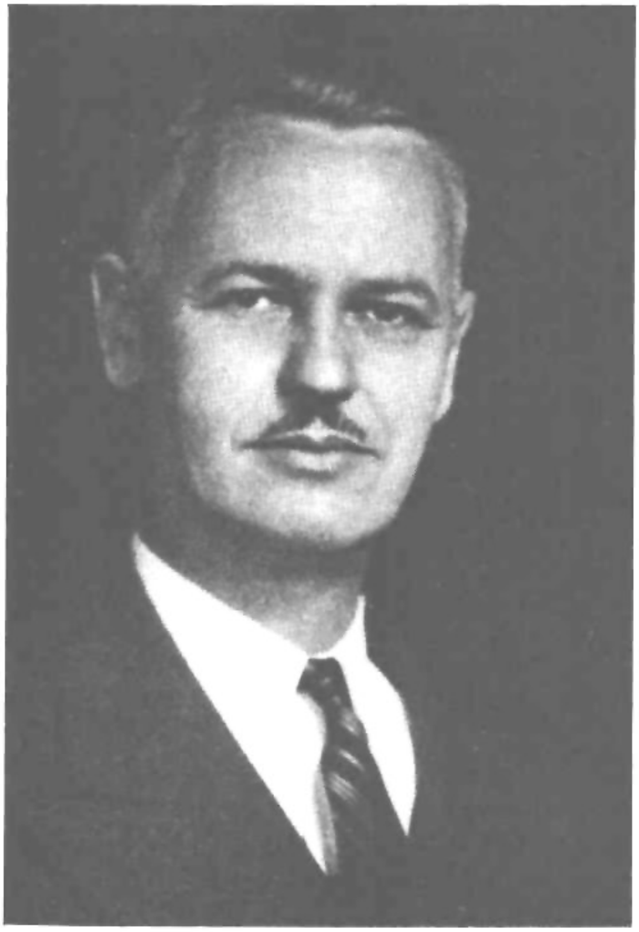
Manual of Nearctic Diptera



C. H. Curran, 1895–1972

Manual of Nearctic Diptera *Volume 1*

Coordinated by

J. F. McAlpine
B. V. Peterson
G. E. Shewell
H. J. Teskey
J. R. Vockeroth
D. M. Wood

Biosystematics Research Institute
Ottawa, Ontario

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AUTHORS

C. P. ALEXANDER, B.Sc., Ph.D.
39 Old Town Road, Amherst, MA 01002, U.S.A.

GEORGE W. BYERS, B.S., M.S., Ph.D.
Department of Entomology, University of Kansas, Lawrence, KS 66045, U.S.A.

EDWIN F. COOK, A.B., A.M., Ph.D.
Department of Entomology, Fisheries and Wildlife, University of Minnesota, 1980 Folwell Avenue, St. Paul, MN 55108, U.S.A.

FELICITY E. A. CUTTEN, B.Sc., Ph.D.
108 Fendalton Road, Christchurch 1, New Zealand

J. ANTONY DOWNES, B.Sc.
Biosystematics Research Institute, Agriculture Canada, Ottawa, Ont. K1A 0C6, Canada

RICHARD H. FOOTE, B.S., D.Sc.
Systematic Entomology Laboratory, S.E.A., A.R., U.S. Department of Agriculture, c/o National Museum of Natural History, Washington, DC 20560, U.S.A.

RAYMOND J. GAGNÉ, B.A., M.S., Ph.D.
Systematic Entomology Laboratory, S.E.A., A.R., U.S. Department of Agriculture, c/o National Museum of Natural History, Washington, DC 20560, U.S.A.

GORDON D. GILL, B.A., M.A., Ph.D.
Department of Biology, Northern Michigan University, Marquette, MI 49355, U.S.A.

J. C. HALL, M.Sc.
Department of Entomology, University of California, Riverside, CA 92521, U.S.A.

D. E. HARDY, A.B., Ph.D.
Department of Entomology, University of Hawaii, 3050 Maile Way, Honolulu, HI 96822, U.S.A.

CHARLES L. HOGUE, B.S., Ph.D.
Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, CA 90007, U.S.A.

H. C. HUCKETT, B.S.A., M.A., Ph.D.
Box 38, R.F.D. 1, Riverhead, NY 11901, U.S.A.

MICHAEL E. IRWIN, B.S., Ph.D.
Agricultural Entomology, University of Illinois and Illinois Natural History Survey, 172 Natural Resources Building, Urbana, IL 61801, U.S.A.

MAURICE T. JAMES, A.B., A.M., Ph.D.
Department of Entomology, Washington State University, Pullman, WA 99164, U.S.A.

L. P. KELSEY, B.S., M.S., Ph.D.
Department of Entomology, University of Delaware, Newark, DE 19711, U.S.A.

H. D. KENNEDY, B.S., M.S.
U.S. Fish and Wildlife Service, U.S. Department of the Interior, P.O. Box 1306, Albuquerque, NM 87103, U.S.A.

EDWARD L. KESSEL, B.S., M.S., Ph.D.
Rose Villa, Apartment 337, 13505 S.E. River Road, Portland, OR 97222, U.S.A.

D. KEITH MCE. KEVAN, B.Sc., A.I.C.T.A., Ph.D., F.R.S.E. (Edinburgh)
Department of Entomology and Lyman Entomological Museum and Research Laboratory, Macdonald Campus of McGill University, Macdonald College P.O., Ste. Anne de Bellevue, Que. H9X 1C0, Canada

LLOYD V. KNUTSON, B.A., M.S., Ph.D.
Insect Identification and Beneficial Insects Introduction Institute, S.E.A., A.R., U.S. Department of Agriculture, Agricultural Research Center - West, Beltsville, MD 20705, U.S.A.

LEIF LYNEBORG, Ph.D.
Zoologisk Museum, Universitetsparken 15, DK 2100, Copenhagen, Denmark

T. C. MAA, Ph.D.
Box 991, Tunghai University, Taichung 400, Taiwan

WAYNE N. MATHIS, B.S., Ph.D.
Department of Entomology, National Museum of Natural History, N.H.B. 169, Smithsonian Institution, Washington, DC 20560, U.S.A.

J. F. MCALPINE, B.S.A., M.Sc., Ph.D.
Biosystematics Research Institute, Agriculture Canada, Ottawa, Ont. K1A 0C6, Canada

D. R. OLIVER, B.A., M.A., Ph.D.
Biosystematics Research Institute, Agriculture Canada, Ottawa, Ont. K1A 0C6, Canada

L. L. PECHUMAN, B.S., M.S., Ph.D.
Department of Entomology, Cornell University, Ithaca, NY 14850, U.S.A.

T. MICHAEL PETERS, B.S., M.S., Ph.D.
Department of Entomology, University of Massachusetts, Amherst, MA 01003, U.S.A.

B. V. PETERSON, B.S., M.S., Ph.D.
Biosystematics Research Institute, Agriculture Canada, Ottawa, Ont. K1A 0C6, Canada

LAWRENCE W. QUATE, Ph.D.
P.O. Box 51, Poway, CA 92064, U.S.A.

O. W. RICHARDS, M.A., D.Sc., F.R.S.
89 St. Stephen's Road, London W13 8JA, England

H. ROBINSON, B.S., M.A., Ph.D.
Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, U.S.A.

CURTIS W. SABROSKY, A.B., M.S., Sc.D. (Hon.)
Systematic Entomology Laboratory, S.E.A., A.R., U.S. Department of Agriculture, c/o National Museum of Natural History, Washington, DC 20560, U.S.A.

EVERT I. SCHLINGER, B.S., Ph.D.
Department of Entomology, University of California, Berkeley, CA 94720, U.S.A.

G. E. SHEWFLL, B.Sc. (Agr.), M.Sc.
Biosystematics Research Institute, Agriculture Canada, Ottawa, Ont. K1A 0C6, Canada

KENNETH G. V. SMITH, M.I.Biol., F.Z.S., F.R.E.S.
Department of Entomology, British Museum (Natural History), Cromwell Road, London SW7 5BD, England

Á. SOÓS, Ph.D., D.Sc.
Zoology Department, Hungarian Natural History Museum, H-1088 Budapest VIII, Baross utca 13, Hungary

K. A. SPENCER, B.A., D.Sc.
Exwell Farm, Bray Shop, Callington PL17 8QJ, Cornwall, England

WALLACE A. STEFFAN, B.S., Ph.D.
Department of Entomology, B. P. Bishop Museum, 1355 Kalihi Street, P.O. Box 19000-A, Honolulu, HI 96819, U.S.A.

GEORGE C. STEYSKAL
Systematic Entomology Laboratory, S.E.A., A.R., U.S. Department of Agriculture, c/o National Museum of Natural History, Washington, DC 20560, U.S.A.

ALAN STONE, Ph.D.
5308 Wriley Road, Bethesda, MD 20016, U.S.A.

H. J. TESKEY, B.Sc., M.S.A., Ph.D.
Biosystematics Research Institute, Agriculture Canada, Ottawa, Ont. K1A 0C6, Canada

F. C. THOMPSON, B.S., Ph.D.
Systematic Entomology Laboratory, S.E.A., A.R., U.S. Department of Agriculture, c/o National Museum of Natural History, Washington, DC 20560, U.S.A.

WILLIAM J. TURNER, A.B., M.S., Ph.D.
Department of Entomology, Washington State University, Pullman, WA 99164, U.S.A.

J. R. VOCKEROTH, B.A., M.A., D.Phil.
Biosystematics Research Institute, Agriculture Canada, Ottawa, Ont. K1A 0C6, Canada

DONALD W. WEBB, B.Sc., M.Sc.
Section of Faunistic Surveys and Insect Identification, Illinois Natural History Survey, Natural Resources Building, Urbana, IL 61801, U.S.A.

RUPERT L. WENZEL, A.B., Ph.D.
Division of Insects, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605, U.S.A.

M. R. WHEELER, B.A., Ph.D.
Department of Zoology, University of Texas, Austin, TX 78712, U.S.A.

J. WILCOX, Ph.D.
Science and Education Administration, U.S. Department of Agriculture, 7551 Vista Del Sol, Anaheim, CA 92807, U.S.A.

WILLIS W. WIRTH, B.S., M.S., Ph.D.
Systematic Entomology Laboratory, S.E.A., A.R., U.S. Department of Agriculture, c/o National Museum of Natural History, Washington, DC 20560, U.S.A.

D. M. WOOD, B.A., M.A., Ph.D.
Biosystematics Research Institute, Agriculture Canada, Ottawa, Ont. K1A 0C6, Canada

GRACE C. WOOD, B.Sc., M.Sc.
146 Ruskin Street, Ottawa, Ont. K1Y 4C1, Canada

CONTENTS

INTRODUCTION 1

J. F. McAlpine, B. V. Peterson, G. E. Shewell, H. J. Teskey,
J. R. Vockeroth, and D. M. Wood

GENERAL

The main purpose of this new *Manual of Nearctic Diptera* is to provide an up-to-date, well-illustrated, easily interpretable means for identifying the families and genera of two-winged flies of America north of Mexico. It is also designed to be a basic reference to a wide spectrum of biosystematic information on Diptera for professional biologists, teachers, students, and informed amateurs.

Historically, the Manual is built upon earlier great works on the biosystematics of Nearctic Diptera. It was planned as a two-volume replacement for Curran's (1934) well-known *Families and Genera of North American Diptera*. Just as Curran's manual resulted from a desire and a necessity to improve on Samuel Williston's (1888, 1896, 1908) classic *Manual of North American Diptera*, this one was inspired by a desire, first voiced in the early 1960's by G. E. Shewell, to update Curran's manual. The appearance in 1965 of a magnificent new *Catalog of the Diptera of America North of Mexico* (Stone *et al.* 1965) provided the immediate incentive and foundation for such an undertaking. It, more than anything else, prompted the late James G. Chillcott, then leader of the Diptera Section, Entomology Research Institute (now Biosystematics Research Institute), to initiate the project. It was formally authorized by the Research Branch, Agriculture Canada, on January 20, 1966, under the leadership of Dr. Chillcott, with assistance by an editorial group consisting of J. F. McAlpine, B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, and D. M. Wood. In all, 52 collaborating specialists are involved (*see* Acknowledgments). For a time following Dr. Chillcott's death in April 1967, the project remained at a standstill. Progress in subsequent years under the successive leadership of G. E. Shewell, J. F. McAlpine, B. V. Peterson, and D. M. Wood has been slow but steady. Both volumes were originally intended to be published simultaneously, but managerial and financial exigencies have made it necessary to publish Volume 1 before Volume 2. It is expected that the first volume will be followed shortly by the second volume, bringing the project to its long-awaited fulfillment.

Volume 1 contains 48 chapters, the first five relating to both volumes. These five include the introduction, chapters dealing with the morphology and terminology of the adult and larval stages, and chapters containing keys to the families of the order based on both adults and larvae. Thus Volume 1 is necessary for the full use of Volume 2. The treatments of the 24 families of the Nematocera and the 19 families of the orthorrhaphous Brachycera comprise the remaining 43 chapters of Volume 1.

The forthcoming Volume 2 will contain a few chapters dealing with the order as a whole, namely, discussions on the habits and environments of Diptera and on the evolution and phylogeny of the families and higher categories. However, as these chapters serve mainly to supplement the general knowledge of the order, Volume 1 is basically independent of Volume 2. The 65 families of the Muscomorpha (Cyclorrhapha) will be treated in separate chapters in Volume 2, to complete the sections for the 108 Nearctic families recognized in the order.

The chapters treating the families each contain a comprehensive morphological description of the adult fly. Short descriptions are provided for the egg, the larva, and the pupa when these stages are known. Keys for identifying all the genera of the Nearctic region for each family are presented for the adult stage and, when feasible, for the larval and pupal stages. Discussions on biology, behavior, classification, distribution, and fossil representation are also included. A list of references appears at the end of each chapter.

We have not included a section on collecting, mounting, and preparing flies because good treatments of these aspects are already available, for example, those by Martin (1977) and Oldroyd (1958).

Although the Manual is designed for a wide array of workers from amateurs to specialists, some fundamental knowledge is necessary for its use. A working familiarity with entomological terminology and methodology, as well as some training in basic taxonomic principles, is essential. Chapters 2 and 3 on the morphology and terminology of adults and larvae are the main background chapters for Volumes 1 and 2. There is no glossary as such, but all morphological terms are indexed and explained at appropriate places in the text. Volume 1 has its own index to morphological terms and taxonomic names. Volume 2 will contain a similar but more comprehensive index covering both volumes.

The chapters are numbered consecutively throughout both volumes for convenient cross-reference to all subjects and figures contained in the Manual. The classification of the families and higher taxa, shown in the accompanying table, is basically an evolutionary one, beginning with the primitive families of the Tipulomorpha and ending with the highly evolved superfamilies and families of the Muscomorpha. This arrangement follows fairly closely that proposed by Hennig (1973) but incorporates some modifications suggested by Griffiths (1972) and Steyskal (1974). It also reflects certain

Classification of the Nearctic families of the order Diptera

Infraorder	Superfamily	Family (and chapter)
	SUBORDER NEMATOCERA	
Tipulomorpha	Tanyderoidea	Tanyderidae (6)
	Tipuloidea	Tipulidae (7)
Blephariceromorpha	Blephariceroidea	Blephariceridae (8)
	Deuterophlebioidea	Deuterophlebiidae (9)
	Nymphomyioidea	Nymphomyiidae (10)
Axymyiomorpha	Axymyioidea	Axymyiidae (11)
Bibionomorpha	Pachyneuroidea	Pachyneuridae (12)
	Bibionoidea	Bibionidae (13)
	Sciaroidea	Mycetophilidae (14) Sciaridae (15) Cecidomyiidae (16)
Psychodomorpha	Psychodoidea	Psychodidae (17)
	Trichoceroidea	Trichoceridae (18)
	Anisopodoidea	Anisopodidae (19)
	Scatopsoidea	Scatopsidae (20) Synneuridae (21)
Ptychopteromorpha	Ptychopteroidea	Ptychopteridae (22)
Culicomorpha	Culicoidea	Dixidae (23) Chaoboridae (24) Culicidae (25)
	Chironomoidea	Thaumaleidae (26) Simuliidae (27) Ceratopogonidae (28) Chironomidae (29)
	SUBORDER BRACHYCERA	
Tabanomorpha	Tabanoidea	Pelecorhynchidae (30) Tabanidae (31) Athericidae (32) Rhagionidae (33)
	Stratiomyoidea	Xylophagidae (34) Xylomyidae (35) Stratiomyidae (36)
Asilomorpha	Asiloidea	Therevidae (37) Scenopinidae (38) Vermileonidae (39) Mydidae (40) Apioceridae (41) Asilidae (42)
	Bombylioidea	Acroceridae (43) Nemestrinidae (44) Bombyliidae (45) Hilarimorphidae (46)
	Empidoidea	Empididae (47) Dolichopodidae (48)
Muscomorpha Aschiza	Lonchopteroidea	Lonchopteridae (49)
	Platypezoidea	Platypezidae (50) Phoridae (51)
	Syrphoidea	Syrphidae (52) Pipunculidae (53)

(continued)

Classification of the Nearctic families of the order Diptera

Infraorder	Superfamily	Family (and chapter)
	SUBORDER BRACHYCERA (*concluded*)	
Muscomorpha		
Schizophora—Acalyptratae	Conopoidea	Conopidae (54)
	Nerioidea	Cypselosomatidae (55) Micropezidae (56) Neriidae (57)
	Diopsoidea	Tanypezidae (58) Strongylophthalmyiidae (59) Psilidae (60) Diopsidae (61)
	Tephritoidea	Lonchaeidae (62) Otitidae (63) Platystomatidae (64) Pyrgotidae (65) Tephritidae (66) Richardiidae (67) Pallopteridae (68) Piophilidae (69)
	Opomyzoidea	Clusiidae (70) Acartophthalmidae (71) Odiniidae (72) Agromyzidae (73) Opomyzidae (74) Anthomyzidae (75) Aulacigastridae (76) Periscelididae (77) Asteiidae (78) Milichiidae (79) Carnidae (80) Braulidae (81)
	Sciomyzoidea	Coelopidae (82) Dryomyzidae (83) Sciomyzidae (84) Ropalomeridae (85) Sepsidae (86)
	Lauxanioidea	Lauxaniidae (87) Chamaemyiidae (88)
	Sphaeroceroidea	Heleomyzidae (89) Trixoscelididae (90) Chyromyidae (91) Rhinotoridae (92) Sphaeroceridae (93)
	Ephydroidea	Curtonotidae (94) Drosophilidae (95) Diastatidae (96) Camillidae (97) Ephydridae (98) Chloropidae (99) Cryptochetidae (100) Tethinidae (101) Canacidae (102)
Schizophora—Calyptratae	Muscoidea	Scathophagidae (103) Anthomyiidae (104) Muscidae (105)
	Oestroidea	Calliphoridae (106) Oestridae (107) Sarcophagidae (108) Rhinophoridae (109) Tachinidae (110)
	Hippoboscoidea	Hippoboscidae (111) Nycteribiidae (112) Streblidae (113)
TOTAL		108 families

advances in our knowledge of the evolutionary relationships of various groups that have become apparent through the joint efforts of all the coordinating specialists in the Biosystematics Research Institute. These aspects, as indicated previously, will be treated fully in chapters on evolution and phylogeny in the second volume.

In all, the Manual treats about 2150 genera distributed among 108 families. No new taxa are proposed. By comparison, Curran's manual treated 2031 genera, but many of these were strictly Neotropical, and he recognized only 81 families. Sabrosky (1967) placed the number of valid Nearctic genera at 1974 and recognized 105 families. The number of described Nearctic species of flies now exceeds 18 200, according to information given by Hardy (1976); this figure compares with 5432 at the time of Aldrich's (1905) catalog (Stone *et al.* 1965). In all parts of the Nearctic region the actual number of species of Diptera, including those that are still undescribed, is now estimated at 25 000 – 30 000 (McAlpine *et al.* 1979).

With few exceptions the work covers only families, genera, and species that occur in the Nearctic region as defined and mapped by Griffiths (1979). The Nearctic region consists of Canada and the contiguous United States including all of Alaska and Florida. Greenland and Bermuda are also included. In the Beringian area the present territorial boundary between the United States and the Soviet Union is accepted as the boundary between the Nearctic and Palaearctic regions. In Mexico the interior plateau, as far south as Tehuantepec, is considered to be mainly Nearctic. The boundary between the Nearctic and Neotropical regions in Mexico follows the boundaries between oak–pine forest or mesquite–grassland areas or desert, at higher elevations (Nearctic), and tropical thorn or broad-leaved evergreen forest at lower elevations (Neotropical). The Diptera of the Mexican Plateau are relatively poorly known, and their treatment throughout the Manual is therefore incomplete. Occasionally, extralimital species have been cited by way of example or have been used to illustrate particular characters. Some genera that are as yet unrecorded from the Nearctic region but which occur in adjacent areas are included in keys to genera, because they might reasonably be expected to occur in the Nearctic.

Some points of style used in the general descriptions and in the keys should be noted. Throughout the Manual, only one side of the insect is described. Accordingly the singular is used for single pairs or structures (e.g. antenna, fore tarsus); the plural is usually used when several homonomous structures occur on each side (e.g. legs, tarsi, claws, pulvilli, empodia), when more than two similar structures occur in a symmetric grouping (e.g. ocelli), or when a single median structure results from the fusion of paired elements (e.g. labella). When subgenera are distinguished in the keys they are indicated by using parentheses; for example, *Tipula* (*Bellardina* Edwards) and *Tipula* (*Tipula* Linnaeus) are two subgenera of the genus *Tipula* Linnaeus.

New illustrations have been specially prepared for the Manual, showing many structural details that previously were uncertain or unknown. A few have been redrawn from other sources and, for these, acknowledgments are made where they appear. The first illustration in each family chapter is a habitus figure depicting a representative member of each family, usually a species belonging to the type genus. For families with very varied appearance, several habitus figures are given. All lateral views show the left side, but wings are presented as dorsal views of the right wing. An improved method for showing side-by-side dorsal and ventral views, especially of terminalia, is used. This method involves showing slightly more than half of the left side in both dorsal and ventral views separated by a narrow space, as in, for example, Figs. 2.59, 8.13, and 20.19. Illustrations are individually numbered and labeled with the genus and species names and the sex; captions to figures provide the authors of species names appearing on each plate, as well as the full names for all parts labeled with abbreviations. Figure numbers begin at Fig. 1 in each chapter. References to figures appearing within each chapter are made by using the figure number only, without including the chapter number. However, when reference is made in one chapter to a figure appearing in another chapter, the chapter number is included with the figure number; for example, mention in Chapter 2 of Fig. 4.6 refers to Fig. 6 in Chapter 4. Chapter numbers are also included with the figure numbers at the beginning of the captions for each plate.

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C. P. Alexander
  Ptychopteridae, Tanyderidae, Tipulidae (adults), Trichoceridae

George W. Byers
  Tipulidae (larvae)

J. G. Chillcott (deceased)
  Originator and general organizer of the project, project leader 1966–1967

Edwin F. Cook
  Chaoboridae, Scatopsidae, Synneuridae (with B. V. Peterson)

Felicity E. A. Cutten
  Nymphomyiidae (with D. Keith McE. Kevan)

J. Antony Downes
  Ceratopogonidae (with Willis W. Wirth), Habits and Environments of Diptera (Vol. 2)

Richard H. Foote
  Tephritidae (with George C. Steyskal) (Vol. 2)

Raymond J. Gagné
Cecidomyiidae
Gordon D. Gill
Heleomyzidae (Vol. 2.)
J. C. Hall
Bombyliidae
D. E. Hardy
Bibionidae, Pipunculidae (Vol. 2)
W. Hennig (deceased)
General assistance, especially in morphology, phylogeny, and classification
Charles L. Hogue
Blephariceridae
H. C. Huckett
Anthomyiidae (Vol. 2), Muscidae (with J. R. Vockeroth) (Vol. 2)
Michael E. Irwin
Therevidae (with Leif Lyneborg)
Maurice T. James
Rhagionidae (with William J. Turner), Stratiomyidae, Xylomyidae, Xylophagidae
L. P. Kelsey
Scenopinidae
H. D. Kennedy
Deuterophlebiidae
Edward L. Kessel
Platypezidae (Vol. 2)
D. Keith McE. Kevan
Nymphomyiidae (with Felicity E. A. Cutten)
Lloyd V. Knutson
Empididae (with George C. Steyskal), Sciomyzidae (with George C. Steyskal) (Vol. 2)
Leif Lyneborg
Therevidae (with Michael E. Irwin)
T. C. Maa
Hippoboscidae (with B. V. Peterson) (Vol. 2)
Wayne N. Mathis
Ephydridae (with Willis W. Wirth) (Vol. 2)
J. F. McAlpine
Acartophthalmidae (Vol. 2), Camillidae (Vol. 2), Chamaemyiidae (Vol. 2), Chyromyidae (Vol. 2), Cryptochetidae (Vol. 2), Curtonotidae (Vol. 2), Cypselosomatidae (Vol. 2), Diastatidae (Vol. 2), Lonchaeidae (Vol. 2), Odiniidae (Vol. 2), Pallopteridae (Vol. 2), Periscelididae (Vol. 2), Piophilidae (Vol. 2), Rhinotoridae (Vol. 2); Morphology and Terminology—Adults; Key to Families—Adults; Evolution and Phylogeny of Families and Higher Categories of Diptera (with D. M. Wood) (Vol. 2); coordinator for Anthomyiidae (Vol. 2), Asteiidae (Vol. 2), Carnidae (Vol. 2), Cecidomyiidae, Clusiidae (Vol. 2), Drosophilidae (Vol. 2), Milichiidae (Vol. 2), Otitidae (Vol. 2), Platypezidae (Vol. 2), Platystomatidae (Vol. 2), Psilidae (Vol. 2), Pyrgotidae (Vol. 2), Richardiidae (Vol. 2), Ropalomeridae (Vol. 2), Sepsidae (Vol. 2), Strongylophthalmyiidae (Vol. 2), Tanypezidae (Vol. 2), Tephritidae (Vol. 2); member of editorial group; project leader 1969–1975; scientific editor
D. R. Oliver
Chironomidae
L. L. Pechuman
Tabanidae (with H. J. Teskey)
T. Michael Peters
Dixidae
B. V. Peterson
Anisopodidae, Apioceridae, Braulidae (Vol. 2), Diopsidae (Vol. 2), Hippoboscidae (with T. C. Maa) (Vol. 2), Lonchopteridae (Vol. 2), Nycteribiidae (with Rupert L. Wenzel) (Vol. 2), Phoridae (Vol. 2), Simuliidae, Streblidae (with Rupert L. Wenzel) (Vol. 2), Synneuridae (with Edwin F. Cook), Thaumaleidae (with Alan Stone); coordinator for Bibionidae, Blephariceridae, Chloropidae (Vol. 2), Conopidae (Vol. 2), Deuterophlebiidae, Heleomyzidae (Vol. 2), Micropezidae (Vol. 2), Mydidae, Neriidae (Vol. 2), Pipunculidae (Vol. 2), Scatopsidae, Sciomyzidae (Vol. 2); member of editorial group; project leader 1975–1978
Lawrence W. Quate
Psychodidae (with J. R. Vockeroth)
O. W. Richards
Sphaeroceridae (Vol. 2)
H. Robinson
Dolichopodidae (with J. R. Vockeroth)
Curtis W. Sabrosky
Asteiidae (Vol. 2), Carnidae (Vol. 2), Chloropidae (Vol. 2), Milichiidae (Vol. 2)
Evert I. Schlinger
Acroceridae
G. E. Shewell
Calliphoridae (Vol. 2), Lauxaniidae (Vol. 2), Sarcophagidae (Vol. 2); member of editorial group; project leader 1967–1969
Kenneth G. V. Smith
Conopidae (Vol. 2)
Á. Soós
Clusiidae (Vol. 2)
K. A. Spencer
Agromyzidae (Vol. 2)
Wallace A. Steffan
Sciaridae
George C. Steyskal
Dryomyzidae (Vol. 2), Empididae (with Lloyd V. Knutson), Micropezidae (Vol. 2), Otitidae (Vol. 2), Platystomatidae (Vol. 2), Psilidae (Vol. 2), Pyrgotidae (Vol. 2), Richardiidae (Vol. 2), Ropalomeridae (Vol. 2), Sciomyzidae (with Lloyd V. Knutson) (Vol. 2), Sepsidae (Vol. 2), Strongylophthalmyiidae (Vol. 2), Tanypezidae (Vol. 2), Tephritidae (with Richard H. Foote) (Vol. 2)
Alan Stone
Culicidae, Thaumaleidae (with B. V. Peterson)
H. J. Teskey
Aulacigastridae (Vol. 2), Nemestrinidae, Pelecorhynchidae, Tabanidae (with L. L. Pechuman), Trixoscelididae (Vol. 2), Vermileonidae; Morphology and Terminology—Larvae; Key to Families—Larvae; coordinator for Agromyzidae (Vol. 2), Athericidae, Empididae, Hilarimorphidae, Ptychopteridae, Rha-

gionidae, Scenopinidae, Sphaeroceridae (Vol. 2), Stratiomyidae, Tanyderidae, Therevidae, Tipulidae, Trichoceridae, Xylomyidae, Xylophagidae; member of editorial group

F. C. Thompson
Syrphidae (with J. R. Vockeroth) (Vol. 2)

William J. Turner
Rhagionidae (with Maurice T. James)

J. R. Vockeroth
Anthomyzidae (Vol. 2), Coelopidae (Vol. 2), Dolichopodidae (with H. Robinson), Muscidae (with H. C. Huckett) (Vol. 2), Mycetophilidae, Opomyzidae (Vol. 2), Psychodidae (with Lawrence W. Quate), Scathophagidae (Vol. 2), Syrphidae (with F. C. Thompson) (Vol. 2), Tethinidae (Vol. 2); coordinator for Canacidae (Vol. 2), Dryomyzidae (Vol. 2), Ephydridae (Vol. 2), Sciaridae; member of editorial group

Donald W. Webb
Athericidae, Hilarimorphidae

Rupert L. Wenzel
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Drosophilidae (Vol. 2)

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Mydidae

Willis W. Wirth
Canacidae (Vol. 2), Ceratopogonidae (with J. Antony Downes), Ephydridae (with Wayne N. Mathis) (Vol. 2)

D. M. Wood
Axymyiidae, Oestridae (Vol. 2), Pachyneuridae, Rhinophoridae (Vol. 2), Tachinidae (Vol. 2); coordinator for Asilidae, Acroceridae, Bombyliidae, Ceratopogonidae, Chaoboridae, Chironomidae, Culicidae, Dixidae, Nymphomyiidae; Evolution and Phylogeny of Families and Higher Categories of Diptera (with J. F. McAlpine) (Vol. 2); member of editorial group; project leader 1978—

Grace C. Wood
Asilidae

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MORPHOLOGY AND TERMINOLOGY—ADULTS 2

J. F. McAlpine

INTRODUCTION

Scope. This chapter deals primarily with the skeletal morphology of adult flies, particularly as applied in identification and classification. A similar chapter on the immature stages, prepared by H. J. Teskey, follows. A major difficulty for the student of Diptera is the plethora of terminologies used by different workers. These variations have arisen because specialists have independently developed terminologies suitable for their own purposes with little concern for homologies. The terms and definitions adopted in this manual are based mainly on the works of Crampton (1942), Colless and McAlpine (1970), Mackerras (1970), Matsuda (1965, 1970, 1976), van Emden and Hennig (1970), Tuxen (1970), and Hennig (1973). The paper by Hennig (1973) is the most up-to-date and most comprehensive review of the anatomy of all stages of Diptera yet produced, and this work in particular should be consulted for many details and references that do not appear here. Some of the terms adopted are conventional and topographical rather than strictly morphological, but an attempt is made to apply terms consistently throughout the order. For example, the terms katepisternum and paramere, both long employed in the Nematocera and some orthorrhaphous Brachycera, are adopted in the Muscomorpha (cyclorrhaphous Brachycera) in place of sternopleuron and postgonite, respectively. Such changes may cause some confusion for awhile, but the advantages of adopting a standard, universally acceptable terminology outweigh the short-term inconvenience.

Most of the morphological terms applied to adults throughout the manual are listed and defined in this chapter. However, additional ones with restricted application are sometimes found in the various family sections. Preferred terms appear in boldface at first appearance, sometimes followed in parentheses by the corresponding singular (*sing.*) or plural (*pl.*) form in boldface and by common synonyms in lightface; this synonymy is not intended to be complete. There is no glossary, but all terms used in the manual are defined in the text and entered in the index. In the index, the page number for the principal entry appears in boldface. For terms not included in the index, the reader can consult comprehensive glossaries, such as those by Torre-Bueno (1937) and Tuxen (1970), and the taxonomic glossary for mosquitoes by Knight (1970), Knight and Laffoon (1970*a*, 1970*b*, 1970*c*, 1971), and Laffoon and Knight (1971).

Orientation and relationship of parts. A fly is basically a bilaterally symmetric, horizontally oriented, forwardly progressing animal. Its body can be divided into three primary anatomical planes oriented at right angles to each other (Fig. 1): ***sagittal*** (vertical longitudinal) ***planes***, the median one of which passes through the central axis of the body; ***horizontal planes***, also parallel to the long axis; and ***transverse planes***, at right angles to the long axis and to the other two planes. The head end is ***anterior*** or ***cephalic***, and the hind end is ***posterior*** or ***caudal***; the upper surface is ***dorsal***, and the lower one is ***ventral***. A line traversing the surface of the body in the median sagittal plane is the ***median line*** (meson) and an area symmetrically disposed about it is the ***median area***. An intermediate line or zone is termed ***sublateral***, and the outer zone, including the side of the insect, is ***lateral***. Structures lying farther from the median sagittal plane than do other structures are referred to as ***lateral***, and those nearer this plane as ***medial***. Similarly, parts of appendages and other attached structures that lie farther from the body are referred to as ***distal*** or ***apical***, and those nearer to the body as ***proximal*** or ***basal***. Many of these terms can be combined to give convenient descriptive words such as dorsolateral and anteroventral. Terms such as mesal for medial, and mesad, laterad, and distad for medially, laterally, and distally, are often found in entomological works, but as stated by Mackerras (1970) there is no good reason for using them.

All terms are used in relation to the morphologically horizontal position of the insect with its legs and wings fully extended laterally, regardless of its particular attitude. Consequently, care must be taken in defining surfaces and bristles, especially those of the legs (Fig. 1).

General organization. As in all insects, the body of an adult fly is divided into three familiar regions, ***head***, ***thorax***, and ***abdomen***, each with its specially modified ***appendages*** (Figs. 2, 3). The segmentation of the insect head is controversial; a review of various theories is presented by Matsuda (1965). The head is usually considered to consist of three ***preoral segments***, namely an ***acron***, an ***antennal segment***, and an ***intercalary segment***; and three ***gnathal*** (postoral) ***segments***, namely a ***mandibular***, a ***maxillary***, and a ***labial segment***. The thorax consists of three primary segments, and the abdomen of 11. Sclerotization occurs in dorsal and ventral plates of each segment and extends from just anterior to each ***intersegmental groove*** for a varying distance toward the posterior end of the segment (Figs. 5, 6). The entire dorsum of a segment is referred to as the ***tergum***, and the entire venter, as the ***sternum***. The terms ***tergite*** and ***sternite*** were originally proposed for the sclerotized subdivisions (sclerites) of each surface, but they are now

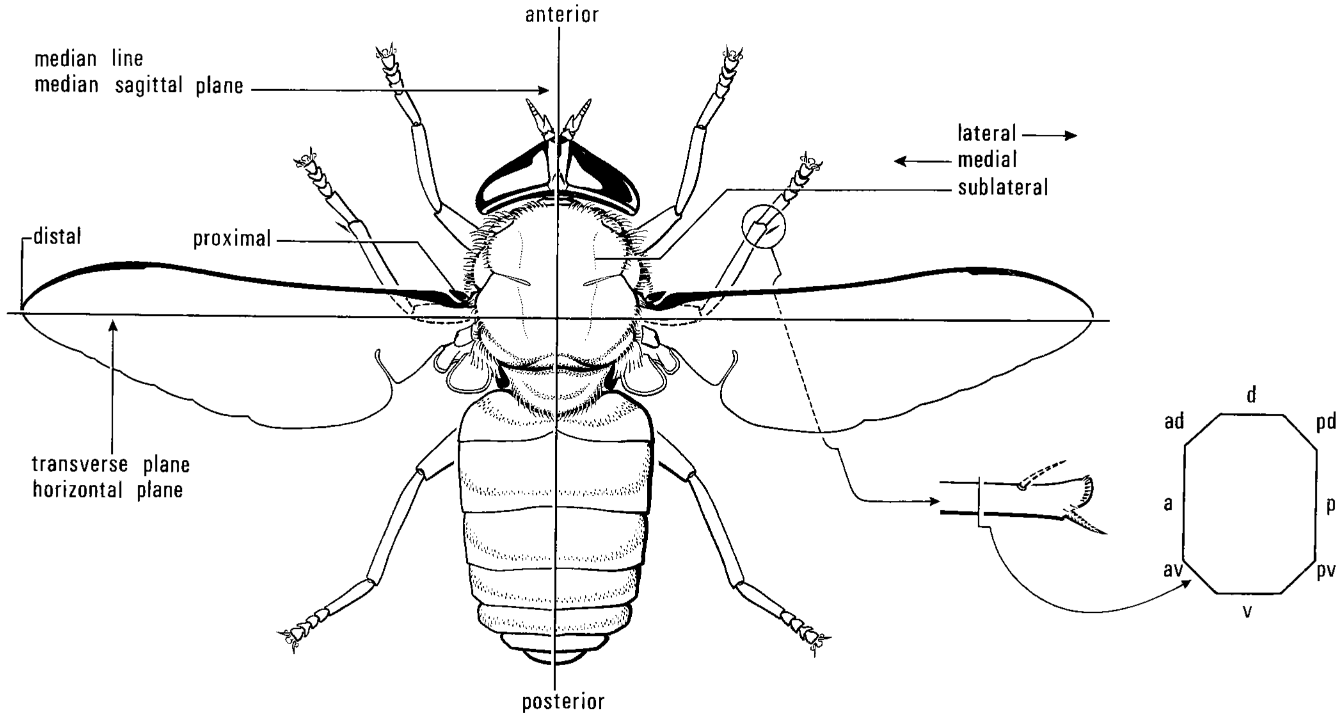


Fig. 2.1. A generalized fly, *Tabanus americanus* Forster, to show orientation and anatomical planes. *Inset:* Vertical section through distal portion of right mid tibia to show external surfaces.
Abbreviations: a, anterior; ad, anterodorsal; av, anteroventral; d, dorsal; p, posterior; pd, posterodorsal; pv, posteroventral; v, ventral.

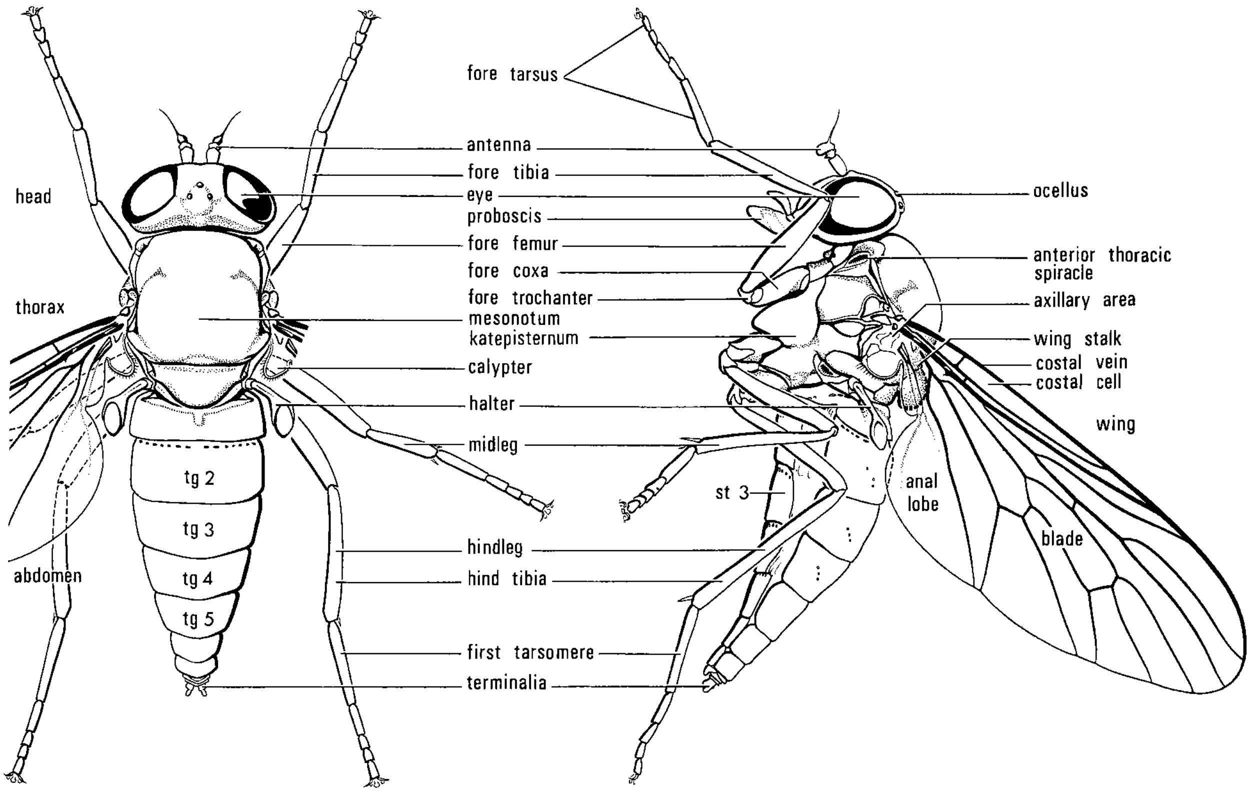
commonly used almost synonymously with tergum and sternum. The unsclerotized part of the segmental ***cuticle*** between two adjacent tergal or sternal plates is the ***intersegmental*** or ***conjunctival membrane*** (Figs. 4, 5); it usually folds inwardly, and portions of it sometimes become sclerotized. In this way intersegmental sclerites arise and a secondary, functional segmentation may be imposed on the primary metameric segmentation (Figs. 5, 6). The preceding inflected part of each segment, called the ***antecosta***, is indicated externally by the ***antecostal suture***, and the sclerotized secondary strip anterior to this suture is the ***acrotergite*** dorsally and the ***acrosternite*** ventrally. Sclerotized infoldings called ***apodemes*** also develop and project into the body to add strength and to provide attachments for muscles. The apodemes arising from the antecostae of the mesonotum, metanotum, and first abdominal tergum are called ***phragmata*** (*sing.* ***phragma***) (Fig. 7).

In the abdomen the side or ***pleuron*** (*pl.* ***pleura***) of the body remains membranous. But in the thorax where greater rigidity is required, strengthening sclerites develop in the ***pleural membrane***; these, together with the tergal and sternal plates, form a kind of box with precisely limited capacity for distortion. In the head, where little or no flexibility is needed, all the sclerites become fused into a single, strong ***head capsule***.

Most appendages such as ***antennae, palpi***, and ***legs*** are paired structures consisting of segmented tubes with flexible joints called ***articulations*** between the segments; the ***wings*** and ***halteres*** are specialized outgrowths of the thorax. The ***tracheae*** of the respiratory system open at segmental ***spiracles*** on each side. Various parts of the ***integument*** may be more or less covered with ***vestiture*** of different kinds. ***Macrotrichia*** (*sing.* ***macrotrichium***) or ***setae*** (*sing.* ***seta***), which include ***bristles***, ***hairs***, and ***setulae***, are connected with nerves and are surrounded at the base by a membranous ring or socket called an ***alveolus*** (*pl.* ***alveoli***). ***Microtrichia*** are superficial extensions of the cuticle, such as the very fine hairs on wing membranes and the ***pruinescence*** (pollinosity) that dulls the surface of many sclerites. The disposition of bristles and hairs is called ***chaetotaxy*** (Figs. 65, 66) and it is extremely important in the taxonomy of flies. Likewise, the extent, intensity, and patterns of ***pruinose*** (pollinose) areas are often of taxonomic value. Markings of any sort that are broader than a line are usually referred to as ***bands*** if they are transverse, and ***stripes*** if they are longitudinal.

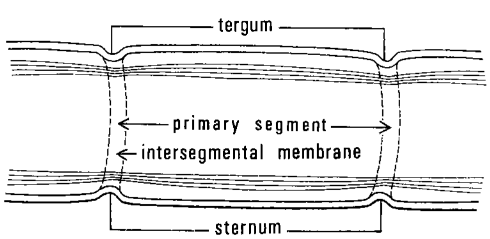
HEAD

Externally, the main parts of the head capsule (Figs. 8–11) are the ***compound eyes***, the ***genae*** (*sing.* ***gena***; bucca, cheek, jowl), and the ***subgenae*** laterally; the ***vertex*** (epicranium) dorsally; the ***frons*** (postfrons, front), ***face*** (prefrons), and ***clypeus*** (anteclypeus, prelabrum) anteriorly; and the ***postcranium*** (occiput), including the ***occiput*** above and the ***postgenae*** below, posteriorly. The ***antennae*** (*sing.* ***antenna***) and ***mouthparts*** are



2 Symphoromyia montana ♀

3 Symphoromyia montana ♀



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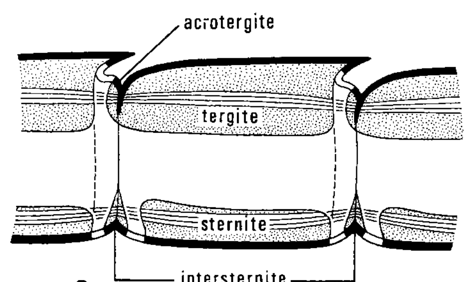

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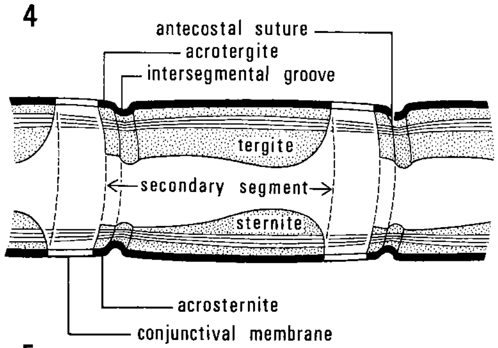

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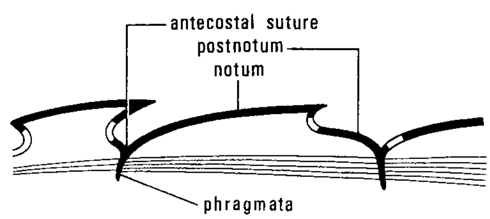

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Figs. 2.2–7. Main divisions and parts of Diptera: (2) dorsal and (3) lateral view of *Symphoromyia montana* Aldrich, to show main anatomical divisions and parts; (4–7) diagrams of primary and secondary segmentation, based on Snodgrass (1935) and Matsuda (1970), showing (4) primary, (5) simple secondary, and (6) more advanced secondary segmentation and (7) dorsal sclerites of thorax in section.

Abbreviations: st, sternite; tg, tergite.

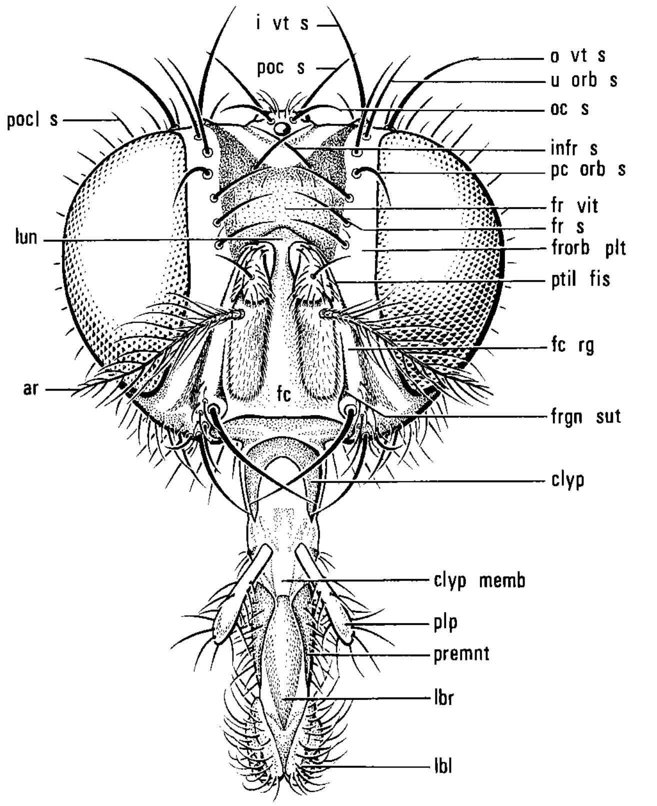
appendages. The parts of the head are defined principally by reference to the ***occipital foramen*** (through which pass the nerve cords, esophagus, aorta, and salivary ducts), the ***ocelli*** (*sing.* ***ocellus***), the insertions of the antennae, the margins of the eyes, the ***subcranial cavity*** (oral cavity), and the ***anterior tentorial pits***. The inner skeleton is formed by the ***tentorium*** (Fig. 51). Basically the tentorium consists of paired ***anterior***, ***dorsal***, and ***posterior tentorial arms***. The anterior tentorial arms arise from the anterior tentorial pits and the posterior arms arise from the ***posterior tentorial pits***. The dorsal tentorial arm is believed to be an outgrowth of the anterior arm (Matsuda 1965), which it joins near the junction of the anterior and posterior arms (Bonhag 1951). All three arms are frequently reduced and more or less consolidated in Diptera. In more primitive insects a median plate called the ***corpotentorium*** is sometimes formed between the two sides of the tentorium, but this plate is poorly developed or absent in Diptera. Likewise, in many insect groups the apices of the two posterior arms are fused medially, forming a ***tentorial bridge*** (Snodgrass 1935). This bridge also appears to be incomplete or absent in most Diptera. The anterior tentorial pits are sometimes poorly developed or absent, particularly in the Muscomorpha (cyclorrhaphous Brachycera); they are very large in some Nematocera, e.g. Culicidae, Chaoboridae (Fig. 24.4), and Chironomidae, and they are also easily seen in some Tabanomorpha, for example in the Tabanidae (Figs. 31.2–4). The posterior tentorial pits, at the ventral ends of the postoccipital suture, are usually less evident (Fig. 11).

Eye. The eyes usually occupy most of the side of the head, but they may be greatly reduced or absent, especially in cavernicolous and some parasitic forms. When the eyes are so large that they meet or almost meet on the median line the condition is referred to as ***holoptic*** (Fig. 10), and when they are widely separate, as ***dichoptic*** (Fig. 8). The tendency toward a holoptic condition is usually restricted to the male, where it is associated with swarming and aerial mating (McAlpine and Munroe 1968). Both the male and the female are holoptic in some members of some families, e.g. Blephariceridae, Thaumaleidae, Acroceridae, Bombyliidae, Empididae, and Pipunculidae, and they are nearly so in Synneuridae and in some Anthomyiidae. In some Nematocera, e.g. most Sciaridae (Fig. 15.4) and some Cecidomyiidae (Fig. 16.1), the eyes are narrowly connected by an ***eye bridge***. Externally each eye consists of many ***facets***, which are the corneas of individual ***ommatidia*** (*sing.* ***ommatidium***). The upper facets may be larger than the lower ones and sometimes, e.g. Aulacigastridae, the anterior ones are larger than the posterior ones. Occasionally, as in some Blephariceridae (Fig. 8.1), Axymyiidae (Figs. 11.1–2), and in the cecidomyiid genus *Trisopsis* (Fig. 16.4), the eyes are divided into dorsal and ventral parts. Eye color varies considerably among species; a pattern of bands or patches of contrasting colors are often evident in life, as shown in the Tabanidae (Figs. 31.1–4). The spaces between the facets are often provided with fine hairs, which are frequently longer and denser in the male than in the female, especially in the Muscomorpha. Usually there are three ocelli in a triangular arrangement on a more or less distinct ***ocellar triangle*** (ocellar plate, vertical triangle) or ***ocellar tubercle***; the anterior (median) ocellus, or the two posterior ocelli, or all three ocelli are sometimes absent. Some Chironomidae and Simuliidae, especially those with reduced compound eyes, have a small dark bulla near the posterior margin of the eye, e.g. *Oreadomyia albertae* Kevan & Cutten-Ali-Khan (Fig. 29.113) and *Twinnia* sp. (Fig. 27.2). This bulla is assumed to be a remnant of the larval eye; in the Simuliidae it is called a ***stemmatic bulla***.

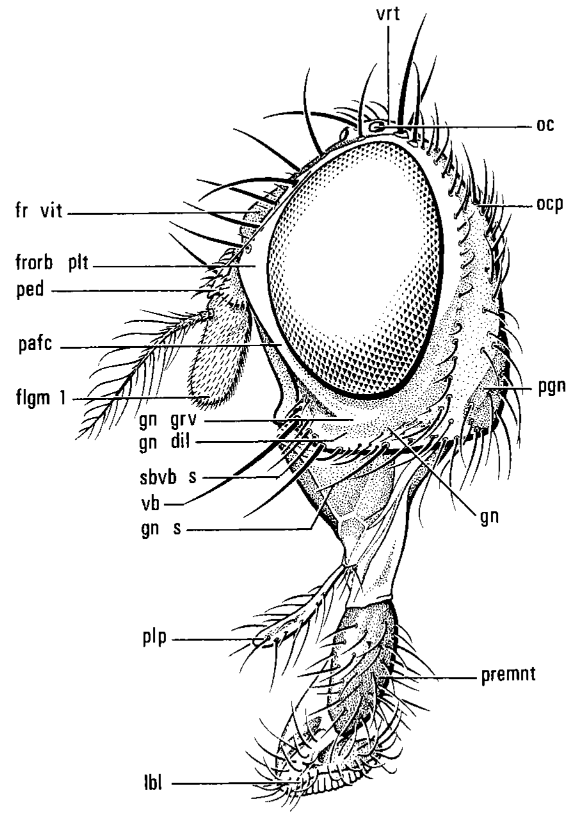
Vertex. The median portion of the upper extremity of the head, bounded by the eyes laterally, the occiput posteriorly, and the frons anteriorly, is called the vertex (Figs. 9, 65). It is a relatively indefinite area, containing the ocellar triangle medially and, at least in the Mus-

Figs. 2.8–11. Head of *Hylemya alcathoe* (Walker): (8) anterior, (9) left lateral, and (11) posterior view of female; (10) anterior view of male. Note dichoptic condition of female (8) and holoptic condition of male (10).

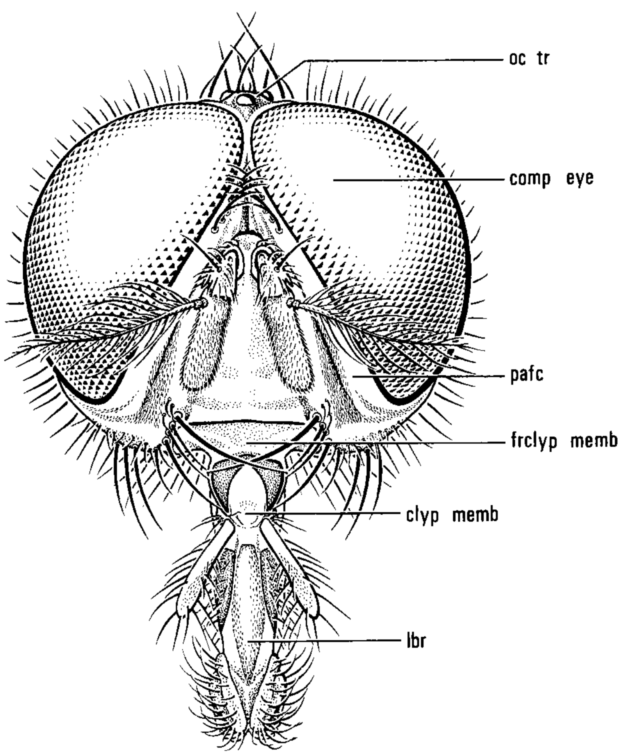
ar, arista
clyp, clypeus
clyp memb, clypeolabral membrane
comp eye, compound eye
fc, face
fc rg, facial ridge
flg, flagellum
flgm, flagellomere
frclyp memb, frontoclypeal membrane
frgn sut, frontogenal suture
frorb plt, fronto-orbital plate
fr s, frontal seta
fr vit, frontal vitta
gn, gena
gn dil, genal dilation
gn grv, genal groove
gn s, genal seta
hyps brg, hypostomal bridge
infr s, interfrontal seta
i vt s, inner vertical seta
lbl, labella
lbr, labrum
lun, lunule
m ocp scl, median occipital sclerite
oc, ocellus
ocp, occiput
ocp for, occipital foramen
ocp s, occipital seta
oc s, ocellar seta
oc tr, ocellar triangle
o vt s, outer vertical seta
pafc, parafacial
pavt s, paravertical seta
pc orb s, proclinate orbital seta
ped, pedicel
pgn, postgena
plp, palpus
pocl s, postocular seta
poc s, postocellar seta
premnt, prementum
ptil fis, ptilinal fissure
p tnt pit, posterior tentorial pit
sbvb s, subvibrissal setula
spc s, supracervical setae
u orb s, upper orbital seta
vb, vibrissa
vrt, vertex



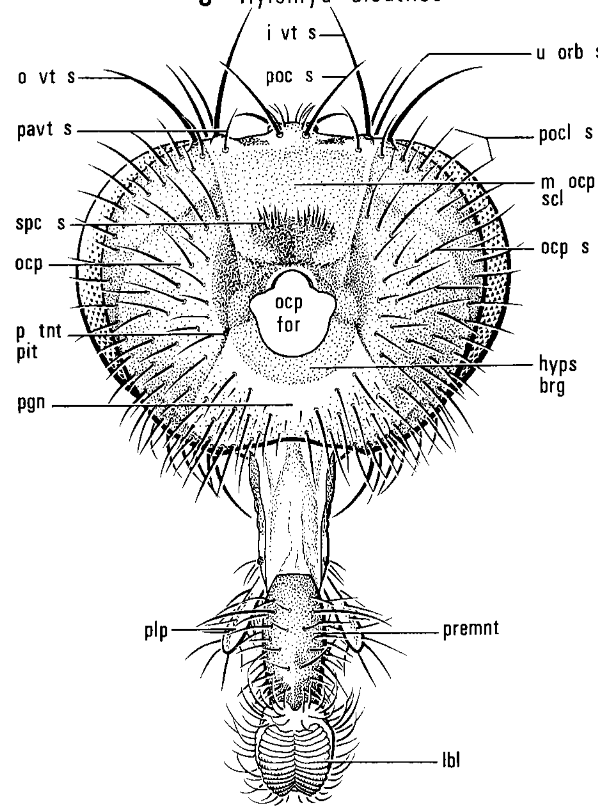
8 Hylemya alcathoe ♀



9 Hylemya alcathoe ♀



10 Hylemya alcathoe ♂



11 Hylemya alcathoe ♀

comorpha, the paired ***orbital plates*** (vertical plates) (*see* "Frons") laterally. In the Nematocera the term vertex is sometimes applied to most of the area here designated as the frons (*see* "Frons"). In many families, especially in the Muscomorpha (Figs. 8–11, 65, 66), ***inner*** and ***outer vertical***, ***paravertical***, and ***postocellar bristles*** are present; typically, ***ocellar bristles*** arise on the ocellar triangle near the anterior ocellus, but they are sometimes displaced. These bristles as well as those on the occiput in the higher Diptera were treated in detail by Steyskal (1976).

Frons. In a generalized insect the frons extends from the vertex to the ***frontoclypeal*** (epistomal) ***suture***, between the two anterior tentorial pits. These landmarks are not always clear, and some dipterists (de Meijere 1916, Hendel 1928, Crampton 1942, Hennig 1973) have adopted convenient topographical definitions of the frontal areas. The area dorsal to the insertions of the antennae (morphologically the postfrons) is usually called the frons, and the frontal area above the clypeus and below the antennae (morphologically the prefrons) is usually referred to as the face (*see* "Face").

In the Nematocera and orthorrhaphous Brachycera the frons is a simple, rather uniformly sclerotized plate, usually without specialized sclerites and bristles. In some Tabanomorpha, e.g. Tabanidae (Figs. 31.9–11), it has shining areas or ***calli*** (*sing.* ***callus***), which are distinguished according to their positions as, for example, the ***median callus***, the ***basal callus,*** and the ***subcallus***. In the Muscomorpha the frons is of particular phylogenetic and systematic importance. In the Aschiza (Fig. 4.95) it is still uniformly sclerotized as in most lower Diptera, but in the Schizophora (Figs. 8, 10, 65) it has undergone characteristic modifications associated with the formation of a ***ptilinum*** (Hennig 1973). The ptilinum, which has been secondarily lost in some Sciomyzidae, is a peculiar, invaginated, sac-like organ armed with small scales (Strickland 1953), and it lies immediately above the bases of the antennae. It is everted with pulsating motions during emergence of the adult and assists the adult to escape from its puparium and the surrounding substrate. The arcuate slit through which the ptilinum is everted is called the ***ptilinal fissure*** (Fig. 8); its lateral extremities nearly coincide with the upper limits of the frontogenal sutures (*see* "Face"). After emergence the ptilinum is retracted within the head capsule and is hidden from view, but its position is marked by the ptilinal fissure. A crescentic median plate lying between the ptilinal fissure and the bases of the antennae is called the ***lunule*** (Fig. 8). A transverse groove, suggestive of an incipient ptilinal fissure and outlining a lunule-like area, is evident in some Aschiza, e.g. some Syrphidae and Platypezidae, as well as in some lower Brachycera, e.g. some Xylophagidae (Figs. 34.7, 34.10), Stratiomyidae, Rhagionidae (Fig. 33.1), Athericidae (Figs. 32.2–3), and Tabanidae (Figs. 31.7–11, subcallus); although no ptilinum is present in these groups, the external area in question may bear some relation to the lunule and ptilinal fissure in the Schizophora (Crampton 1942, p. 18). In the Schizophora the frons (exclusive of the ocellar triangle, treated under "Vertex") is differentiated into a relatively elastic, median ***frontal vitta*** (interfrons, mesofrons) and paired, lateral ***fronto-orbital plates*** (orbits, parafrontal plates) (Fig. 8). Primitively each fronto-orbital plate extends from the vertex to the lower extremity of the frons, e.g. Neriidae and Clusiidae (Fig. 4.114); but with progressive lateral extension of the membranous frontal vitta in some groups, e.g. Heleomyzidae, the lower portion of each fronto-orbital plate is virtually obliterated (Fig. 4.98). However, a broad ***frontal plate*** sometimes arises secondarily from the resclerotized lower lateral margin of the frons (Hennig 1973). Thus each fronto-orbital plate may be differentiated into an upper orbital plate continuous with the vertex and a lower frontal plate continuous with the ***parafacials*** (*see* "Face") (Fig. 4.99). In acalyptrate families the frontal plate is frequently very narrow or undifferentiated, e.g. Heleomyzidae (Figs. 4.98, 4.112), but where it is secondarily enlarged, e.g. Tephritidae, it is at least partially separated from the orbital plate (Fig. 4.99). In the Calyptratae both the orbital plate and the frontal plate are usually strongly developed, but they are fused and practically indistinguishable from each other (Figs. 8, 65).

The frontal vitta frequently bears ***interfrontal setae*** or ***hairs*** or both (Fig. 8); it may also have heavily sclerotized, sometimes bristled ***interfrontal plates***, as in the Sphaeroceridae and the Milichiidae (Figs. 4.117, 4.143, 4.149). Bristles on the fronto-orbital plates can be referred to simply as ***fronto-orbital setae*** or ***setulae***. For purposes of distinction, however, those on the orbital plate are called ***orbital setae*** or ***setulae*** (superior orbital setae or setulae), and those on the frontal plate are called ***frontal setae*** or ***setulae*** (inferior orbital setae or setulae). Orbital setae may be differentiated further as ***upper*** and ***lower orbital setae***; they are usually reclinate, proclinate, or lateroclinate (Figs. 8, 65, 66). Similarly frontal setae may be differentiated as ***upper*** and ***lower frontal setae***; they, too, may be reclinate, proclinate, lateroclinate, or inclinate (Figs. 8, 65, 66), but usually at least some of the stronger frontal setae are more or less inclinate. In acalyptrate families the frontal setae arise laterally to the orbital setae (Fig. 4.99), but in the Calyptratae the frontal setae usually arise medially to the orbital setae (Figs. 8, 65). In holoptic males (Fig. 10) and a few holoptic females throughout the order the frons is virtually obliterated; frequently in these cases the orbital setae are also lost.

Face. The anteromedial portion of the head, bounded dorsally by the insertions of the antennae, ventrally by the frontoclypeal suture, and laterally by the eyes, is the face. In most Nematocera (Figs. 17.2–3, 24.4) and many orthorrhaphous Brachycera (Figs. 32.2–3), this sclerite is relatively small, and often what at first sight appears to be the face is in fact the clypeus. In bloodsucking groups in which the clypeus is enlarged, e.g. Culicidae (Fig. 25.46), Ceratopogonidae (Figs. 28.46–47), Simuliidae (Figs. 27.3–6), and Tabanidae (Figs. 31.2–4), the face is practically obliterated. However, in a few Nematocera, e.g. Anisopodidae (Fig. 48) and Blephariceridae, the face is fairly large and exposed but not nearly so large as in most Asilomorpha (Figs. 40.2, 40.5) and Muscomorpha (Fig. 8). Its larger size in higher Diptera appears to be correlated with the development of a movable proboscis.

In most Diptera each side of the face is marked by a suture that runs dorsally from the anterior tentorial pit toward the base of the antenna. These grooves are the ***frontogenal sutures*** (Matsuda 1965) (Fig. 8), and the median ***facial plate*** lies between them. In addition, in the Schizophora the two arms of the ptilinal fissure run ventrally outside the frontogenal sutures and form the inner margins of the parafacials (Fig. 8). Each parafacial abuts the fronto-orbital plate dorsally and the gena ventrally. Lying between the inner margin of each parafacial and the corresponding frontogenal suture is a strip, often convex and usually narrow, called the ***facial ridge*** (vibrissal ridge). Each facial ridge fades out dorsally, but ventrally it terminates in a more or less angular prominence, the ***vibrissal angle***, which frequently bears one or more strong bristles, the ***vibrissae*** (*sing.* ***vibrissa***; oral vibrissae) (Figs. 8, 9, 66). Both the facial ridges and the parafacials may be bare or setose; in the Tachinidae, especially, setae which are frequently present on the facial ridge are called ***supravibrissal setae*** (Fig. 66). The median facial plate is usually bare, but it is haired in some groups. In the Asilidae and related families it sometimes bears a cluster of hairs and bristles called the ***mystax*** (Figs. 42.36–42). Frequently, especially in the Schizophora, the facial plate has a pair of longitudinal ***antennal grooves*** (foveae) separated by a median ridge, the ***facial carina.*** The facial carina may be continuous with the lunule, e.g. Lonchaeidae (Fig. 4.109). Sometimes, as in many Piophilidae, the facial plate is concave and membranous along the midline (Fig. 4.110). In other cases, e.g. Ephydridae, it is entirely sclerotized and prominently convex (Fig. 4.155); in some Syrphidae (Fig. 4.126) and a few acalyptrates (Fig. 4.112) it is tuberculate. The ***lower facial margin*** is sometimes called the epistoma, but this term should be avoided because it is ambiguous (Crampton 1942, pp. 16–17).

Clypeus. The clypeus lies between the face and the labrum, and it supports the cibarial dilator muscles. It is limited dorsally by the frontoclypeal suture and anteriorly by the ***clypeolabral articulation.*** In the Muscomorpha, the clypeus is reduced to a narrow, usually U-shaped sclerite that is separated from the lower margin of the face by a broad, flexible ***frontoclypeal membrane*** (Figs. 8, 10). In most Nematocera and many orthorrhaphous Brachycera the clypeus is a relatively large, shield-shaped sclerite occupying a facial rather than a subcranial position (Figs. 17.2–3, 24.4, 32.2–3). In many representatives, especially those with well-developed piercing and sucking mouthparts, the clypeus is greatly enlarged at the expense of the face. In a few groups such as the Blephariceridae and some *Xylophagidae* (Fig. 34.7) (but not the Mycetophilidae, contrary to Crampton 1942), the clypeus is divided into a proximal ***postclypeus*** and a distal ***anteclypeus.*** Here the anteclypeus is more or less deflected under the face as in many higher Diptera, perhaps indicating that the peculiar U-shaped clypeus of the Muscomorpha is in fact derived from the anteclypeus only (Crampton 1942). Throughout the Muscomorpha the clypeus is firmly connected internally by means of lateral apodemes to the skeleton of the ***cibarial pump*** (Fig. 58). The entire stirrup-shaped structure, including the external U-shaped clypeus, is called the ***fulcrum.***

The region between the lower margin of the eye and the subcranial cavity consists of the gena above (Fig. 9) and a narrow, usually hairless strip, the subgena, below. The ***subgenal suture***, which begins at the anterior tentorial pit and runs posteroventrally, separates these two sclerites. Sometimes the two sclerites are collectively called the cheek. Anterodorsally the gena unites with the lower extremity of the fronto-orbital plate in lower Diptera (Figs. 15.2–3, 34.7) and with the facial ridge and the parafacial in the Muscomorpha (Figs. 8, 9). Both the gena and the subgena are more or less fused posteriorly where they join with the postgena (Fig. 9). The gena is usually haired and sometimes also bears outstanding ***genal bristles***, which should not be confused with vibrissae (*see* "Face"). The setulae along the anteroventral margin of the gena are referred to as the ***subvibrissal setae*** or ***setulae*** (oral setae or setulae, peristomal hairs) (Figs. 9, 66). In the schizophorous Muscomorpha there is a weakened, often depressed and groove-like area near the ventral limits of the ptilinal suture and the juncture of the gena and the parafacial (Figs. 9, 66). This area is called the ***genal groove*** (cheek groove, facial impression, facial warp, mediana, transverse impression, vibrissarium). It is usually bare and is particularly conspicuous in the Calyptratae, where it distinctly separates the parafacial above from the gena below. In many muscoid flies the hairy, strongly sclerotized portion of the gena lying below the genal groove and extending forward toward the vibrissal angle is called the ***genal dilation*** (occipital dilation, metacephalon) (Figs. 9, 66). The subgena is usually very narrow and bare; its lower extremity forms the lateral margin of the subcranial cavity. In the Tipulomorpha the clypeus, genae, subgenae, and related structures are fused and elongated to form a snout-like ***rostrum*** (Fig. 64). The position of the palpi, which are always attached immediately below the distal edge of the head capsule, serves to indicate where elongation has taken place.

In groups with a more or less retractable proboscis, the lower surface of the head has a well-developed subcranial cavity for reception of the basal part of the proboscis. In the Nematocera and certain orthorrhaphous Brachycera this cavity is little more than a depression, and in forms with typical piercing and sucking mouthparts, e.g. Culicidae, Ceratopogonidae, Simuliidae, and Tabanidae, it is absent. Likewise, it is relatively poorly developed in orthorrhaphous forms with rigidly fixed, projecting mouthparts, e.g. many Asilidae. On the other hand it is well developed in the Empididae and the Dolichopodidae. It is best developed, however, in the Muscomorpha, where it appears to be correlated with the development of the very mobile, jointed proboscis so characteristic of higher Diptera.

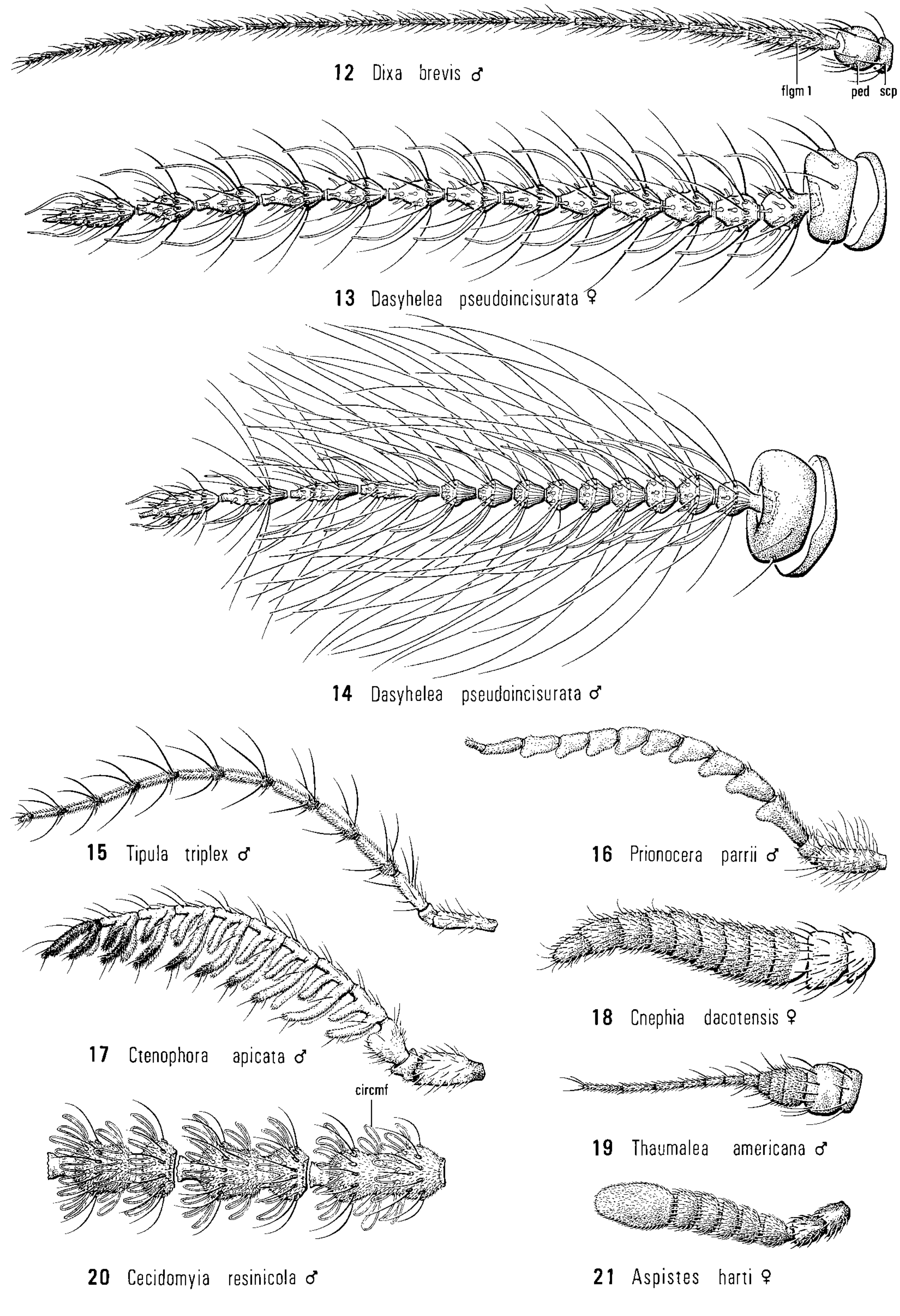
Postcranium. The entire posterior surface of the head capsule (Fig. 11) is the postcranium. It is usually rounded in outline and may be strongly convex as in most Nematocera, flattened as in most Muscomorpha, or concave as in the Bombyliidae and the Pipunculidae. The principal landmarks are the occipital foramen and the posterior tentorial pits. According to Snodgrass (1935, p. 112) the narrow rim of the occipital foramen is the ***postocciput***; it is separated from the remainder of the postcranium by the ***postoccipital suture***. The upper half of the postcranium, the occiput, merges ventrally with the postgenae, which occupy the portion of the postcranium below the occipital foramen. The occiput of many orthorrhaphous Brachycera and all Muscomorpha contains a distinct ***median occipital sclerite*** (epicephalon, cerebrale), the upper margin of which passes over the vertex into the ocellar triangle (Fig. 11). This sclerite is indistinct or absent in the Nematocera (Hendel 1928). According to Crampton (1942) the ventral closing of the head capsule is formed by the median approximation and fusion of the postgenae. The fused median area is called the ***hypostomal bridge*** (pseudogula). It is closed in most Diptera but apparently is open in at least some species of Tanyderidae and Anisopodidae (Crampton 1942, Figs. 2H and 2K). Exclusive of the bristles on the vertex (*see* "Vertex") the principal bristles on the occiput are the ***postocular*** and ***occipital bristles*** and the ***supracervical setulae*** (Fig. 11).

Antenna. The antennae are a pair of mobile, segmented, sensory appendages arising from membranous ***antennal sockets*** between the frons and the face. They vary extensively in structure (Figs. 12–45) and sometimes exhibit strong sexual dimorphism (Figs. 13, 14). They furnish excellent taxonomic characters and are much used in the classification of the Diptera. The basic number of antennal parts or segments is three. The basal segment is called the ***scape***; the second segment, which encloses ***Johnson's organ***, a mass of receptor cells for detecting movements of the flagellum, is called the ***pedicel***; and the remaining part, which contains varying numbers of ***flagellomeres***, is called the ***flagellum*** (Fig. 12). According to Hennig (1973) the basic number of flagellomeres is fourteen in the Nematocera (Figs. 12–21), eight in the primitive Brachycera (Figs. 22–30), three in the Asilomorpha (Figs. 31–36), and four in the Muscomorpha (Figs. 37–45). The scape is usually short and sometimes, as in the Culicidae and the Hippoboscidae, rudimentary. The pedicel may be enlarged as in all Culicomorpha (Figs. 12–14) (except the Simuliidae) and in some Tabanidae, or it may be elongated as in many Conopidae (Fig. 38) and Sciomyzidae (Fig. 39); in the Calyptratae and some other Muscomorpha, it is marked dorsally by a longitudinal ***antennal seam*** (Figs. 43–45).

The flagellum is the most variable section. The thread-like form found in many Nematocera, e.g. Dixidae (Fig. 12), is called filiform; when the flagellomeres bear whorls of hairs as in the Culicomorpha (Figs. 13, 14), the antennae are called verticillate or plumose; if each flagellomere has one or more extensions as in certain Tipulidae (Figs. 16, 17), it is described as serrate or pectinate; if the flagellomeres are broad and flat, as in the mycetophilid genus *Keroplatus*, the antennae are said to be foliaceous. The nodose type occurring in many Nematocera, e.g. Cecidomyiidae, is called moniliform. Usually some or all of the flagellomeres bear sensory hairs, bristles, pegs, or related structures, or some combination of these. In many cecidomyiids they are provided with continuous thread-like sensoria called ***circumfila*** (*sing.* ***circumfilum***) (Fig. 20).

In higher Diptera the first flagellomere (postpedicel) is usually enlarged and the distal segments are reduced to a ***stylus*** or an ***arista*** (Figs. 23–45). A stylus is usually rigid and either terminal or subterminal, whereas an arista is usually more slender and bristle-like, and may arise dorsally as well as apically. However, there is no sharp distinction between the two. An arista-bearing antenna is called aristate, and a stylus-bearing one is called stylate. The arista is dorsal if it arises on the top of the first flagellomere, and terminal if it arises at the apex; it may be bare, plumose, or pectinate according to the number and arrangement of the hairs it bears. The primary number of ***aristomeres*** in the Muscomorpha is three; in the Syrphoidea, however, it is usually reduced to two. Wherever an arista occurs in the lower Brachycera, e.g. some Stratiomyidae, Rhagionidae, Empididae, and Dolichopodidae, it is usually two-segmented. In stylate forms the segmentation is sometimes not apparent. The arista is occasionally greatly reduced or absent, as in the acalyptrate family Cryptochetidae and in the phorid genus *Abaristophora*.

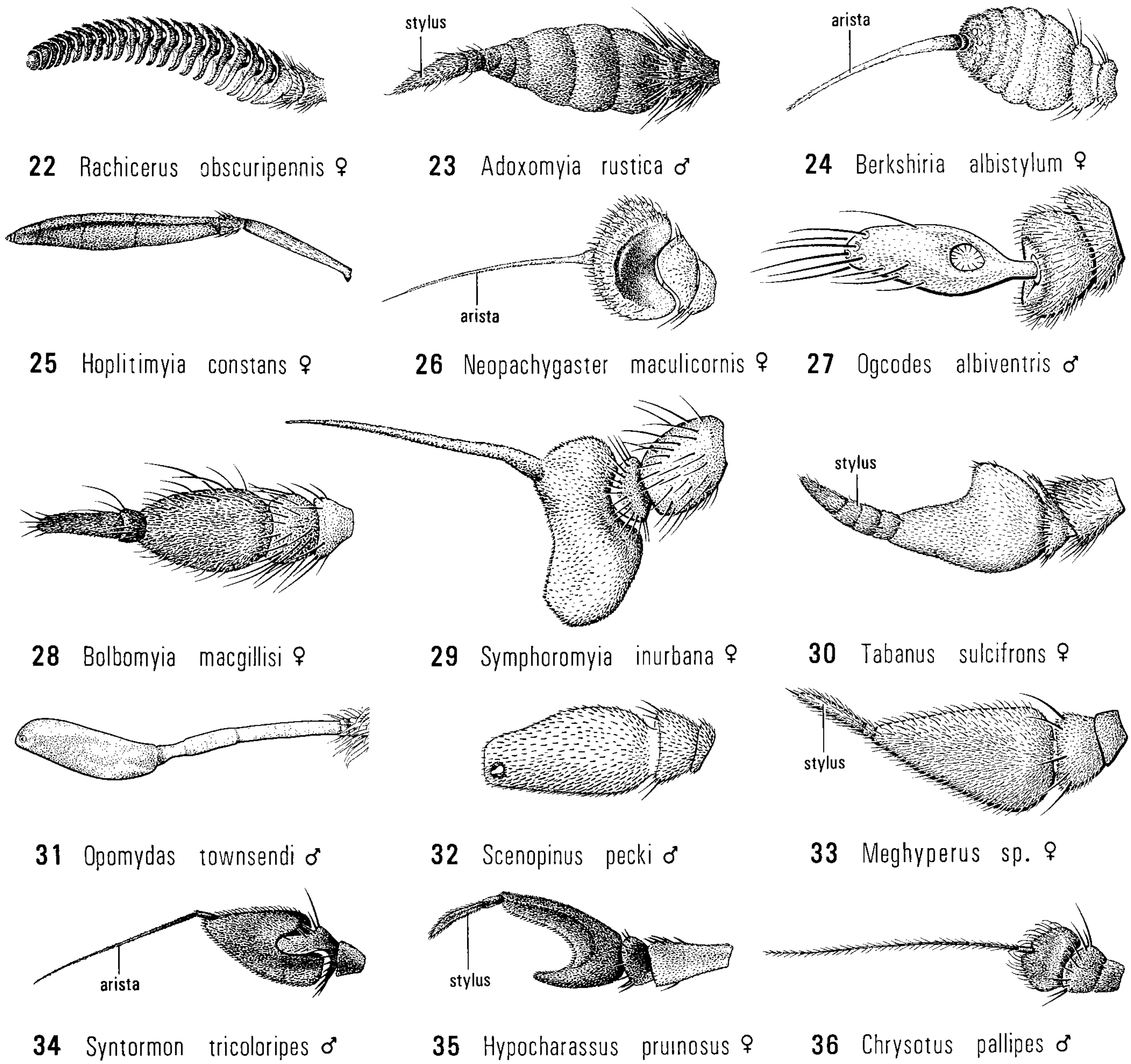
Mouthparts. The mouthparts (Figs. 46–63) form a tubular sucking organ, the ***proboscis***. In general there are two main types, the piercing and sucking type found in bloodsucking and predacious groups such as biting flies (Figs. 46, 47), Asilidae (Figs. 53, 54), and Empididae; and the lapping and sucking, nonbiting type found in the Anisopodidae (Figs. 48, 49), Tipulidae, Chironomidae, and Stratiomyidae and in most higher Diptera (Figs. 50–63). However, both these types vary considerably. Typically, the proboscis consists of three unpaired and two paired elements (Figs. 46, 47). The three unpaired elements are the ***labrum*** (labrum–epipharynx), forming the dorsal wall of the proboscis; the ***labium***, forming the ventral wall of the proboscis; and



Figs. 2.12–21. Left antennae of Nematocera, left lateral view: (12) *Dixa brevis* Garrett; (13) female and (14) male of *Dasyhelea pseudoincisurata* Waugh & Wirth; (15) *Tipula triplex* Walker; (16) *Prionocera parrii* (Kirby); (17) *Ctenophora apicata* Osten Sacken; (18) *Cnephia dacotensis* (Dyar & Shannon); (19) *Thaumalea americana* Bezzi; (20) *Cecidomyia resinicola* (Osten Sacken); (21) *Aspistes harti* Malloch.
Abbreviations: circmf, circumfilum; flgm, flagellomere; ped, pedicel; scp, scape.

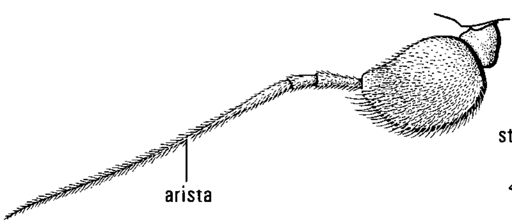
the ***hypopharynx***, projecting between the other two elements. The two paired elements, also arising between the labrum and the labium, are the ***mandibles*** anterolaterally and the ***maxillae*** (*sing.* ***maxilla***) posterolaterally.

The labrum is derived from a single preoral lobe (Snodgrass 1944), and although its ventral surface is frequently called the ***epipharynx***, this structure is an integral part of the labrum. Situated on each side of the base of the epipharynx is a small sclerite called the ***torma*** (*pl.* ***tormae***). It belongs to the epipharynx and connects with the clypeus at the lateral ends of the clypeolabral suture (Peterson 1916). Tormae are best developed in Nematocera and orthorrhaphous Brachycera that have mouthparts adapted for piercing, as in the Simuliidae (Fig. 27.8) and the Ceratopogonidae (Fig.

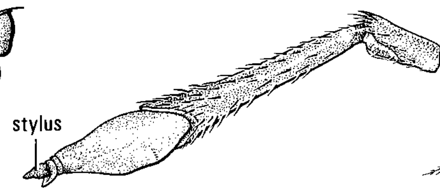


Figs. 2.22–36. Left antennae (except Fig. 34) of orthorrhaphous Brachycera, left lateral view: (22) *Rachicerus obscuripennis* Loew; (23) *Adoxomyia rustica* (Osten Sacken); (24) *Berkshiria albistylum* Johnson; (25) *Hoplitimyia constans* (Loew); (26) *Neopachygaster maculicornis* (Hine); (27) *Ogcodes albiventris* Johnson; (28) *Bolbomyia macgillisi* Chillcott; (29) *Symphoromyia inurbana* Aldrich; (30) *Tabanus sulcifrons* Macquart; (31) *Opomydas townsendi* (Williston); (32) *Scenopinus pecki* Kelsey; (33) *Meghyperus* sp.; (34) *Syntormon tricoloripes* Curran, right antenna, left side; (35) *Hypocharassus pruinosus* (Wheeler); (36) *Chrysotus pallipes* Loew.

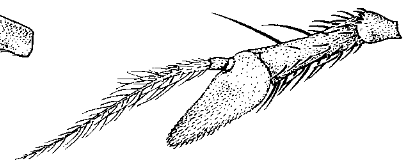
28.46); they are usually not evident in higher Diptera. Peterson (1916) wrongfully interpreted the reduced clypeus in the Muscomorpha as tormae. Externally the labrum is hinged to the clypeus by the ***clypeolabral suture*** or ***membrane***; internally its epipharyngeal surface forms the top of the ***food canal***. The labrum is sometimes rather soft and membranous, as in *Rhabdophaga* (Cecidomyiidae), *Mycetobia* (Anisopodidae), *Chironomus*, and *Scenopinus*; small and flap-like, as in *Trichocera* and most Mycetophilidae; strongly sclerotized and blade-like, as in many bloodsucking and predacious flies; elongate with its sides curled ventromedially to form a closed food canal, as in the Culicidae (Fig. 47); moderately developed, as in most Muscomorpha (Figs. 55–60); or heavily sclerotized with strong, tooth-like projections laterally, as in the Dolichopodidae (Figs. 50–52). The hypopharynx forms the bottom of the food canal in most Diptera; it is usually stylet shaped and contains the ***salivary canal***. In the Asilidae (Figs. 53, 54) it forms the piercing implement, like a hypodermic syringe, for injecting paralyzing saliva into prey. Internally at the bases of the labrum and the hypopharynx, especially in the Muscomorpha, are sometimes found two sclerites, a stirrup-shaped fulcrum proximally (its external, U-shaped dorsal plate forms the clypeus), and a crescentic ***hyoid sclerite*** distoventrally (Figs. 55, 59). Both are associated with the ***cibarial pump*** (food pump) at the base of the food canal. The apices of both the labrum and hypopharynx sometimes have tooth-like serrations in bloodsucking flies.



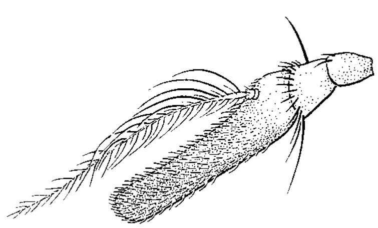
37 Conicera dauci ♀



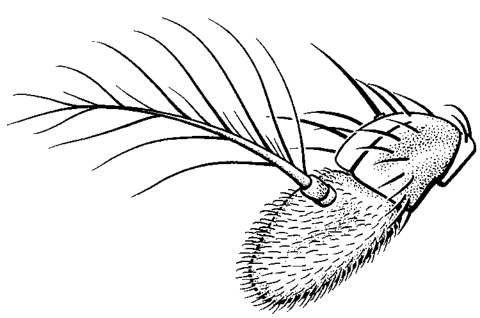
38 Physocephala furcillata ♂



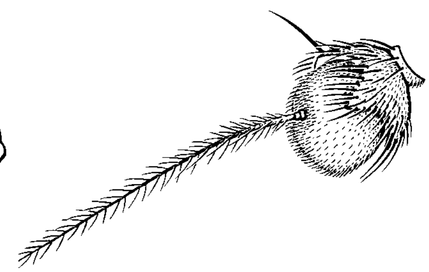
39 Dictyacium ambiguum ♀



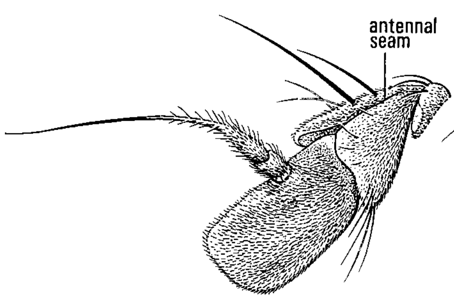
40 Lauxaniella femoralis ♀



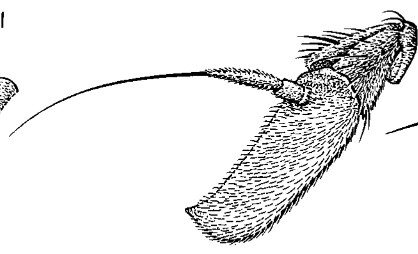
41 Drosophila colorata ♂



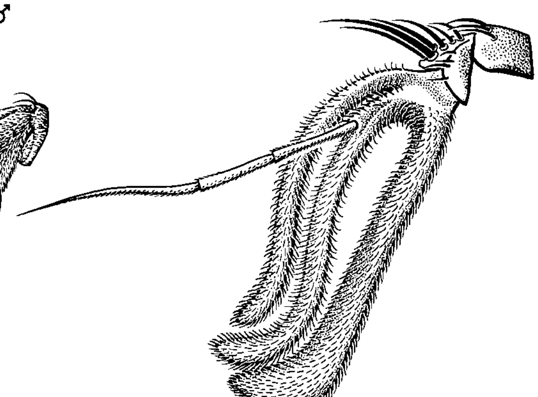
42 Clusia lateralis ♀



43 Cordilura ustulata ♂



44 Chaetosa palpalis ♂



45 Dichocera tridens ♂

Figs. 2.37–45. Left antennae of Muscomorpha, left lateral view: (37) *Conicera dauci* (Meigen); (38) *Physocephala furcillata* (Williston); (39) *Dictyacium ambiguum* (Loew); (40) *Lauxaniella femoralis* (Loew); (41) *Drosophila colorata* Walker; (42) *Clusia lateralis* (Walker); (43) *Cordilura ustulata* Zetterstedt; (44) *Chaetosa palpalis* (Coquillett); (45) *Dichocera tridens* (Walton).

Functional mandibles are found in the female only. They are usually flattened, blade-like structures, but in the Culicidae (Figs. 46, 47) they are slender and stylet-like. Frequently they are serrate along the median margins. Functional mandibles are present in the Tanyderidae, most Blephariceridae, and some Psychodidae; in most families of Culicomorpha, e.g. Dixidae, Culicidae, Ceratopogonidae, Simuliidae, and some Chaoboridae and Chironomidae; and in some Tabanoidea, e.g. Athericidae, Rhagionidae, and Tabanidae. Vestigial mandibles usually occur in the male of species in which the female has mandibles, but they are never functional. In the Tabanoidea, however, they are absent in the male and present in the female, only. No case is known where they are present in the male but absent in the female. When present in either sex they fit between the labrum and the hypopharynx (Fig. 47).

The maxillae are also stylet-like, but they retain more evidence of their derivation from primitive leg-like appendages and are therefore more complex than mandibles. Each maxilla is composed of a basal ***cardo*** and a distal ***stipes***. The stipes bears the principal maxillary blade (endite). It has been interpreted by some authors (Crampton 1942, Snodgrass 1944) as the galea, but by others (Imms 1944, Wenk 1962, Hennig 1973) as the ***lacinia***; the latter interpretation is adopted here. The stipes also bears a maxillary palpus, usually referred to as the palpus; it has five segments in many Nematocera, two in most orthorrhaphous Brachycera, and one in most Muscomorpha. The third segment bears a characteristic ***sensory area***, which is invaginated as a ***sensory pit*** or ***vesicle*** in many Nematocera (Fig. 48). The entire palpus shows sexual dimorphism in several instances throughout the order and it is absent in certain representatives of many groups.

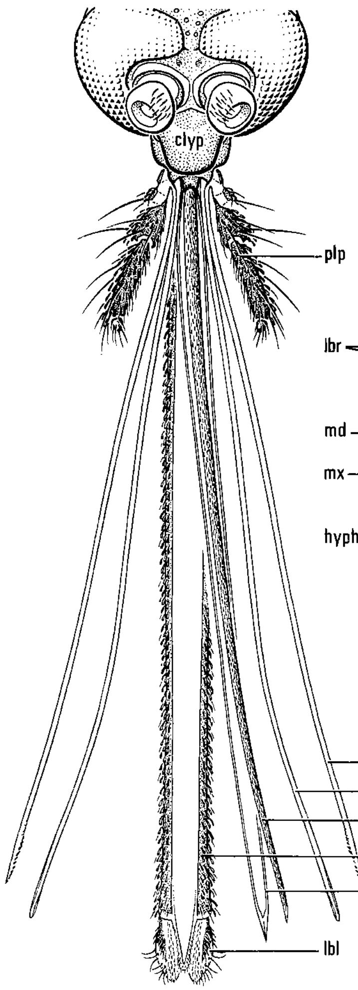
The labium, derived from a pair of united second maxillae (Snodgrass 1935), is the largest of the mouthparts. It usually forms a trough in which the other mouthparts lie. Basically it consists of a proximal ***postmentum*** (mentum of Crampton 1942) and a distal ***prementum*** (theca, part of haustellum of some authors). The postmentum is frequently greatly reduced or absent, but it is sometimes present as a distinct plate as in the anisopodid genus *Sylvicola*, and it is very long in the Chilean genus *Tanyderus*. The prementum is one of the most important of the labial sclerites. At its distal end it bears the ***labella*** (*sing.* ***labellum***) derived from a pair of united two-segmented labial palpi; the two-segmented condition is plesiomorphic and is most evident in primitive Nematocera, e.g. Blephariceridae and Tanyderidae. The labella usually consist of two membranous, cushion-like lobes. In the Brachycera, and perhaps rarely in the Nematocera (Hennig 1973), the inner surfaces of these lobes are furnished with varying numbers of small, sclerotized, trachea-like grooves called ***pseudotracheae*** (*sing.* ***pseudotrachea***) (Figs. 58, 61–63), which radiate from the terminus of the food canal. These microcanals, best known in the Calliphoridae (Graham-Smith 1930), serve to distribute saliva and to take up dissolved food. In association with the pseudotracheae, many muscoid flies have developed small ***prestomal teeth***, which are used as rasping structures for rupturing surfaces and breaking up food particles. In bloodsucking forms such as *Stomoxys* (Figs. 55–57) and *Glossina*, the labella are greatly reduced, but the prestomal teeth (Fig. 57) are relatively large and are the main implements used for piercing. In some forms, e.g. the tipulid genus *Geranomyia*, certain Blephariceridae, and the empidid species *Empis clausa* Coquillett, the labella are very long and slender. In other cases, e.g. the mycetophilid genus *Mycetophila*, they are extremely broad.

This discussion shows that although the mouthparts of all Diptera are primarily adapted for sucking up liquid or liquefied food, the components of the proboscis vary considerably among groups both in structure and in function. Even among the so-called biting flies with typical piercing and sucking mouthparts, there are marked differences in the ways the parts are inserted and are utilized during feeding. In bloodsucking Nematocera and tabanoids the actual incision is made by the stylet-like mandibles. In mosquitoes all six stylets, namely the labrum, the two mandibles and maxillae, and the hypopharynx, are inserted into the wound during feeding. In black flies, however, and probably also in some insectivorous ceratopogonids, the labrum is folded against the external surface of the host so that only five stylets are inserted into the wound. In predatory Dolichopodidae the sides of the labrum are armed with blade- and tooth-like processes, called the ***epipharyngeal armature*** (Fig. 51), that are presumably used for cutting and tearing tissues; in these species, also, the labrum is probably inserted into the wound during feeding.

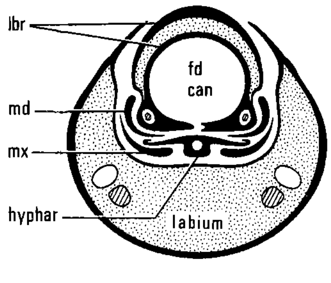
In all the above forms the labium and the labella are not inserted. However, in higher Diptera such as *Stomoxys* and *Glossina*, the prestomal teeth of the labella

Figs. 2.46–52. Mouthparts of Culicidae, Anisopodidae, and Dolichopodidae: (46) *Aedes canadensis* (Theobald), anterior view, with parts displayed to show forms and relationships; (47) *Culex pipiens* Linnaeus, cross section through proboscis (after Hennig 1973); (48) *Sylvicola fenestralis* (Scopoli), anterior view; (49) *S. fenestralis*, cross section through proboscis; (50) *Condylostylus sipho* (Say), cross section through proboscis; (51) *C. sipho*, anterolateral view of proboscis showing relationship with cibarium and tentorium, with (52) enlargement of right epipharyngeal armature.

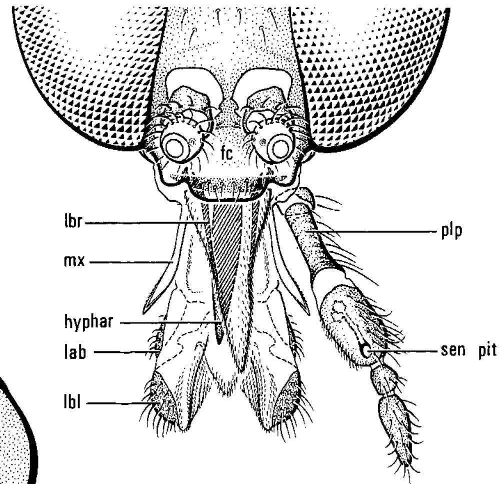
Abbreviations: ant soc, antennal socket; a tnt pit, anterior tentorial pit; cib, cibarium; clyp, clypeus; epiphar arm, epipharyngeal armature; fc, face; fd can, food canal; hyphar, hypopharynx; lab, labium; lbl, labellum; lbr, labrum; md, mandible; mx, maxilla; plp, palpus; sen pit, sensory pit; tnt, tentorium.



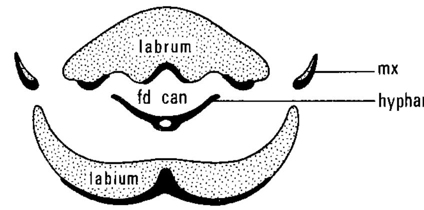
46 Aedes canadensis ♀



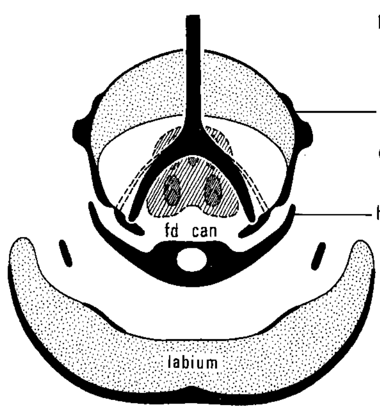
47 Culex pipiens ♀



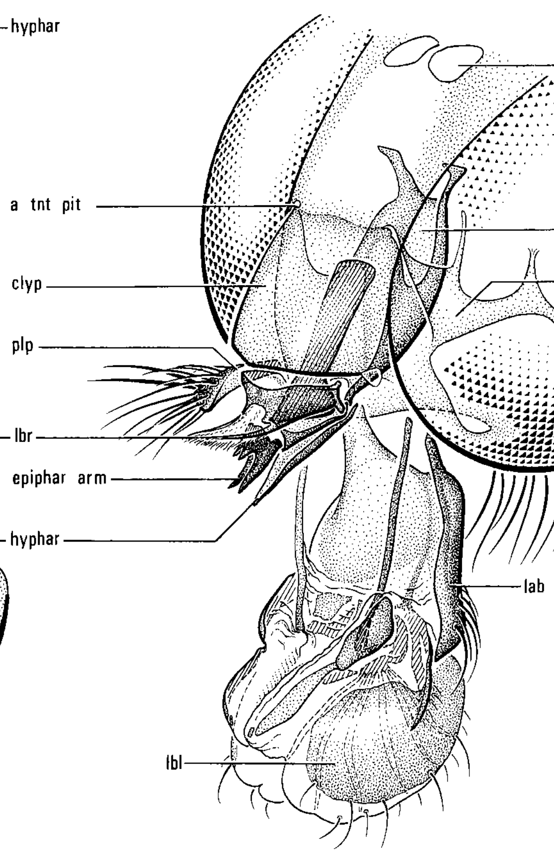
48 Sylvicola fenestralis ♀

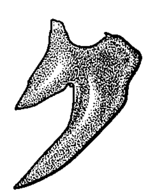


49 Sylvicola fenestralis ♀

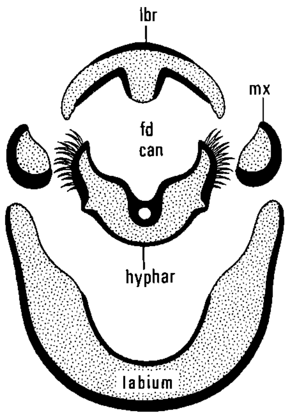


50 Condylostylus sipho ♀

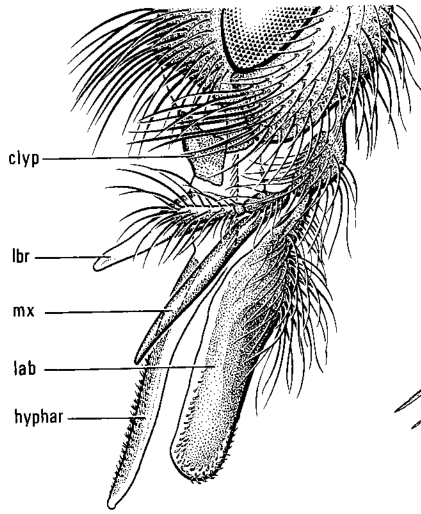




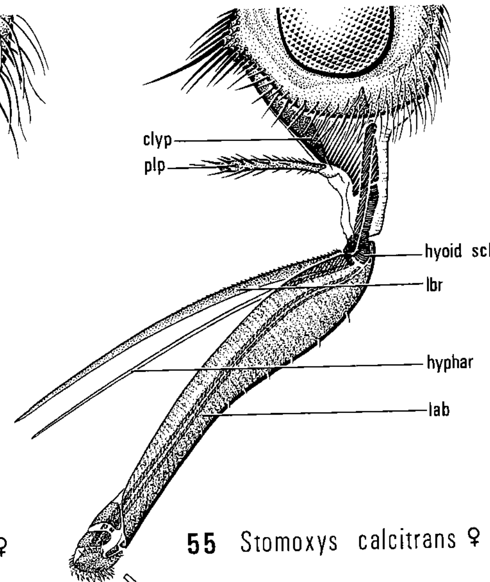
51 Condylostylus sipho ♀ 52



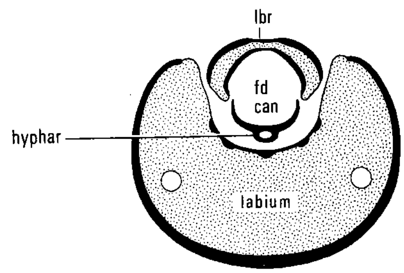
53 Laphria thoracica



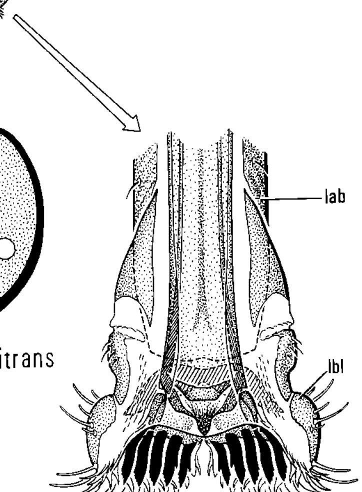
54 Laphria thoracica ♀



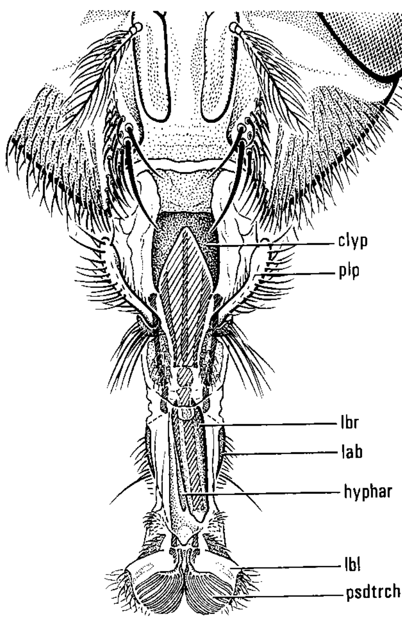
55 Stomoxys calcitrans ♀



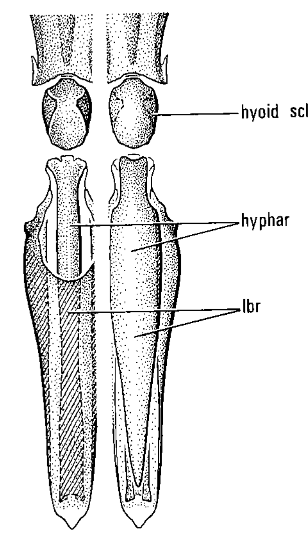
56 Stomoxys calcitrans



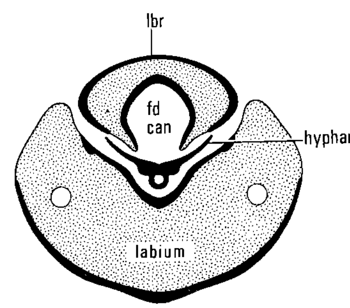
57 Stomoxys calcitrans ♀



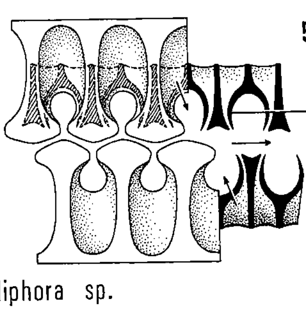
58 Calliphora vomitoria ♀



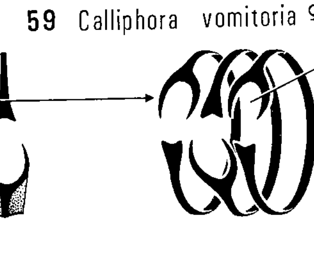
59 Calliphora vomitoria ♀



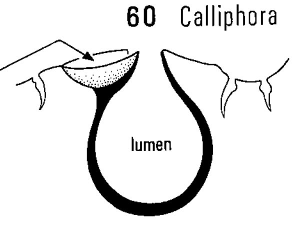
60 Calliphora vomitoria



61 Calliphora sp.



62 Calliphora sp.



63 Calliphora sp.

have become the effective cutting tools; in these flies both the labrum and the labium, including the reduced labella, are inserted into the host during feeding.

In Diptera that are neither predacious nor bloodsucking, which include most of the order, food is imbibed by applying the soft labella to liquid substances such as nectar or to dry food sources such as pollen grains and dried honeydew that have first been suitably liquefied with saliva.

THORAX

The segments of the thorax (Figs. 64–66) are the ***prothorax***, ***mesothorax***, and ***metathorax***. An outstanding feature of the Diptera is that the mesothorax is greatly enlarged to accommodate the muscles for the single pair of wings, whereas both the prothorax and metathorax are very reduced. The prefixes pro-, meso-, and meta- are usually attached to the different sclerites of the corresponding thoracic segments, e.g. prosternum, mesonotum, and metepimeron, but because of the predominance of the mesothorax, the prefix meso- is frequently omitted when referring to the sclerites of that segment (*see* "Mesothorax"). These prefixes are not to be confused with ante-, pre-, and post-, which are used to define particular parts of each sclerite, e.g. antepronotum, prescutellum, and postpronotum.

Basically each thoracic segment of an insect has a dorsal tergal plate, the ***notum***; a lateral plate, the ***pleuron***; and a ventral plate, the ***sternum***. Generally, the notum can be more or less divided into the ***prescutum***, ***scutum***, and ***scutellum***; in the Diptera, however, this division of the notum is usually made only for the mesonotum. The lateral pleural sclerites are considered to have been derived from subcoxal elements of ancestral legs, which became incorporated into the body wall. They consist of an anterior ***episternum*** and a posterior ***epimeron*** separated by a ***pleural suture*** which runs between the leg base and the wing base and serves to strengthen the pleuron. The episternum may be divided into an upper ***anepisternum*** and a lower ***katepisternum***; the epimeron may similarly be separated into the ***anepimeron*** and the ***katepimeron***. These general terms can all be modified by the suffixes pro-, meso-, and meta- to designate the particular segment of the thorax with which they are associated. However, as indicated above, when referring to the sclerites of the mesothorax, all these terms are usually used unmodified except for the term mesonotum. The principal thoracic landmarks in the Diptera are the attachments of the head, abdomen, legs, wings, and halteres, and the ***anterior*** (mesothoracic) and ***posterior*** (metathoracic) ***thoracic spiracles***. In the Diptera, as in all insects, true prothoracic spiracles are absent, but the mesothoracic spiracles frequently migrate forward and hence are often incorrectly called the prothoracic spiracles (*see* "Mesothorax").

Prothorax. The head is joined to the thorax by a membranous area of the prothorax called the ***cervix*** (neck), which bears one to three pairs of ***cervical sclerites***. The ***pronotum*** is usually clearly divided into anterior and posterior parts; the ***antepronotum*** (anterior pronotum) is best developed in the Nematocera, especially the Tipulidae (Fig. 64), in which the lateral portions are enlarged to form a pair of prominent ***antepronotal lobes***. The ***postpronotum*** (posterior pronotum), better developed in higher Diptera (Figs. 65, 66), is usually intimately associated with the mesonotum, and its posterolateral margins form the ***postpronotal lobes*** (humeri, humeral calli). The number, size, and position of the ***postpronotal*** (humeral) ***bristles*** provide useful taxonomic characters in many groups throughout the order, especially in higher Diptera. Laterally the ***propleuron*** may be rather indistinctly divided into an anterior ***proepisternum*** and a small ***proepimeron***; together, the two parts usually form an arch over the base of the anterior coxa, especially in higher Diptera (Fig. 66). The ***propleural suture*** that separates them is usually at least partly obliterated; it is most apparent along the ventral margin, running from just above the anterior coxa toward the anterior spiracle. The proepimeron blends into the fused junction of the mesopleural katepisternum and anepisternum. The presence or absence of ***proepisternal*** (propleural) ***bristles*** and hairs is important in the taxonomy of many families, especially in higher Diptera; the same is true for ***proepimeral*** (stigmatal) ***bristles***. The principal sternal sclerite is the ***prosternum***, which may be divided externally into an anterior ***presternum*** and a posterior ***basisternum***. The prosternum is usually separated from adjacent sclerites by a membrane, but it is sometimes joined with the proepisternum by a sclerotized ***precoxal bridge*** (Fig. 4.162). The morphology of the prothorax, especially the prosternum, in acalyptrate flies was treated in detail by Speight (1969).

Figs. 2.53–63. Mouthparts of Asilidae, Muscidae, and Calliphoridae: (53) *Laphria thoracica* Fabricius, cross section through proboscis; (54) *L. thoracica*, lateral view; (55) *Stomoxys calcitrans* (Linnaeus), lateral view; (56) *S. calcitrans*, cross section through proboscis; (57) *S. calcitrans*, enlargement of labella, front view, showing prestomal teeth; (58) *Calliphora vomitoria* (Linnaeus), anterior view; (59) *C. vomitoria*, enlargement of labrum, hypopharynx, and hyoid sclerite, dorsal and ventral views; (60) *C. vomitoria*, cross section through proboscis; (61) enlargement of pseudotracheae of *Calliphora* sp. (adapted from Graham-Smith 1930), showing openings to main lumen and pseudotracheal rings as seen externally, (62) alternating relationships of the bifid and flattened extremities of three consecutive pseudotracheal rings as seen from the external surface, and (63) interbifid space at bifid extremity and flattened portion at opposite extremity of a pseudotracheal ring as seen from the side view.

Abbreviations: clyp, clypeus; fd can, food canal; hyoid scl, hyoid sclerite; hyphar, hypopharynx; lab, labium; lbl, labellum; lbr, labrum; mx, maxilla; plp, palpus; psdtrch, pseudotrachea.

Mesothorax. The ***mesonotum*** (Figs. 64–66) includes the entire dorsum of the mesothorax. Its three basic components are the ***prescutum***, the ***scutum*** (mesoscutum, mesonotum), and the ***scutellum***; it also includes a fourth part posteriorly, the ***postnotum*** (metanotum, postscutellum), which is probably derived from an intersegmental acrotergite. Unfortunately, many dipterists have misapplied the term mesonotum to the scutum only.

The true prescutum, as opposed to an anterior portion of the scutum that Curran and others incorrectly called the prescutum, is greatly reduced in the Diptera. A portion of the ***prescutal suture*** (prescutoscutal suture, pseudosuture), separating the prescutum from the scutum, is evident in some Nematocera, e.g. Tipulidae, Blephariceridae, Axymyiidae, and Psychodidae; its position coincides closely with the ***prescutal pits*** (humeral pits, humeral scars, tuberculate pits, pseudosutural foveae) present in some Tipulidae (Fig. 64), Ceratopogonidae, and Chironomidae. In the mature pupa these pits lie beneath the bases of the pupal horns. In many Nematocera and orthorrhaphous Brachycera the posterolateral margin of the prescutal area is traversed by a longitudinal suture, probably the base of the ***lateral parapsidal suture*** (notaulice), which marks off a narrow lateral sclerite called the ***paratergite***; this sclerite is believed to be a vestige of the prescutum (Colless and McAlpine 1970, Hennig 1973).

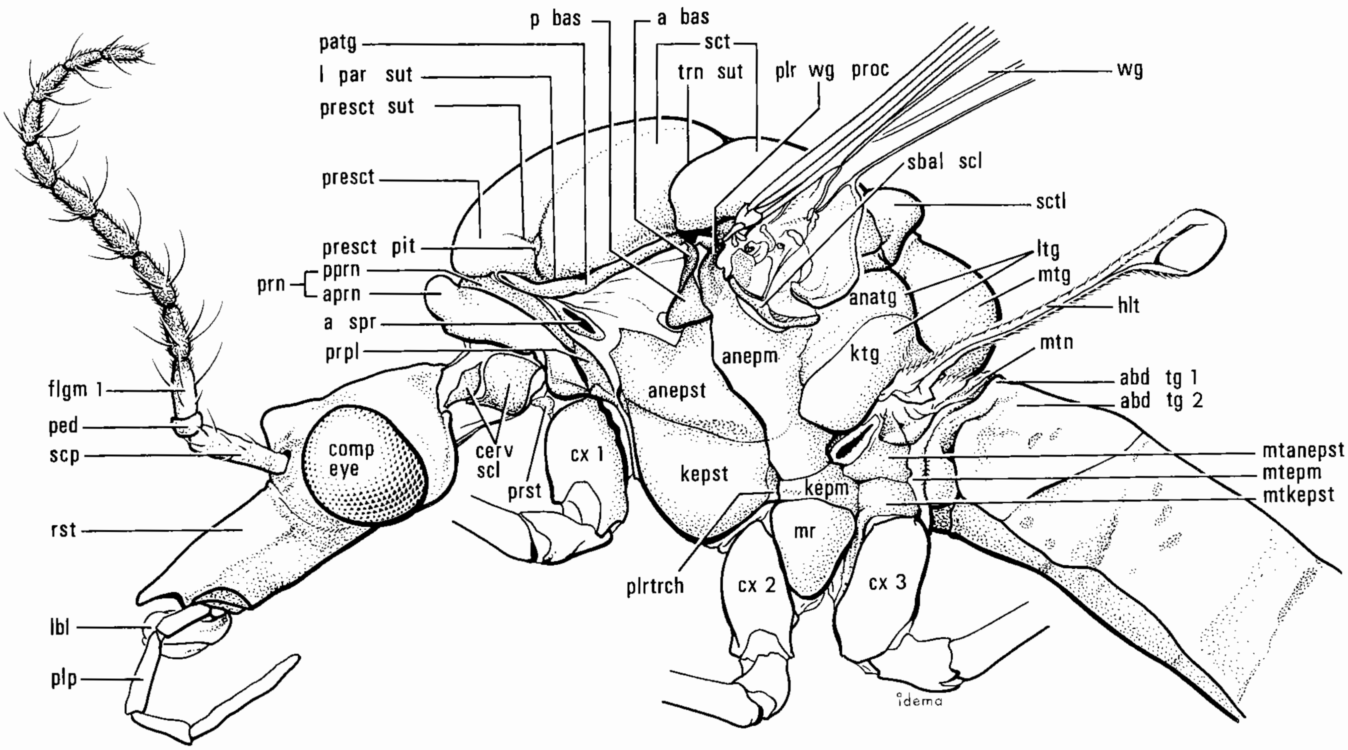


Fig. 2.64. Morphology and terminology of head and thorax of *Tipula trivittata* Say, lateral view.

a bas, anterior basalare
abd tg, abdominal tergite
anatg, anatergite
anepm, anepimeron
anepst, anepisternum
aprn, antepronotum
a spr, anterior spiracle
cerv scl, cervical sclerite
comp eye, compound eye
cx, coxa
flgm, flagellomere
hlt, halter
kepm, katepimeron
kepst, katepisternum
ktg, katatergite
lbl, labellum
l par sut, lateral parapsidal suture
ltg, laterotergite
mr, meron
mtanepst, metanepisternum
mtepm, metepimeron
mtg, mediotergite
mtkepst, metakatepisternum
mtn, metanotum
patg, paratergite
p bas, posterior basalare
ped, pedicel
plp, palpus
plrtrch, pleurotrochantin
plr wg proc, pleural wing process
pprn, postpronotum
presct, prescutum
presct pit, prescutal pit
presct sut, prescutal suture
prn, pronotum
prpl, propleuron
prst, prosternum
rst, rostrum
sbal scl, subalar sclerite
scp, scape
sct, scutum
sctl, scutellum
trn sut, transverse suture
wg, wing

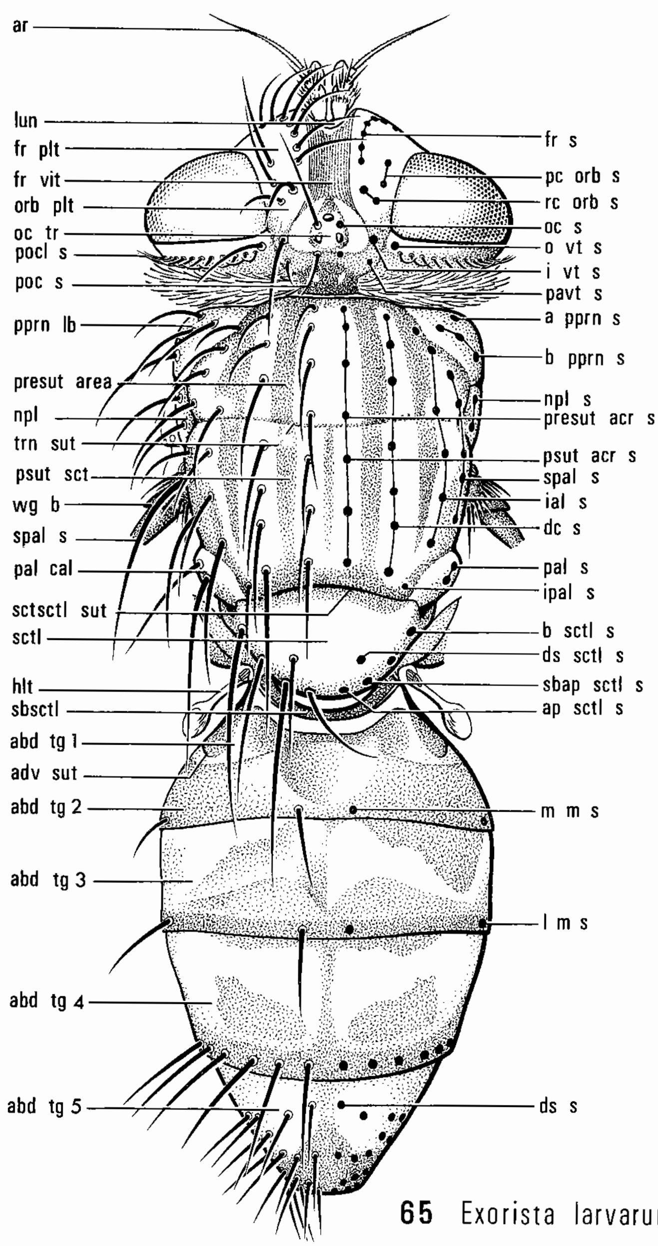
The true scutum occupies most of the thoracic dorsum in the Diptera, and its gross development is an outstanding apomorphic character of the order. Because of its greatly expanded condition and concomitant distortion, the homologies of its features are not easily recognized. A predominant feature of the scutum in most Diptera is the ***transverse suture***, sometimes incorrectly called the transcutal or scutal suture. It is derived from a pair of lateral sutures that divide the scutum into an anterior ***presutural area*** (prescutum of Curran and others) and a posterior ***postsutural area*** (scutum of some authors). Each half of this suture arises laterally in front of the ***anterior notal wing process*** and continues toward the midline of the scutum. In the Tipulidae and some related families, e.g. Ptychopteridae, these sutures meet on the midline, forming a characteristic V-shaped groove, but in most other groups they are weaker and do not meet in the middle. In most Calyptratae, however, and in some acalyptrate families, e.g. Somatiidae, they also meet in the middle. They tend to be more directly transverse in higher Diptera than in most Nematocera. In certain forms, e.g. all Bibionomorpha and most Culicomorpha, they are scarcely evident. The origin and homology of the transverse suture is somewhat controversial. The terms transcutal suture or scutal suture are certainly incorrect. The true transcutal suture is a continuation of the ***tergal fissure***, which is located between the ***median*** and ***posterior notal wing processes***, whereas the transverse suture arises in front of the anterior notal wing processes. Matsuda (1970) interpreted the transverse suture of the Diptera as the lateral parapsidal sutures, which arise from the lateral extremities of the prescutal suture in plecopteroid and neuropteroid orders. This interpretation accords well with that of Hendel (1928) and with the observable facts in many Diptera. As pointed out by Hendel (1928), the suture that separates the paratergite from the lateral margin of the scutum in many Nematocera is continuous with the transverse suture; together these sutures in the Diptera appear to be homologous with true lateral parapsidal sutures in lower orders. Any or all of the following additional sutures can be distinguished on the scutum of various Diptera. The paired, more or less longitudinally aligned ***parapsidal sutures*** arise from the prescutal sutures and continue caudally in a sublateral (dorsocentral) position in many Nematocera; they are particularly strong in certain Psychodidae. A distinct ***median scutal*** (acrostichal) ***suture*** is often very distinct in the Chironomidae and the Chaoboridae; it is also present in many Psychodidae and in some Bibionomorpha. The ***scutoscutellar suture***, separating the scutum and the scutellum, is the hindmost transcutal suture. Two other short, paired, more or less transverse sutures are sometimes present between the transverse suture and the scutoscutellar suture, namely a true ***scutal*** (transcutal) ***suture*** anteriorly near the tergal fissure, and a ***posterolateral scutal suture*** posteriorly. The following designations are applied to other features of the scutum. In the higher Diptera (Figs. 65, 66) the anterolateral region of the scutum, between the postpronotal lobe and the wing base, is a clearly delimited, sunken area called the ***notopleuron***; this area corresponds closely to the sclerite called the paratergite in many Nematocera and may be partially homologous. The swollen area lying just behind the lateral extremities of the transverse suture and anteromedial to the anterior notal wing process is called the ***prealar callus***. Similarly the swollen area between the scutellum and the posterior base of the wing, marked off anteriorly by the posterolateral scutal suture and posteriorly by the scutoscutellar suture, is called the ***postalar callus***. A ridge running from the anterolateral angle of the scutellum to the wing base is called the ***postalar ridge***, and the ventrolateral surface below the postalar ridge is called the ***postalar wall*** (postalar declivity). The lateral margin of the scutum immediately above the attachment of the wing is the ***supra-alar area***. Sometimes, as in the Blephariceridae, Deuterophlebiidae, Simuliidae, and Thaumaleidae, this area is modified to form a distinct concavity, the ***supra-alar depression***, over the wing base. The upper margin of this depression is called the ***supra-alar ridge***.

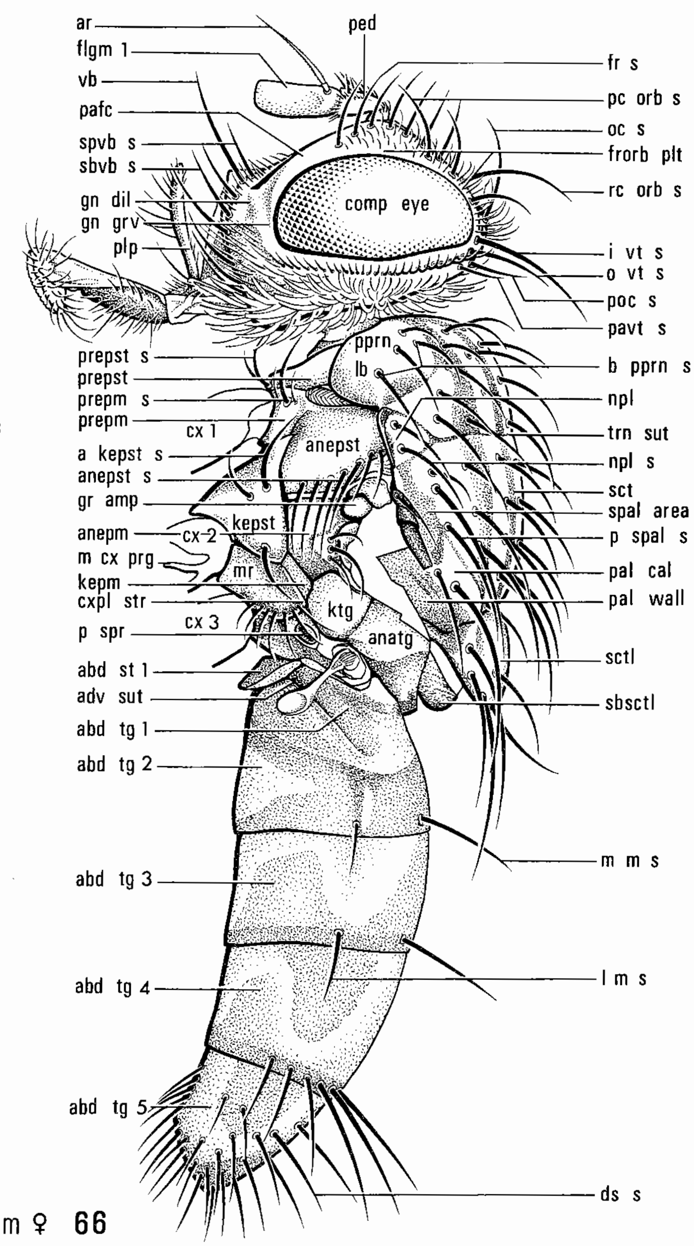
The scutellum is a clearly defined, rounded or triangular lobe bounding the posterior margin of the scutum. In the Diptera it is almost always evaginated and its apex frequently projects roof-like over the postnotum, more so in higher Diptera than in the Nematocera. It is grossly developed in the Celyphidae and is unusually elongate in certain Stratiomyidae and Piophilidae. Frequently it is immediately preceded by a small, transverse, lenticular bulge, the ***prescutellum***. A ridge running from the base of the lower calypter to the anterolateral angle of the scutellum is called the ***suprasquamal ridge***. A largely membranous area between the suprasquamal ridge and the lower margin of the postalar wall is called the ***tympanal fossa***. It is usually strengthened by a rib-like sclerite called the ***tympanal ridge***. In many Muscomorpha, at least, the tympanal ridge is forked anteriorly and forms a single Y; in some families such as the Calliphoridae and the Oestridae it is doubly forked and forms a double Y. In these groups the two lowermost arms enclose a membranous ***tympanic pit*** that opens toward the base of the wing. The tympanal fossa, the tympanal ridge, and the tympanal pit are best seen in a posterodorsal view with the wing in a downward position.

The postnotum has been incorrectly called the metanotum and the postscutellum by some authors; it includes all the parts behind and below the scutellum. The postnotum is sometimes large and exposed, especially in the Nematocera (Fig. 64), or relatively small and withdrawn, as in the Tabanidae. It consists of a ***mediotergite*** and two ***laterotergites*** (pleurotergites, metapleura), one on each side. The mediotergite sometimes has a median suture or groove, as in most Chironomidae (Figs. 29.26–29) and Chaoboridae (Fig. 24.5). The anterior (dorsal) portion of the mediotergite is usually concave, but in some forms, especially the Tachinidae (Fig. 66), this area is differentiated as a convex, transverse, lenticular bulge, the ***subscutellum*** (postscutellum, infrascutellum). Each laterotergite extends down to the posterior thoracic spiracle and is sometimes divided into a dorsal ***anatergite*** and a ventral ***katatergite*** (Fig. 64).

The chaetotaxy of the thoracic sclerites, shown in Figs. 65 and 66, is extremely important in taxonomy.

The ***mesopleuron*** includes the entire pleuron of the mesothorax and is divided by the pleural suture into an anterior ***episternum*** and a posterior ***epimeron***. The pleural suture is relatively straight in most Nematocera, but it follows an increasingly zigzag course in higher Diptera. The episternum is divided transversely by the ***anapleural suture*** into an upper part, the ***anepisternum*** (mesopleuron of many dipterists), and a lower part, the ***katepisternum*** (sternopleuron, preepisternum). Similarly the epimeron is transversely divided into the ***anepimeron*** (pteropleuron) and the ***katepimeron*** (barrette), separated by the ***transepimeral suture*** (anepimeral suture of Crampton). The anepisternum is divided by a membranous area, the ***anepisternal cleft*** (episternal fissure, basalar cleft), which extends downward in front of the pleural suture to the anapleural suture. In the Simuliidae the anepisternal cleft is unusually large and is referred to as the ***anepisternal membrane*** (pleural membrane). The parts of the anepisternum lying on each side of this cleft are sometimes given different names, as in the Chironomidae (see Hansen and Cook 1976). Posterodorsally, in the mouth of the anepisternal cleft and near the lower base of the wing, is a relatively small, usually subdivided sclerite called the ***basalare*** (Fig. 64). It is derived from the anepisternum and provides a base for the insertion of wing muscles (Snodgrass 1935). The





65 Exorista larvarum ♀ **66**

anterior part of the basalare, called the ***anterior basalare***, is usually joined dorsally to the scutum just behind the lateral extremity of the transverse suture by a narrow strip which, in the Tipulidae, is called the ***prealar bridge***. The posterior part, called the ***posterior basalare***, is usually attached posteroventrally to the anterodorsal margin of the epimeron. The posterior basalare is sometimes setose, as in certain Asilidae.

The anterior spiracle lies toward the anterodorsal angle of the anepisternum, near the junction of the pronotum and the mesonotum.

The mesothoracic katepisternum is a constant, easily recognized feature throughout the order, but its interpretation and naming is rather contradictory and confusing (Hennig 1973). It is always greatly extended ventrally at the expense of the ***mesosternum***, the ventral sclerite of the mesothorax. The mesosternum is reduced in the Diptera to a narrow, usually wholly internal phragma, and early workers incorrectly assumed that it was combined with the katepisternum. Hence, the katepisternum is frequently, but inappropriately, called the sternopleuron (sternopleurite of Crampton 1925), especially in systematic works. Crampton (1909) proposed the name katepisternum for the part of the episternum lying below the anapleural suture. He interpreted this large sclerite in the Diptera as the "fusion product of the katepisternum [erroneously called katepimeron in text, but correctly called katepisternum in figures and resumé], part of the trochantin, and a portion of the antecoxal laterale." In his figures of *Tipula* and *Musca* he labeled it as the "katepisternal complex (ES_{KX})." According to Matsuda (1970) the sclerite in question is derived from anapleural, not katapleural, elements, and this interpretation adds to the confusion concerning its proper name. The name katepisternum has usually been applied in Crampton's (1909) sense in the Nematocera and it has often been applied in the same sense in the orthorrhaphous Brachycera and the Muscomorpha (Crampton 1942, Bonhag 1949, Downes 1955). However, some authors (Rees and Ferris 1939, Matsuda 1970, Saether 1971, Hansen and Cook 1976) misapplied the term katepisternum in the Diptera to a small sclerite of katapleural origin, the ***pleurotrochantin*** (Fig. 64) of Crampton (1925, 1942), which is known only in *Tipula* (Rees and Ferris 1939), *Plecia* of the Bibionidae (Crampton 1925), and the Culicomorpha (Crampton 1925). These same authors (except Crampton) used the term preepisternum for the major portion of the katepisternum. The name preepisternum was first used by Hopkins (1909) for an anterior part of the episternum of *Dendroctonus* (Coleoptera). Subsequent usage of the term by Snodgrass (1909, 1910, 1959), Comstock (1920), Imms (1925), Rees and Ferris (1939), and Matsuda (1970) is inconsistent and contradictory. For the Diptera, at least, it is preferable to retain the names katepisternum and pleurotrochantin for the sclerites in question. The katepisternum (Figs. 64–65) is usually a simple, convex, somewhat triangular sclerite, with or without ***katepisternal bristles*** or ***setulae*** or both. In some Simuliidae it is divided into an upper and a lower

Figs. 2.65–66. Morphology, chaetotaxy, and terminology of body of *Exorista larvarum* (Linnaeus), in (65) dorsal and (66) lateral views.

abd st, abdominal sternite
abd tg, abdominal tergite
acr s, acrostichal seta
adv sut, adventitious suture
a kepst s, anterior katepisternal seta
anatg, anatergite
anepm, anepimeron
anepst, anepisternum
anepst s, anepisternal seta
a pprn s, anterior postpronotal seta
ap sctl s, apical scutellar seta
ar, arista
b pprn s, basal postpronotal seta
b sctl s, basal scutellar seta
comp eye, compound eye
cx, coxa
cxpl str, coxopleural streak
dc s, dorsocentral seta
ds s, discal seta
ds sctl s, discal scutellar seta
flgm, flagellomere
frorb plt, fronto-orbital plate
fr s, frontal seta
fr vit, frontal vitta
gn dil, genal dilation
gn grv, genal groove
gr amp, greater ampulla
hlt, halter
ial s, intra-alar seta
ipal s, intrapostalar seta
i vt s, inner vertical seta
kepm, katepimeron
kepst, katepisternum
ktg, katatergite
l m s, lateral marginal seta
lun, lunule
m cx prg, mid coxal prong
m m s, median marginal seta
mr, meron
npl, notopleuron
npl s, notopleural seta
oc s, ocellar seta
oc tr, ocellar triangle
orb plt, orbital plate
o vt s, outer vertical seta
pafc, parafacial
pal cal, postalar callus
pal s, postalar seta
pal wall, postalar wall
pavt s, paravertical seta
pc orb s, proclinate orbital seta
ped, pedicel
plp, palpus
pocl s, postocular setae
poc s, postocellar seta
pprn, postpronotum
pprn lb, postpronotal lobe
prepm, proepimeron
prepm s, proepimeral seta
prepst, proepisternum
prepst s, proepisternal seta
presut acr s, presutural acrostichal seta
presut area, presutural area of scutum
p spal s, posterior supra-alar seta
p spr, posterior spiracle
psut acr s, postsutural acrostichal seta
psut sct, postsutural scutum
rc orb s, reclinate orbital seta
sbap sctl s, subapical scutellar seta
sbsctl, subscutellum
sbvb s, subvibrissal seta
sct, scutum
sctl, scutellum
sctsctl sut, scutoscutellar suture
spal area, supra-alar area
spal s, supra-alar seta
spvb s, supravibrissal seta
trn sut, transverse suture
vb, vibrissa
wg b, wing base

part by a horizontal groove called the ***katepisternal sulcus*** (mesepisternal groove) (Figs. 27.10, 27.12–13).

The mediodorsal margin of the anepimeron extends dorsally and articulates with the wing; this extension is called the ***pleural wing process*** (subalifer). In Calyptratae its basal portion bears a bulbous swelling; this structure, first discovered and named in the Calliphoridae (Lowne 1890–1895), is called the ***greater ampulla*** (*pl.* ***ampullae***; infra-alar bulla, subalar knob) (Fig. 66). It is greatly inflated in many Syrphidae but is undeveloped in the Nematocera and in all acalyptrate families except the Periscelididae and the Ropalomeridae, as well as some Psilidae, Sciomyzidae, and Tephritidae. Behind the pleural wing process in most Diptera a well-developed ***subalar sclerite*** (subalar ridge, vallar ridge) lies in the subalar membrane between the insertion of the wing and the dorsal margin of the anepimeron. In the Syrphidae the posteroventral margin of this sclerite is produced to form the ***plumule***, and the anterodorsal portion is frequently inflated to form one or more peculiarly shaped dilations. The so-called ***vallar bristles***, present in some Sciomyzidae, arise on the subalar sclerite. In certain Calyptratae, e.g. Calliphoridae and Sarcophagidae, the swollen anterior part is called the ***lesser ampulla***. The occurrence of both the greater and the lesser ampullae may be correlated with the ability to make bee-like buzzing sounds. The transepimeral suture extends from near the hindmost point of the bend in the lower portion of the pleural suture toward the posterior (metathoracic) spiracle. The katepimeron is a narrow, more or less horizontal sclerite immediately below the transepimeral suture (Figs. 64, 66). It lies along the dorsal rim of the ***meron*** (meropleuron, hypopleuron) and is sometimes separated from it, as in some Sarcophagidae, Calliphoridae, Muscidae, and Tachinidae, by a suture-like depression called the ***coxopleural streak*** (Fig. 66). When the lower margin of the katepimeron is indistinguishably fused with the meron, the two sclerites together are called the ***meropleurite***. The meron is particularly strongly developed in some primitive families such as the Tanyderidae, Ptychopteridae, Blephariceridae, and Axymyiidae; in the Mycetophilidae, Sciaridae, and Cecidomyiidae, however, it is greatly reduced. The chaetotaxy of it and the adjoining katepimeron affords useful taxonomic characters in many families, especially in the Calyptratae.

The mesosternum is mostly invaginated in the Diptera, but it is relatively large and exposed in the Deuterophlebiidae, the Nymphomyiidae, some Blephariceridae, and some Anisopodidae. It is also wide and exposed in the tipulid genera *Gnophomyia* and *Chionea* (Matsuda 1970).

Metathorax. The metathorax is reduced and its dorsum, the ***metanotum***, is usually scarcely visible externally (Fig. 64). The metanotum connects the mesothoracic postnotum to the first abdominal tergite and is a narrow, transverse band extending from the base of one halter to the other. It is relatively large and exposed only in a few forms, e.g. Psychodidae and the xylophagid genus *Coenomyia*; usually, it is concealed beneath the base of the first abdominal tergite.

Laterally the ***metapleural suture*** extends from the coxa to the halter and separates the ***metapleuron*** into the ***metepisternum*** anteriorly and the ***metepimeron*** posteriorly (Fig. 64). A clear division of the metepisternum into a dorsal ***metanepisternum*** and a ventral ***metakatepisternum*** occurs, for example, in the tipulid genus *Dolichopeza*, but this division is usually indistinct. An intersegmental suture separating the metepisternum from the mesothoracic meron can usually be distinguished; it runs ventrally from the posterior spiracle, thence anteromedially between the mesothoracic and metathoracic coxae. The metepimeron is frequently closely associated with the anterolateral extremities of the first abdominal tergite. Sometimes, especially in groups with petiolate abdomens, the two metepimera become fused ventromedially behind the bases of the hind coxae to form a ***postcoxal bridge***.

The ***metasternum***, like the mesosternum, is usually almost entirely invaginated. However, a small external metasternum is present in the Deuterophlebiidae and the Nymphomyiidae. The area lying between and in front of the metathoracic coxae in higher Diptera (basisternum of Crampton 1942), sometimes referred to as the 'metasternum' as in Syrphidae, is probably at least partially derived from the pleuron.

Wing. In the Diptera only the front or mesothoracic pair of wings is developed as functional flight organs; the metathoracic pair is reduced to small club-like structures, the ***halteres*** (*sing.* ***halter***). This feature is an outstanding apomorphic character of the order. Other special features of dipterous wings are discussed under venation below.

For convenience the wing is treated under three headings: the ***axillary area*** containing the ***axillary plates*** between the lateral margins of the notum and the bases of the wing veins, the basal ***stalk*** containing the bases of the wing veins and associated plates and membranes, and the ***blade*** or main area of the wing (Fig. 3).

The axillary area is illustrated in Fig. 68. The anterior margin of the wing is called the ***costal margin***. The most proximal plate, at the extreme base of the costal margin, is the ***tegula*** (costal plate, epaulet); the adjacent, more distal plate, articulating with the base of the ***costa*** (***C***), is called the ***basicosta*** (humeral plate, subepaulet). In addition to these two plates there are at least three axillary plates. The ***first axillary plate*** articulates with the anterior notal wing process and the ***subcostal sclerite***. The ***second axillary plate*** articulates proximally with the first axillary plate, anteriorly with the base of the ***radius*** (***R***), posteriorly with the ***third axillary plate***, and ventrally with the pleural wing process. The third axillary plate articulates with the posterior notal wing process, the bases of the ***cubitus*** (***Cu***) and the ***anal vein***

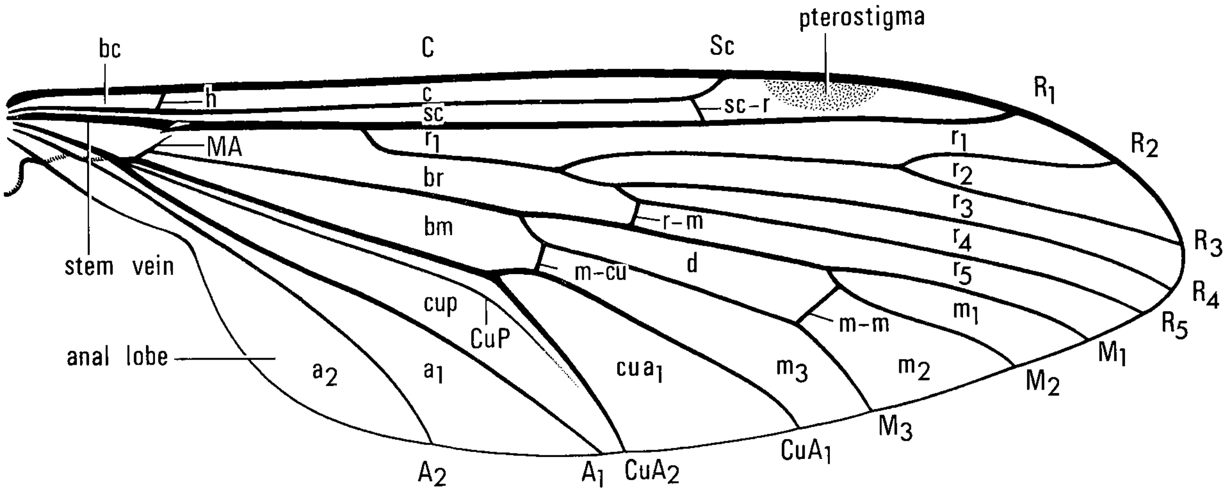
(*A*), and the second axillary plate. Sometimes a ***fourth axillary plate***, lying more or less proximal to the third axillary plate, has been distinguished (Bonhag 1949); it is really the apical part of the posterior notal wing process that has become more or less detached (Snodgrass 1935). Lying in the median area of the wing base more or less distal to the second and third axillary plates is a pair of hinged plates called the ***proximal*** and ***distal median plates*** (m and m′ of Snodgrass 1935). The proximal median plate (m of Snodgrass 1935, m′ of Bonhag 1949) is really part of the third axillary plate (Snodgrass 1952) derived from the basal parts of M and Cu (Matsuda 1970). It is separated from the distal median plate by a ***basal fold***. The distal median plate is a secondary sclerite that must have segregated simultaneously with the formation of the basal fold (Matsuda 1970). The posterobasal portion of the axillary membrane, joining the hind margin of the wing to the thorax, forms two basal lobes called the ***calypteres*** (*sing.* ***calypter***; squamae, squamulae). The proximal lobe, called the ***lower calypter*** (basicalypter, squamula thoracica), begins as a narrow, membranous ligament arising from the furrow between the scutellum and the postnotum and ends where the more distal lobe, the ***upper calypter*** (disticalypter, squamula alaris), folds sharply over it. The upper calypter is believed to be homologous with the jugal region or neala of higher insects, e.g. Neoptera, including the jugal lobe of the Mecoptera (Hennig 1973). It is usually larger than the lower calypter, but in some groups, e.g. Tabanidae, Acroceridae, and many Calyptratae, the lower calypter is larger than the upper one. The fringe of hairs along the posterior margin of each calypter is called the ***calyptral fringe***, and the fold between the two lobes is the ***calyptral fold***.

The wing stalk is also illustrated in Fig. 68. It contains the bases of all the main wing veins as well as their basal plates and basal brace veins. The subcostal sclerite, linking the ***subcosta*** (***Sc***) with the first axillary plate, is wedged between the basicosta and the anteroproximal margin of the basal section of R. The basal section of R is called the ***stem vein*** (incorrectly called remigium by some dipterists); it is usually marked off apically by a transverse, suture-like constriction close to the level of the ***humeral crossvein*** (***crossvein h***); the broad proximal part of the stem vein corresponds to the median plate of Hamilton (1971, 1972*a*, 1972*b*, 1972*c*). The posterior margin of the wing stalk usually has a broad lobe called the ***alula*** (axillary lobe). Proximally this lobe is continuous with the upper calypter and distally it is usually separated from the rest of the wing by an indentation called the ***alular incision***. The alula represents a newly acquired feature of the Diptera (Hennig 1973); it is usually absent or poorly developed in the Nematocera, except in Anisopodidae, but is usually relatively large in the Brachycera.

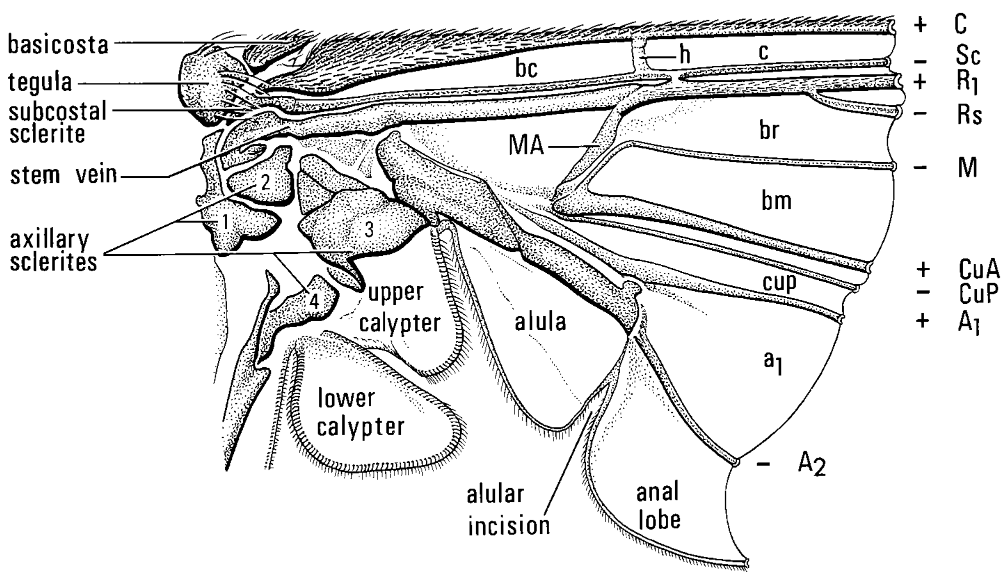
The wing blade is illustrated in Figs. 67 and 69. Frequently, especially in the Nematocera and in orthorrhaphous Brachycera, a sharply defined, somewhat thickened, opaque or pigmented area called the ***pterostigma*** is evident in the membrane near the point where R_1 joins C; according to Arnold (1964), it marks the position of a costal blood sinus. In the Diptera the ***anal lobe*** is a rather flexible, more or less triangular area, containing at most two branches of the anal vein, both of which may be atrophied.

The venation of the wing varies greatly throughout the order (Figs. 4.1–76) and is of fundamental taxonomic value. The veins are essentially remnants of the body hemocoel (Martynov 1930, Arnold 1964). They develop from cuticularized blood lacunae, which are usually occupied by tracheae during morphogenesis (Carpenter 1966). The system adopted here for interpreting and naming the veins and cells is fundamentally the Redtenbacher (1886) system, usually referred to as the Comstock–Needham (1898–1899) system, as improved by workers such as Comstock (1918), Comstock and Needham (1922), Lameere (1923), Martynov (1930), Carpenter (1966), Hennig (1973), Séguy (1973), and Kukalova-Peck (1978); Carpenter's review of this controversial subject is exceptionally clear and concise. This system is founded on the recognition in insect wings of six primary veins that Redtenbacher called the ***costa*** (***C***), ***subcosta*** (***Sc***), ***radius*** (***R***), ***media*** (***M***), ***cubitus*** (***Cu***), and ***anal vein*** (***A***). In the most generalized condition each of these veins consists of two main branches: a convex (+) anterior branch (A) and a concave (−) posterior (sectoral) branch (P) (Kukalova-Peck 1978) (Fig. 68). Primitively both branches of each vein arose from a common basal blood sinus (Kukalova-Peck 1978), and both branches of each vein were further branched. In many modern insects, especially those with membranous wings, the subsequent branches frequently retain some degrees of their original convex or concave properties. Correlation of this fundamental pattern of venation and ***fluting*** (alternating ridges and valleys) in the wings of both fossil and living members of the Pterygota is the principal basis for homologizing the wing veins in all orders.

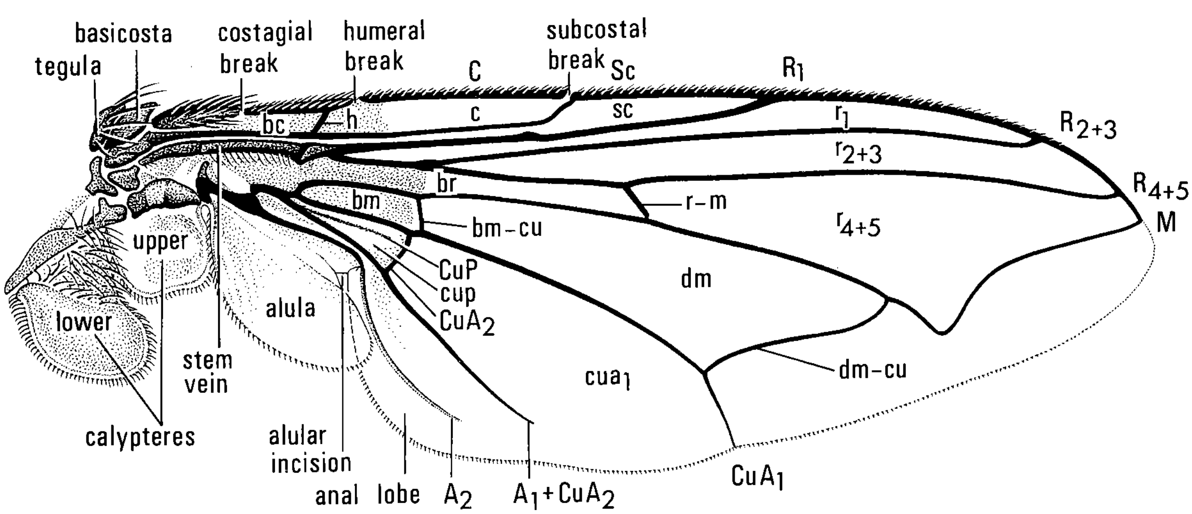
Although this interpretation is accepted for the origins of the veins, traditionally established names for some veins do not entirely conform with the system. In practical taxonomy the names usually applied to the C, Sc, R, and M veins in all orders do not reflect their anterior (A) or posterior (P) (sectoral) origins. For the sake of simplicity new, perhaps more appropriate, names (*see* Wootton 1979) are not introduced here for the Diptera. Both C and Sc are represented by single veins called simply C and Sc. In the case of R, the anterior branch (RA in the strict sense) is called $\boldsymbol{R_1}$, and the remaining four posterior branches making up the posterior branch (RP in the strict sense) or ***radial sector*** (***Rs***) are called $\boldsymbol{R_2}$, $\boldsymbol{R_3}$, $\boldsymbol{R_4}$, and $\boldsymbol{R_5}$, rather than RP_1, RP_2, RP_3, and RP_4 or Rs_1, Rs_2, Rs_3, and Rs_4. In the case of M the anterior branch (***MA***) is extremely reduced and never reaches the wing margin. The components of the posterior branch (***MP***) are called $\boldsymbol{M_1}$, $\boldsymbol{M_2}$, and $\boldsymbol{M_3}$.



67 Ground-plan of Diptera wing



68 Tabanus americanus ♀



69 Paralucilia wheeleri ♀

However, in the case of Cu the A and P designations have often been used for naming the branches, for purposes of clarity. Accordingly, the forked anterior branch of Cu (***CuA***) consists of ***CuA_1*** and ***CuA_2***; the posterior branch of Cu is ***CuP***. In the case of A the anterior branch is called ***A_1*** and the posterior branch is ***A_2*** (Figs. 67, 69).

The nearest approach to the primordial venation of pterygote insects is found in fossil Paleoptera. Special features of the Neoptera, to which the Diptera belong, are as follows: the ability to flex the wings over the back, the fusion of MA with R (Martynov 1930), sometimes the fusion of M_4 with CuA, and the partial to complete loss of the primary fluting of many of the veins in the central portion of the wing (Kukalova-Peck 1978). Generally also C, Sc, and R are subparallel along the anterior margin of the wing, whereas the others are directed more or less fanwise in the posterior part of the wing. The Tanyderidae (Fig. 4.1) and the Psychodidae (Fig. 4.2) show what is believed to be the most primitive venational pattern of the Diptera. The following features of the supposed primordial venation of the order (Fig. 67) are the most distinctive.

- C completely surrounds the wing but is strongest along the anterior margin.
- Sc has one free longitudinal vein. Some authors (Alexander 1927, 1929; Friend 1942; Hennig 1954; Colless and McAlpine 1970) assume that Sc is primitively two-branched (Sc_1 and Sc_2) near its apex. In this assumption the transverse vein between Sc and R_1 is interpreted as a branch (Sc_2) that fuses with R_1; it is believed to reappear as a separate vein only in the Australian tanyderid *Nothoderus australiensis* Alexander. Other workers (Curran 1934, Hamilton 1972*a*) treat the transverse vein between Sc and R_1 as the subcostal-radial crossvein (sc-r), a common feature of neuropteroid wings. In the latter interpretation the so-called free Sc_2 of *Nothoderus* might be considered a ***secondary veinlet*** in the vicinity of the pterostigma, also a common feature in neuropteroid groups. The matter is of little or no taxonomic importance, and because there is no unequivocal evidence that Sc_2 ever occurs in the Diptera it seems preferable to omit any reference to it.
- The base of R has a transverse suture-like constriction marking off the stem vein.
- Rs has four free veins (R_2 to R_5).
- The base of M is atrophied, giving the appearance that M arises from Cu.
- MA occurs as a short, transverse vein (arculus, brace vein, phragma; see Hennig 1968) between MP and R.
- MP has only three free branches, M_1 to M_3 (Comstock 1918, Friend 1942, Hennig 1973). M_4 never occurs as a separate, free vein in the Diptera, and for practical taxonomic purposes it seems preferable to adopt Comstock's (1918) recommendation to omit any reference to it in the designation of veins throughout the order. Comstock (1918) believed that it coalesced with either M_3 or CuA_1. Tillyard (1926) interpreted CuA_1 as a free M_4. However, the distinctive nature of the ***cubital fork*** throughout the Diptera and the strong convexity of both its branches (as opposed to a primitively concave condition in all branches of MP) indicate that the vein in question is primarily derived from CuA rather than from M_4.
- CuA has two free branches (CuA_1 and CuA_2), these forming a distinctive cubital fork.
- CuP is weak and untracheated; it lies close behind CuA and never reaches the wing margin.
- A consists of a strong convex anterior branch (A_1) and a weak concave posterior branch (A_2).
- The following ***crossveins*** are present: ***humeral*** (***h***), ***subcostal-radial*** (***sc-r***) (Sc_2 of some authors),

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Figs. 2.67–69. Dorsal views of right wing to show structure and venation: (67) wing stalk and blade of hypothetical primitive Diptera; (68) axillary area and wing stalk of *Tabanus americanus* Forster; (69) complete wing of *Paralucilia wheeleri* (Hough).

veins

A_1, A_2; branches of anal veins
C, costa
Cu, cubitus
CuA, anterior branch of cubitus
CuA_1, CuA_2; anterior branches of cubitus
CuP, posterior branch of cubitus
M, media
M_1, M_2, M_3; posterior (sectoral) branches of media
MA, anterior branch of media
R, radius
R_1, anterior branch of radius
R_2, R_3, R_4, R_5; posterior (sectoral) branches of radius
Rs, radial sector
Sc, subcosta

cells

a_1, a_2; anal
bc, basal costal
bm, basal medial
br, basal radial
c, costal
cua_1, anterior cubital (cubital fork)
cu*p*, posterior cubital
d, discal ($1m_2$)
dm, discal medial
m_1, m_2, m_3; medial
r_1, r_2, r_3, r_4, r_5; radial
sc, subcostal

crossveins

bm-cu, basal medial-cubital*
dm-cu, discal medial-cubital
h, humeral
m-cu, medial-cubital*
m-m, medial
r-m, radial-medial
sc-r, subcostal-radial

* Crossvein bm-cu is the same as crossvein m-cu, but the designation 'b'm-cu is used to distinguish crossveins bm-cu from m-cu when both occur.

radial-medial (***r-m***) (anterior crossvein, ta), ***medial-cubital*** (***m-cu*** or ***bm-cu***) (tb, possibly the base of M_4), and ***medial*** (***m-m***) (M_2-M_3). The ***sectoral crossvein*** (***crossvein r-s***) between R_1 and R_2 is considered to be absent by Alexander (1927, 1929), but this opinion is not universal.

- The following closed ***cells*** are present: ***basal costal*** (***bc***), ***costal*** (***c***), ***subcostal*** (***sc***), ***basal radial*** (***br***) (1st basal), ***basal medial*** (***bm***) (2nd basal), and ***discal*** (***d***) ($1M_2$) [see discal medial cell (cell dm), p. 33].

The following peculiarities and transformation series are among the most important venational specializations that occur within the Diptera (see Figs. 4.1–76).

C fades out and becomes absent beyond the insertions of R and M in the Deuterophlebiidae, in some Blephariceridae, in all Chironomoidea, in all Bibionomorpha except Cecidomyiidae, in all Stratiomyoidea, in most Empididae, in all Dolichopodidae, and in all Muscomorpha except the Lonchopteridae and some Platypezidae (*Opetia*). One to three weakenings or ***costal breaks*** frequently occur in the Diptera, especially in the Schizophora (Fig. 69). Usually these breaks are located proximal to the insertion of Sc. They are believed to be special points for flexing the wings during flight (Hennig 1971, p. 30; 1973, p. 192), and they are also associated with folds in the wing during pupation (Hennig 1973, p. 192). The most frequent break occurs just proximal to where Sc joins C or to the point where it would join C if Sc were complete. A similar break, occurring almost as frequently, is located slightly distal to crossvein h. The third break, considerably less frequent than the others, is found slightly proximal to crossvein h and marks off a short, thickened, relatively heavily bristled section at the base of C, the ***costagium*** (Séguy 1973). None of these breaks have been previously named, and it is here proposed to call them the ***costagial***, ***humeral***, and ***subcostal breaks***. Costal breaks are rare in the Nematocera and lower Brachycera. One to several are found in some Psychodidae (Fig. 4.2), and one, corresponding to the humeral break, is fairly common in the Ceratopogonidae (Figs. 4.15–16). A somewhat similar interruption occurs in the Cecidomyiidae at the point near the apex of the wing where C is suddenly attenuated (Fig. 4.22). This characteristic may indicate that the thickening of C on the posterior margin of the wing in this family is a secondary condition. All three main breaks usually occur in the Calyptratae (Fig. 69). All or none may occur in other Schizophora (Figs. 4.53–76) providing many useful characters for separating the various taxa.

Both the apex of Sc and crossvein sc-r are weak or absent in many groups. Sometimes the end of Sc is atrophied but crossvein sc-r remains, as in many Tipulidae. Sometimes the ends of both Sc and crossvein sc-r disappear, as in many Empididae (Figs. 4.42–44) and in all Drosophilidae. Occasionally Sc joins R_1, possibly through the agency of a reduced crossvein sc-r, as in some Tipulidae and Empididae, in some Dolichopodidae (Fig. 4.46), in some Platypezoidea (Fig. 4.49) except Platypezidae, and in some acalyptrates. Although crossvein sc-r is seldom recognized in the Muscomorpha, it is clearly present and complete in some Syrphidae (Fig. 4.51) and Conopidae (Fig. 4.53). In most other Muscomorpha there is a peculiar swelling on R_1 near the point where Sc bends forward (Fig. 69); this thickening is probably a remnant of crossvein sc-r.

The anterior convex branch of R (R_1) is practically always present as a free unbranched vein. Plesiomorphically Rs is dichotomously twice branched to form R_2 and R_3, and R_4 and R_5 (Fig. 67), but as stated above, four free branches are retained only in the Tanyderidae (Fig. 4.1) and the Psychodidae (Fig. 4.2). In all other Diptera one or more of these branches has been lost by fusion or atrophy (Figs. 4.3–76). Apparently reductions from the original four branches to three branches, two branches, one branch, or complete absence evolved in different ways in the various groups of Diptera (Hennig 1954). In the Tipulidae the apex of R_2 curves forward and is permanently attached to R_1 (capture of R_2 by R_1), usually in the manner of a crossvein (Alexander 1927, 1929). Alexander (1927, 1929) believes that R_2 is atrophied in the Culicomorpha, Bibionomorpha, and Brachycera, but many authors do not agree. In the Culicomorpha, for example, most workers see the first branch of the three-branched radial sector as a free R_2 and the last branch as a fusion product of R_4 and R_5 (R_{4+5}) (Figs. 4.11–14). Many workers (Hennig 1954, 1973; Colless and McAlpine 1970) ascribe the loss of R_2 in the Brachycera and all Nematocera except the Tipulidae to a fusion of R_2 with R_3 (R_{2+3}). Also, in many Nematocera, e.g. some Tipulidae, the Ptychopteridae, the Trichoceridae, and some Psychodidae, the base of R_4 is fused with the base of R_3, described as a capture of R_4 by R_3. In addition, a ***supernumerary radial crossvein*** sometimes occurs between R_4 and R_5 in the Tanyderidae and the Tipulidae (Alexander 1929). A similar venational pattern occurs in some orthorrhaphous Brachycera, e.g. certain Asilidae (Fig. 4.32), Nemestrinidae, and Bombyliidae (Fig. 4.36). Here, what appears to be the entire basal connection of R_4 is sometimes retained (Fig. 4.32), but frequently it is reduced to a ***stump vein*** (Fig. 4.36). From these patterns Alexander (1929), following Shannon and Bromley (1924), concluded that in all Brachycera where the free tip of R_4 is retained, e.g. Tabanomorpha, Asilomorpha, and Muscomorpha, R_4 is connected to R_5 through the agency of a supernumerary crossvein. This theory, like Alexander's theory relating to the loss of R_2, is not accepted by all workers as being as broadly applicable as Alexander concluded. Thus, some differences are to be expected in the names applied to some veins in the radial sector by different workers.

As indicated above, MA fuses with R shortly after its origin. The brace vein between MP and R is derived from MA, but a high convexity lying close behind the last branch of Rs in most species is probably a secondary aerodynamic feature. This convexity is unusually elongated and pigmented in the Syrphidae, where it is called the ***spurious vein*** (Figs. 4.51–52). Although it is untracheated, it functions as an afferent blood vessel in this family (Arnold 1964). Somewhat similar ***false veins*** or fold-like thickenings (usually concave) in the wing membrane between the main veins occur sporadically throughout the order, but especially in families of the Nematocera where the main veins are weak or reduced. Such a false vein is often evident between the posterior branch of M and CuA_1 in the Ceratopogonidae (Figs. 4.15–16), Chironomidae (Fig. 4.13), Simuliidae (Fig. 4.18), Mycetophilidae (Fig. 4.19), Cecidomyiidae (Fig. 4.22), and Scatopsidae (Fig. 4.26). There is a tendency throughout the Diptera for M_2 and M_3 to coalesce with adjacent veins or to disappear. Frequently M_{1+2} bends forward and joins R_{4+5}, and in cases where the bend is relatively sharp, as in certain Syrphidae (Fig. 4.52) and in many Calyptratae (Fig. 69), the apical portion is sometimes referred to as the 'apical crossvein'.

Primitively in the Diptera the true discal cell is present and bounded proximally by the base of M_3, posteriorly by a long, free vein (probably M_3), and distally by a true crossvein m-m (Fig. 67). However, in some Nematocera, some orthorrhaphous Brachycera, and all Muscomorpha in which a 'discal cell' is present, M_3 disappears or combines with ***crossvein m-m*** to form the ***discal medial-cubital crossvein*** (***crossvein dm-cu***; posterior crossvein, tp) and joins CuA_1 near its base (Figs. 4.6–7, 4.34, 4.36–37, 4.41–42, etc.). In this way cell m_3 is eliminated and a new ***discal medial cell*** (***cell dm***) abuts directly on the cubital fork, as in all Muscomorpha (Fig. 69). Moreover, crossvein dm-cu, which closes cell dm distally, is something more than the original crossvein m-m. It now connects M and CuA_1 rather than M_2 and M_3. This transformation series is best seen by comparing the wings of certain Vermileonidae (Fig. 4.35), Apioceridae (Fig. 4.31), Bombyliidae (Figs. 4.36–37), Empididae (Figs. 4.41–42), and Platypezidae (Fig. 4.48).

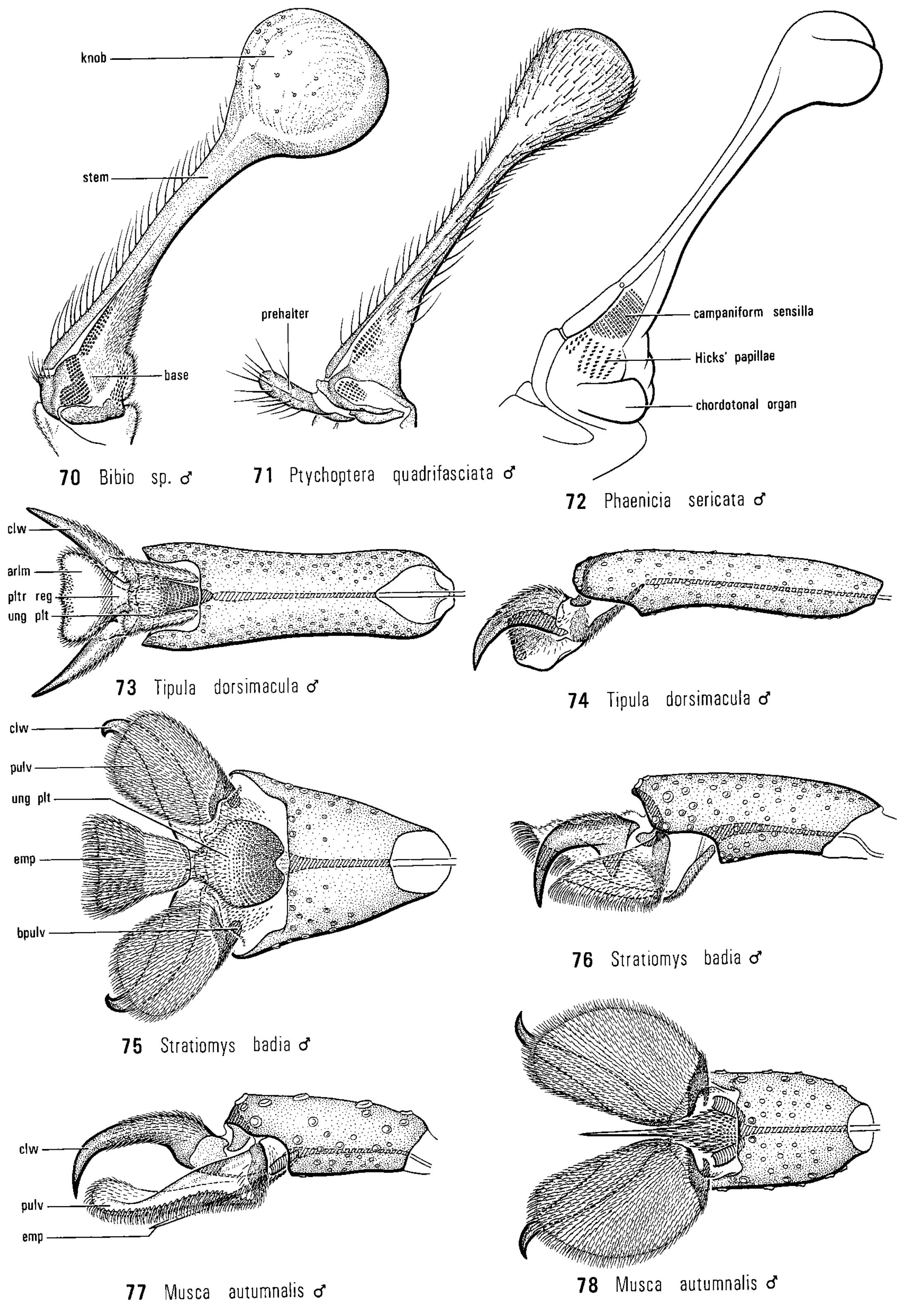
In most orthorrhaphous Brachycera and Muscomorpha CuA_2 joins A_1, enclosing CuP and forming a closed ***posterior cubital cell*** (***cell cup***) (anal cell of most dipterists) (Fig. 69). The size and shape of this cell is governed by the position of CuA_2, which ends on A_1 instead of reaching the wing margin, and it provides many useful taxonomic characters. For example, cell cu*p* is much longer in the Syrphoidea (Figs. 4.51–52) than in most Schizophora (Figs. 4.53–76); it is relatively squarely closed in most schizophorous Muscomorpha but has an angular point in the Tephritidae (Fig. 4.56) and many Otitidae (Fig. 4.55); it is usually short but present throughout the schizophorous Muscomorpha (Figs. 4.53–76), but it is sometimes very small or absent in many acalyptrate families (Figs. 4.58, 4.65, 4.67–68) because of the absence of CuA_2. CuP is weak and untracheated in all Diptera and is seldom used as a taxonomic character. It is usually more strongly developed in the Nematocera and lower Brachycera than in the Muscomorpha. In the Muscomorpha it is strongest in the Syrphidae.

Primitively A_1 is complete and reaches the wing margin as a free vein, but there is a strong tendency, especially in the Muscomorpha, for it to be abbreviated and even absent. When it is absent, as in the Chloropidae (Fig. 4.68) and the Ephydridae (Fig. 4.67), cell cu*p* is also absent. A_2 ends before the wing margin in all Diptera except the Tipulidae (Fig. 4.6) and the Trichoceridae (Fig. 4.8). Its sharp curvature toward A_1 (Fig. 4.73) is an apomorphic feature of all Fanniinae (Muscidae). The anal lobe varies greatly in size and shape throughout the order (Figs. 4.1–76). It is larger and more angulate in flies that swarm and complete the initial stages of mating while in flight than in weaker fliers that mate while grounded (McAlpine and Munroe 1968). Sometimes characters of the anal lobe are expressed in terms of the ***anal cell*** (axillary cell), which usually includes all of the wing surface behind A_1, exclusive of the alular lobe. Additional venational peculiarities are described under the different families in which they occur.

Diptera wings show a wide array of colorations and designs (de Meijere 1916); these color patterns provide useful characters in many families throughout the order. Clear wings are often described as hyaline and darkened ones as infuscated or fumose. Predominantly fumose wings with clear or pale punctuations are termed irrorated (Fig. 4.56); the clear areas are called irrorations. Dark areas are usually referred to as spots or bands, and wings possessing them are spotted, mottled, or banded.

The wing surfaces sometimes bear both macrotrichia and microtrichia. Except in many Nematocera macrotrichia are usually restricted to the veins; occasionally, as in the Culicidae (Fig. 4.14), they form scales, and in the Psychodidae (Fig. 4.2) they are lanceolate. Microtrichia may be relatively long and easily seen or very short and fine. They vary in density from partially to completely absent to uniformly very dense; bare areas on the wings of some groups, e.g. Stratiomyidae, Syrphidae, and Hippoboscidae, provide useful taxonomic characters (Vockeroth 1957). The structure of the wing membrane itself has scarcely been investigated; in the Simuliidae both surfaces are covered with small, raised buttons from which wax filaments extend through the cuticle (Hannay and Bond 1971). Information concerning various chordotonal organs and sensilla found on the wings of flies is summarized by Fudalewicz-Niemczyk (1963).

Halter. The halteres (Figs. 70–72) are reduced and highly specialized metathoracic wings; they serve as balancing organs to maintain stability in flight (Faust 1952, Pringle 1948), and their original development in the Diptera was probably an adaptation for aerial swarming (McAlpine and Munroe 1968, p. 1167). Each halter has three main parts: the ***base*** (scabellum), the ***stem*** (pedicel), and the ***knob*** (capitulum). The base is provided with a variety of sense organs, including ***chordotonal organs***, ***Hicks' papillae***, and other ***campaniform sensilla*** (Hennig 1973); a peculiar appendage, the ***pre-***



Figs. 2.70–78. Halteres and acropods: dorsal view of halter of (70) *Bibio* sp., (71) *Ptychoptera quadrifasciata* Say, and (72) *Phaenicia sericata* (Meigen) (redrawn from Pringle 1948); ventral and lateral views of acropod of (73, 74) *Tipula dorsimacula* Walker, (75, 76) *Stratiomys badia* Walker, and (77, 78) *Musca autumnalis* De Geer.

Abbreviations: arlm, arolium; bpulv, basipulvillus; clw, claw; emp, empodium; pltr reg, plantar region; pulv, pulvillus; ung plt, unguitractor plate.

halter, arises from the base in the Ptychopteridae (Fig. 71). The stem sometimes bears rows of setulae, corresponding to the setulae on C and other main veins of the fore wing, as in the Tipulidae, the Pachyneuridae, and the Tanypezidae. The knob is bulb-shaped, and according to Brauns (1939) it usually contains large-sized cells. In mature specimens it varies from whitish to brown or black. Black-knobbed halteres frequently serve as a useful character at the species level as in *Leptometopa halteralis* Coquillett (Milichiidae), at the generic level as in *Melanagromyza* (Agromyzidae), and at the family level as in Lonchaeidae.

Legs. Each leg consists of a ***coxa*** (*pl.* ***coxae***), ***trochanter***, ***femur*** (*pl.* ***femora***), ***tibia*** (*pl.* ***tibiae***), and ***tarsus*** (*pl.* ***tarsi***) (Figs. 2, 3). The structure of these segments differs in the ***foreleg***, ***midleg***, and ***hindleg*** (pro-, meso-, and meta-thoracic legs), and all legs sometimes show striking modifications on all segments. The diversity of leg structure provides many taxonomic characters in most families throughout the order. The different leg surfaces are ascertained by imagining that all the legs are fully extended laterally, parallel to each other and at right angles to the main axis of the body. Thus each segment of each leg has an anterior, posterior, dorsal, and ventral surface (Fig. 1). Other surfaces are named on the same basis, e.g. anterodorsal and posteroventral.

All coxae articulate dorsally with a ***coxifer*** or pleural process at the ventral end of the pleural suture of each thoracic segment. Ventrally the fore coxa articulates with the side of the exposed prosternum. The mid and hind coxae adjoin their corresponding invaginated ***furcasterna***. Usually all coxae are short and stout, but in some forms with raptoral legs, e.g. certain Empididae (Fig. 47.2), the fore coxa is as long as or longer than the femur and relatively slender. In the Mycetophilidae all coxae are rather long. The mid coxa is divided into an anterior region, the ***eucoxa***, and a posterior region, the meron. The meron is more or less incorporated with the lower portion of the epimeron (*see* "Mesopleuron"). To restore the mobility of the mid coxa, its eucoxa is transversely divided into a ***basicoxa*** and a ***disticoxa***. Examples of special coxal processes include the ***mid coxal prong*** of most Muscomorpha (Fig. 66) (absent in the Platypezidae, the Pipunculidae, the Conopidae, and most Pyrgotidae), the hooked spines on the mid coxa of *Fannia* (Muscidae) and *Amphipogon* (Piophilidae), and the male ***coxal processes*** in some Mycetophilidae. The fore and mid coxae, at least, of most species have one or more discrete clusters of sensory setulae near their outer bases.

The trochanter is usually small and immovably united with the femur, as in most insects. From a taxonomic standpoint it is relatively unimportant in the Diptera. In many Syrphidae and Sarcophagidae it bears a spur, a tubercle, or specialized setae.

The femora and tibiae are usually about the same length and are almost always the longest of the leg segments. Both are extremely long and slender in many Tipulomorpha, but the femora are usually stouter than the tibiae. The fore femur is particularly strongly developed in forms with raptorial forelegs, e.g. some Ceratopogonidae, certain Empididae (Figs. 47.2, 47.8), and a few Ephydridae. All femora may be armed with specialized spines, tubercles, or processes, especially on the ventral surfaces. In many groups the distal end of the anteroventral surface of the fore femur bears a comb-like row of spinules called a ***ctenidium*** (*pl.* ***ctenidia***); frequently one bristle in this position is outstanding and it is sometimes referred to as a ***ctenidial spine*** (Fig. 4.140). Similar ctenidia may be found on the other femora. Sometimes, as in the Sepsidae and in *Hydrotaea* (Muscidae), special modifications of the fore femur and tibia occur in the male for holding the wings of the female during copulation. The hind femur and tibia of the male of *Sepedon* (Sciomyzidae) are bent in a peculiar fashion, and the femur is provided with stout processes, also for use during mating. A crest-like, sound-producing ***scraper*** occurs on the posterior surface of the hind femur as part of a stridulation mechanism (*see* "Abdomen") in certain Agromyzidae and Chamaemyiidae (von Tschirnhaus 1972). The hind femur of a few forms, e.g. Megamerinidae and *Meromyza* (Chloropidae), are unusually strongly developed.

The tibiae are usually provided with serially arranged setulae and bristles, and they may also possess spurs, spines, flanges, and various kinds of processes and ctenidia. Sometimes, as mentioned above, the armature varies between the sexes, and special clasping modifications are developed in the male for holding the female during copulation. The tibiae may bear apical combs of setulae, as in many Chironomidae (Figs. 29.59–66) and Anisopodidae (Figs. 19.8–10); in some families, e.g. Mycetophilidae, articulated ***spurs*** are present (Figs. 14.79–80); in others, e.g. Bibionidae (Figs. 13.4–5) and Scatopsidae, the fore tibia has strong digging spines utilized for depositing the eggs in the ground. In the Calyptratae, there is sometimes an outstanding posterodorsal bristle called the ***calcar*** situated on the hind tibia at or beyond the middle. Specialized areas occur on the tibiae in several families; examples include the ***tibial organ*** (sensory area) on the hind tibia of many Chloropidae (Anderson 1977) and a similar area called the ***osmeterium*** (*pl.* ***osmeteria***) on the hind tibia of some Sepsidae. In the Sepsidae these specialized areas have been interpreted as producers of a sexual scent substance (Šulc 1928–1929). Hennig (1973) suggested that perhaps a similar tibial gland that Kazjakina (1966) found in *Dolichopus*, and a gland in the proximal section of the fore tibia of the ocydromioid section of the Empididae described by Tuomikoski (1966), have a similar function.

Virtually all Diptera have five ***tarsomeres*** (tarsal segments) on all legs (Figs. 2, 3). They are called ***first*** (basitarsus, metatarsus, proximal tarsal segment), ***second***, ***third***, ***fourth***, and ***fifth*** (distitarsus) ***tarsomeres***. All the first tarsomeres are greatly shortened in the trichocerid genus *Paracladura* (Fig. 18.6). The number of tarsomeres, however, is reduced only in a few Cecidomyiidae and Phoridae. In the cecidomyiid subfamilies Cecidomyiinae and Porricondylinae the first tarsomere is very short and more or less fused with the second tarsomere (Fig. 16.81), but in the tribe Heteropezini (Porricondylinae) there may be as few as two distinguishable tarsomeres. In the myrmecophilous phorid genus *Myrmosicarius*, the four distal tarsomeres of the female are completely fused (Borgmeier 1929). All tarsomeres are generously provided with various setae, setulae, sensory hairs, and chemoreceptors. The first tarsomere, especially on the foreleg and hindleg, is frequently modified. In the male of certain Drosophilidae the first tarsomere of the foreleg bears ***sex combs***; in the male of Coelopidae and Dryomyzidae it usually has a number of stout setae and a ventral claw-like process. In the male of the dolichopodid genus *Enlinia* the entire tarsus is sometimes greatly modified (Steyskal 1975). Peculiar structures also occur on the first tarsomeres of the midleg and hindleg in some members of these groups. The male of the dolichopodid genus *Campsicnemus* often has a greatly modified mid tarsus. The female of *Eurygnathomyia* (Pallopteridae) has two unusually stout bristles arising from the ventral surface of the first tarsomere of the foreleg only. The male of certain species of *Hylemya* (Anthomyiidae) possesses a series of long, closely placed setae on the dorsal surface of the first tarsomere of the midleg. The male of *Lonchaea striatifrons* Malloch (Lonchaeidae) has several stout setae ventrally near the base of the first tarsomere of the hindleg. The first tarsomere of the hindleg is swollen in the male of several families, especially some Bibionidae (Fig. 13.1), Empididae (Fig. 47.1), and Platypezidae (Fig. 4.124); in the Platypezidae the other segments of the hind tarsus are also sometimes greatly broadened and flattened. In the Sphaeroceridae the first tarsomere of the hindleg is unusually short and stout (Fig. 4.149). Each first tarsomere of *Bittacomorpha* (Ptychopteridae) contains a tracheal sac, possibly for assisting in its peculiar drifting flight (Brues 1900; Alexander, Ch. 22).

On the distal end of the fifth tarsomere is the ***acropod*** (posttarsus, also sometimes inappropriately called the pretarsus) (Figs. 73–78). It is a small terminal segment believed to be homologous with the dactylopodite of a crustacean limb (de Meijere 1901). Because it is so closely associated with the fifth tarsomere it is usually wrongly regarded as an integral component of that segment. Its evolutionary development in the Diptera provides some characters that are of fundamental importance in the general classification of the order. The principal sclerite of the acropod is the ventrally located ***unguitractor plate***; distally it bears a pair of ***claws*** (ungues), and proximally it is attached to the distal margin of the fifth tarsomere. The distal end of the acropod sometimes protrudes as a median, more or less membranous, sac-like ***arolium***. The ventral surface of the arolium sometimes forms a ***plantar region*** that merges with the distal end of the unguitractor plate. An unpaired median process, the ***empodium*** (*pl.* ***empodia***), arising from the ventral or plantar region of the arolium, is usually present; when present it is ***pulvilliform*** or ***setiform*** in structure. On each side of the acropod near the lateral margins of the unguitractor plate is a small sclerite called the ***basipulvillus***; this pair of plates provide the bases for a pair of flap-like processes, the ***pulvilli*** (*sing.* ***pulvillus***). Both the pulvilli and the empodium act as adhesive organs and sometimes possess hollow hairs called ***retineriae*** (*sing.* ***retineria***), through which a viscous substance is secreted.

The presence or absence of pulvilli or an empodium or both, together with the form of the empodium, serve as important characters in the Diptera. So far as is known true pulvilli are absent in the Tipulomorpha (Figs. 73, 74) and the Psychodomorpha (Hennig 1973). They are present in some form in practically all other groups. A discrete empodium is also lacking in the Tipulomorpha; here the arolium forms a simple, rounded, sac-like median lobe. But some form of a distinct empodium can usually be distinguished in all other families. A pulvilliform empodium occurs in certain Ptychopteridae, in most Bibionomorpha (absent in many Mycetophilidae), in most Tabanomorpha (Figs. 75, 76), and in a few Asilomorpha [Acroceridae (Fig. 43.36), some Nemestrinidae, several clinoceratine Empididae, and the dolichopodid genus *Hydrophorus*]. A setiform empodium occurs in most Culicomorpha (Figs. 29.73–76) and Asilomorpha, and in practically all Muscomorpha (Figs. 77, 78).

Besides being organs of locomotion, the legs of Diptera serve many other purposes. The fore tarsus is usually provided with chemoreceptors for tasting; several contact chemoreceptors have also been found on the tibiae and femora (Hennig 1973). Almost certainly, all tarsi are used as tactile organs. The forelegs of many Chironomidae and the hindlegs of the Culicidae are used somewhat like antennae. As mentioned above, the forelegs of certain Ceratopogonidae, Empididae, and Ephydridae have become raptorial, and in the male of certain groups these and other legs are frequently modified for holding onto the female during copulation. Nearly all flies use their legs to clean and preen themselves, and comb and brush-like patches of setulae are sometimes present in various places for these purposes. In many groups the legs are peculiarly decorated for sexual or combative display. Frequently the color patterns of legs in the Diptera appear to mimic similar patterns found in the Hymenoptera. For example, the forelegs of some Micropezidae simulate ichneumonid antennae in having a transverse white band and in being vibrated in front of the head. Similarly, the forelegs of many Syrphidae simulate the antennae of aculeate Hymenoptera. Such patterns are assumed to be protective adaptations.

ABDOMEN

As in all insects, the abdomen of a fly (Figs. 79–141) is primitively composed of 11 segments. The terminal portion, consisting of the rudiments of segment 11, namely a pair of ***cerci*** (*sing.* ***cercus***) and the ***anus***, is called the ***proctiger*** (anal segment). There is no evidence of a 12th segment.

By inference, the primitive number of ***abdominal spiracles*** (stigmata) in the Diptera is eight, and eight pairs still occur in the female of some Tipulidae, Bibionidae, Chironomidae, Thaumaleidae, Stratiomyidae, Scenopinidae, Rhagionidae, Mydidae, Apioceridae, and Asilidae (Crampton 1942). But the occurrence of seven pairs is typical of the Diptera in general, and a maximum of this number in the male is an apomorphic character of the order (Hennig 1973). Loss of certain spiracles is relatively common throughout the order. Abdominal spiracles are said to be missing entirely in *Deuterophlebia*, *Nymphomyia*, and *Psychoda phalaenoides* (Linnaeus) (Tokunaga 1936), and the absence of spiracles 6 and 7 is fairly common, especially in the male of many Schizophora and in the female of almost all Muscidae. In male Schizophora, the number of abdominal spiracles (five or six pairs versus seven pairs) is sometimes a useful taxonomic character at family and subfamily levels (Griffiths 1972). In both sexes the spiracles are usually borne in the pleural membrane just below the lateral margins of the tergites (Figs. 79, 98, 111, 134); frequently some or all of them become enclosed within the lateral extremities of the tergites, as in the Calyptratae (Figs. 104, 137). Usually each spiracle is associated with its own segment, but some shifting may occur, especially of spiracles 6 and 7 in the male of the Muscomorpha and of spiracle 7 only in the female of the Scathophagidae and the Anthomyiidae (Fig. 104).

The genital opening is located anteroventrally to the anus in both sexes. The female genital opening is between sternites 8 and 9 (Hennig 1973) and serves to identify those two segments in that sex. The ***aedeagus*** (copulatory organ, intromittent organ, mesosome, penis, phallosome, phallus) is the male organ that bears the genital opening or openings; it arises immediately behind sternite 9 and serves to identify sternites 9 and 10 in the male.

The basal segments of the abdomen (preabdomen), consisting of segments 1–5 or 1–6, are frequently broader than the terminal portion of the abdomen, referred to as the ***terminalia*** (postabdomen, hypopygium) (Figs. 79, 109, 112). The distinction between the basal and terminal sections is much more evident in the Muscomorpha (Figs. 109, 134), especially, than in more primitive Diptera (Figs. 79, 112). The terminalia consist of the terminal complex of modified genital and anal segments, plus any adjacent segments that show modifications for copulation and oviposition.

Basically each abdominal segment consists of a dorsal tergite and a ventral sternite connected laterally by the pleural membrane. The density, size, and arrangement of hairs and bristles on any or all of both the tergites and sternites frequently provide useful taxonomic characters. Of special interest are one or more pairs of peculiar ***sensory setulae*** (alphasetae, sensilla trichodia) that are frequently present on the anterior margin of the sternites (Fig. 135); these setulae are very persistent and serve to mark the positions of sternites even when the sternites are displaced or atrophied, as they are in the rotated terminalia of the male Muscomorpha. Similar setulae are sometimes present on the tergites as well. Abdominal glands, such as dermal glands, scent-producing organs, ampullae, or tubes, occur in several groups (Hennig 1973, pp. 204–205). A ***stridulatory file***, activated by a ***resonator ridge*** on the hind femur, is present on the lateral extremities of the fused ***syntergite 1 + 2*** and on the pleural membrane in both the male and the female of certain representatives of a few families, e.g. Agromyzidae and Chamaemyiidae (von Tschirnhaus 1972). An abdominal stridulation organ that interacts with the wings occurs in certain Tephritidae (Hennig 1973).

A general trend toward shortening of the abdomen is evident throughout the order. Although exceptions occur, the abdomen is usually longer and more slender, and with more of the terminal segments exposed, in the Nematocera and orthorrhaphous Brachycera than in the Muscomorpha. This shortening takes place by coalescence of the basal segments, reduction or coalescence of terminal segments, telescopic retraction of the terminal segments into proximal segments, or downward and forward folding (flexion) of the terminal segments, or some combination of these ways.

Tergite 1 is almost always shortened and closely associated with tergite 2 (Young 1921). In the Muscomorpha (Figs. 110, 134) it is reduced to a narrow band and is fused with tergite 2 to form syntergite 1 + 2. This syntergite is usually marked laterally by a transverse suture of varying degrees of completeness, called the ***adventitious suture***. Sternite 1, also, is usually more or less reduced and is sometimes closely associated with sternite 2 (Figs. 112, 137). It is said to be absent in a few forms, e.g. *Anopheles* (Culicidae), *Mydas, Lonchoptera, Pipunculus*, and *Copromyza* (Sphaeroceridae) (Young 1921); probably it is frequently fused with sternite 2, as in the Tabanidae (Bonhag 1951). Fusion of various abdominal tergites sometimes occurs; for example tergites 2 and 3 are fused in the Ptychopteridae and several tergites are fused in certain Tachinidae and Cryptochetidae. Abdominal segments 3–5 are frequently much reduced in the Asteiidae.

Lateral extension of the abdominal tergites is characteristic of the Calyptratae; the lateral margins of tergites 2–5 therefore sometimes extend over the reduced, frequently narrow sternites. In many Tachinidae the sternites are so reduced that the tergites almost encircle the segments. The enclosure of the spiracles in the margins of the tergites, which is especially characteristic in the Calyptratae (Fig. 137), may be related to this lateral expansion of the tergites.

In some Muscomorpha, especially in the Calyptratae, sternite 5 of the male is excised posteriorly and forms part of the male copulatory apparatus; frequently it is adorned with ***sternal processes***, lobes, tubercles, setae, and other modifications (Fig. 137). In a few groups, e.g. Micropezidae and Sepsidae, somewhat similar processes sometimes occur on some of the preceding sternites as well.

In the Nematocera and orthorrhaphous Brachycera segments 6–8 of both sexes are usually more or less permanently exposed in much the same manner as the more proximal segments. Throughout the Muscomorpha there is an increased tendency for more of these segments to be telescoped into each other and withdrawn into segment 5 in the female, or folded into a ventral ***genital pouch*** in the membrane adjoining the posterior margin of sternite 5 in the male. In discussing both male and female terminalia the ***pregenital segments*** are sometimes distinguished from the ***postgenital segments***; the pregenital segments of the terminalia refer to those segments proximal to the main genital opening, and the postgenital segments are those distal to it. In the Nematocera and lower Brachycera usually only the segments beyond segment 7 are modified for some aspect of reproduction. In males of the Muscomorpha (Figs. 132–138) both the tergal and sternal elements of the pregenital segments, namely segments 6, 7, and 8, are more or less reduced, asymmetric, and often fused into a composite sclerite or ***syntergosternite*** (Figs. 134, 137) (first genital sclerite, prehypopygial sclerite, protandrium) (*see* "Flexion and rotation," last paragraph).

Female terminalia. Representative female terminalia are illustrated in Figs. 79–110. In higher Brachycera the segments beyond segment 5 or 6 form a more or less tapered tube with various modifications for egg laying. Often in the Diptera all the elements of the terminalia, including the cerci, are called the ***ovipositor*** (oviposition tube, oviscapt, ovicauda), but the dipterous ovipositor as such is not homologous with the true orthopteroid-type ovipositor. The orthopteroid ovipositor is formed from two pairs of appendages, the anterior and posterior gonapophyses, that arise from sternites 8 and 9, respectively, whereas the dipterous ovipositor may also include elements of segments that are proximal to and distal to segments 8 and 9. Moreover, it has no gonapophyses, at least on sternite 9.

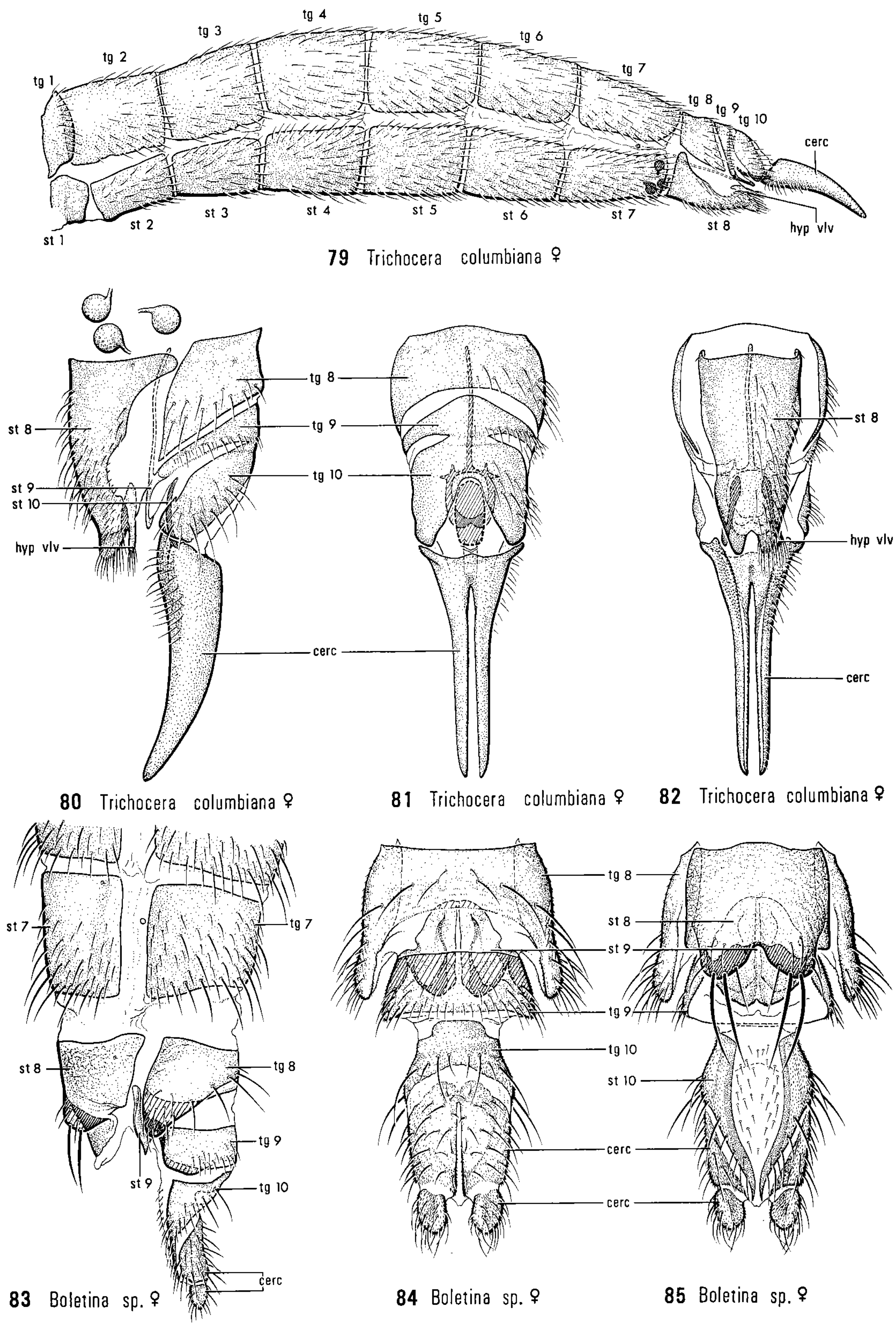
The ***genital opening*** (genital aperture, genital orifice, gonotrema, reproductive opening, vulva) between segments 8 and 9 leads to a pouch-like or tubiform ***genital chamber*** (vagina, atrium). In the Diptera, as in most insects, the paired oviducts unite to form a common oviduct that opens by means of the ***primary gonopore*** in the dorsal wall of the genital chamber. A saccate, dorsal invagination of the genital chamber called the ***bursa*** (bursa copulatrix, bursa inseminalis) occurs in some families, e.g. Tipulidae (Byers 1961, Frommer 1963), Culicidae (Laffoon and Knight 1971), and Asilidae (Reichardt 1929), but it is not known how widely this structure is distributed in the order (Hennig 1973). In the Muscomorpha the anterior portion of the genital chamber is sometimes enlarged for retaining developing eggs and is called the ***uterus*** (ovisac), which is distinguished from the posterior part, the ***vagina***. In the Hippoboscoidea, the larvae develop in the uterus until they are ready to pupate. In viviparous Sarcophagidae and Oestridae the uterus has an enlarged pouch for retaining developing larvae. In most Tachinidae the uterus is lengthened and often coiled for retaining developing eggs.

The internal structures of ectodermal origin associated with the female reproductive system include the ***spermathecae***, the ***accessory glands*** (appendicular glands, colleterial glands, parovaria), and the ***ventral receptacle***.

The spermathecae are more or less spherical or cylindrical, usually heavily sclerotized, strongly differentiated receptacles in which the spermatozoa are stored and from which the spermatozoa are released onto the eggs as they are passed from the oviduct. They are located at the ends of slender ***spermathecal ducts*** that lead to the ***spermathecal openings***. The predominant number of spermathecae in all major sections of the Diptera is three (Sturtevant 1925–1926, Hennig 1958), and three is considered the basic number for the order (Downes 1968, Hennig 1973) as opposed to one in most other orders. However, their number is frequently reduced to two or one, and in a few groups, e.g. most Chamaemyiidae (Figs. 107, 108), there are four. The spermathecae may be relatively smooth and spherical, wrinkled and cylindrical, telescoped, or corkscrew-like in shape. Sometimes they are weakly sclerotized, and in the few instances where they have been reported absent the faintly differentiated membranous sacs have probably been overlooked.

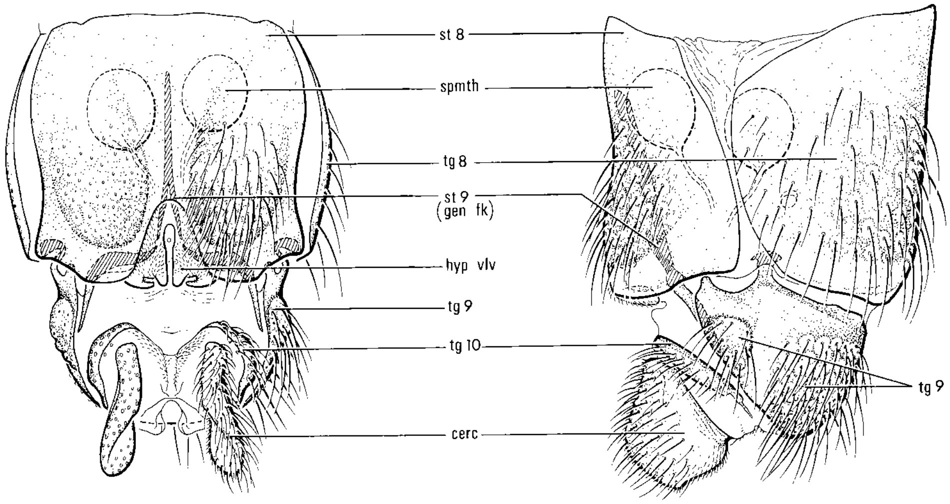
Primitively there are three separate spermathecal openings, and they are located on a free, relatively unmodified sternite 9 (Downes 1968). This condition still exists in a few primitive families, e.g. Blephariceridae, Tanyderidae, and some Tipulidae, but in most Nematocera a common spermathecal duct opens on sternite 9 some distance behind the primary gonopore (Downes 1968). Usually the spermathecal opening is found internally, in the dorsal wall of the genital chamber. In the Nematocera and many orthorrhaphous Brachycera it is often associated with modified derivatives of sternite 9.

The accessory glands are unsclerotized organs that are usually associated with egg laying. One or two are usually present, depending on the species or group (Sturtevant 1925–1926).. Generally, they produce an adhesive for attaching eggs to a substrate or for gluing the eggs together in a mass as they are laid. In some pupiparous groups, e.g. Glossinidae and Hippoboscidae,



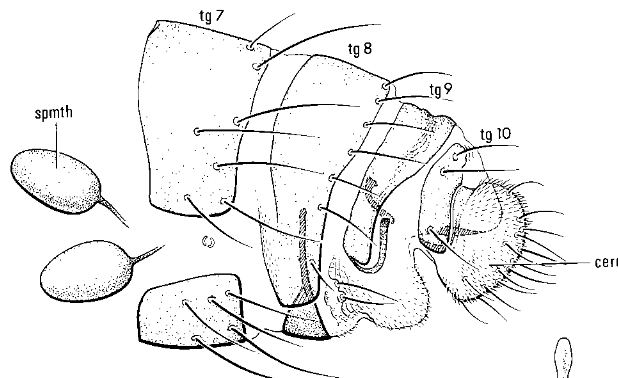
Figs. 2.79–85. Female abdomens and terminalia: (79) left lateral view of entire abdomen of *Trichocera columbiana* Alexander; (80) left lateral, (81) dorsal, and (82) ventral views of terminalia of *T. columbiana*; (83) left lateral, (84) dorsal, and (85) ventral views of terminalia of *Boletina* sp. (Fig. 83 drawn to larger scale than Figs. 84 and 85).

Abbreviations: cerc, cercus; hyprct, hypoproct; hyp vlv, hypogynial valve; st, sternite; tg, tergite.

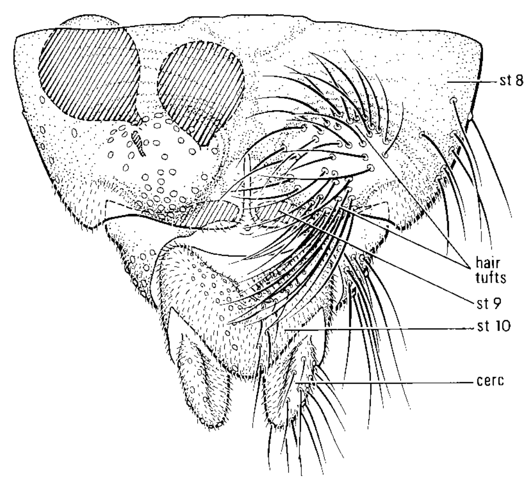


86 Chironomus plumosus ♀

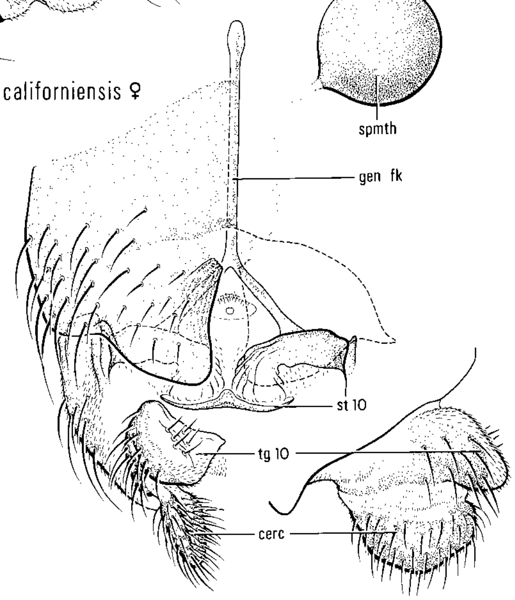
87 Chironomus plumosus ♀



88 Leptoconops (Brachyconops) californiensis ♀



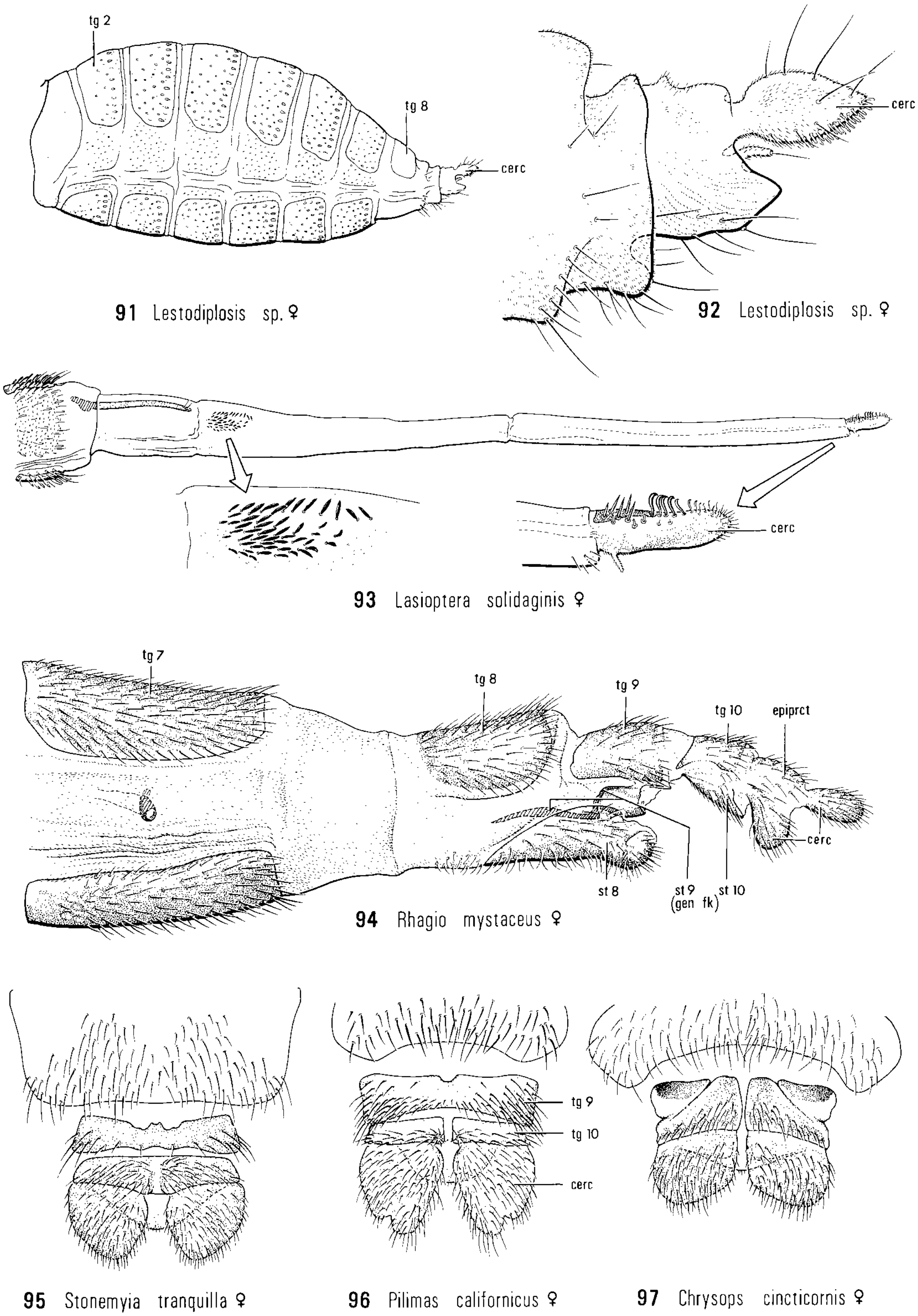
89 Probezzia concinna ♀



90 Prosimulium decemarticulatum ♀

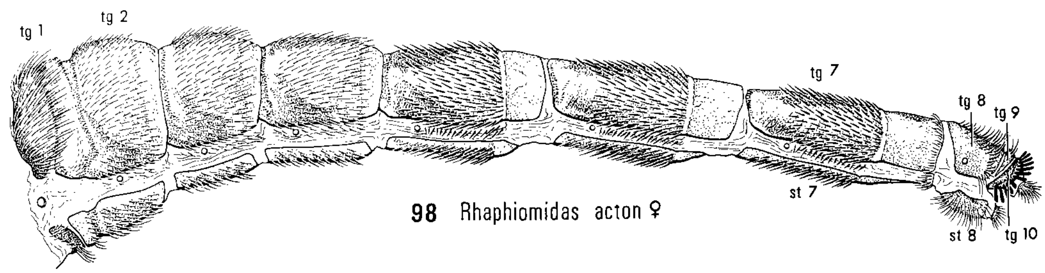
Figs. 2.86–90. Female terminalia of Culicomorpha: (86) ventral and (87) left lateral views of *Chironomus plumosus* (Linnaeus); (88) *Leptoconops* (*Brachyconops*) *californiensis* Wirth & Atchley, left lateral view; (89) *Probezzia concinna* (Meigen), ventral view; (90) *Prosimulium decemarticulatum* (Twinn), ventral and left lateral (*inset*) views.

Abbreviations: cerc, cercus; gen fk, genital fork; hyprct, hypoproct; hyp vlv, hypogynial valve; spmth, spermatheca; st, sternite; tg, tergite.

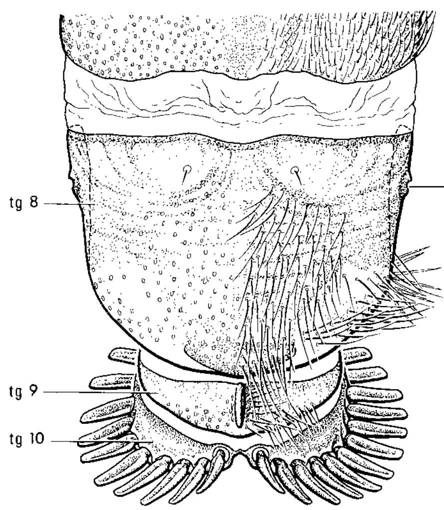


Figs. 2.91–97. Female abdomens and terminalia of Cecidomyiidae and Tabanomorpha: (91) entire abdomen and (92) terminalia in greater detail of *Lestodiplosis* sp., left lateral view; (93) specialized terminalia of *Lasioptera solidaginis* Osten Sacken, left lateral view; (94) abdomen of *Rhagio mystaceus* (Macquart), left lateral view; (95) terminalia of *Stonemyia tranquilla* (Osten Sacken); (96) terminalia of *Pilimas californicus* (Bigot) and (97) terminalia of *Chrysops cincticornis* Walker, dorsal view, showing various conditions of tergites 9 and 10.

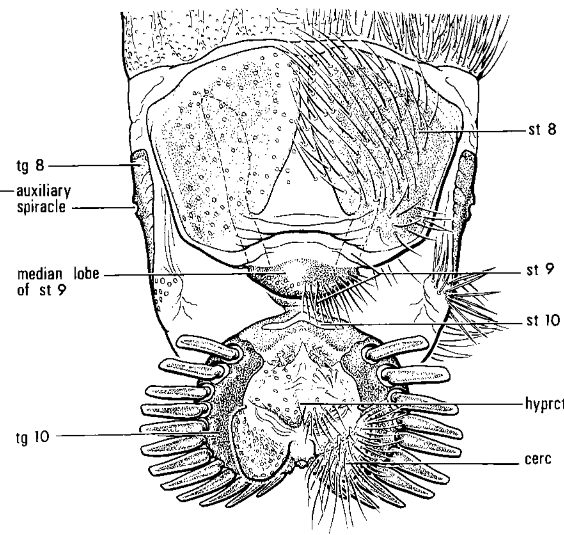
Abbreviations: cerc, cercus; gen fk, genital fork; st, sternite; tg, tergite.



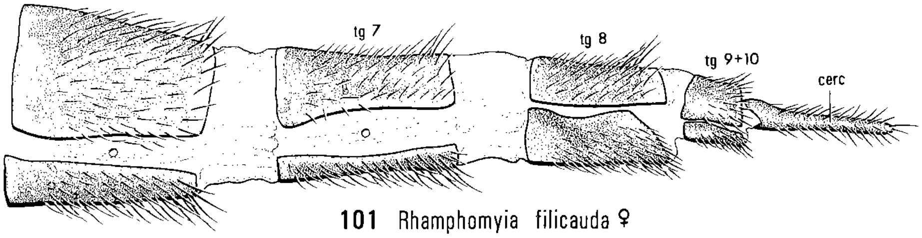
98 Rhaphiomidas acton ♀



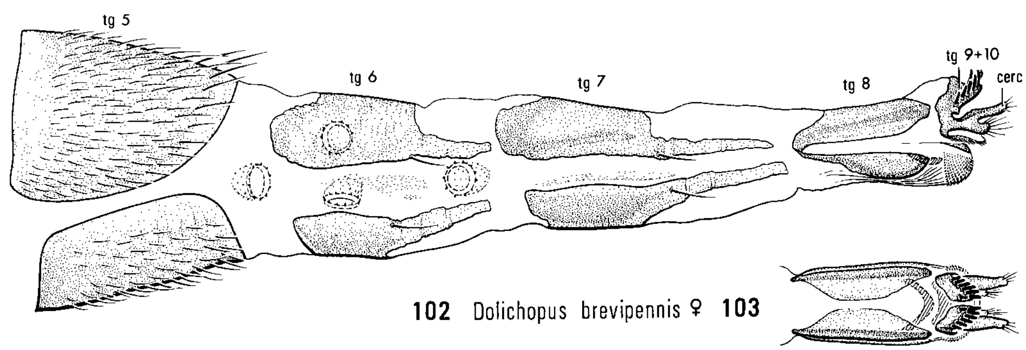
99 Rhaphiomidas acton ♀



100 Rhaphiomidas acton ♀



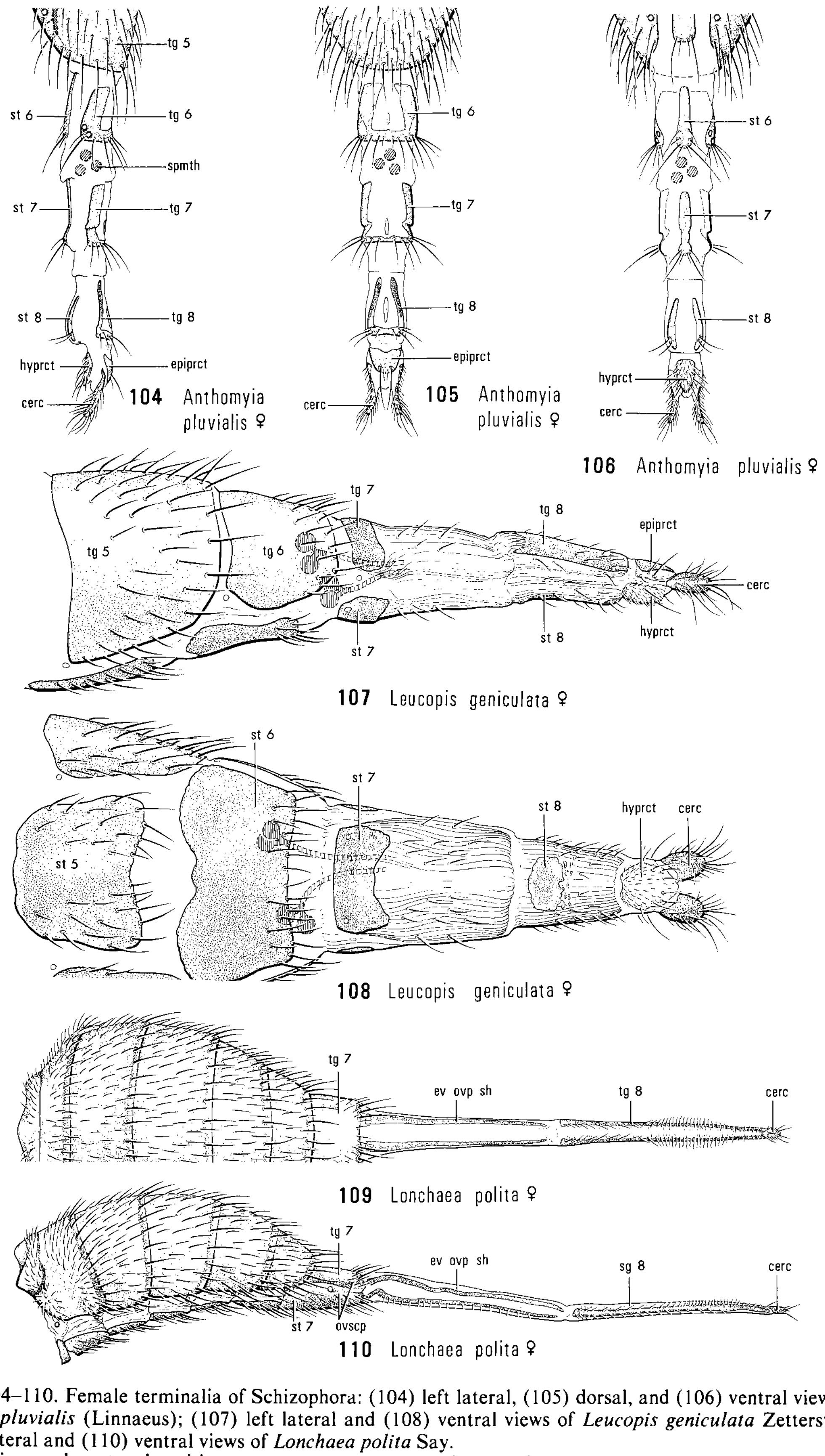
101 Rhamphomyia filicauda ♀



102 Dolichopus brevipennis ♀ 103

Figs. 2.98–103. Female abdomens and terminalia of Asilomorpha: (98) left lateral, (99) dorsal, and (100) ventral views of entire abdomen of *Rhaphiomidas acton* Coquillett (Apioceridae); (101) *Rhamphomyia filicauda* Henriksen & Lundbeck (Empididae), left lateral view; (102) left lateral and (103) ventral views of *Dolichopus brevipennis* Meigen.

Abbreviations: cerc, cercus; hyprct, hypoproct; st, sternite; tg, tergite.



Figs. 2.104–110. Female terminalia of Schizophora: (104) left lateral, (105) dorsal, and (106) ventral views of *Anthomyia pluvialis* (Linnaeus); (107) left lateral and (108) ventral views of *Leucopis geniculata* Zetterstedt; (109) left lateral and (110) ventral views of *Lonchaea polita* Say.

Abbreviations: adv sut, adventitious suture; cerc, cercus; epiprct, epiproct; ev ovp sh, eversible ovipositor sheath; hyprct, hypoproct; ovscp, oviscape; sg, segment; spmth, spermatheca; st, sternite; tg, tergite.

they serve as 'milk glands' for the nourishment of the larvae. They may be pear-shaped, subspherical, long and cylindrical, or complex ramose structures. The ducts of the accessory glands open into the anterodorsal part of the genital chamber, usually close behind the spermathecal openings.

The ventral receptacle is known only in certain acalyptrate families (Sturtevant 1925–1926). It arises from the anteroventral portion of the genital chamber and functions as a sperm reservoir. It may be a simple membranous pocket, as in *Thaumatomyia* (Chloropidae); a long, fine, much coiled tube, as in *Stegana* (Drosophilidae); or a large, heavily sclerotized pouch, as in Ephydridae. Unlike other uterine pouches that may also occur, the ventral receptacle never has a muscular wall of its own.

In the Nematocera and orthorrhaphous Brachycera the pregenital segments of the female terminalia are usually relatively unmodified. The membranous intersegmental region between them is short and the sclerites themselves usually remain more or less permanently exposed. There is a trend, however, beginning with the orthorrhaphous Brachycera (especially in the Rhagionidae, Fig. 94) and progressing through the Muscomorpha in which the main segments of the terminalia become more slender and more widely spaced, with relatively long, membranous intersegmental regions to permit a greater degree of telescoping. Special names have not been applied to the parts of segment 6, but segment 7 is modified to form a bulbous ***oviscape*** in several family groups of the Muscomorpha, e.g. Nerioidea, Tephritoidea (Figs. 109, 110), and Agromyzidae. Frequently, especially in the Calyptratae, spiracle 7 becomes shifted forward to segment 6, which thus exhibits two pairs of spiracles (Fig. 104). In many cases throughout the order, but especially in the Muscomorpha, both the tergites and the sternites of segments 7 and 8 are mainly membranous and they are sometimes reduced to elongate, single or paired strips or rods (Fig. 106). In the piercing-type ovipositor of the Tephritoidea (Figs. 109, 110) both the tergite and sternite of segment 8 are divided into elongate rods to form the main shaft of the ovipositor tube. Sometimes segment 8 is referred to as the ***gynium***; thus, in the Tipulidae at least, its tergite and sternite are called the ***epigynium*** and the ***hypogynium*** (subgenital plate), respectively. A pair of processes arising from the hypogynium, possibly homologous with the anterior gonapophyses of the orthopteroid ovipositor, are called ***hypogynial valves*** (hypovalvae, sternal valves, ovipositor lobes) (Figs. 79–82). A single, median plate in the same position in the Blephariceridae is called the ***hypogynial plate*** (oviscapt).

The tergites and sternites of segments 9 and 10 are present in the basic pattern of the Diptera (Hennig 1973). They are clearly evident in several primitive groups (Saether 1977), including the Tipulidae (Frommer 1963), the Sciaridae (Colless and McAlpine 1970), orthorrhaphous Brachycera (Nagatomi and Iwata 1976), and the Tabanoidea (Stuckenberg 1973). They are said to be present in some Syrphidae (Lehrer 1971) and are also evident in some Phoridae, e.g. *Spinophora*. As noted above, sternite 9 is usually highly modified and is frequently greatly reduced or absent. In many Nematocera and orthorrhaphous Brachycera it occurs as a mainly internal ***genital fork*** (furca, vaginal apodeme) in the dorsal wall of the genital chamber; differences in its shape sometimes provide useful taxonomic characters, as in the Simuliidae (Fig. 90). The ***preatrial*** and ***postatrial sclerites*** of the Culicidae are probably also derived from sternite 9. Nagatomi and Iwata (1976) reported that sternite 9 is usually absent in orthorrhaphous Brachycera, but they evidently did not realize that the structure that they called the genital fork is a derivative of sternite 9 (Bonhag 1951, pp. 156–157). In most Muscomorpha, however, sternite 9 is indistinguishable or absent. Tergite 9 is usually present as a dorsal plate in the Nematocera and orthorrhaphous Brachycera, but beginning in the Asilomorpha and throughout the Muscomorpha it is usually indistinguishably fused with a composite sclerite sometimes incorrectly called the epiproct or it is absent (Herting 1957).

Tergite 10 is frequently present as a dorsal plate in the Nematocera (Figs. 79–90) and orthorrhaphous Brachycera (Figs. 94–103). Sometimes it is closely associated or fused with tergite 9. It is sometimes divided into two plates, which often become very small or disappear (Nagatomi and Iwata 1976). In many orthorrhaphous Brachycera, e.g. Mydidae, Asilidae, Apioceridae (Figs. 98–100), Therevidae, Scenopinidae, and Dolichopodidae (Figs. 102, 103) (for references, see Hennig 1973), tergite 10 (not tergite 9 as interpreted by Hennig and others) is divided into a pair of spine-bearing hemitergites, sometimes called acanthophorites, used for digging during oviposition; these structures have usually been wrongly assumed to be derived from tergite 9 (Adisoemarto and Wood 1975, Irwin 1976). Sternite 10 (intra-anal plates of the Tipulidae, ventral plates of the Tabanidae) may be fused with sternite 11 or virtually absent (Frommer 1963, Bonhag 1951).

The true proctiger, possibly including vestiges of segment 11, is the anus-bearing region behind segment 10. Some authors refer to elements of segment 11 in some primitive families (Frommer 1963, Tipulidae; Bonhag 1951, Tabanidae), but in general no separate tergite (true epiproct) or sternite (true hypoproct) of segment 11 is found in the female Diptera. Because of the absence of segment 11 and because segment 10, especially, is so closely integrated with the true proctiger, the term is often extended by dipterists to include all the structures behind segment 9.

The paired cerci are usually the most prominent elements of the proctiger. Each cercus is primitively two-segmented in the female of both the Nematocera and the Brachycera, but it is independently reduced to one segment in many groups in both suborders, e.g. most

Nematocera, Athericidae, Tabanidae, and Nemestrinidae, and perhaps all Asilomorpha and Muscomorpha (Hennig 1973, Nagatomi and Iwata 1976, Saether 1977). They are sometimes well developed and elongate as in the Tipulidae and Trichoceridae (Figs. 79–82), or reduced to tiny lobes (Figs. 99,108). In lower Diptera, as in most insects, they are activated by muscles from segment 10. In certain Cecidomyiidae (Fig. 93) and in the Tephritoidea (Figs. 109, 110) the cerci are fused and form the apex of the piercing-type ovipositor.

The anus opens on the midline between the cerci in a more or less apicoventral position.

Male terminalia. The eight main elements of the male terminalia (Figs. 111–141) in the basic pattern of the Diptera are as follows:

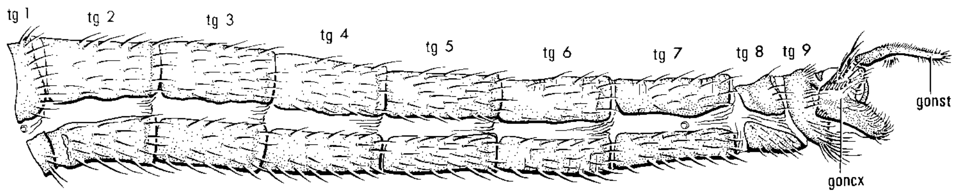
- tergite 9, the ***epandrium*** (genital arch)
- sternite 9, the ***hypandrium*** (Gabelplatte, penis sheath of the Syrphidae, vinculum of the Calliphoridae)
- a pair of primitively two-segmented arms, the ***gonopods*** (claspers, forcipate claspers, anterior gonapophyses, pregonites, harpagones, parameres) arising posterolaterally on sternite 9 and consisting of a basal ***gonocoxite*** (basimere, basistyle, side-piece) and a distal ***gonostylus*** (distimere, dististyle, clasper)
- a pair of unsegmented paraphallic processes, the ***parameres*** (harpes, parandrites, paraphyses, penis valves, posterior gonapophyses), situated between the posterolateral base of the aedeagus and the dorsomedial base of the gonocoxite
- a median phallic organ, the aedeagus, arising behind sternite 9
- a reduced ***tergite 10***, which is closely associated with tergite 9 and tends to form a pair of lateral lobes, the ***surstyli*** (*sing.* ***surstylus***)
- a simple ***sternite 10*** (ventral epandrial plate)
- the vestigial tergite and sternite of segment 11, more or less consolidated to form a proctiger bearing the cerci and the anus.

These eight items comprise the basic elements of the male terminalia in most orders of insects (Snodgrass 1935, Sharov 1966, Tuxen 1970, Matsuda 1976), but they vary greatly in occurrence and form. In the Diptera, as in other orders, they provide an unparalleled array of taxonomic characters. For convenience tergite 9, the epandrium, is discussed in conjunction with tergite 10. The remaining elements are discussed in the order they are listed.

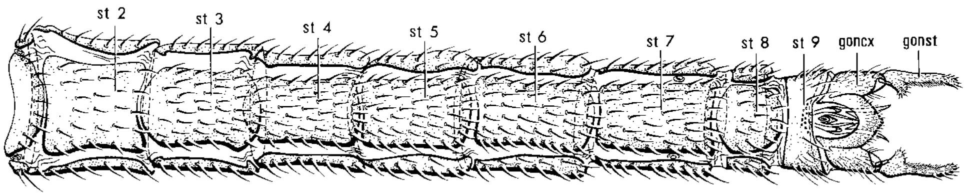
Sternite 9, the hypandrium, is usually considerably modified in the male Diptera. In many Nematocera it is joined laterally with tergite 9, the epandrium, and the two together are then frequently called the ***basal ring*** (genital ring) (Figs. 114, 119). There is also a strong tendency for the gonopods to become fused with sternite 9, in which case the sternite is often virtually obliterated and replaced by the more or less fused bases of the gonopods (Figs. 122, 11.4–5). In the Muscomorpha (Figs. 135, 141) the hypandrium is usually somewhat U-shaped, with the arms of the U more or less encompassing the base of the aedeagus. Single median and paired lateral hypandrial apodemes sometimes project internally. Throughout the order there is a tendency for a pair of lobes to occur medially at the posterior margin of the hypandrium, between the inner ventral bases of the gonocoxites and the anteroventral base of the aedeagus. These lobes are usually at least partially fused medially and frequently form an ***aedeagal guide*** (adminiculum, penis guard, phallosome) (Figs. 133, 135, 140). In some Tipulidae and Anisopodidae (Fig. 19.16) they form a complex, elongate, ventromedial process; in other Tipulidae they form a transverse plate. In the Tabanoidea the fused lobes appear to be united laterally with the fused parameres and thus form the anteroventral wall of the cone-shaped ***aedeagal sheath*** (penis sheath, tegmen) (Figs. 32.6, 33.14). In many Muscomorpha they are fused with the posterior median extremity of the hypandrium and project trough-like around the anteroventral surface of the aedeagus (Figs. 135, 140).

Much confusion exists concerning the interpretation and naming of the parts here called gonopods and parameres, the homologies of which are still disputed throughout the endopterygote orders (for reviews, see especially Scudder 1971 and Matsuda 1976). The crux of the dispute rests mainly on whether the pair of large, primitively two-segmented arms on the posterior margin of sternite 9, the gonopods of this manual, that occur in most pterygote insects including the Diptera, are homologous with the primitive two-segmented appendages (gonopods) on the posterior margin of sternite 9 in Thysanura (Apterygota) (Griffiths 1972). The two-segmented arms associated with sternite 9 (gonopods) in such endopterygote orders as Mecoptera, Trichoptera, Hymenoptera, and Diptera are generally thought to be homologous with each other, and most workers except Crampton (1938, 1941, 1942) and Snodgrass (1957, 1963) believe that they are homologous with the gonopods of Thysanura (Sharov 1966, Mackerras 1970, Matsuda 1976). Also, it is generally agreed that Coleoptera is one of a few orders in which the male does not have elements that can be referred to these gonopods (Snodgrass 1935, Lindroth and Palmén 1970, Matsuda 1976). The significance of this last statement relates to the application of the name paramere.

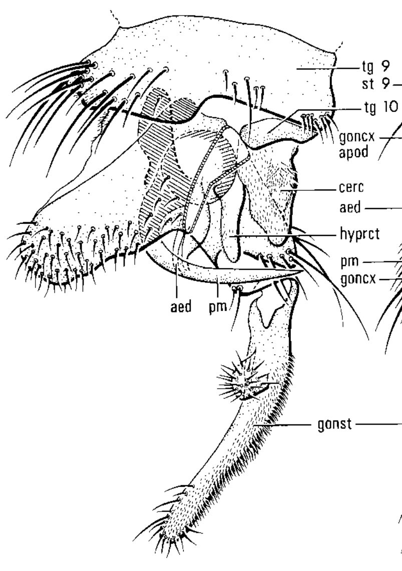
Interpretation of both the gonopods and the parameres in the Diptera is complicated by the fact that the name paramere was applied to the gonopods by such workers as Crampton (1938, 1941, 1942) and Snodgrass (1957, 1963). In these last papers, Snodgrass postulated that the primitive gonopods were lost not only in the Coleoptera but in all endopterygote insects and were replaced during ontogeny by parameres. As a result of this argument, he also concluded that these new para-

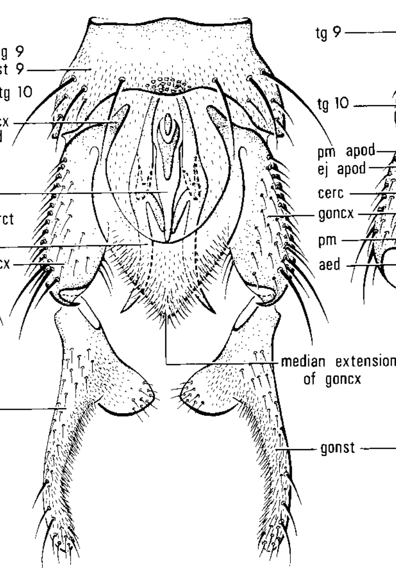


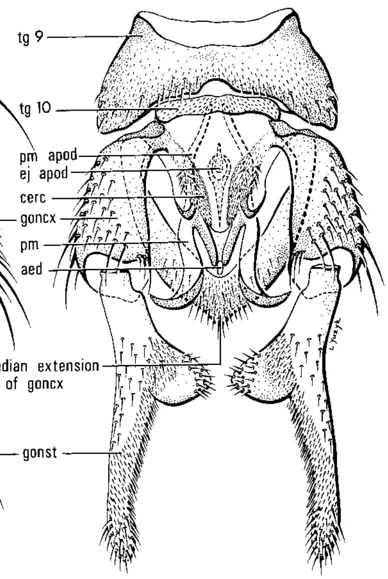
111 Trichocera garretti ♂



112 Trichocera garretti ♂





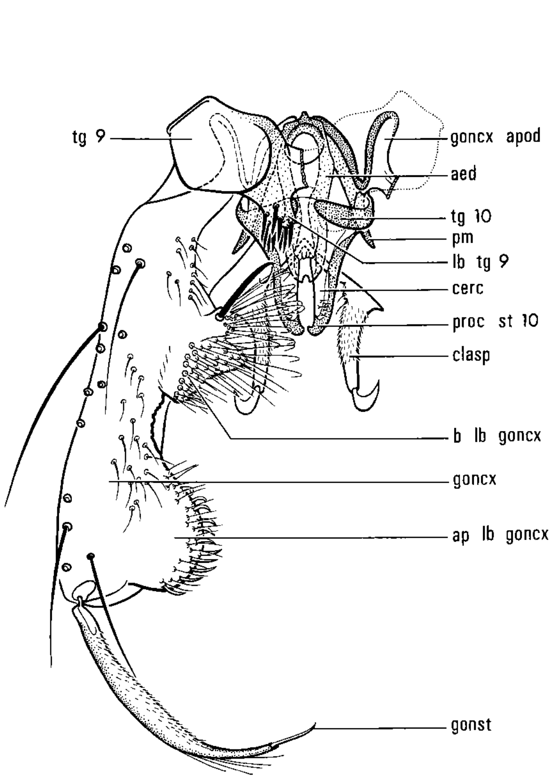


113 Trichocera garretti ♂ **114** Trichocera garretti ♂ **115** Trichocera garretti ♂

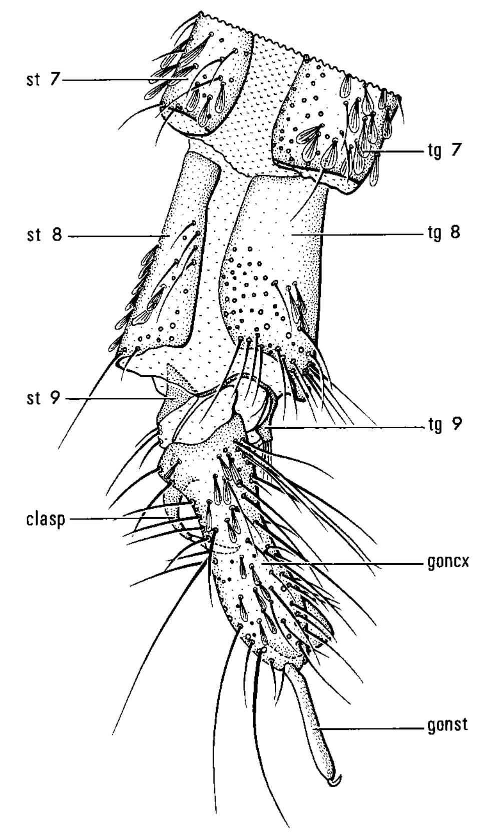
Figs. 2.111–115. Male abdomen and terminalia of *Trichocera garretti* (Alexander): (111) left lateral and (112) ventral views of entire abdomen; (113) left lateral, (114) ventral, and (115) dorsal views of terminalia.

Abbreviations: aed, aedeagus; cerc, cercus; ej apod, ejaculatory apodeme; goncx, gonocoxite; goncx apod, gonocoxal apodeme; gonst, gonostylus; hyprct, hypoproct; pm, paramere; pm apod, parameral apodeme; spm pmp, sperm pump; st, sternite; tg, tergite.

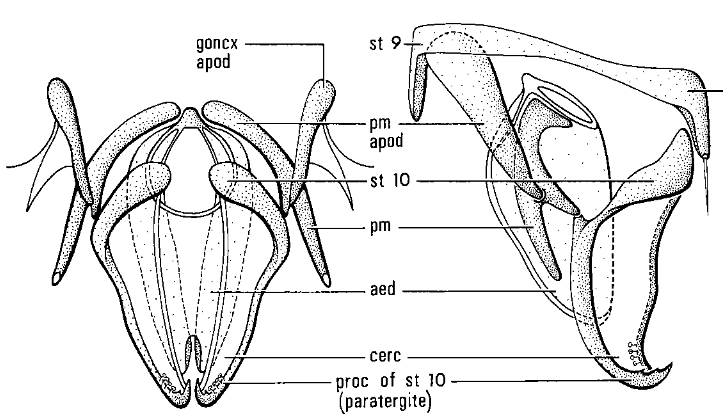
meres became secondarily two-segmented, and that the pair of paraphallic lobes that are named parameres in our discussion and that occur at the base of the aedeagus in most endopterygote insects including the Diptera are paraphyses (parandrites of Crampton 1938) of secondary origin. This argument is a reversal of his previous conclusions (Snodgrass 1935), and it appears to be wrong for most endopterygote orders, including the Diptera (Sharov 1966, Mackerras 1970, Matsuda 1976). Crampton himself (1938, p. 5) cautioned that, "The evidence thus far produced by those who maintain that the genital forceps (gonopods) of Hymenoptera represent the parameres of Coleoptera is not entirely satisfactory," and he only accepted it provisionally as a working hypothesis. It is unfortunate that he disregarded these reservations in his later papers. Mackerras



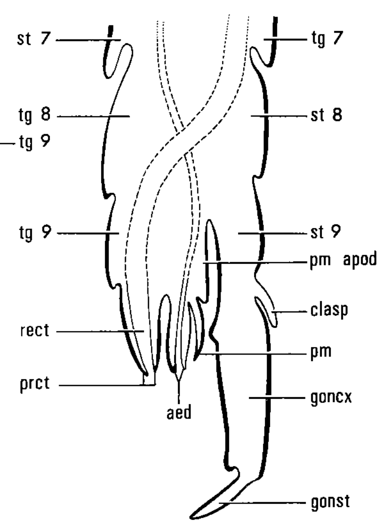
116 Aedes hexodontus ♂



117 Aedes grossbecki ♂



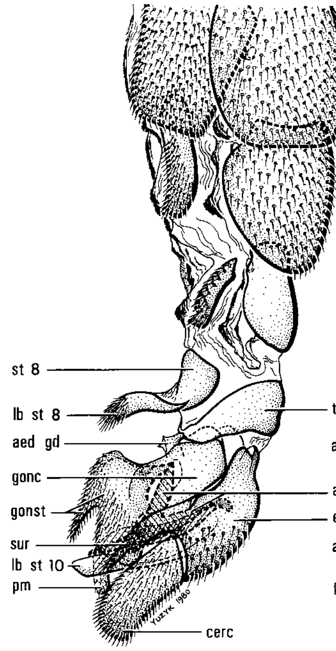
118 Aedes stimulans ♂ **119** Aedes stimulans ♂



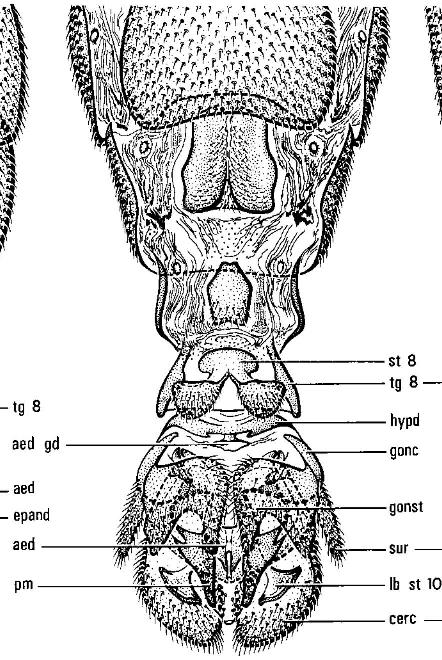
120 Aedes sp. ♂

Figs. 2.116–120. Male terminalia of Culicidae: (116) *Aedes hexodontus* Dyar, dorsal view (after Wood *et al.* 1979); (117) *Aedes grossbecki* Dyar & Knab, left lateral view, before rotation (redrawn from Knight and Laffoon 1971); (118) dorsal and (119) left lateral views (diagrammatic) (redrawn from Matheson 1944) of *Aedes stimulans* (Walker) showing details of aedeagus and associated parts; (120) longitudinal section (diagrammatic) through distal abdominal segments and terminalia of *Aedes* sp. subsequent to 180° rotation, with sclerotized areas indicated by thicker lines (redrawn from Edwards 1920).

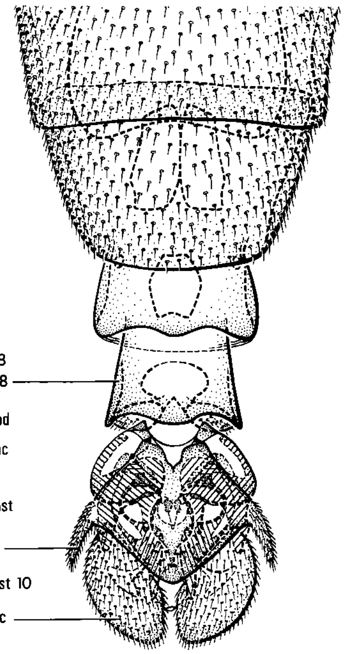
Abbreviations: aed, aedeagus; ap lb goncx, apical lobe of gonocoxite; b lb goncx, basal lobe of gonocoxite; cerc, cercus; clasp, claspette; goncx, gonocoxite; goncx apod, gonocoxal apodeme; gonst, gonostylus; lb tg 9, lobe of tergite 9; pm, paramere; pm apod, parameral apodeme; prct, proctiger; proc st 10, process of sternite 10 (paratergite); rect, rectum; st, sternite; tg, tergite.



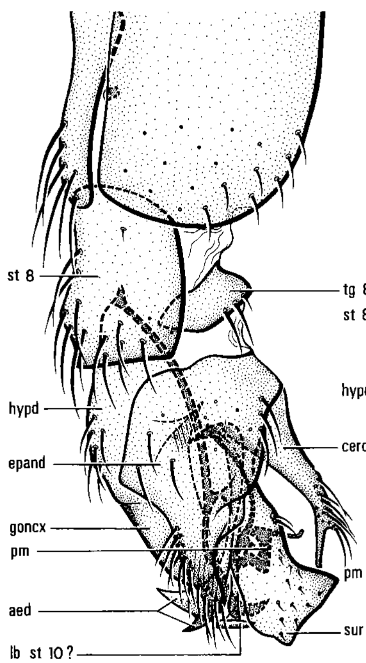
121 Xylomya tenthredinoides ♂



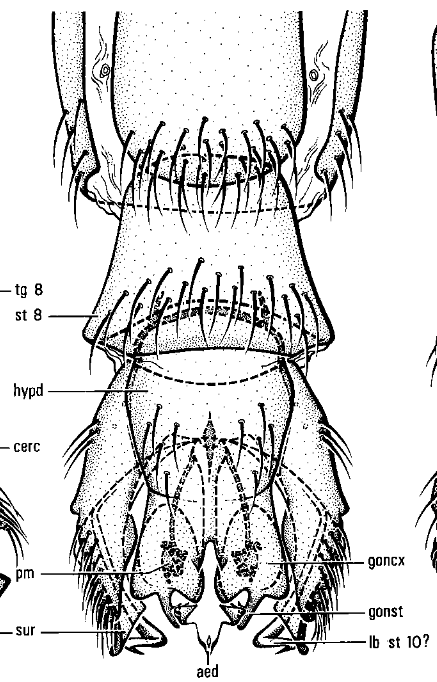
122 Xylomya tenthredinoides ♂



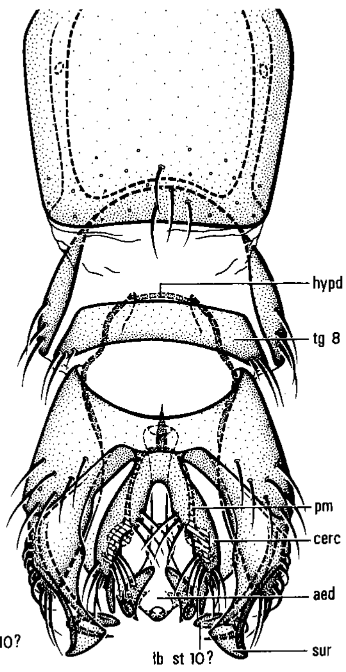
123 Xylomya tenthredinoides ♂



124 Gloma luctuosa ♂



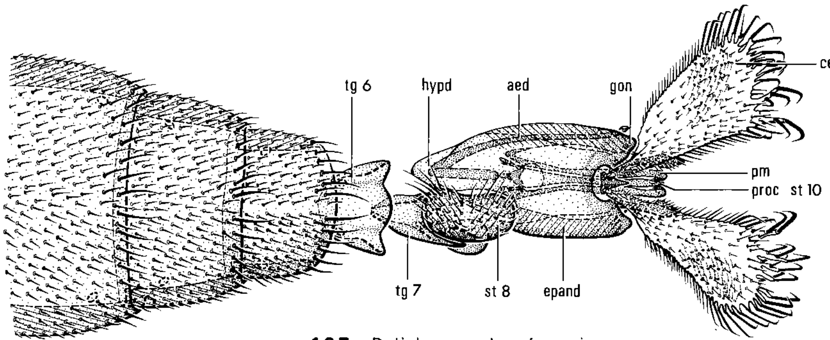
125 Gloma luctuosa ♂



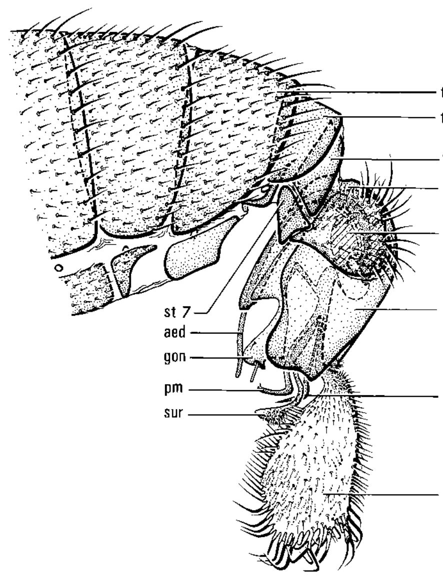
126 Gloma luctuosa ♂

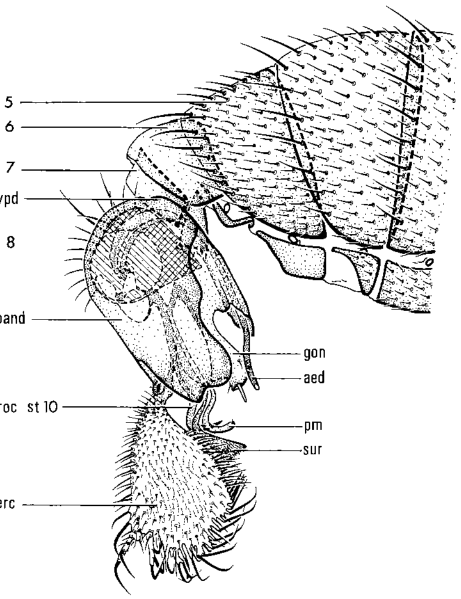
Figs. 2.121–126. Male terminalia of Xylomyidae and Empididae: (121) left lateral, (122) ventral, and (123) dorsal views of *Xylomya tenthredinoides* (Wulp); (124) left lateral, (125) ventral, and (126) dorsal views of *Gloma luctuosa* Melander.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; a 1b sur, anterior lobe of surstylus; cerc, cercus; epand, epandrium; goncx, gonocoxite; goncx apod, gonocoxal apodeme; gonst, gonostylus; hypd, hypandrium; hyprct, hypoproct; 1b st, lobe of sternite; 1b tg, lobe of tergite; p 1b sur, posterior lobe of surstylus; pm, paramere; pm apod, parameral apodeme; st, sternite; sur, surstylus; tg, tergite.



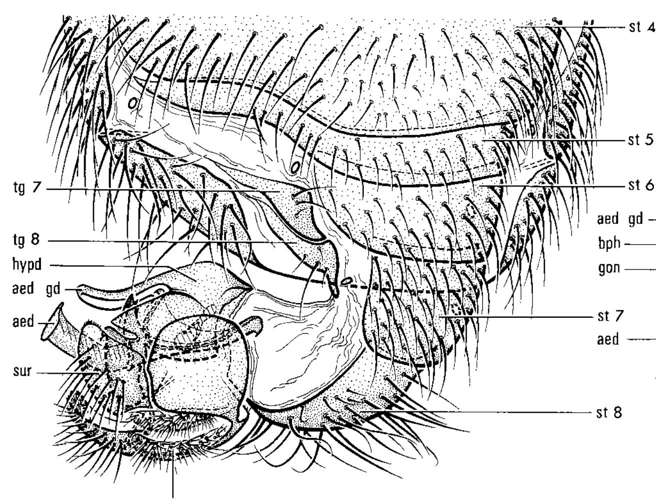
127 Dolichopus brevipennis ♂

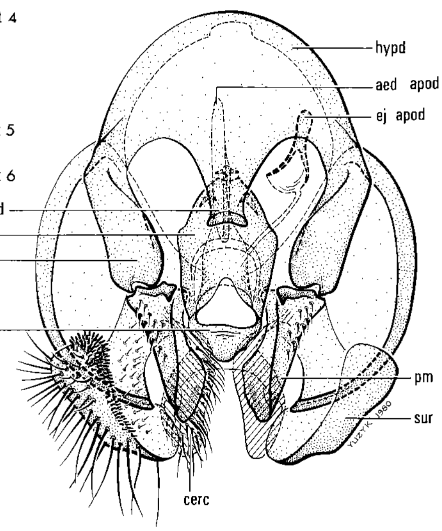




128 Dolichopus brevipennis ♂

129 Dolichopus brevipennis ♂



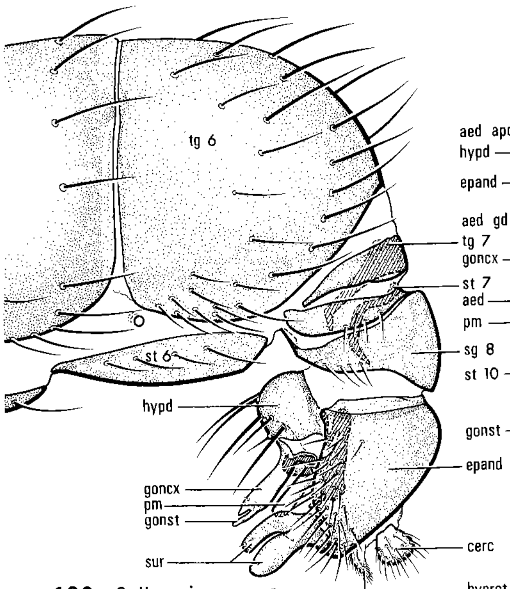


130 Syrphus ribesii ♂

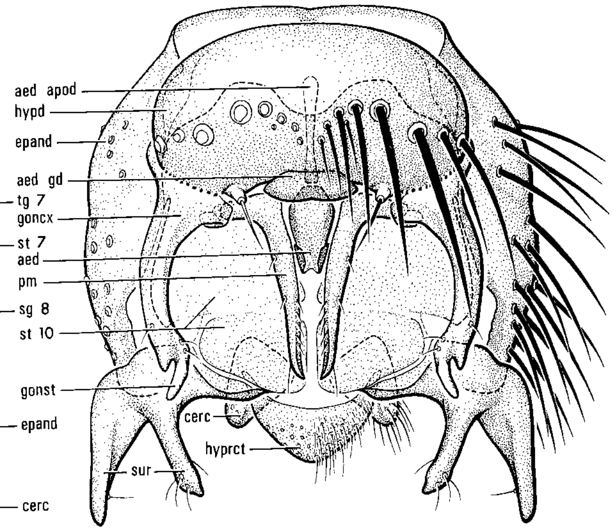
131 Syrphus ribesii ♂

Figs. 2.127–131. Male abdomen and terminalia of Dolichopodidae and Syrphidae: (127) dorsal, (128) left lateral, and (129) right lateral views of *Dolichopus brevipennis* Meigen; (130) *Syrphus ribesii* (Linnaeus), ventral view of apical portion of abdomen with terminalia in normal resting position; (131) *S. ribesii*, ventral view of terminalia.

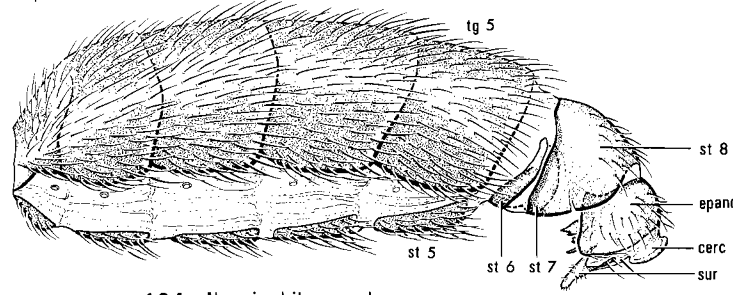
Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; bph, basiphallus; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; gon, gonopod; hypd, hypandrium; pm, paramere; proc st 10, process of sternite 10; st, sternite; sur, surstylus; tg, tergite.



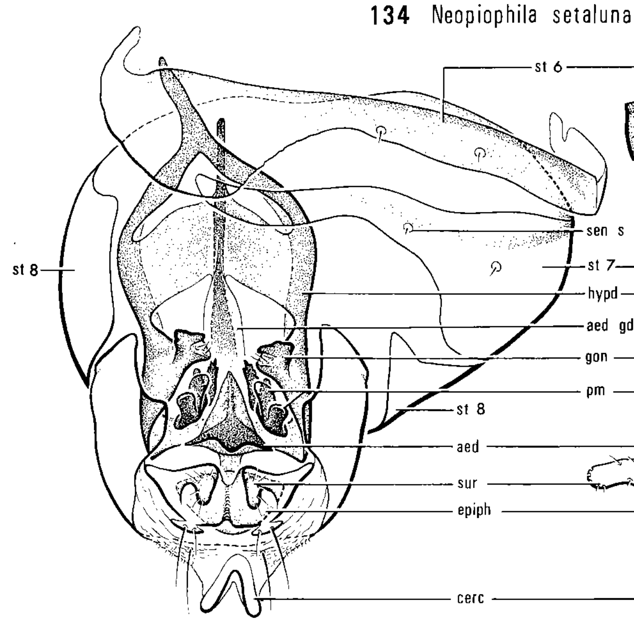
132 Callomyia sp. ♂



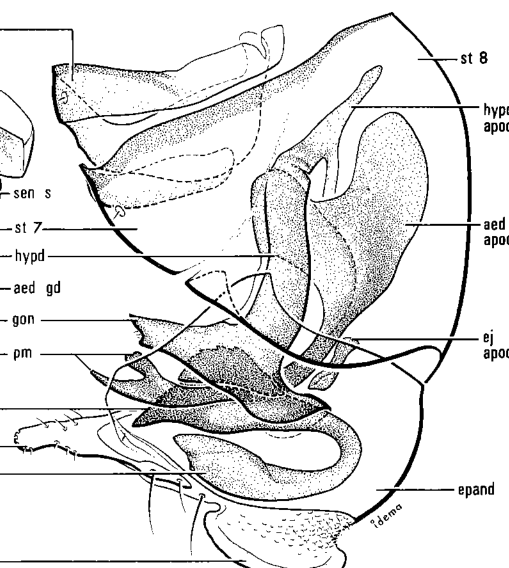
133 Callomyia sp. ♂



134 Neopiophila setaluna ♂



135 Neopiophila setaluna ♂



136 Neopiophila setaluna ♂

(1970, p. 27) summed up the matter as follows: "The weight of probability still lies with the gonocoxite theory for the endopterygotes, and it would seem undesirable to depart from it without further evidence." That conclusion is adopted here for the Diptera.

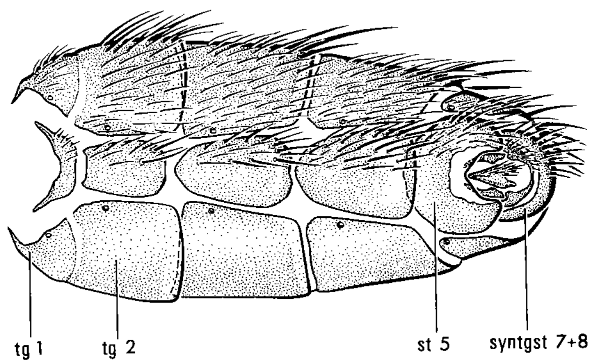
The gonocoxite articulates proximally with the posterior margin of the hypandrium and distally bears the gonostylus. In form, the gonocoxite may be relatively simple as in *Trichocera* (Figs. 113–115) or complex as in the Culicidae (Figs. 116, 117) with closely associated ***claspettes*** and with ***apical***, ***subapical***, and ***basal lobes***; sometimes it is very large as in *Axymyia* (Figs. 11.4–5) and sometimes it is greatly reduced as in most Muscomorpha (Figs. 135, 138–141); it may be free from the hypandrium as in the Trichoceridae (Fig. 114), *Cramptonomyia* (Pachyneuridae (Figs. 12.3–4), and the Culicomorpha (Figs. 116, 117) or fused with the hypandrium as in *Axymyia* (Figs. 11.4–5) and many other Bibionomorpha and Muscomorpha. The so-called claspettes found in many Culicidae (Fig. 116) and somewhat similar lobes sometimes called by the same name among other Nematocera, e.g. Cecidomyiidae (Figs. 16.93), are among the most striking processes associated with the gonocoxite; in the Culicidae, at least, they arise proximally in the membrane between the bases of the gonocoxites, anteroventral to the base of the aedeagus (compare this position with that of the parameres below) and may be homologous with the aedeagal guide of other Diptera. Frequently, especially in the Nematocera and orthorrhaphous Brachycera, each gonocoxite has a conspicuous internal ***gonocoxal apodeme***. The distal ends of the gonocoxal apodemes are usually widely separated from each other, but in some Ceratopogonidae (Fig. 28.101) and most if not all Chironomidae (Figs. 29.77–110) they are fused. The gonostylus may be simple as in most Trichoceridae (Figs. 113–115) or complex as in *Hesperinus* (Bibionidae) and many Tipulidae (Figs. 7.3–6); toothed or untoothed as in the Cecidomyiidae (Figs. 16.85, 16.87); and relatively large as in many Nematocera, much reduced as in *Callomyia* (Platypezidae) (Figs. 132, 133), or absent or combined with the gonocoxite as in all Schizophora (Figs. 135–141). In the Nematocera and orthorrhaphous Brachycera both the gonocoxite and the gonostylus are usually preserved, but it is not unusual for the gonostylus to be reduced and fused with the gonocoxite. In the Muscomorpha, however, the gonopod (pregonite) is usually reduced to a simple lobe on the hypandrium (Figs. 135, 136, 138–141) and only rarely is the primitive two-segmented condition apparent, e.g. in *Callomyia* (Platypezidae) (Figs. 132, 133). In the Syrphoidea, however, no discrete gonopodal lobe is evident (Figs. 130, 131). Some workers (Crampton 1942, van Emden and Hennig 1970, Hennig 1976*a*) are reluctant to homologize these lobes in the higher Diptera with gonopods and refer to them by the noncommital term pregonites. The position, the sometimes two-segmented condition, and the general resemblance of them in the Platypezidae and certain orthorrhaphous Brachycera leave little doubt that they are, in fact, homologous structures throughout the Diptera (Hennig 1976*b*). It seems desirable to adopt the more explicit term, gonopod, for them in the Muscomorpha as in the Nematocera and orthorrhaphous Brachycera.

With regard to the true parameres, as defined in this manual, it is generally accepted that they are derived from secondary divisions of the primary phallic lobes, and that they are primitively unsegmented (Snodgrass 1935, 1957, 1963; Scudder 1971; Matsuda 1976). They are located between, and articulate with, the base of the aedeagus and the dorsomedial base of each gonocoxite. They occur regularly in most orders, and in the Diptera they constitute an important part of the genital complex. It is these lobes in the Coleoptera (in which gonopods are absent) that Verhoeff (1893) first named parameres, and it is these lobes that Snodgrass (1957) insisted are paraphallic lobes derived from the primary phallic lobes of segment 10. Unfortunately, in the Diptera they are sometimes confused with additional lobes or processes associated with the gonocoxite; for example, Scudder (1971) misinterpreted the claspette, which in the Culicidae arises near the proximal inner ventral surface of each gonocoxite, as a paramere.

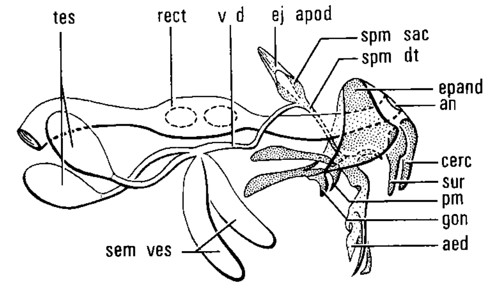
The parameres (Figs. 113–115, 116, 118, 119, 121–126, 130–133, 135, 136, 140, 141) are surprisingly constant throughout the order and only rarely are they indistinguishable or absent. Normally the base of each paramere articulates with the basal posterolateral extremities of the aedeagus and with the base of the gonocoxal apodeme arising from the proximal dorsomedial rim of the gonocoxite. Usually each paramere is subtended by an internal ***parameral apodeme*** for muscle attachment. The parameres serve as accessory structures for supporting and directing the aedeagus, and perhaps also for protecting the aedeagus while it is

Figs. 2.132–136. Male abdomen and terminalia of Platypezidae and Piophilidae: (132) *Callomyia* sp., left lateral view of apical portion of abdomen with terminalia in normal resting position; (133) *Callomyia* sp., ventral view of terminalia; (134) left lateral view of entire abdomen with terminalia slightly unfolded from normal resting position, (135) ventral view of terminalia and adjoining sclerites, and (136) left lateral view of terminalia and adjoining sclerites of *Neopiophila setaluna* McAlpine.

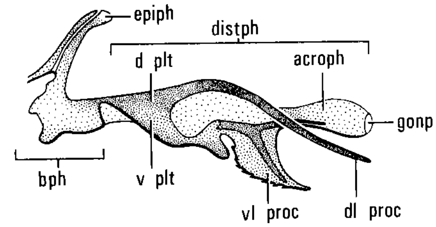
Abbreviations: adv sut, adventitious suture; aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; a 1b sur, anterior lobe of surstylus; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; epiph, epiphallus; gon, gonopod; goncx, gonocoxite; gonst, gonostylus; hypd, hypandrium; hypd apod, hypandrial apodeme; hyprct, hypoproct; p 1b sur, posterior lobe of surstylus; pm, paramere; sen s, sensory seta; sg, segment; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite.



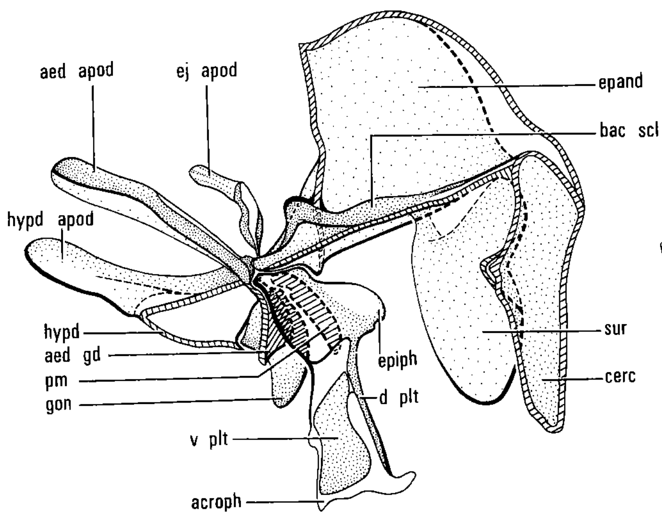
137 Melanophora roralis ♂



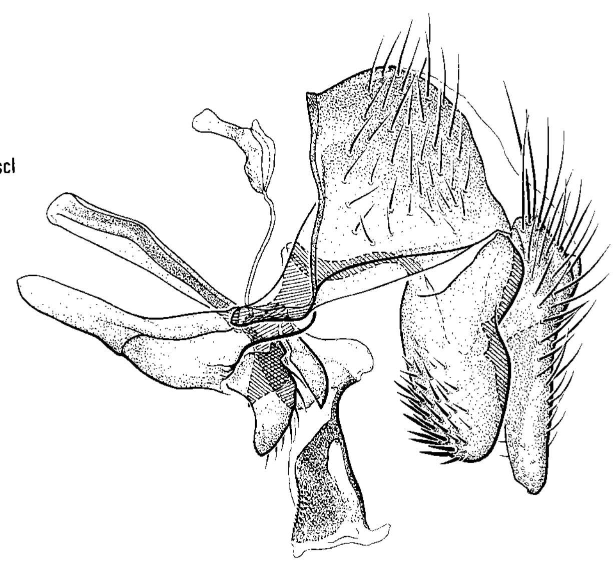
138 Phormia regina ♂



139 Pollenia rudis ♂



140 Masistylum arcuatum ♂



141 Masistylum arcuatum ♂

Figs. 2.137–141. Male abdomen and terminalia of Calyptratae: (137) *Melanophora roralis* (Linnaeus) (Rhinophoridae), ventral view of entire abdomen with terminalia in normal resting position; (138) *Phormia regina* (Meigen) (Calliphoridae), longitudinal section (diagrammatic) through distal abdominal segments and terminalia showing vas deferens and ejaculatory duct looped around rectum before reaching base of aedeagus (redrawn from Crampton 1942); (139) *Pollenia rudis* (Fabricius) (Calliphoridae), details of aedeagus and associated parts in left lateral view; (140) *Masistylum arcuatum* (Mik) (Tachinidae), longitudinal section of terminalia in left lateral view; (141) *M. arcuatum*, normal terminalia in left lateral view.

Abbreviations: acroph, acrophallus; aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; an, anus; bac scl, bacilliform sclerite; bph, basiphallus; cerc, cercus; distiph, distiphallus; dl proc, dorsolateral process; d plt, dorsal plate; ej apod, ejaculatory apodeme; epand, epandrium; epiph, epiphallus; gon, gonopod; gonp, gonopore; hypd, hypandrium; hypd apod, hypandrial apodeme; pm, paramere; rect, rectum; sem ves, seminal vesicle; spm dt, sperm duct; spm pmp, sperm pump; spm sac, sperm sac; st, sternite; sur, surstylus; syntgst, syntergosternite; tes, testicle; tg, tergite; vl proc, ventrolateral process; v d, vas deferens.

not in use (Hennig 1976*a*, 1976*b*). Usually they are relatively small, simple, and more or less triangular; they are lightly to heavily sclerotized and sometimes even bear strong setulae or spines, e.g. Simuliidae (Figs. 27.65–73). In some groups, especially in the Muscomorpha, they are rather complicated with several lobes, e.g. *Microsania* of the Platypezidae and *Neopiophila* of the Piophilidae (Figs. 135, 136). In other cases they are largely fused with the basiphallus, e.g. some Cecidomyiidae (Fig. 16.87). In most Tabanoidea they are somewhat membranous and fused to form at least the dorsal wall of a conical aedeagal sheath, which together with the fused aedeagal guides encloses the aedeagus (Fig. 33.14). In the Asilidae this sheath encloses only the base of the aedeagus (Theodor 1976). In the Syrphoidea, where the gonopods are atrophied, the parameres are often unusually exposed and prominent (Figs. 130, 131).

There has been a general hesitancy to accept the homology of the parameres throughout the Diptera. Although long recognized and called parameres in the Nematocera and certain orthorrhaphous Brachycera, the neutral term, postgonites, is the name most commonly applied to them in the Muscomorpha. Some workers (Hennig 1976*b*) postulated that the postgonites of the Muscomorpha may be derived from the gonostylus. However, their position and relationship to the gonopod and the aedeagus leave scarcely any doubt that they are homologous with the parameres of lower Diptera, as suggested by van Emden and Hennig (1970, p. 139). It seems timely to adopt a uniform terminology for them throughout the order.

The aedeagus exhibits a great variety of forms, and in many families it provides the best specific characters available. It develops from tissues behind sternite 9, and most authors regard it as a derivative of segment 10. Its primary function is to transfer sperm to the female reproductive system, usually by the direct transfer of free sperm into one or more spermathecae or to a site in the bursa near the spermathecal opening or openings. In the Chironomidae, Thaumaleidae, Ceratopogonidae, and Simuliidae, the sperm is transferred in a gelatinous envelope, the ***spermatophore***, to the female genital chamber. In these four families the aedeagus is mainly membranous and nondistensible. In the Ceratopogonidae (Figs. 28.98–119) the sclerotized ventral portion, possibly a specialized aedeagal guide, is called the aedeagus; in the Simuliidae (Figs. 27.51–73) the same structure is called the ***ventral plate***. The aedeagus is usually elongate in species that deliver free sperm and short and rather bursa-like in those that produce a spermatophore. It is exposed in most Diptera, but in some forms, e.g. most Tabanoidea, it is enclosed within the aedeagal sheath (Fig. 32.6). In some acalyptrates, e.g. Celyphidae, *Amiota* (Drosophilidae), *Dasiops* (Lonchaeidae), *Minettia* (Lauxaniidae), and some Piophilidae (Fig. 135), the aedeagus is greatly reduced or absent.

The external wall of the aedeagus is usually at least partially sclerotized and frequently consists of many different plates, processes, spines, and lobes (Fig. 139). It is not possible to homologize all the parts that have been distinguished and named by different authors in different families, but a number of basic elements can usually be distinguished, especially in higher Diptera. These include: a proximal ***basiphallus*** (phallobase, phallophore, theca); a distal ***distiphallus*** (juxta, phallus); one to three membranous internal tubes, the ***endophallus***,[1] which unite proximally with the sperm ducts; and one or more distal openings, the ***gonopores*** (phallotremata).

The basiphallus is the sclerotized basal sector of the aedeagus. Usually it is relatively short and simple, but in many Schizophora, especially Tephritoidea, it is very elongate and convoluted or coiled. Internally it is usually subtended by an ***aedeagal apodeme*** (ejaculatory apodeme, phallapodeme, Tragplatte). When present in the Nematocera and most orthorrhaphous Brachycera (Fig. 125) the aedeagal apodeme is a simple internal extension of the aedeagus, and it lies more or less in the same plane as the aedeagus. In the Muscomorpha, however, it is separated from the basiphallus by a membranous articulation, and it joins the basiphallus at a distinct angle (Figs. 136, 140) (Hennig 1976*b*). Here it may be free and wedge- or Y-shaped, a condition referred to as ***cuneiform***, or it may be at least partially fused with the median internal surface of the hypandrium (Fig. 136), namely ***fultelliform***. Externally the contraction of the muscles attached to the aedeagal apodeme in the Nematocera and orthorrhaphous Brachycera results in compression of the closely associated ***sperm pump*** (ejaculator, ejaculatory bulb, ejaculatory pump). Contraction of the muscles attached to the aedeagal apodeme in the Muscomorpha results in exsertion of the aedeagus (Hennig 1976*b*). Externally the basiphallus also sometimes bears, especially in the Brachycera, an external process called the ***epiphallus*** (spinus), arising from its posteromedial surface (Figs. 135, 136, 140, 141).

The term distiphallus is usually applied to the relatively discrete apical section of the aedeagus of higher Diptera, but perhaps it may also be a useful term for the apex of the aedeagus in some lower Diptera. In the Tanyderidae, the Blephariceridae, and other primitive Diptera the apex of the aedeagus is three-branched (Downes 1968). Each branch carries a separate seminal duct, the endophallus, ending in an independent gonopore. This condition is correlated with three external spermathecal openings in the female, which are spaced to correspond to the three gonopores of the male (Edwards 1929, Downes 1968). In the Tabanoidea the aedeagus is distinctly three-branched (Fig. 32.6), but there is no stem-like section separating the basiphallus (endophallic hilt) and the distiphallus, and only the central branch contains an endophallic tube. The two lateral branches, called ***aedeagal tines*** (endophallic

[1] It is unfortunate that Hennig (1976*b*) used this term for the entire aedeagus.

tines), arise directly from the basiphallus; at their bases they are directed anteriorly but they quickly curve dorsally and thence posteriorly on each side of the main central branch. During copulation they are forced through the opening of the aedeagal sheath together with the central branch that bears the gonopore. This condition is correlated with a single internal spermathecal opening in the female. The distiphallus of higher Diptera may also be trifid in representatives of many families, e.g. Asilidae, Empididae, Syrphidae, Pipunculidae, Platystomatidae, Sarcophagidae, and Tachinidae, and here also the corresponding spermathecal openings are located internally in the oviduct. Throughout the Diptera, many departures from the tripartite condition occur, namely from a bipartite condition in the Phlebotominae of the Psychodidae to a simple tube in most Cecidomyiidae (Figs. 16.83–110), and from a swollen structure, the ***glans***, at the end of a long, coiled, or convoluted basiphallus such as is found in the Tephritoidea to the very complicated structure found in some Calyptratae (Fig. 140). Numerous terms have been created for the individual parts of the distiphallus, especially in the Muscomorpha (Roback 1954, Lopes 1956, and Lopes and Kano 1968, Sarcophagidae; Saltzer 1968, Calliphoridae; Nowakowski 1962 and Steyskal 1969, Agromyzidae; McAlpine 1973, Platystomatidae; Hennig 1974 and 1976*a*, Anthomyiidae). Although many of these terms are applicable only to particular families, a basic pattern is emerging (Hennig 1976*a*), and at least some of the parts, such as the ***acrophallus*** bearing the gonopores, are recognizable in different families. Some of these parts are shown in Fig. 140 and are labeled according to the terminology applied by Saltzer (1968) and Hennig (1976*a*). For a study on the function and relationships of various parts of the male and female terminalia in the Sarcophagidae, see Lopes and Kano (1968).

Some additional internal parts (Fig. 138) that function in the transfer of sperm and that are closely associated with the aedeagus are the sperm pump and one or more ***sperm ducts*** (ejaculatory ducts). A sperm pump occurs in all species that create a closed system for transfer of free sperm during copulation; it is undeveloped or absent in species that produce a spermatophore (Downes 1968). When present it is supplied by the common duct of the testes, the ***vas deferens***, and it consists of a sac at the base of the aedeagus, the ***sperm sac*** (vesica, ejaculatory sac, Samenspritze). In the Nematocera and orthorrhaphous Brachycera it is closely associated with the aedeagal apodeme, and the muscles that operate it are sometimes attached directly to the aedeagal apodeme, which has been incorrectly labeled ejaculatory apodeme by some workers. In the Muscomorpha, however, the sperm pump is completely separate from the aedeagal apodeme and it has its own median unpaired process, the ***ejaculatory apodeme***, for muscle insertions (Figs. 135, 140) (Hennig 1976*b*).

The epandrium is the principal dorsal sclerite, tergite 9, of the genital segment (andrium). It is always connected with its ventral sternite, the hypandrium, and with modified rudiments of tergite 10, posteriorly. Frequently, especially in higher Diptera, a pair of lateral lobes called the surstyli, now believed to be derived from tergite 10, project clasper-like from the posterolateral margins of the epandrium. These lobes have often been considered to be secondary processes of the epandrium (Crampton 1942, Hennig 1958) but, as postulated by Steyskal (1957) and McAlpine (1962, 1967) and as later shown by Hennig's (1976*a*, 1976*b*) detailed studies, they originate from laterally displaced portions of tergite 10.

In the Nematocera the epandrium is frequently reduced and fused laterally with the hypandrium to form a basal ring (Figs. 114, 119). Sometimes it occurs as a free, variously developed plate, e.g. Synneuridae (Fig. 21.5). In many cases it is extremely reduced and possibly combined with tergite 10, e.g. Anisopodidae (Fig. 19.14) and in other cases it is relatively large and free from tergite 10, e.g. most Bibionomorpha (Figs. 11.5, 12.4). In orthorrhaphous Brachycera the epandrium is usually relatively larger than in the Nematocera. In the Asilomorpha, e.g. Apioceridae (Figs. 41.15–16), the Asilidae, and the Empididae (Fig. 124), it is frequently deeply cleft dorsally, and its sides appear capable of clasper-like functions. Sometimes, especially in the Empididae, the epandrium has its own surstylus-like lobes, even though true surstyli are also present, as in *Gloma* (Figs. 124–126) and *Oreogeton* (McAlpine 1967).

In the Nematocera tergite 10 sometimes occurs as a simple, weakly sclerotized dorsal strip behind the epandrium, as in the Trichoceridae (Fig. 115) (Hennig 1973), but in a few cases it bears surstyli. Perhaps the most generalized surstyli observed in the order are those found in the family Ptychopteridae (Crampton 1942). In the genus *Bittacomorpha* they are directly attached to the lateral extremities of tergite 10 (not tergite 9 as indicated by Crampton 1942), which, though very narrow, is still complete on the dorsum. Similar surstyli also occur in other Ptychopteridae (Hennig 1973, Just 1973, called cerci), Blephariceridae, some Tipulidae (Byers 1961, called tergal arms), some Mycetophilidae, for example the genus *Symmerus* (Hennig 1973), and some Synneuridae (Figs. 21.4–5). In these cases tergite 10 is divided medially and appears as two more or less lateral lobes articulated with the posterolateral margins of the epandrium. In many Nematocera, however, tergite 10 is lost or indistinguishably fused with tergite 9. Likewise, in orthorrhaphous Brachycera tergite 10 sometimes varies in form. In the Rhagionidae, for example, it may be present as a free, transverse sclerite, or it may be divided on the midline into two variously reduced lateral sclerites, or it may be completely atrophied (Stuckenberg 1973). It takes the form of clasper-like surstyli in some Xylophagidae (Figs. 121–123), Stratiomyidae, Asilidae, Empididae (Figs. 124–126), and Dolichopodidae (Figs. 128, 129) (Crampton 1942).

In the Muscomorpha (Figs. 130–139) the epandrium is usually a strongly developed, more or less saddle-shaped sclerite, and the presence of articulated surstyli is a basic feature of practically all families (Hennig 1976*b*). Some authors (Hennig 1936, Griffiths 1972) have postulated that tergite 9 is lost in the Muscomorpha and that the epandrium in this group is the fusion product of the gonocoxites (periandrial theory of Griffiths 1972). However, Hennig himself (1976*a*, 1976*b*) presented detailed evidence to show that "this interpretation is certainly wrong." Matsuda (1976) declared that the periandrial idea is not acceptable because both the gonopods and the epandrium sometimes occur together, as shown in Fig. 10 of Griffiths' (1972) work, and Andersson (1977) also rejected it on several grounds. Occasionally in Muscomorpha two pairs of closely associated surstylar lobes are present (Steyskal 1957, McAlpine 1963). An ***anterior surstylar lobe*** is clearly evident as a separate entity in the conopid genus *Zodion* (Steyskal 1957, Fig. 4) and in the chamaemyiid genus *Cremifania* (McAlpine 1963, Figs. 11 and 12). This lobe appears to be a secondary lobe of the epandrium. The posterior lobe, or true surstylus, derived from tergite 10 and articulated with the epandrium, is much more common. In many acalyptrate groups, however, these two pairs of lobes become more or less integrated and give the appearance of a single divided surstylus, e.g. Dryomyzidae, Sciomyzidae, Heleomyzidae, and many Tephritoidea. Here the lobes can be distinguished as ***inner*** and ***outer surstyli***, e.g. most Tephritoidea, or as ***anterior, median***, and ***posterior surstylar lobes***, e.g. Lonchaeidae. In a few cases, e.g. Tethinidae, the epandrium may even have additional surstylus-like lobes. In some families, e.g. most Sepsidae and the Chamaemyiidae, the surstyli are secondarily reduced and fused with the epandrium. The various lobes of the surstyli sometimes bear different types of hairs, spines, and processes. In many Tephritidae the distal end of the inner surstylus bears several strong teeth, the ***prensisetae*** (Munro 1947). These are probably homologous with the strong teeth on the posterior lobe of the surstylus in many Lonchaeidae and Otitidae.

Sternite 10, like tergite 10, is usually present in some form in Diptera (Steyskal 1957, McAlpine 1967, Hennig 1976*a* and 1976*b*), and it too is closely associated with the epandrium. Normally it is located in the ventral wall of the epandrium behind and dorsal to the aedeagus. Its evolution can be followed from primitive Nematocera, e.g. Blephariceridae, Ptychopteridae, and Anisopodidae, through the Brachycera into the Schizophora. In the Nematocera it is sometimes referred to simply as sternite 10, e.g. Anisopodidae (Fig. 19.18) and Synneuridae (Fig. 21.5), but often it is so reduced or membranous that it cannot be distinguished from the hypoproct, e.g. Cecidomyiidae (Figs. 16.87, 16.102, 16.113). In the Brachycera it has been given different names in different families, e.g. ventral lamella of the proctiger (Karl 1959, in Asilidae), sternite 10 (Vockeroth 1969, in Syrphidae), ventral proctigeral sclerite or second ventral proctigeral sclerite (Ulrich 1972, in Empididae), bacilliform sclerites (Crampton 1942, in Calliphoridae), processi longi (German authors), interprameral sclerite (Griffiths 1972, in Muscomorpha), and ventral epandrial sclerite (Hennig 1976*b*, in Brachycera). Primitively it occurs as a simple plate that joins anteriorly with the posterior margins of the hypandrium, laterally with the inner margins of the surstyli when present or with the margins of tergite 10, and posteriorly with the hypoproct. It is relatively simple in the Synneuridae (Fig. 21.5), Ropalomeridae (Steyskal 1957), Ironomyiidae and Platypezidae (McAlpine 1967), and Rhagionidae, Empididae, Platypezidae, and Lonchopteridae (Hennig 1976*b*). Sometimes, e.g. some Anisopodidae (Fig. 19.16) and Xylophagidae (Fig. 122), it bears elongate processes. Commonly throughout the order it becomes more or less divided medially as in *Dioctria* (Asilidae), and in the Calyptratae, especially, it is divided into two rod-like struts, the ***bacilliform sclerites*** (processi longi), that connect the inner bases of the surstyli with the posterior arms of the hypandrium.

The proctiger is the anus-bearing region behind segment 10. Primitively in the Insecta it consists of a dorsal plate, the ***epiproct***; a pair of lateral lobes, the ***paraprocts***; a ventral plate, the ***hypoproct***; and the cerci. All these are probably derived from the 11th and last true somite (Snodgrass 1935, 1963). True paraprocts have not been identified in the Diptera (Crampton 1942, p. 93). The processes, sometimes called paraprocts in the Culicidae, are derived from segment 10 and, therefore, are not true paraprocts. The epiproct is usually weakly developed or absent, but the hypoproct is a relatively constant feature. Frequently it is fused with sternite 10 and in many instances is indistinguishable as a separate sclerite. Embryologically the cerci arise as appendages of segment 11, between the bases of the paraprocts and the epiproct. They sometimes form a conspicuous and important part of the proctiger in the Diptera, e.g. in the Dolichopodidae (Figs. 127–129), but frequently, especially in the Nematocera (Figs. 111–120), they are weakly developed and practically indistinguishable. In their generalized condition they occur as a pair of hairy lobes on either side of the anus. In contrast to a primitive two-segmented condition in the female Diptera, the cerci in the male are only one-segmented, as in the Mecoptera (Hennig 1973). They are said to be absent in the male of all Tipulomorpha (Hennig 1973), but here they are probably incorporated in the proctiger or so-called anal segment, as in the Culicidae (Figs. 118, 119). In other nematocerous groups, e.g. Synneuridae (Figs. 21.5, 21.6), they are more sharply delimited from adjacent parts. In the Dolichopodidae (Figs. 127–129) they are frequently highly developed and ornamented. In most acalyptrate families, and no doubt in the basic pattern of the Muscomorpha, they are simple, relatively weakly sclerotized lobes (Figs. 135, 136). In the Calyptratae (Figs. 137, 138, 141), they form strongly sclerotized, elongate processes (mesolobes); here the two cerci are often fused at their bases but separated distally, and they articulate directly with the surstyli; in other groups, e.g. *Chaetolonchaea* of the Lonchaeidae and many Sarcophagidae and Tachinidae, they are sometimes completely fused together. The anus always opens between the cerci, behind and above the base of the aedeagus. Sometimes it is an important landmark.

Flexion and rotation. The apical portion of the male abdomen is frequently bent or folded forward ventrally, dorsally, or laterally (Figs. 142–146). Such bending is called ***flexion***, and it may be categorized as ***ventroflexion***, ***dorsoflexion***, or ***lateroflexion***, respectively. Flexion is termed ***facultative*** when it is voluntary and temporary, and ***obligatory*** when it is fixed and permanent.

In addition to being flexed, the male terminalia may be twisted through 90° to 360° about the long axis of the abdomen (Figs. 120, 138). Such twisting is called ***rotation***, and it, also, is facultative when it is temporary, and obligatory when it is fixed permanently. Rotation through 180° (Fig. 120), best known in the Culicidae, results in true ventral structures coming to lie in a dorsal position. Such a condition is called ***inversion***, and it can be recognized by reference to the relative positions of the aedeagus and the proctiger. When the terminalia are inverted the anus is ventral to the genital opening, whereas the reverse situation occurs when the terminalia are not inverted. Rotation through 360° (Fig. 138), which occurs in all Muscomorpha, is called ***circumversion***. In all forms with circumverted terminalia the anus and the genital structures are restored to their original positions, but the main internal ducts of the genital system, the nervous system, and the tracheal system are twisted around the hind gut (Fig. 138).

Both flexion and rotation are adaptations for mating and for storing the terminalia when not in use, and both have evolved repeatedly in different ways in different groups within the order. An understanding of the various conditions now existing rests upon the following points.

Courtship and mating in the Diptera consists of a chain of sign stimulus–response reactions (Stich 1963), beginning with contact of the sexes and ending in sperm transfer. Plesiomorphically, the initial stages of mating (contact and coupling) are believed to take place during flight (McAlpine and Munroe 1968), and the final stages (ejaculation and sperm transfer) usually occur while the mating pair rests on a substrate. Apomorphically, the initial stages may occur on a substrate, and the final stages during flight.

The ***initial coupling position*** (pose of Lamb 1922) frequently differs from the ***final mating position*** (position of Lamb 1922, also see Richards 1927). For coupling, both sexes usually, if not always, face in the same direction and are said to assume a ***unidirectional orientation*** (Figs. 142–146), but for the final stages of mating, the two sexes of many species face in opposite directions and are said to assume a ***tail-to-tail orientation*** (Figs. 142*b,c*; 143*b,c*; 144*a*; 146*a*).

With regard to flexion of the terminalia, the simplest situation is found in groups such as the Chironomidae and the Simuliidae, in which the abdomen is relatively slender and tubular. During coupling the end of the abdomen is voluntarily ventroflexed to bring the ventral surface of the male terminalia in contact with the ventral surface of the female terminalia (Figs. 142, 142*a*). The aedeagus is then able to join with the spermathecal opening or openings. In all Diptera in which the one or more spermathecal openings are located internally in a bursa or common oviduct, the ventral surface of the aedeagus is placed adjacent to the dorsal surface of the bursa or oviduct (inverse correlation of genitalia, as opposed to direct correlation, according to Lamb 1922; see also Richards 1927, Griffiths 1972, Hennig 1973). In some Nematocera, however, the male terminalia are permanently dorsoflexed, e.g. Blephariceridae. This condition also occurs in some orthorrhaphous Brachycera, e.g. some Empididae, but in the Dolichopodidae the male terminalia are permanently lateroflexed (Figs. 127–129, 145, 145*a*). In the Muscomorpha, they are usually permanently ventroflexed. In the basic pattern of the Diptera the male terminalia were probably relatively unflexed during rest but were capable of being voluntarily flexed ventrally and forward during coupling.

With regard to rotation, the simplest situation is found in groups such as the Simuliidae and the Tabanidae, where the terminalia are unrotated and apparently incapable of facultative twisting. Here the initial coupling position is unidirectional as in all Diptera, with both sexes vertically upright, male above and female below (Figs. 142, 142*a*). The final mating position is tail-to-tail, and because there is no rotation of the terminalia, one of the pair, usually the male, must lie upside down (Fig. 142*c*). In this position the male is completely helpless, and locomotion of the coupled pair usually depends on the female. Therefore when exposed, both partners are vulnerable to predators and other

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Figs. 2.142–146. Copulatory positions of Diptera. In these sketches the sexes are distinguished by male and female symbols (♂ ♀), and the dorsal (posterior) surface of the aedeagus is indicated by a small black triangle. The sketches in the left column show positions taken by different groups during initial coupling of the pairs, and those in the right column show alternative positions taken during the final stages of copulation. Figs. 142 and 143 relate to groups in which there is no permanent rotation of the male terminalia. Figs. 144 and 145 relate to groups in which the male terminalia are permanently rotated through 180°, i.e. inverted; and Fig. 146 relates to the Muscomorpha (=Cyclorrhapha) in which the male terminalia are permanently rotated through 360°, i.e. circumverted. In Fig. 142*b* the terminalia of both the male and female are each facultatively rotated through 90°. In Fig. 142*a* the male terminalia are ventroflexed and those of the female are dorsoflexed; but the reverse is true in Fig. 143*a*. In Fig. 145*a* the male terminalia are permanently dextrally lateroflexed.

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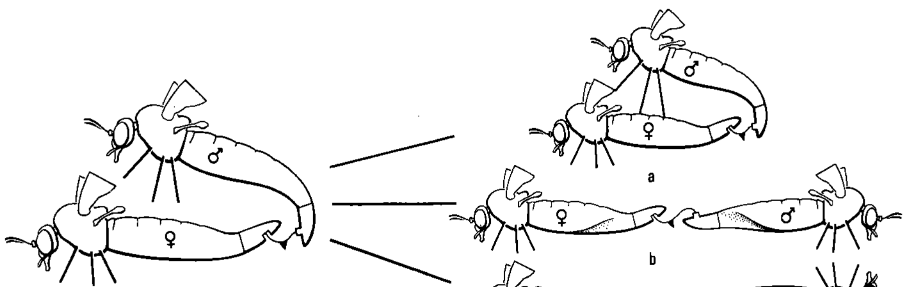
unfavorable environmental factors. This vulnerability probably explains, to some extent, why most Diptera have evolved various means, through rotation of the terminalia, to remain vertically upright during the final stages of mating. Because the rotation is effected in different ways, at different ontogenetic times, and at different morphological points in different groups it is believed to have arisen independently many times within the order (Richards 1927). It begins with facultative inversion of the terminalia in which up to 180° of



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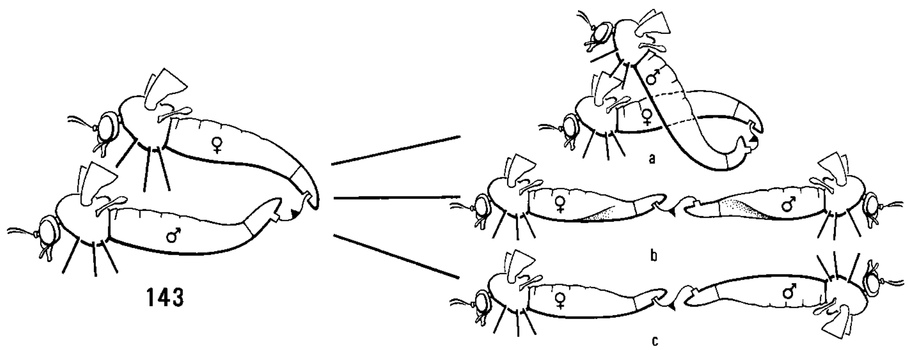

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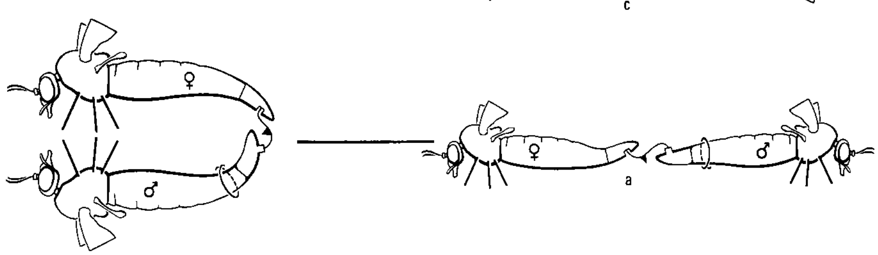

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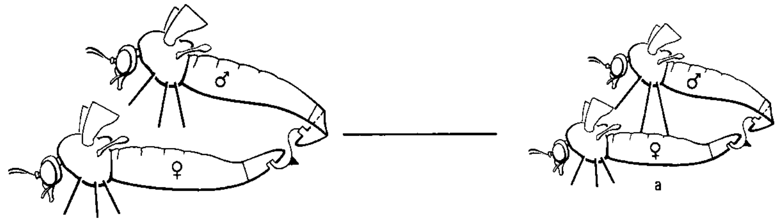

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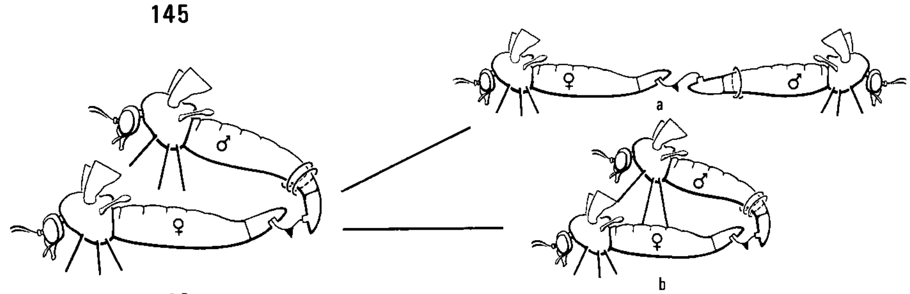

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rotation is spread over a number of segments, as in certain Bibionomorpha, followed by obligatory inversion, as in the Culicidae, where the terminalia are permanently rotated 180° between segments 7 and 8, and culminating with circumversion (360° rotation) in the Muscomorpha.

Details on flexion and rotation are still unrecorded for most Diptera, but the information that is known permits the following summary.

In the Tipulomorpha permanent inversion occurs in some Tipulidae, e.g. some eriopterine tipulids (Richards 1927), including *Styringomyia*, *Molophilus*, *Amphineurus* (Crampton 1942), and *Erioptera* subgenus *Ilisia* (Alexander, Ch. 7); in the Tipulinae at least partial inversion occurs in *Macromastix* (Crampton 1942), *Brachypremna*, and *Megistocera* (Frommer 1963). However, it is uncertain when it occurs and what segments are involved. Permanent inversion of segment 9 and the proctiger takes place in the tanyderid *Protoplasa fitchii* (Crampton 1942); according to Hennig (1973), inversion is distributed over several segments in this family. In the Psychodomorpha permanent inversion of the male terminalia is a normal feature of Psychodidae (Feuerborn 1922*b*; Richards 1927; Quate, Ch. 17), but additional details are unknown. A full 180° rotation occurs in all *Sylvicola* (Anisopodidae). Inversion in both the Tipulomorpha and the Psychodomorpha probably occurs after the adults emerge. As already noted, inversion is perhaps best known and documented in the Culicidae and in a few marine Chironomidae with wingless females. In the Culicidae 180° obligatory rotation of all the parts of the male terminalia beyond segment 7 occurs after emergence but before copulation. Practically all of the twisting is effected between segments 7 and 8, with little or no dragging of the preceding sclerites out of their true ventral or dorsal positions. Internally the genital duct, at least, is crossed over the hind gut (Fig. 120). Rotation of 180° is recorded for the Dixidae (Feuerborn 1922*a*, Richards 1927, Crampton 1942) and the Chaoboridae (Cook 1956). In the Ceratopogonidae inversion may or may not occur depending on the genus, tribe, or subfamily (Richards 1927, Downes 1978), and it is usually facultative rather than obligatory. Inversion, when it occurs, always takes place after emergence, sometimes before and sometimes during copulation; when it occurs during copulation partial counter-rotation sometimes follows so that the terminalia of males that have mated show degrees of rotation between 0° and 180°. In this family most of the rotation occurs between segments 8 and 9, but one and sometimes two previous segments are also involved (Downes 1978). According to Tokunaga (1935) inversion of the terminalia in the marine chironomid *Telmatogeton* is accomplished during the pupal stage, but in most Chironomidae rotation occurs facultatively during copulation (Fittkau 1968, Dordel 1973). Sometimes it is spread over a number of segments and sometimes it is restricted to the more terminal ones. In the Culicidae, the Chaoboridae, and the Ceratopogonidae, at least, permanent rotation may occur ***clockwise*** (dextral) or ***counterclockwise*** (sinistral).

In the Bibionomorpha 180° rotation is recorded for certain Mycetophilidae, e.g. *Diadocidia* (Lindner 1923), and at least 90° rotation is evident in the preserved males of many species of *Mycomya*. In the Pachyneuridae up to 90° rotation is present in pinned males of most species of *Pachyneura* and in *Cramptonomyia*. In one species of the sciarid genus *Bradysia*, all degrees of rotation from 0° to 180° are evident; here rotation obviously occurred after emergence of the adult, but whether it was before or during copulation is not known.

In orthorrhaphous Brachycera permanent inversion of the terminalia to 180° rotation occurs in most Acroceridae and Bombyliidae, but it is not known when it takes place. In the Asilomorpha 90° rotation is evident in some Scenopinidae, e.g. *Pseudotrichia* and *Belosta*. In the Asilidae 90° rotation is evident in the male of many Dasypogoninae, where inversion usually takes place during copulation. In the subfamily Laphriinae, however, the terminalia are permanently rotated 180° (Hull 1962), but whether it occurs before or after the adult emerges is unknown. A 90° rotation also occurs for many Empididae in the subfamilies Tachydromiinae, Ocydromiinae, and Hybotinae; here the terminalia are frequently permanently rotated 90° (Bährmann 1960, Kessel and Maggioncalda 1968, Griffiths 1972) and in most cases some of the sclerites are asymmetric (Smith 1969). Complete permanent inversion occurs in the empidid genus *Microphorus* (McAlpine 1967). In the Dolichopodidae, sternite 8 is rotated clockwise 90° to a more or less lateral position (Figs. 127, 128). The remainder of the terminalia is rotated an additional 90° in the same direction, and then lateroflexed to the right. The terminalia are therefore inverted and lie against a membrane in the right side of the abdomen, opposite the ventral surface of sternite 8, with the cerci and aedeagus directed anteroventrally (Figs. 127–128); the outer surface of sternite 8 is exposed on the left side. From the consolidated appearance of the terminalia throughout the family both inversion and lateroflexion probably occur during the pupal stage in the Dolichopodidae.

In male Muscomorpha (Figs. 130–141) rotation has proceeded beyond 180° to about 360°, resulting in circumversion of the terminalia. This condition appears to have occurred only once and is considered to be a synapomorphic character of the Muscomorpha. The first 180°, representing permanent inversion, always takes place in the puparium before emergence, but the final 180°, resulting in circumversion, may take place immediately after emergence from the puparium, and it is reversible during the final stage of mating in at least some Platypezidae (Kessel 1968). In most cases, however, circumversion is accomplished before emergence from the puparium and is irreversible. The first 180° of rotation always occurs in the vicinity of segment 8. Some dragging of sternites 6 and 7 into the left side of the abdomen is usually apparent. Also, sternite 7, tergite 8, and sternite 8 usually become more or less fused into a single syntergosternite that occupies a more or less dorsal position. The final 180° of circumversion occurs between segments 8 and 9, restoring the genital and postgenital parts to their true dorsal and ventral positions. The sclerites of segments 6, 7, and 8, whether fused or not, are frequently asymmetric and partially to wholly atrophied. Where the vestiges of these segments appear symmetric as in some Drosophilidae and many muscoids, the symmetry is undoubtedly a secondary phenomenon.

Permanent ventroflexion is always correlated with circumversion and results in the terminalia being folded forward about 180° into a protective, more or less membranous genital pouch behind sternite 5 in the vicinity of sternites 6 and 7. In certain Aschiza, e.g. Syrphidae and Platypezidae, and perhaps also in some primitive Schizophora such as Lonchaeidae, ventroflexion may be completed immediately after the adult emerges from the puparium. But in most Schizophora, and certainly in all Calyptratae, ventroflexion, like circumversion, is accomplished before the fly emerges from the puparium.

As mentioned above, many male Diptera in Empidoidea and Muscomorpha show pronounced asymmetries in the sclerites of abdominal segments 6–8 (Figs. 127–136). These conditions occur primarily in forms that have permanently rotated terminalia, but some workers (Griffiths 1972, Emmert 1972) believe they arose independently of rotation; according to them such asymmetries are primarily associated with flexion of the terminalia and the formation a genital pouch for protecting the genital apparatus. The relative reduction or retention of the tergites and sternites of segments 6–8 is particularly important in the Muscomorpha (Griffiths 1972). The presence or absence of spiracles 6 and 7, also of considerable taxonomic significance, especially in the Schizophora, appears to be partially correlated with the preservation or loss of these sclerites.

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MORPHOLOGY AND TERMINOLOGY—LARVAE 3

H. J. Teskey

INTRODUCTION

Diptera larvae are extremely variable. Head structures range from a well-developed exposed capsule with mouthparts adapted for biting and chewing, to variously reduced structures partially or completely retracted within the thorax with mouthparts altered for piercing and rasping. Rarely, the head skeleton is essentially absent. The segments of the larval body may be variously fused or subdivided, conspicuously swollen in portions, or cylindrical or compressed. Some or all segments may bear filamentous or tuberculous outgrowths of various kinds.

The variation is so great that no individual or concise combination of characters exists by which Diptera larvae can be distinguished from all other insect larvae. The only character common to all Diptera larvae, but also found in representatives of several other orders, is the absence of jointed thoracic legs. This feature, when coupled with the fact that the majority of free-living Diptera larvae are rather slender with active directional movement, serves to distinguish most Diptera larvae. Most legless larvae of other orders are rather swollen, with movements that appear slow and undirected.

HEAD

The great diversity in head structure can be systematized according to certain morphological trends that correspond somewhat with the phylogeny of the Diptera. Three broad categories of head structure have been distinguished based on the degree of reduction and the amount of retraction within the thorax of the head capsule, and on the structure and plane of movement of the mandibles. A well-developed, fully exposed head capsule with mandibles usually bearing teeth and operating in a horizontal or oblique plane is termed ***eucephalic*** (Brauer 1883) and typifies the larvae of most Nematocera. A ***hemicephalic*** head capsule is more or less reduced or incomplete posteriorly and partially retracted within the thorax, with sickle-shaped mandibles operating in a vertical plane. Such a head capsule is mainly found among the orthorrhaphous Brachycera. Further reduction and retraction of the head capsule within the thorax coupled with the development of an internal pharyngeal skeleton produces the ***acephalic*** condition, the term used to describe the characteristically shaped ***cephalopharyngeal skeleton*** that typifies larvae of the Muscomorpha (*see* "Muscomorpha").

Although these terms are useful in defining general trends, they are not entirely mutually exclusive. Exceptions to their application include the Tipulidae, a nematocerous family with a head capsule that is more or less extensively reduced posteriorly and partially retracted within the thorax. The tipulid mandibles vary from stout and toothed, adapted for chewing, to slender and sickle-shaped, for piercing. But they are almost always opposed to each other in a horizontal plane. The head capsule of some blephariceridlarvae is eucephalic except for a slight dissolution of the capsule dorsolaterally. Although the head capsule of the Cecidomyiidae is classed as hemicephalic or acephalic, the family is undoubtedly referable to the Nematocera. Another nematocerous family, the Synneuridae, essentially lacks any vestige of a head capsule and is the only truly acephalic example. On the other hand larvae of the brachycerous families Therevidae and Scenopinidae appear to have well-developed, fully exposed head capsules with the only brachycerous features being the slender, sickle-shaped mandibles operating in a vertical plane and the slender, sclerotized ***metacephalic rod*** (capsule rod, manubrium) (*see* "Cranium") articulated posteriorly to the head and extending into the prothorax.

Despite such exceptions these fundamental concepts form the basis of the following detailed discussion, showing how the three successive types of head capsules are derived. Trends in the evolution of head structures other than those already mentioned are also discussed. Because the acephalous condition represented by the cephalopharyngeal skeleton of the Muscomorpha constitutes such a major transition, it is treated separately from the Nematocera and orthorrhaphous Brachycera.

Nematocera and orthorrhaphous Brachycera

Cranium. The eucephalic head capsule consists mainly of the ***cranium***. The cranium is the sclerotized external cuticle of the head to which the mouthparts are attached anteriorly and in which the muscles operating these mouthparts and the ***pharynx*** (*see* "Pharynx") originate. It comprises three sclerites, namely a middorsal ***frontoclypeal apotome*** (cephalic apotome) and a pair of lateral sclerites called the ***genae*** (Fig. 1). These sclerites are separated by lines of weakness termed ***ecdysial lines***. The integument splits along these lines during molting. The ecdysial lines bordering the frontoclypeal apotome are normally rather prominent. Either they appear in the form of an inverted Y as in a few larvae of the Bibionoidea or, more commonly, they lack the stem line and resemble a U or a V with the two arms reaching the occiput separately although very close together. The ecdysial lines on the head are continuous with a single middorsal ecdysial line on the thoracic segments. Sometimes one median ecdysial line, or rarely, as in the Ptychopteridae, a pair of such lines is present ventrally. Although these ventral lines rarely split at ecdysis, they sometimes function as a hinge permitting outward movement of the two halves of the head when the dorsal ecdysial lines split (Hinton 1963).

The ecdysial lines in the larvae have commonly been homologized with sutures that occur in the adult insect. The arms of the Y have been termed the frontal sutures, and the stem has been called the coronal suture; both together have been called epicranial sutures. In line with this terminology the area synonymous with the frontoclypeal apotome has commonly been referred to as the frontoclypeus. Although there is some merit in retaining the sutural names for the ecdysial lines, Snodgrass (1947) has shown that the lines are not sutures in the strict sense but are simply lines of weakness and that the area enclosed by the ecdysial lines is not entirely homologous with the frontoclypeus of the adult form. Instead, Snodgrass applied the name apotome, meaning "part cut out", to this area. The name apotome alone, or cephalic apotome as is sometimes applied, is not fully descriptive, however. According to a generally accepted rule proposed by Snodgrass (1947), all muscles associated with the pharynx, cibarium, and epipharyngeal surface of the labrum originate on, and help define, the frontoclypeus. As these muscles originate on the frons and clypeus of most larvae it seems preferable to retain the name frontoclypeus in the form frontoclypeal apotome for the sclerite, despite the few known exceptions to the rule, for example larvae of the Tipulidae (Chiswell 1955).

A frontoclypeal suture between the frons and the clypeus is rarely evident in Diptera larvae. However, evidence of these two areas can often be obtained from muscle insertions. The clypeus bears the muscles dilating the ***cibarium*** (preoral cavity), which is the roof of the mouth, whereas the frons serves for attachment of the pharyngeal muscles and the muscles operating the ***tormae*** (*sing. torma*) and ***premandibles*** (messors) of the labrum (Snodgrass 1947) (*see* "Labrum").

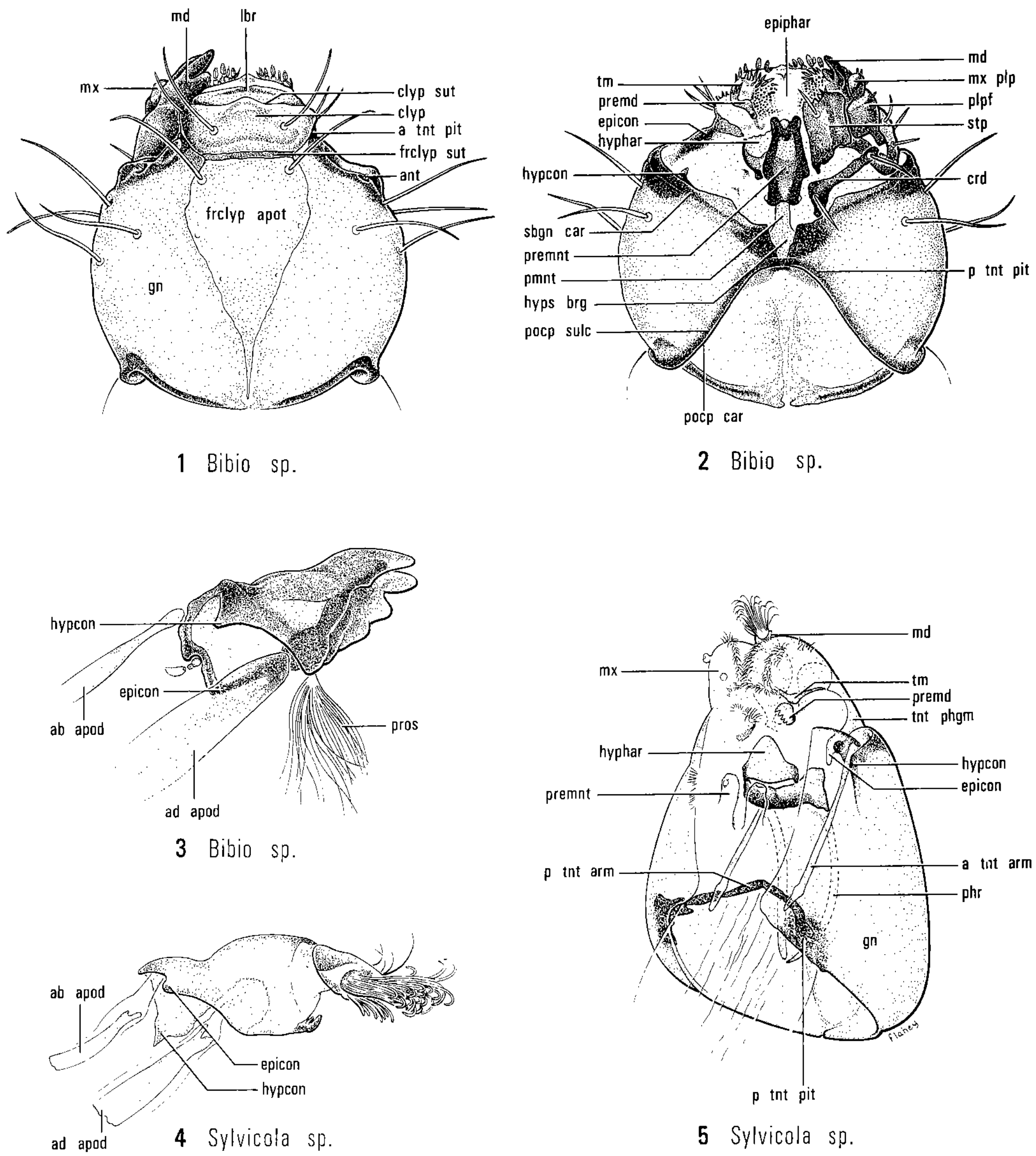
The genae comprise the greatest area of the eucephalic head capsule. Because the frontoclypeal apotome narrows posteriorly and a ventral gular sclerite is lacking, the genae normally border the entire occipital foramen. The edges bordering the occipital foramen are normally thickened and strengthened to form a ***postoccipital carina***, which may be delimited anteriorly by a slight groove, the ***postoccipital sulcus*** (postoccipital suture) (Fig. 2). Ventrolaterally on the postoccipital sulcus, or the area where the sulcus would be expected to run, a slightly more heavily sclerotized area, sometimes bearing a slight depression on each side, is often present. These depressions are the ***posterior tentorial pits***. The anterior edge of each gena is also somewhat thickened to strengthen it for articulation of the mouthparts. This thickened border is called the ***subgenal margin***.

The retraction of the head capsule within the thorax and the associated reduction in the extent of the cranial elements of the capsule characteristic of the hemicephalic condition occur to some degree in all families of the orthorrhaphous Brachycera as well as in the Tanyderidae, the Tipulidae, the Axymyiidae, and the Cecidomyiidae of the Nematocera (Figs. 7.66–67, 16.5, 31.51–54, 39.5, 42.76–77, 47.57). The retraction is permanent in these groups because the integument and some of the muscles controlling head movement have acquired new insertions, usually from near the middle of the cranium to immediately behind the mouthparts.

The extent of the reduction of the head capsule of orthorrhaphous Brachycera is quite variable. The reduction appears to begin with desclerotization of the posterior margin followed by disappearance of desclerotized cuticle. Thus, the head capsule of the Stratiomyidae is complete except for a relatively large occipital opening (Fig. 36.59). In the Tabanidae (Fig. 31.56) substantial reductions to the posteroventral areas of the head capsule occur. Here desclerotization has resulted in isolated small posterolateral lenticular sclerites. Although these appear detached from the rest of the capsule, they are united by a transparent cuticle that also extends somewhat ventrally to unite with the apical portion of a pair of ***tentorial arms*** (*see* "Tentorial Arms"). The cranium of the Rhagionidae and the Vermileonidae is reduced to a convex, posteriorly truncate dorsal plate leaving the entire ventral side of the head capsule open (Figs. 33.22, 39.4). In some representatives of the Rhagionidae a tendency to median longitudinal desclerotization of this plate can be seen. Similar desclerotization of the dorsal plate is carried even further in the Apioceridae, the Mydidae, and the Asilidae (Figs. 40.29, 42.78–79) where the posterior two-thirds or more of the dorsal plate is reduced to relatively broad, paired bars united for some or all of their length by a transparent cuticle. In the Dolichopodidae and the Empididae this trend has resulted in slender, disconnected, paired rods that in the Dolichopodidae are somewhat expanded caudally (Figs. 47.58, 48.41, 48.43). Division of the retracted elements of the cranium into paired structures does not occur universally, however. In the Therevidae and the Scenopinidae, for example, only a single rod is present (Figs. 37.24, 38.12).

The single rod-like retracted portion of the cranium in the Therevidae and the Scenopinidae is separated from the exposed portion of the cranium by a distinct suture. The beginning of this development possibly occurs in larvae of *Coenomyia* (Xylophagidae). Here, the retracted posterior portion of the head capsule is less heavily sclerotized than the exposed anterior portion, particularly along the median line, and it is distinctly notched laterally at the point of attachment with the thoracic integument where a pair of thoracic muscles are inserted (Fig. 34.15). In larvae of *Xylophagus* (Xylophagidae), the exposed portion of the head capsule is similar to that of *Coenomyia*, but the retracted portion consists of two relatively short, sublateral rods flexibly hinged to the anterior portion of the cranium. A similar type of articulation (although in some cases involving only one median rod) exists in larvae of the Therevidae, Scenopinidae, Mydidae, Apioceridae, Asilidae, Empididae, and Dolichopodidae (Figs. 37.24, 38.12, 40.29, 42.78–79, 47.58, 48.41, 48.43). In all such cases the articulated rods are called metacephalic rods (capsule rod of Melin 1923, manubrium of Cook 1949).

A broad range of cranial reduction analogous to that described above occurs in the single family Tipulidae. The initial reduction consists of shallow dorsolateral incisions and loss of the thickened postoccipital margins (Figs. 7.67, 7.77). From this stage the head capsule becomes reduced to three or four slender rods (Figs. 7.76, 7.83, 7.88). However, in these cases none of the rods involve the tentorial arms.



Figs. 3.1–5. Head capsule features: (1) dorsal and (2) ventral views of *Bibio* sp. (Bibionidae) with right mandible and maxilla removed; (3) right mandible of *Bibio* sp., ventromedial view; (4) left mandible of *Sylvicola* sp. (Anisopodidae), lateral view; (5) ventrolateral view of head capsule of *Sylvicola* sp. with left mandible and maxilla removed (*continued*).

Abbreviations: ab apod, abductor apodeme; ad apod, adductor apodeme; ant, antenna; a tnt arm, anterior tentorial arm; a tnt pit, anterior tentorial pit; clyp, clypeus; clyp sut, clypeolabral suture; crd, cardo; ecdys ln, ecdysial line; epicon, epicondyle; epiphar, epipharynx; frclyp apot, frontoclypeal apotome; frclyp sut, frontoclypeal suture; gn, gena; hypcon, hypocondyle; hyphar, hypopharynx; hyps brg, hypostomal bridge; lbr, labrum; md, mandible; mx, maxilla; mx plp, maxillary palpus; phr, pharynx; plpf, palpifer; pmnt, postmentum; pocp car, postoccipital carina; pocp sulc, postoccipital sulcus; premd, premandible; premnt, prementum; pros, prostheca; p tnt arm, posterior tentorial arm; p tnt pit, posterior tentorial pit; sbgn car, subgenal carina; stp, stipes; tm, torma; tnt phgm, tentorial phragma.

The retraction of the head capsule in the Axymyiidae has not resulted in any weakening of the hind margin.

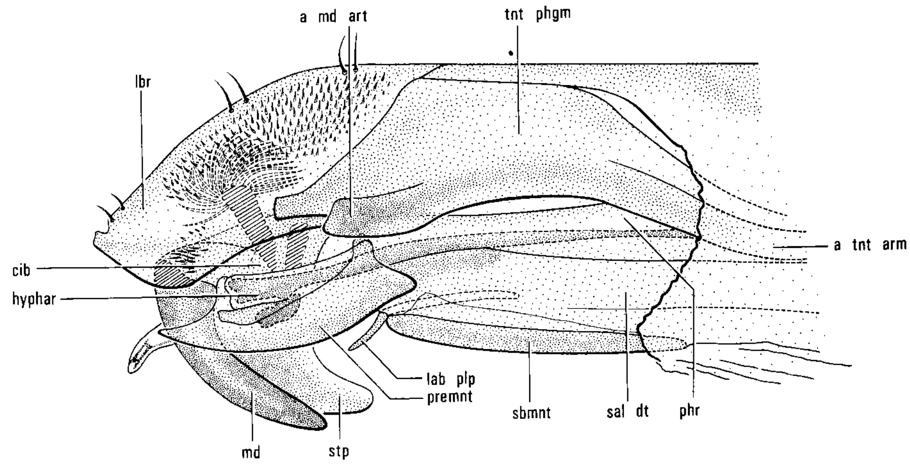
Tentorial arms. The ***tentorium*** is the internal skeleton of the head and it is present as a plesiomorphic structure in many larvae of the Nematocera and Brachycera (Hennig 1973, Anthon 1943*b*). However, it has become more or less extensively reduced or lost in several groups of Nematocera, e.g. Tipulidae, Sciaroidea, Psychodidae, Ptychopteridae, and Chironomoidea. With the notable exceptions of the Tipulidae and the Sciaroidea, the greater rigidity provided to the head capsule in these groups by a solid ventral connection between the genae, the hypostomal bridge (*see* "Ventral Region of Head Capsule"), seems to compensate for the loss or reduction of the tentorium. The tentorium in the eucephalic head consists basically of chitinized, rod-like invaginations from two pairs of ***tentorial pits***. The posterior pair of pits is located ventrolaterally on the postoccipital sulcus (Figs. 2, 5) and the anterior pair is located behind the ***anterior*** (dorsal) ***mandibular articulation*** adjacent to the ecdysial lines (Figs. 1, 5). The invaginations from the posterior tentorial pits in the basic scheme extend transversely toward each other and unite to form a bridge-like ***posterior tentorial arm***, while the paired ***anterior tentorial arms*** extend backward to meet the posterior arms (Fig. 5). The tentorium may also include a pair of short ***dorsal arms*** as outgrowths of the anterior arms to the cranial wall near the base of the antennae. This most primitive arrangement of the tentorium apparently exists among Diptera larvae only in some Anisopodidae (Anthon 1943*a*). The tentorium may be reduced, usually beginning with the failure of the posterior arms to unite, followed by complete loss of the posterior arms, and then by loss of the anterior arms. However, it has been suggested (Hennig 1973) that in the Sciaridae all that remains of the tentorium are the posterior arms forming the posterior of two ventral points of union or abuttment of the genae (Fig. 15.33).

The internal structure of ridges and braces associated with or near the ends of the anterior tentorial arms is often very complex and has been described and illustrated at some length by Anthon (1943*b*) and Cook (1949). The development of a pair of internal ***tentorial phragmata*** (*sing.* ***tentorial phragma***; vertical plates, pharynx supports) is of great importance because it constitutes a trend, possibly beginning among some Nematocera, further developed among the orthorrhaphous Brachycera, and culminating in the Muscomorpha. These tentorial phragmata are flattened, plate-like invaginations of the tentorial pits and of adjacent sutures. Cook (1944) called these sutures, in part, the paraclypeal folds in the Culicidae. He then initiated the name paraclypeal phragmata for the invaginations, which most subsequent authors have used for the tentorial phragmata. However, Hartley (1963) pointed out that the paraclypeal phragmata of orthorrhaphous Brachycera may not be homologous with those in the Nematocera. Indeed this seems to be the case, for in some Nematocera, e.g. Blephariceridae, some Psychodomorpha, and some Culicomorpha, a portion of the lateral margin of the clypeus appears to fold or bend inwardly. This fold is anterior to and often more or less separated from the anterior tentorial pit and its incipient tentorial phragma (Fig. 5). It is to this structure that Cook gave the name paraclypeal phragma. The paraclypeal phragma commonly bears the anterior mandibular articulation, although in the Culicidae this articulation is on a slender extension of the fold to the hypopharynx called the ***cibarial bar*** (Cook 1949). The paraclypeal phragma apparently fuses with the tentorial phragma and the tentorial elements of the composite structure become dominant in the Brachycera. It therefore seems preferable to follow Roberts (1971*a*) in calling these structures in the Brachycera the tentorial phragmata, especially as the tentorium is undoubtedly a major part of the structure. The anterior tentorial arms project from the lower posterior margin of the phragmata and constitute a prominent feature of the head of most Brachycera (Figs. 6, 8, 12). The tentorial arms are especially well-developed in this group because they have assumed greater importance as major points of attachment for mandibular adductor muscles to compensate for the reduction of the cranium.

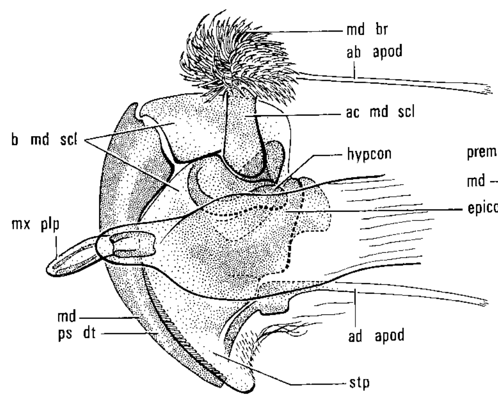
In those Asiloidea and Empidoidea in which the metacephalic rods have a basal line of weakening, the tentorial arms have a similar suture or weak point at their junction with the tentorial phragmata (Figs. 8; 47.58). Roberts (1969*b*) also reports such a weakening in the articulation point on the tentorial arms of *Rhagio* (Rhagionidae), but this weakened point is absent in the related genus *Chrysopilus* (Rhagionidae).

Ventral region of head capsule. The morphology of the ventral side of the head capsule of many nematocerous larvae is controversial. Specifically, the problem concerns the origin of a sclerotized, anteriorly toothed plate, the ***hypostoma*** (hypostomium, hypochilum, labial plate, maxillary plate, prementum), situated below the mouthparts in larvae of many Tipulidae, Psychodidae, and Culicomorpha. Some claim that the hypostoma is a derivative of the labium (Cook 1944), and others believe its origin is with the subgenal region of the cranium (Anthon 1943*b*). Until further detailed comparative morphological study provides an answer to this argument, the terminology of Anthon (1943*b*) is accepted here.

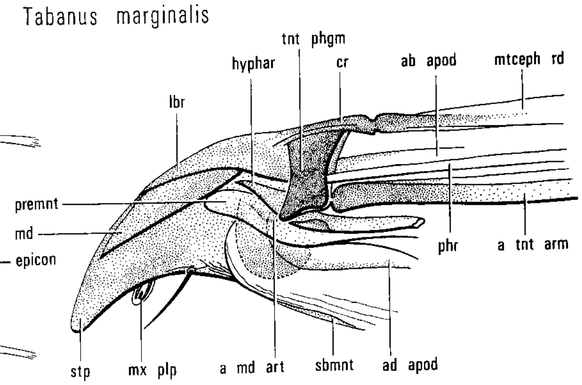
In the most primitive condition of the ventral region of the head capsule, as exemplified by the Bibionidae and the Anisopodidae, the genae are widely separated (Fig. 5) or a narrow, bridge-like extension between the genae is present in front of the occipital foramen (Fig. 2). This bridge is commonly referred to as the ***hypostomal bridge*** (subgenal bridge). In the membranous zone anterior to the hypostomal bridge unmistakable parts of the labium can be recognized. According to Anthon (1943*a*) these are most extensive in *Olbiogaster* (Anisopodidae) and include a ***submentum***, a ***mentum***, a ***prementum***, ***glossae***, and ***labial palpi***. In representatives



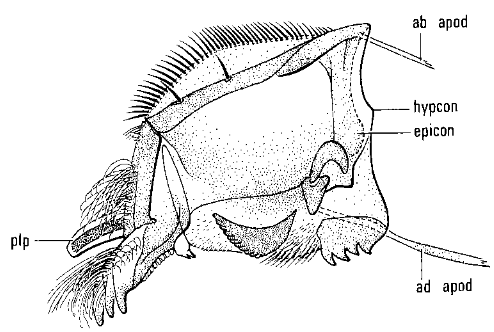
6 Tabanus marginalis



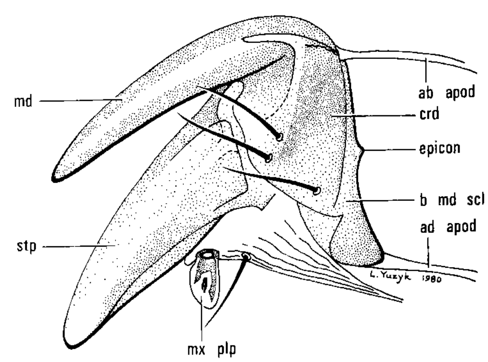
7 Tabanus marginalis



8 Promachus sp.



9 Odontomyia sp.



10 Promachus sp.

Figs. 3.6–10. Head capsule features (*concluded*): (6) lateral view of anterior portion of head capsule of *Tabanus marginalis* Fabricius (Tabanidae) with left mandibular–maxillary complex and portion of head capsule removed; (7) left mandibular–maxillary complex of *T. marginalis*, lateral view; (8) lateral view of anterior portion of head capsule of *Promachus* sp. (Asilidae) with left mandibular–maxillary complex and portion of head capsule removed; (9) left mandibular–maxillary complex of *Odontomyia* sp. (Stratiomyidae), lateral view; (10) left mandibular–maxillary complex of *Promachus* sp., lateral view.

Abbreviations: ab apod, abductor apodeme; ac md scl, accessory mandibular sclerite; ad apod, adductor apodeme; a md art, anterior mandibular articulation; a tnt arm, anterior tentorial arm; b md scl, basal mandibular sclerite; cib, cibarium; cr, cranium; crd, cardo; epicon, epicondyle; hypcon, hypocondyle; hyphar, hypopharynx; lab plp, labial palpus; lbr, labrum; md, mandible; md br, mandibular brush; mtceph rd, metacephalic rod; mx plp, maxillary palpus; phr, pharynx; plp, palpus; premnt, prementum; ps dt, poison duct; sal dt, salivary duct; sbmnt, submentum; stp, stipes; tnt phgm, tentorial phragma.

of the Bibionidae the labium is somewhat reduced, although usually ***postmental elements*** (a union of both submentum and mentum) and ***premental elements*** are present (Fig. 2). A similar situation exists in the Tanyderidae (Crampton 1930), the Blephariceridae (Anthon and Lyneborg 1968), and the Ptychopteridae. Among some other larvae of the Nematocera the hypostomal bridge is lengthened, correspondingly reducing the labium to only the premental elements. In the extreme condition, as exemplified by the Simuliidae and some Chironomidae (Figs. 27.80–81, 29.119–127), the hypostoma is well developed. It is apparently used for scraping food such as algae from submerged surfaces. Anthon (1943*b*) demonstrated the progressive development of the hypostomal bridge and the resulting displacement of the labium anteriorly, and finally somewhat internally, above the hypostoma until it becomes closely appressed to the hypopharynx. In these cases the prementum and hypopharynx appear to be combined as a single unit; the only means for differentiating the two is the position of the ***salivary duct***, which opens in a pocket between the ventral wall of the hypopharynx and the prementum.

This hypothesis on the development of the hypostomal region seems to be supported by modifications of the region shown in the Tipulidae. In representatives of this family the hypostoma itself is often more or less divided medially, with each half quite obviously situated at the apex of an uninterrupted, sclerotized forward extension of the subgenal margin of the cranium (Figs. 7.76–77, 7.87).

Part of the difficulty with the hypothesis stems from Anthon's (1943*a*) own illustrations of *Olbiogaster* (Anisopodidae) and *Ptychoptera* (Ptychopteridae). The ventral sclerites lying between the genae appear to be homologous in the two genera and differ only in the degree to which they are separated from the genae. However, in *Olbiogaster* he names these sclerites the submentum and the mentum and in *Ptychoptera* the hypostomal bridge and the hypostoma.[1] The mentum in *Olbiogaster* and the hypostoma in *Ptychoptera* are apically toothed and look identical. Reduced premental elements lie above these toothed structures in close association with the hypopharynx.

Larvae of the Chironomidae bear other distinctive structures on the ventral surface of the head capsule that are important in the systematics of the family. On either side of the hypostoma in many members of the family are ***paralabial plates*** that may be marginally toothed (Fig. 29.118), striate (Figs. 29.119–120), or fringed with setae (Figs. 29.123, 29.125, 29.127). In larvae of the Tanypodinae the hypostoma is membranous and above it, apparently derived from the prementohypopharyngeal complex, is a sclerotized apically toothed plate called the ***ligula*** (Figs. 29.117–118).

[1] Originally spelled hypostomium and used incorrectly as such by many subsequent authors.

A rather generalized labium is retained in most orthorrhaphous Brachycera. A large submentum and a smaller prementum often with labial palpi are found in the Tabanidae, some Stratiomyidae, and the Asiloidea (Figs. 6, 8; 37.26, 40.29). The submentum is lost but the prementum is retained, usually in a rather membranous condition, in other orthorrhaphous Brachycera. Like the Nematocera, it is closely bound to the hypopharynx. Again, the salivary duct is a useful landmark in distinguishing the hypopharynx.

Labrum. The labrum, or so-called upper lip, is continuous anteriorly with the frontoclypeal apotome, with no apparent separation in many cases. However, a clypeolabral suture may be present (Fig. 1). The basic form of the labrum in nematocerous larvae is a relatively broad, dorsoventrally compressed lobe. However, in the larvae of several families of Nematocera and in all of the orthorrhaphous Brachycera the labrum assumes a rather slender, laterally compressed, wedge-like appearance, probably in conjunction with rotation of the plane of movement of the mandibles toward a vertical axis (Figs. 5, 11). The ventral surface of the labrum is called the ***epipharynx*** (palatum). It usually bears a variety of setae, hairs, or spines that are sometimes generally distributed or, commonly, grouped into brushes or combs. These structures play an important part in the feeding process. They serve either by directing food materials toward the mouth as is done, for example, by the highly evolved labral brushes or fans of the Culicidae (Figs. 25.23, 25.26–27) and the Simuliidae (Fig. 27.76), or by cleaning the mandibles. The movement of the brushes and fans is mediated by muscles inserted on one or two pairs of small sclerites set in the mainly membranous surface of the epipharynx (Figs. 5; 29.119–122, 29.131–133). Chief among these is a flat, trapezoidal or triangular sclerite called the ***torma*** *(pl.* ***tormae***), on each side at the lateral angle between the labrum and the clypeus; the torma sometimes embraces the basal corners of the labrum where it either articulates with, or is fused with, a ***dorsal labral sclerite*** (labral plate). The median end of the torma usually projects anteromedially on the epipharynx. A second sclerite, the ***premandible***, is sometimes present and articulates posteriorly with each torma. It is often incorrectly considered a part of the torma. The free end usually bears one or more teeth or spines sometimes resembling a comb. The motion that these sclerites impart to the labral brushes is produced by one or two pairs of labral retractor muscles originating on the frontoclypeal apotome. Another sclerite on the epipharynx with an associated brush of setae is a median ***epipharyngeal bar*** (palatal bar) that lies between the premandibles and behind the median ends of the tormae. This sclerite is usually V or U shaped or is sometimes divided medially. Paired labral compressor muscles are inserted on this sclerite and are attached to the median dorsal labral sclerite. The epipharyngeal bar is present in larvae of many Nematocera (Fig. 29.119) but is absent in others such as the Tipulidae (Matsuda 1965).

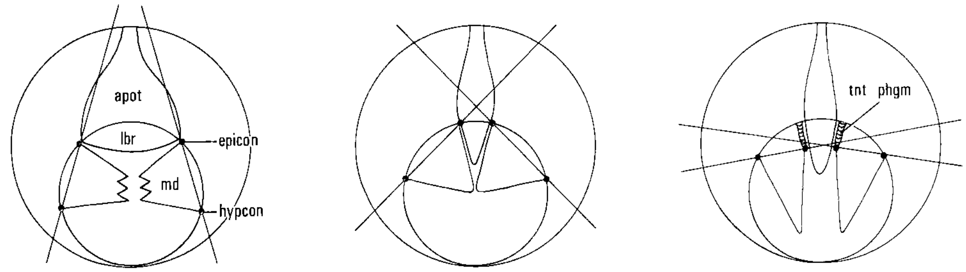


Fig. 3.11. Diagrammatic representation of rotation of plane of mandibular movement resulting from narrowing of labrum, shift of mandibular articulations, and development of tentorial phragmata.

Abbreviations: apot, apotome; epicon, epicondyle; hypcon, hypocondyle; lbr, labrum; md, mandible; tnt phgm, tentorial phragma.

The development of all of these sclerites and the hairs and spines associated with them among the Nematocera is extremely varied and of great taxonomic importance. A variable number of cibarial dilator muscles are also inserted on the epipharynx, on the postlabral portion. They usually have their opposite attachment on the clypeus.

All of the above sclerites and associated spines and brush-like groupings of hairs are absent in larvae of the orthorrhaphous Brachycera. However, hairs apparently used for cleaning the mandibles and, in some cases rather numerous but more generally distributed, are normally present in representatives of this group.

Mandible. Anthon (1943*b*) and Hennig (1973) considered the larval mandibles to be primitively two segmented. This condition exists most conspicuously in larvae of two genera of the Tipulidae (*Ulomorpha* and *Pilaria*) (Fig. 7.89), the Trichoceridae, the Anisopodidae (Fig. 4), the Ptychopteridae, and most orthorrhaphous Brachycera. The subdivision of the brachycerous mandibles is probably a secondary condition and therefore unrelated to that in the Nematocera.

The mandibles of several families of the Nematocera, especially those families in which the mandibles operate in a horizontal plane in opposition to one another, appear to retain some biting and chewing function. Accordingly, there is often a distal toothed incisor lobe and a proximal molar lobe (Fig. 3). One or both lobes may bear tufts of hairs. The hair tuft nearest the molar surface on the upper paralabral surface is called the ***prostheca***. These hair tufts apparently function in cleaning the epipharynx and the maxillae just as the hairs on the epipharynx clean the mandible as it moves in and out. The hairs are directed inward so that food particles are forced toward the mouth.

Mandibles of some other Nematocera, e.g. some Tipulidae and Chironomidae, are claw-like, with a reduction in the number of teeth on the incisor surface and a loss of the molar grinding area (Figs. 7.83, 7.89, 29.117–118). This alteration in form appears to be associated with a major trend in the Nematocera, culminating in the Brachycera, to rotation of the mandibles from a horizontal plane through movement first in an oblique direction and finally to a vertical plane with the mandibles parallel to one another (Cook 1949, Schremmer 1951).

The mandible has two points of articulation, an anterior ***epicondyle*** and a posterior ***hypocondyle***. The hypocondyle articulates laterally on the subgenal margin of the cranium, whereas the point of articulation of the epicondyle is normally closely associated with the proximal end of the anterior tentorial arm near the anterior angle of union of the genae and the frontoclypeal apotome. Rotation of the mandible is due to a shifting of its points of articulation. This shift apparently takes place in two steps (Fig. 11). The first is a movement of, at least, the epicondyle higher on the curve of the cranium. This repositioning is normally accompanied by a narrowing of the labrum and the frontoclypeal apotome, and it is characteristic of the larvae of all Psychodomorpha. The second step is displacement downwardly or inwardly of the anterior articulation on the developing tentorial phragma. This conformation is the case in many Psychodomorpha and in all orthorrhaphous Brachycera. In the Culicidae, however, the anterior articulation is on the cibarial bar.

In many families of the orthorrhaphous Brachycera there is a strong tendency for the mandibles and maxillae to become fused. Cook (1949) discussed this development in the Tabanidae, the Stratiomyidae, and the Therevidae. De Meijere (1916) and Bischoff (1924) also treated the subject extensively. The fusion is most extensive in the Stratiomyidae where the respective structures cannot be clearly differentiated except for the maxillary palpi (Fig. 9). Extensive modifications have taken place here involving membranization and the addition of complex groups of hairs apically. The apical portion of the mandible appears also to have been lost. The whole structure functions in sweeping food materials into the mouth (Cook 1949, Roberts 1969*b*). In most other representatives of the orthorrhaphous Brachycera the fusion has not progressed to the point where the mandible and maxilla cannot be distinguished. They are, however, very closely linked both spatially and in movement. The inner membranous surface of the maxilla is attached to the ***basal mandibular sclerite***.

With the exception of the Bombylioidea, the mandible of the orthorrhaphous Brachycera is basically subdivided with a slender, pointed, heavily sclerotized, usually curved apical blade that articulates dorsally to an inner basal mandibular sclerite (Figs. 7, 10). The basal mandibular sclerite bears two condyles in the Tabanomorpha as in all Nematocera, namely an inner epicondyle, articulating with the tentorial phragma, and an outer hypocondyle, which articulates with the anterolateral margin of the cranium. However, the hypocondyle has been lost in many Asiloidea and in the Empidoidea. This loss is the first appearance of a condition that is normal to all Muscomorpha. The reduction of the mandible to a single articulation in the Asiloidea is probably associated with the much larger, more heavily sclerotized maxilla that is present in these larvae (Figs. 10; 40.29, 42.78–79). The maxilla has its own connection with the sides of the cranial plate through the ***cardo*** (*see* "Maxilla") and inwardly has a membranous connection with the basal mandibular sclerite. The mandible is thus wedged between a solidly mounted maxilla and the labrum so that it cannot stray from its vertical movement and has little need for the hypocondyle.

The corresponding situation in the larvae of the Empididae and the Dolichopodidae is clouded by the reduction and skeletonization of their head capsules (Figs. 47.58, 48.41, 48.43). In these families a V- or U-shaped sclerite occurs on either side of a median labrum. The outer arm of this sclerite is probably the cardo of the maxilla and the inner arm is the mandible. In addition, one or more maxillary sclerites lie anterior to this V- or U-shaped sclerite, and one of them bears the maxillary palpus. The median portion of the cardo is connected dorsally to the basal mandibular sclerite. A similar formation is seen in the larval head capsule of *Vermileo* (Vermileonidae) (Fig. 39.4).

The basal mandibular sclerite of the Tabanidae comprises three closely linked sclerites (Cook 1949, Teskey 1969). Two of these are apparently subdivisions of the normal basal sclerite but the third is a bar-like ***accessory mandibular sclerite*** that connects with a group of dorsolateral spines (Fig. 7). These spines, called ***mandibular brushes***, are present in most, if not all, Tabanoidea and are unique to this group. They apparently function for anchoring the head capsule within the host, but Roberts (1969*b*) sees their role in *Rhagio* (Rhagionidae) as assisting in locomotion. When the mandible is at rest, the mandibular brush is retracted beneath a fold of integument. But when the mandible is adducted the mandibular brush is pulled from beneath the covering integument by means of its connection with the accessory sclerite, and the spines become erect and lie in a recurved anchoring position. Another feature of some significance in tabanid larvae is a hollow mandible traversed by a poison duct opening subapically on the anterior edge of the blade. The duct runs through the basal sclerite to an inner pore near the hypocondyle and then to a poison gland within the head capsule.

In all Diptera larvae the ***mandibular abductor muscles*** perform the retractive movement of the mandibles and the ***mandibular adductor muscles*** control the closing or downward movements of the mandibles. These muscles are inserted by means of ***apodemes*** on either side of the fulcrum for mandibular movements. When a basal mandibular sclerite is present, the muscle insertions are near the proximal and distal ends of the sclerite (Fig. 10). In tabanid larvae the abductor insertion is on the accessory mandibular sclerite (Fig. 7). Both sets of muscles normally originate on the posterior and lateral walls of the genae and the tentorial arm, when present. With the reduction of the head capsule in the Brachycera, only a few of the mandibular adductor muscles are retained on the remnants of the cranium (in some cases the metacephalic rods) and the origins of the majority of muscle bundles are shifted to the tentorial arms.

Maxilla. The basic structure of the larval maxilla as it exists, for example, in some Tipulidae, the Bibionidae, the Mycetophilidae, the Sciaridae, the Anisopodidae, and the Ptychopteridae consists of a basal cardo and a distal ***stipes***, bearing a one-segmented ***maxillary palpus*** (Figs. 2; 14.99–100, 15.33). The distal extremity of the stipes may be slightly differentiated into two endite lobes, the ***galea*** and the ***lacinia***. The maxillary palpus is sometimes borne on what appears to be a secondary lobe of the stipes called the ***palpifer***. The cardo commonly can be recognized by the two to four well-developed setae that it bears. But very often, with the exception of the palpus which is normally very evident, the homologies of the parts of the maxillae in nematocerous larvae are obscure.

The maxilla of nematocerous larvae is often mostly membranous, perhaps in line with its normal, rather passive role in feeding; aside from a sensory function, it serves to form a ventrolateral margin for the mouth opening within which the mandible can push food particles into the oral cavity. A notable exception to this passive function of the maxilla is found in the larvae of the Sciaroidea. Here the maxilla, especially the stipes, is heavily sclerotized and flattened with a toothed margin (Figs. 14.99, 15.33). It appears to have a function similar to the mandibles in actively rasping the food substrate.

The maxilla of the Asilidae also diverges from the passive role and seems to be specially adapted for a fossorial existence. Here the maxilla is enlarged, well sclerotized, and often somewhat shovel shaped or spatulate apically for digging (Figs. 10; 42.78–79). It also serves to protect the blade-like mandible, which lies in a concavity on its median face. This surface is densely haired, apparently for cleaning the mandible. Distinctive also of the maxilla of larvae of all families of the Asiloidea is the retention of a well-defined cardo which, as mentioned above, bears several hairs. In the Asilidae three hairs are present, judging from the above figures and all the illustrations of Melin (1923). The sclerotized cardo in larvae of the Asilidae is flexibly fused to the dorsal edge of the basal mandibular sclerite. A similar but narrower fusion is seen in the larvae of the Empididae and the Dolichopodidae.

No more than two maxillary muscles have been retained in Diptera larvae. These are inserted in the stipes and have their origin on the genae. Maxillary muscles are reduced to one in some Tipulidae and apparently in all orthorrhaphous Brachycera (Cook 1949). The reduced musculature of the maxilla of the orthorrhaphous Brachycera appears to be associated with the partial fusion of the maxilla with the mandible whereby the inner membranous surface of the maxilla is continuous with the basal mandibular sclerite. The two structures move essentially as a single unit, mediated primarily by the mandibular muscles, thus decreasing the need for well-developed maxillary muscles.

Antenna and eye. The antennae and eyes are borne on the genae. The antenna is normally located near the anterodorsal corner of the sclerite in the vicinity of the anterior mandibular articulation. The maximum number of antennal subdivisions is six in some Chironomidae (Hennig 1973), although this number is very rare. Normally one to three subdivisions are present and they are commonly very short, sometimes no more than a pimple-like projection as in the Bibionidae, many Mycetophilidae, some Psychodidae, the Anisopodidae, and the Ptychopteridae. However, the antenna of the larvae of some Blephariceridae and the Deuterophlebiidae is elongate, and in the Deuterophlebiidae, conspicuously biramous (Figs. 8.7, 9.3). The antenna of the Chaoboridae has evolved into a prehensile structure with apical spines and is used for capturing prey (Figs. 24.9–10). The antenna usually bears various sensory organs whose sensory functions in larvae are poorly understood.

Eyes have been described for only a few larval Diptera, namely *Tipula* (Tipulidae), *Ptychoptera* (Ptychopteridae), the Culicomorpha, *Rhagio* (Rhagionidae), and the Stratiomyidae (Roberts 1971*b*, Hennig 1973). However, they are obviously more widely present judging from published illustrations of many other taxa. Even in their apparent absence, light-sensitive cells are probably present in most larvae. Bolwig (1946) and Hartley (1963) have shown the presence of such cells in a depression on the anterolateral margin of the tentoropharyngeal sclerite of certain cyclorrhaphous larvae (Fig. 12). The eyes in the Nematocera and orthorrhaphous Brachycera are simple ***stemmata*** (*sing.* ***stemma***) consisting at most of a lens or crystalline sphere in the surface of the head capsule beneath which are bundles of elongate visual cells shielded by a cup of black pigment granules. The pigment provides for directional perception of light. In many cases the lens is absent. A precocious adult eye with numerous ommatidia commonly occurs anterior to the larval eye in some larvae of the Chaoboridae and the Culicidae.

Pharynx and associated parts. According to Snodgrass (1935), the cibarium is the food pocket of the preoral mouth cavity, between the base of the hypopharynx and the undersurface of the clypeus. It is followed by the pharynx and then by the esophagus. All three parts are evident in most Nematocera. The dorsal walls of the cibarium and pharynx bear dilator muscles that are inserted on the frontoclypeal apotome. The cibarium or the pharynx, or both, can therefore act as a pumping mechanism. The pharynx of some nonpredacious nematocerous larvae that feed on waterborne particles has a complex filtering apparatus for straining the suspended food particles from the water and then for ejecting the excess water from the mouth. Anthon (1943*b*), Cook (1944), and Snodgrass (1959) described some variations of the ***pharyngeal filter*** and indicated that it occurs in some Tipulidae, the Psychodidae, the Trichoceridae, the Anisopodidae, the Scatopsidae, the Ptychopteridae, and the Culicidae. Anthon and Lyneborg (1968) illustrated the pharyngeal filter of the Blephariceridae. In all these larvae it has the same general form as is shown in Fig. 5.

Contraction of the dilator muscles inserted on the dorsal walls of the cibarium and pharynx, together with closure of the esophagus, enlarges the pharynx, thereby creating a negative pressure that sucks in the water which contains the food particles. The opening to the pharynx is then constricted and the intrinsic muscles in the pharynx are contracted. This action creates sufficient pressure to force the water back through the constriction. During expulsion, the water passes through a filter formed by dense, comb-like fimbriations that retain the very fine food particles.

In larvae of orthorrhaphous Brachycera the pharynx is an elongate tube. This tube has been called, at least in part, the cibarium or the cibarium–pharynx by Cook (1949) and Roberts (1969*b*), even though the portion so named extends well behind the hypopharynx. These writers have perhaps been following a later interpretation by Snodgrass (1947) that the frontal ganglion is situated at the boundary between the cibarium and the pharynx. It seems preferable, however, to maintain in the orthorrhaphous Brachycera the distinction between the cibarium and the pharynx that is based on morphological features of the food canal itself, as is done for the Nematocera at the beginning of this section.

The pharynx is often more or less sclerotized ventrally and membranous dorsally in many brachycerous larvae. A series of muscles inserted in this membranous upper surface and attached to the cranium dorsally serves to dilate the tube so that it can function as a pump, like that described above for nematocerous larvae. The elasticity of the upper membrane and the sclerotized ventral and lateral walls suffices for contraction of the tube. Efficient pumping action is aided by a flaplike valve at the opening of the pharynx, as described for larvae of the Tabanidae (Olsufjev 1936), and by the ability to constrict the esophageal opening. The sclerotization of the pharynx is accompanied, at least in larvae of the Stratiomyidae, the Vermileonidae, the Empididae, and the Dolichopodidae, by fusion of the pharynx with the tentorial phragmata. This condition may be a precursor to the situation that occurs in larvae of the Muscomorpha (see description of head under "Muscomorpha"). Sclerotization of the pharynx and its fusion with the tentorial arms are particularly well developed in the Stratiomyidae, possibly in conjunction with the evolution of a ***pharyngeal grinding mill***. This mill and a similar structure in some Syrphidae, patterned on the principles of a mortar and pestle, is shown in Figs. 36.58–59 and is described by Robert (1969*a*).

A pharyngeal filter is absent in larvae of most orthorrhaphous Brachycera, apparently because most larvae of the group are predatory. Their food, although mainly liquid, is highly concentrated and filtering would serve no real purpose. An exception is found in some Stratiomyidae, which have a pharyngeal filter bearing some similarity to the filter of the larvae of some Muscomorpha. The pharyngeal filter in *Stratiomys* (Stratiomyidae) consists of two lateral, longitudinal grooves in the floor of the pharynx covered by a dense, comb-like series of transversely oriented filaments. The grooves communicate to the exterior anteriorly on either side of the prementum. Excess water is forced through the filaments and along the grooves to the exterior while suspended food particles are retained by the sieving action of the filaments.

Muscomorpha

The larval head of the Muscomorpha departs radically from the heads of more primitive Diptera. The muscomorphan head capsule is difficult to homologize with the more primitive Diptera because a series of connectant groups showing the gradual evolution of the cephalopharyngeal skeleton and associated structures is lacking. This difficulty is evidenced by the differences of opinion expressed in older literature (as summarized by Ludwig 1949 and Hennig 1973). Many workers resorted to postulating completely new structures to explain some of the modifications. However, the muscomorphan head is considered here to represent a logical further development of the features of the head capsule of larvae of the orthorrhaphous Brachycera. The major evolutionary sequences in its development can be interpreted as an extension of trends pointed out by Cook (1949) and repeated above, particularly as they occur in the larval head of orthorrhaphous Brachycera. Chief among these trends are the further reduction, including complete desclerotization, of all external elements of the maxillae and the head capsule, together with loss of all direct connection of the tentorial phragmata with the external body cuticle; complete fusion of the tentorial arms with the pharynx; and additional phragmatal growth posteriorly to the tentorial phragmata and to the fused tentorial arms and pharynx.

In the Muscomorpha the head comprises an outer membranous ***cephalic segment*** (pseudocephalic segment), which anteriorly bears the antennal and maxillary sensory papillae, and the internal ***cephalopharyngeal skeleton*** (Figs. 12, 13). Most descriptions of larvae of the Muscomorpha either make no mention of the cephalic segment being part of the head or they include it with the description of the body segments; this treatment indicates a misunderstanding of its derivation. Such misinterpretation is obviously the case where 12 segments are attributed to the body of muscomorphan larvae. Schremmer (1956) pointed out that the cephalic segment probably originated from the maxillae and from small anterior portions of the head capsule that have become membranous; these membranous portions fuse dorsally over the mandibles and enclose them in a deep atrium (oral pocket). This interpretation explains why the sensory organs of the maxillary palpi and the antennae are in such close proximity. Without such rationalization, this proximity could be explained only by a complex migration. The modification of the maxillae as a sheath for the mandibles occurs among larvae of the orthorrhaphous Brachycera, in particular in some species of the Mydidae and the Asilidae where the median face of each maxilla has a concavity in which the mandible is recessed. The progressively skeletonized appearance of the maxillae in larvae of the Vermileonidae, the Empididae, and the Dolichopodidae indicates that membranization does in fact occur.

The cephalic segment is bilobate anteriorly, with an antennal and a maxillary sensory papilla at the apex of each lobe. These two lobes are referred to as the ***antennomaxillary lobes***. Whereas the two papillae are separated in most larvae, Roberts (1970) showed them both present at the apex of a relatively large two-segmented protuberance in *Myathropa florea* (Linnaeus) (Syrphidae). A second, but much smaller pair of sensory organs, enervated from the maxillary nerve, is present behind the primary pair in *Calliphora* (Calliphoridae) and other larvae (Ludwig 1949, Roberts 1971*a*). This secondary pair is normally located among a series of ***oral ridges*** that radiate from the preoral cavity, and these sensory organs are therefore usually difficult to detect. Homology of the antennal and maxillary sensory papillae has been demonstrated from studies of the nervous system by the above authors and Hartley (1963).

The oral ridges are situated on the antennomaxillary lobes on either side of the preoral cavity. Their function is apparently similar to that of the pseudotracheae of the adult; they serve to direct food-carrying liquids toward the atrium (Figs. 12, 13). They vary widely in structure, although this aspect has apparently not been studied much. The configuration of the ridges has been used diagnostically in some of the European literature but has been generally ignored on this continent. The ridges are, at least in some larvae, made up of rows of minute spicules. They are apparently best developed in some saprophagous syrphid larvae of the tribe Eristalini, which inhabit putrid or stagnant water rich in organic matter. Hartley (1963) and Roberts (1970) described the cephalopharyngeal skeleton of these larvae. Their mandibles are greatly reduced and the cephalopharyngeal skeleton is further retracted within the thorax; the antennomaxillary lobes are thus partially invaginated so that the ridges line an internal cavity. Here they are very pronounced, and each bears a fringe of bristles forming a comb that touches the adjacent ridge. The ridges thus no longer channel food toward the mouth but serve as a coarse filter to separate some of the solid particulate matter from the liquid carrier. The oral ridges and spicules are sometimes used as rasping devices, particularly when the spicules are well developed as in some Platypezidae (Fig. 5.45).

The cephalopharyngeal skeleton normally comprises three main parts: the ***tentoropharyngeal sclerite*** (basal sclerite, pharyngeal sclerite, pharyngosinusal theca), the ***hypopharyngeal sclerite*** (hypostomal sclerite, H-shaped sclerite, intermediate sclerite, labial sclerite, labiohypopharyngeal sclerite), and the ***mandibles*** (mouth hooks) (Figs. 12, 13).

The tentoropharyngeal sclerite consists of a pair of reclining, somewhat U-shaped sclerites on either side of the pharynx. The two arms of each U-shaped sclerite are called the ***dorsal*** and ***ventral cornua*** (*sing.* ***cornu***; wings). The two ventral cornua are fused on each side with the pharynx. The bases of the U-shaped sclerites involving the anterolateral walls represent, at least in part, the tentorial phragmata; the two ventral cornua, which are fused with the pharynx, apparently include the two anterior tentorial arms. In contrast, in the orthorrhaphous Brachycera the tentorial arms project from the ventral edges of the tentorial phragmata; here any fusion with the pharynx involves only the phragmata, and the tentorial arms are always free apically. In the Muscomorpha the ventral cornua are normally somewhat expanded apically to provide an adequate surface for attachment of mandibular and labial muscles. The dorsal cornua probably represent an additional posterior expansion of the tentorial phragmata. Roberts (1971*a*) and Hartley (1963) called the dorsal cornua the clypeal or clypeofrontal phragmata, but this derivation seems doubtful because there is no evidence of such phragmatal growth in larvae of the orthorrhaphous Brachycera from which the Muscomorpha are apparently derived. Both dorsal and ventral cornua may bear conspicuous, clear, unpigmented areas or windows that sometimes continue to the posterior margin and thus appear like sinuses or incisions in the cornua (Fig. 5.79). The dorsal margin of each ventral cornu often has a distinctively shaped projection.

The tentoropharyngeal sclerites may be joined anterodorsally by a dorsal bridge (Fig. 12), which Hartley (1963) and Roberts (1970) derived from the labrum. This bridge is often weak, with a fenestrated appearance. The anterior margins of the tentoropharyngeal sclerite below the dorsal bridge is concave and part of the sclerite behind this concavity is often depressed. In this depression lie visual cells. This depression provides a dark background so that these cells can obtain a directional perception of illumination (Roberts 1971*b*).

The hypopharyngeal sclerite is a more appropriate name morphologically for the sclerite lying between the mandibles and the tentoropharyngeal sclerite than other names that have been applied to it. This sclerite is apparently a fusion product of several structures, of which the hypopharynx is almost certainly a part. A combined name for the components of the sclerites would be too unwieldly. The most commonly used name, hypostomal sclerite, is inaccurate morphologically and could be confused with the postlabial sclerite of the same name in larvae of some Nematocera. It comprises two lateral, more or less longitudinal bars joined ventrally near the middle by a transverse bar; thus, from above and from below, this sclerite resembles the letter H (Fig. 13). The cibarium runs through this supporting structure to connect with the pharynx. The lateral bars articulate with the mandibles anteriorly and are continuous posteriorly with the anteroventral margin of the tentorial phragmata in most if not all Aschiza and in several Schizophora (Figs. 5.3, 5.45, 5.50–51, 5.74); they are separated from the tentorial phragmata by a narrow line of cleavage in all other Schizophora. Therefore the lateral bars may be derived from the tentorium as considered by both Hartley (1963) and Roberts (1970). They are perhaps, at least in part, anterior extensions of the points at which the tentorial phragmata articulate with the mandibles in the orthorrhaphous Brachycera. The salivary duct enters the cibarium just behind the transverse bar. Because this duct opens at the base of the labium, between it and the hypopharynx, in all more primitive Diptera larvae, the transverse bar can reasonably be assumed to be partially derived from one or both of these structures. Traxler (1977) suggested that the entire hypopharyngeal sclerite is of labial and hypopharyngeal origin whereas Ludwig (1949) considers it solely of labial origin; but neither of these proposals have been substantiated. Several small labial sclerites sometimes occur anteriorly, below the hypopharyngeal sclerite, in larvae of at least the Schizophora. These sclerites support the ventral membranous wall of the atrium. The more anterior of these sclerites is sometimes in the form of a transverse bar supporting the labial lobe at the hind margin of the mouth (Fig. 13). Miller (1932) showed this sclerite (his liguloid arch) to have small spines along its leading edge in *Calliphora* (Calliphoridae). The strong, dentate, ventral arch that is a characteristic feature of larvae of the Sciomyzidae (Fig. 5.57) is possibly homologous with this labial sclerite. A pair of labial muscles is attached to the anterior labial sclerite. These muscles serve to dilate the atrium.

Dilation of the atrium creates a negative pressure that draws food-carrying liquids into the cavity. The stream of nutrient-rich liquid is then moved along through the cibarium and pharynx by a similar muscle action.

The labium is commonly much more well developed in larvae of the Aschiza than the Schizophora. In some Phoridae and Platypezidae it consists of a solid, sclerotized continuation of the hypopharyngeal sclerite; its apex is modified to form a rasping structure that functionally may replace the mandibles (Figs. 5.45, 5.50–51). An apically pointed extension from the hypopharyngeal sclerite, similar to the pointed labrum above it, is figured by Hartley (1963) and Roberts (1970) in larvae of *Syrphus* (Syrphidae). However, in *Syrphus* highly modified mandibles are present that articulate with a short dorsal spur from near the middle of this hypopharyngeal-labial sclerite.

A pair of slender sclerotized rods called ***parastomal bars*** project from each side of the anterior margin of the tentoropharyngeal sclerite above the hypopharyngeal sclerite in some Muscomorpha, both in the Aschiza and the Schizophora (Figs. 12; 5.50, 5.58). In some Syrphidae, particularly Syrphinae, and also in first-instar larvae of some Schizophora, these bars converge and fuse anteriorly and have been homologized with the labrum (Hartley 1963, Roberts 1970). This interpretation has some support in such orthorrhaphous Brachycera as the Tabanidae where the epipharyngeal margin of the slender, wedge-shaped labrum is shown by Teskey (1969) to have a narrow band of heavier sclerotization on either side. Because the epipharynx is continuous with the dorsal wall of the pharynx at the point where the tentorial phragmata fuse with the pharynx, it is reasonable to assume that these narrow, sclerotized bands have also fused with the phragmata. The sclerotized bands have remained intact in the higher Diptera, both in their role of supporting the labrum when it is present and in supporting the dorsal wall of the epipharynx. When the free end of the labrum is absent, the parastomal bars may connect with a fenestrated ***epipharyngeal sclerite*** (epistomal sclerite) lying above the anterior extremity of the hypopharyngeal sclerite (Fig. 5.58). Labral sensory organs pass through these fenestrations (Roberts 1971*a*).

The ***mandibles*** (mouth hooks) of the Schizophora are commonly strongly sclerotized, curved, and tapered apically from a widened squarish or triangular base (Fig. 12). They are hollow, and a small pore laterally on the basal portion is the external opening of the lumen. A similar pore occurs in the basal mandibular sclerite of tabanid larvae (Teskey 1969). This similarity, plus the general similarity of the form of the base of the muscomorphan mandible to that of the orthorrhaphous Brachycera, suggests that the structures are homologous and that the two parts of the mandible have become solidly fused. The apical, hooked portion sometimes has accessory teeth along the ventral margin.

The mandibles are articulated proximally with the lateral bars of the hypopharyngeal sclerite, and muscles inserted on the base of the mandible above and below the point of articulation control the up-and-down movement. The upper abductor insertion is directly on the mandible, whereas the lower adductor insertion is on a small sclerite called the ***dental sclerite*** below the base of the mandible, according to Ludwig (1949) and Roberts (1971*a*). If such muscle attachment does occur on the dental sclerite, the sclerite must be attached firmly to the mandibular base. However, Miller (1932) stated that in *Calliphora* (Calliphoridae) the adductor muscle insertion is directly on the mandible. He described a very complex dental sclerite but offered no explanation of its function.

Associated with the mandibles of some Muscidae are accessory oral sclerites below the mandibles (Fig. 5.101). Roberts (1971*a*) illustrated these sclerites in *Limnophora* (Muscidae) and explained their operations, but he suggested nothing about their origin.

Another oral sclerite of a different type is also illustrated by Roberts (1971*a*) and Miller (1932) in larvae of *Calliphora*. This slender, rod-like sclerite, which is slightly expanded at its posterior end, lies in the membranous ridge between the two atria in which the mandibles retract. The function of this sclerite is unknown and it apparently occurs only in *Calliphora* and some close relatives.

The various sclerites of the cephalopharyngeal skeleton described above are found in many shapes and sizes throughout the Muscomorpha, and they provide excellent characteristics for the identification of the various taxa.

Hartley (1963) and Roberts (1971*a*) considered the foregut, or that part of the alimentary canal lying within the cephalopharyngeal skeleton, to comprise three regions: the preoral cavity, the atrium, and the cibarium–pharynx. The ***preoral cavity*** is bounded by the mandibular lobes that bear the ridges converging on the mouth. The ***atrium*** is internal. Its floor bears the labial sclerites and is supported by the transverse bar of the hypopharyngeal sclerite. Its roof bears the epipharyngeal sclerite supported by the parastomal bars. Behind the atrium is the cibarium–pharynx, sometimes bearing longitudinal ridges of the pharyngeal filter.

The above definitions of the terms preoral cavity and atrium are adopted here. However, this interpretation of the cibarium–pharynx does not correspond to Snodgrass' (1935) original definition of the terms that was adopted earlier in this work. In Snodgrass' definition the hypopharynx forms the floor of the cibarium. It is therefore more accurate to call this region the cibarium rather than the cibarium–pharynx and restrict the term pharynx to the portion of the alimentary tract traversing the tentoropharyngeal sclerite that sometimes bears the pharyngeal filter. Moreover, the region is morphologically well defined and can be readily related to the condition in larvae of the Nematocera and orthorrhaphous Brachycera. The term atrium can be retained for the region between the functional mouth and the cibarium. The atrium is essentially unique to the Muscomorpha and was created by the additional retraction of the head, including the mandibles, within the cephalic lobe and the thorax.

As a rule the pharyngeal filter is present only in those larvae of the Muscomorpha that are saprophagous and consume solid food materials suspended in liquid (Keilin 1912). The filter is absent in predatory larvae, as explained previously. The filter is effectively described by Hartley (1963) and Roberts (1971*a*). The lower surface of the pharynx has a series of longitudinal ridges; the free edge of each ridge bears lateral rows of short filaments projecting laterally to meet the filaments of the next row, as shown in Fig. 14. The pharynx is thus divided into a series of ventral channels and one dorsal channel. This filter functions analagously to those of the Nematocera and the Stratiomyidae. Liquid in which food particles are suspended is drawn into the dorsal channel. Then by appropriate pressures and valve closure the liquid is forced through the filamentous sieve into the ventral channels, where it is regurgitated through the mouth.

The musculature of the cephalopharyngeal skeleton has been mentioned here only to the extent needed to explain the operation of certain structures. The complete musculature and nervous systems as they exist in larvae of some Syrphidae and the *Calliphora* (Calliphoridae) is described and illustrated by Hartley (1963), Ludwig (1949), and Roberts (1970, 1971*a*). These descriptions almost certainly can be applied to all larvae of the Muscomorpha.

BODY

Body shape. The body shapes of Diptera larvae are diverse. Most nematocerous larvae, as exemplified by the Tipulidae, the Bibionidae, most Sciaroidea, the Trichoceridae, the Anisopodidae, and the Chironomidae, are subcylindrical (Figs. 7.66, 13.12–14, 14.97, 18.7, 19.19, 29.114–116). Larvae of the Cecidomyiidae, the Tabanidae, and several Muscomorpha such as the Canacidae and the Ephydridae have a fusiform body (Figs. 5.37, 5.62–63, 16.8–9, 31.51–52). Larvae of certain Ceratopogonidae, *Glutops* (Pelecorhynchidae), the Therevidae, and the Scenopinidae have an elongate, serpentine body (Figs. 28.132–134, 30.5, 38.11). Some larvae, for example the Xylophagidae and many Muscomorpha, have a body form that is markedly narrowed anteriorly (Figs. 5.73, 5.76, 5.98, 5.102, 34.11–12). Many Diptera larvae have dorsoventrally flattened bodies. These include the Xylomyidae, the Stratiomyidae, the Lonchopteridae, the Platypezidae, and *Fannia* (Muscidae) (Figs. 5.40–41, 5.47, 5.53, 35.6–7, 36.71–73). The larvae of many Syrphidae and many parasitic forms are very stout (Figs. 5.1, 5.17, 5.33, 5.38, 43.28, 44.4). Part of the body may be conspicuously swollen. The thorax of larvae of the Chaoboridae and the Culicidae is characteristically swollen (Figs. 24.10, 25.33–34). Larvae of the Simuliidae are swollen toward the posterior end (Fig. 27.77). Larvae of *Goniops* (Tabanidae) and the Conopidae are pear shaped (Figs. 5.11, 31.54). The larva of *Microdon* (Syrphidae) is hemispherical (Fig. 5.12).

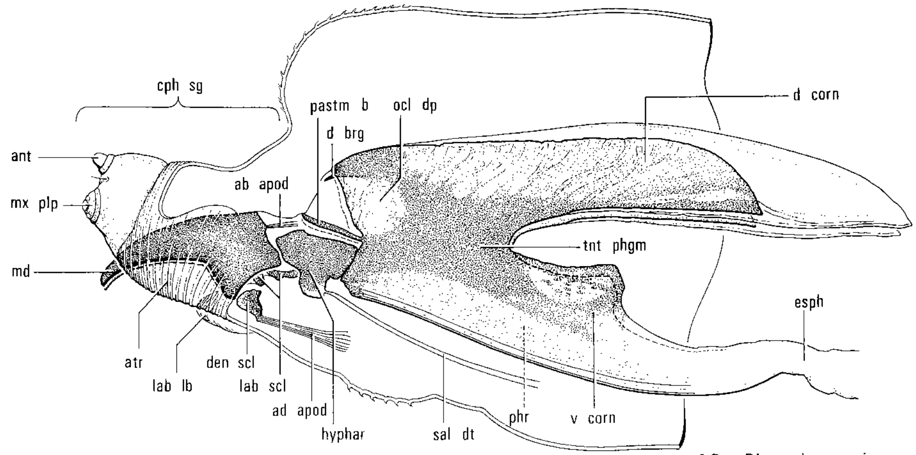
Body segmentation. The number of recognizable body segments is most commonly 12 in the Nematocera and 11 in the Brachycera. Of these, three are always thoracic and the remainder abdominal. Any variance from these numbers is to decrease the number of abdominal segments in the Nematocera and to increase it for the Brachycera. Thus the larvae of the Tipulidae, the Deuterophlebiidae, some Psychodidae, the Trichoceridae, the Anisopodidae, the Ptychopteridae, and the Simuliidae have eight recognizable abdominal segments, whereas the number is further reduced to seven in the Blephariceridae and the Axymyiidae. On the other hand larvae of the Asiloidea commonly have nine recognizable abdominal segments. The ninth abdominal segment is sometimes small and displaced onto the ventral side of the body, as in many Cecidomyiidae and the Scatopsidae.

In all cases where nine abdominal segments are present, the anus is located on the ninth segment. Therefore when only eight abdominal segments are present and the anus is situated ventrally on the terminal segment, a fusion of the eighth and ninth abdominal segments is indicated.

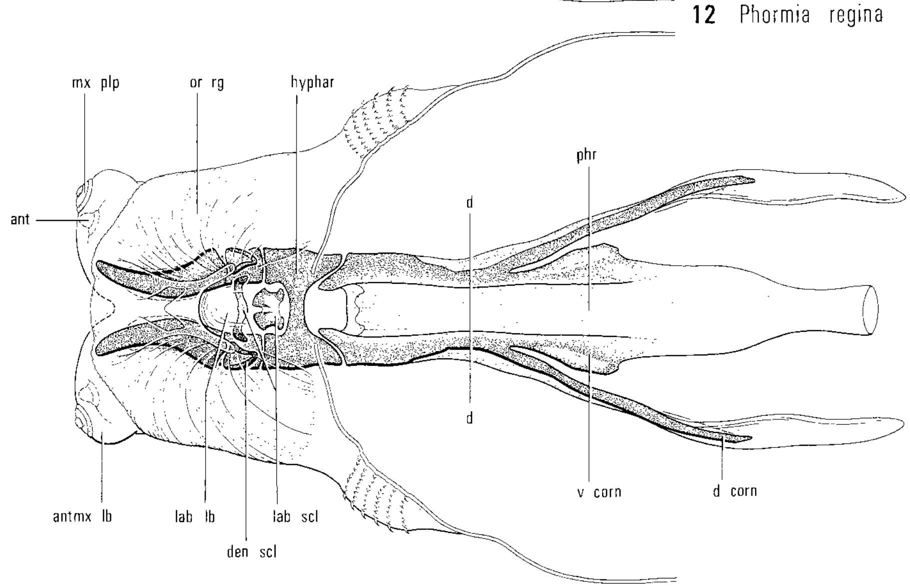
One of the abdominal segments in the Blephariceridae is included in a compound fusion segment involving the head capsule, the three thoracic segments, and the first abdominal segment. The entire larva therefore appears to comprise only seven segments, the first being quite large (Fig. 8.7).

In the embryos of Blephariceridae and several other Nematocera investigated, 13 body segments are initially recognizable but later the above-mentioned fusion, plus fusion of the last four body segments, occurs to produce the apparent seven-segmented condition (Matsuda 1976, Craig 1967). Fusion of the three thoracic segments with each other is an important diagnostic feature of the Chaoboridae, the Culicidae, and the Simuliidae (Figs. 24.10, 25.33–34, 27.77).

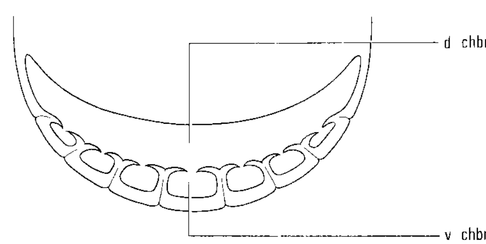
Conversely, subdivision of the segments is a feature of the larvae of several taxa. A narrow intercalary pseudosegment is inserted in front of the prothorax and each of the abdominal segments of *Sylvicola* and *Mycetobia* (Anisopodidae) (Fig. 19.19). The three thoracic and first abdominal segments of larvae of the Psychodinae are commonly divided into two subdivisions, and the following six abdominal segments are each divided into three (Figs. 17.14–15). These subdivisions can usually be differentiated from the true segmental boundaries by slightly less prominent folds in the integument, but the sclerotized plaques present dorsally on many or all



12 Phormia regina



13 Phormia regina



14 Phormia regina

Figs. 3.12–14. Cephalic segment and cephalopharyngeal skeleton of *Phormia regina* (Meigen) (Calliphoridae): (12) left lateral view with left antennomaxillary lobe removed; (13) ventral view, entire; (14) diagrammatic cross section (d-d) of pharyngeal filter.

Abbreviations: ab apod, abductor apodeme; ad apod, adductor apodeme; ant, antenna; antmx lb, antennomaxillary lobe; atr, atrium; cph sg, cephalic segment; d brg, dorsal bridge; d chbr, dorsal chamber; d corn, dorsal cornu; den scl, dental sclerite; esph, esophagus; hyphar, hypopharynx; lab lb, labial lobe; lab scl, labial sclerite; md, mandible; mx plp, maxillary palpus; ocl dp, ocular depression; or rg, oral ridge; pastm b, parastomal bar; phr, pharynx; sal dt, salivary duct; tnt phgm, tentorial phragma; v chbr, ventral chamber; v corn, ventral cornu.

subdivisions are a better indication. Larvae of *Trichocera* (Trichoceridae) have a similar pseudosegmentation (Fig. 18.7).

Larvae of the Therevidae and the Scenopinidae, which closely resemble each other, are unique in having 20 segmental divisions, most of which are so similar as to make the pattern of division difficult to interpret (Fig. 38.11). Slight size and shape differences in alternate units of the 12 segmental divisions beyond the anterior three (thoracic) segments indicate that these comprise six true abdominal segments that have each become subdivided once. The posterior spiracles, which typically occur on the true eighth abdominal segment (*see* "Respiratory System"), are located on the 14th abdominal subdivision; this positioning indicates that the preceding 13th subdivision is probably an undivided seventh abdominal segment. There is no clear guide as to how the true eighth and ninth abdominal segments are divided to produce the terminal four subdivisions.

Similar difficulties in interpreting the true body segmentation occur in some Bibionidae (*Bibio* and *Plecia*), where the posterior spiracles lie on the ninth abdominal division (Figs. 13.12, 13.14). Are these two segments actually subdivisions of the eighth abdominal segment (as suggested by Hennig 1948), or have the posterior spiracles shifted their normal location? A study of the internal anatomy of these segments might answer this question and might also provide an explanation of the odd sequence of subdivisions of the abdomen of larvae of the Therevidae and the Scenopinidae.

Except where obvious fusion occurs, the segments or their subdivisions are usually clearly differentiated from each other. However, sometimes the borders are indistinct, usually because of general integumental wrinkling as in some Syrphidae (Fig. 5.17), which obscures segmental lines. In these cases the true segmentation can often be distinguished by studying the repetitions of the setal patterns of the cuticle.

Cuticle. The cuticle of most Diptera larvae is nonpigmented, weakly or not at all sclerotized, flexible, and elastic. The usual lack of pigment and general sclerotization is perhaps explained by the concealed way of life of most Diptera larvae. The thickness and durability of the cuticle vary considerably among Diptera larva. At one extreme is the very thin membranous cuticle that is characteristic of aquatic Culicomorpha. Larvae of the Sciaroidea and many Muscomorpha living exclusively in concealed niches surrounded by a near-saturated atmosphere, where abrasive forces are at a minimum, also have a thin cuticle. At the other extreme are larvae of the Asilidae, living and moving in relatively dry soil. They have a tough, leathery cuticle that protects them from abrasion and water loss. All gradations are found between these extremes, and the thickness and durability of the cuticle are usually good indicators of the potential stresses found in the habitat occupied by the larva.

Sclerotization of the cuticle is most conspicuous in larvae of *Xylophagus* (Xylophagidae) and related genera. In these larvae, the dorsal surface and, to a lesser extent, the ventral surface of the thorax, as well as the dorsal surface of the terminal segment surrounding the spiracles, bear sclerotized plates (Figs. 34.11–13). Partial or complete sclerotization of the posterior spiracular disc (*see* "Number and Distribution of Spiracles") or structures associated with the spiracles or anus is a feature of many Tipulidae, Scatopsidae, Synneuridae, Culicidae, Psilidae, and others (Figs. 5.86, 7.78–81, 21.6, 25.34). In the Scatopsidae a pair of lobes called adanal lobes, or a shelf above and behind the anus, are sclerotized as well as the tubular processes bearing the posterior spiracles (Fig. 20.26). A variety of sclerotized structures may occur on larvae of the Culicidae; the most prominent of these are usually the subconical respiratory siphon and the so-called saddle covering the dorsal surface of the ninth abdominal segment bearing the anus (Figs. 25.28–32). Additionally, sclerotized tergal plates sometimes occur on other posterior abdominal segments of culicid larvae, and the setal clusters that are so conspicuous a feature of these larvae may also arise from sclerotized plaques.

Some or all of the segmental subdivisions of larvae of the Psychodinae bear sclerotized plates dorsally (Figs. 17.14–15). A ventral, variously shaped sclerite on the prothorax, called the ***sternal spatula*** (breastbone, spatula sternale), is characteristic of many larvae of the Cecidomyiidae (Fig. 16.7). According to Milne (1961) the sternal spatula is used primarily to construct the pupal chamber in soil.

Larvae of the Stratiomyidae and the Xylomyidae have a particularly distinctive armored cuticle. Its rough, reticulate appearance is caused by the deposition of calcium carbonate.

Few Diptera larvae are conspicuously colored. The rather general, greenish or brownish coloration of some Tabanidae and the red of some Chironomidae is imparted by the coloring of the hemolymph. The reddish hemolymph takes on its coloration from hemoglobin (Keilin 1944). The larvae of many of the Cylindrotominae (Tipulidae) and the Syrphidae that live on the surface of plants are greenish. More commonly the color is arranged in surface patterns that change with age of the larvae, for example, many Mycetophilidae and Culicomorpha. The color is bestowed by pigment granules contained in chromatocyte cells of peripheral fat bodies (Hinton 1958, 1960). The coloration of the body sometimes depends on the character and density of cuticular pubescence. Dense microtrichia give a grayish tinge to the body of tipulid larvae. The cuticular microtrichia of some Limoniinae are golden colored.

Generally, larvae that live deep within soil and wood are uniformly whitish or yellowish. Color varies most in larvae that live in litter, under bark, or in water and especially in those larvae that develop on plants or amidst moss.

Cuticular outgrowths on the body surface of Diptera larvae range from minute, fine microtrichia or spicules, to scale-like projections, to simple or greatly modified hairs or setae, through to strong spines and fleshy processes in various combinations. The incidence of such outgrowths on segments preceding the terminal one are reduced among representatives of the schizophorous Muscomorpha. The characteristics of these outgrowths and their distribution provide valuable diagnostic features. The great diversity of arrangement, size, and character of these cuticular structures is indicated below.

When small microtrichia and spicules are present they often cover extensive areas of the integument, as in larvae of some Tipulidae, Bibionidae, Platypezidae, Syrphidae, Aulacigastridae, Sciomyzidae, Drosophilidae, and Ephydridae (Figs. 5.15, 5.41, 5.56, 5.63–64, 7.74–75, 13.12). In these larvae, the microtrichia are evenly distributed and relatively uniform in size. In *Ptychoptera* (Ptychopteridae) the microtrichia are of various sizes; the smaller ones are unevenly distributed and the larger setulae are arranged in multiple transverse and longitudinal rows (Fig. 22.5). The microtrichia in larvae of some Scatopsidae are arranged in a transverse band on each segment; these segments sometimes also bear a secondary pattern of slightly longer setulae arranged in longitudinal rows (Fig. 20.24). Microtrichial pubescence is restricted to areas usually bordering the prolegs (*see* "Locomotory Structures") in larvae of the Tabanidae (Figs. 31.51–52) and constitutes one of the most important diagnostic features of these larvae (Teskey 1969). Stout, thorn-like or scale-like spines are prominent features on all or most segments of larvae of the Oestridae (Figs. 5.33, 5.35).

Large, fleshy processes are the most prominent of cuticular outgrowths. They may occur on all segments or only on the terminal segment. Normally when such projections are present on several segments they become progressively larger toward the caudal end (Figs. 5.14, 5.19, 5.53, 5.55). The projections are sometimes stronger laterally that elsewhere on the body. The occurrence of this feature on several larvae that are dorsoventrally flattened greatly accentuates the flattened condition, as in Lonchopteridae, some Platypezidae, *Periscelis annulata* (Fallén) (Periscelididae), and *Fannia* (Muscidae) (Figs. 5.40–41, 5.47, 5.53, 5.55). The adaptive advantage of having tubercles on more than the terminal segment is sometimes difficult to understand. However, with larvae of the Cylindrotominae (Tipulidae) (Fig. 7.65) one only has to see them in their natural habitat among moss and other vegetation to see how perfectly camouflaged they are.

Tubercles restricted to the terminal segment commonly surround or are adjacent to the posterior spiracles. The number, size, and position of these tubercles is relatively constant for each taxon. In aquatic larvae these tubercles are often fringed with hydrophobic hairs (Figs. 7.72, 7.78–81, 23.10, 36.74, 36.86) that spread out over the water surface. These hairs prevent water from entering the spiracles when the larva takes in air, and they enclose a bubble of air over the spiracles when the larva submerges.

Many larvae bear a few symmetrically arranged setae occurring either alone (Fig. 7.70) or interspersed among a general body covering of microtrichia (Figs. 7.74–75). The setae are usually simple and hair-like, and they vary greatly in size; but sometimes they are club-shaped, stellate, pectinate, plumose, or otherwise variously shaped (Figs. 17.16, 25.33, 28.130). The setae may be present on all segments including the head or, as in larvae of the Scenopinidae, the Therevidae, and the Asilidae, they may be present only on the thoracic and terminal abdominal segments (Figs. 38.11, 42.76–77). The number and distribution of setae are usually similar on the mesothorax and metathorax but this pattern normally differs from the pattern repeated on each of the first seven abdominal segments. The setal pattern on the prothorax differs widely from that on the terminal segment or segments and from that on the mesothorax, the metathorax, and the first seven abdominal segments. A system of setal nomenclature for comparative purposes can often be devised, based on the dorsal, lateral, and ventral locations of specific setae, exclusively differentiated with various modifiers such as inner, mid, outer, pre-, and post-. Such systems are also applicable for naming tubercles. However, the complex setal patterns of some groups cannot be satisfactorily described in this way, and other methods have been devised in some families such as the Culicidae (Knight and Laffoon 1971) and the Phoridae (Schmitz 1938).

Locomotory structures. Diptera larvae lack segmented thoracic limbs. The most common replacements for these limbs are different types and sizes of projections, usually bearing locomotory spinules, on the anterior margins of one or more body segments. These projections are held extended by turgor pressure and are retracted by the action of muscles inserted in the projections. The form and distribution of the projections and the configuration and structure of their spinous covering are of great systematic importance.

Hinton (1955) suggested that the locomotory structures of Diptera larvae have evolved *de novo* many times and he gave to all such structures the name proleg. However, the appendages are basically of two types, and only one of these is called a ***proleg*** here; the other type is called a ***creeping welt*** (locomotory ridge, ambulatory ridge). A third very different type of structure, called a ***suction disc***, occurs in larvae of the Blephariceridae and some Psychodinae. The terms pseudopodia and parapodia have often been applied to fleshy locomotory structures of the abdominal segments in larvae of the Tabanidae, the Athericidae, and the Syrphidae, but not in other larvae bearing such appendages. This differentiation is not justified, however, because such structures do not differ significantly from those structures that are

Number and distribution of prolegs in various groups of Diptera (modified from Hinton 1955)

	Thorax			Abdomen								
	1	2	3	1	2	3	4	5	6	7	8	9
Dixidae				2	0–2							
Chironomidae	2											2
Ceratopogonidae	0–2											1–2
Thaumaleidae	1											1
Simuliidae	1											1
Blephariceridae					2	2	2	2	2	2		
Nymphomyiidae				2	2	2	2	2	2	2		2
Deuterophlebiidae				2	2	2	2	2	2	2		
Tanyderidae												2
Ptychopteridae				2	2	2						
Tipulidae (*Dicranota*)						2	2	2	2	2		
Tabanidae				6–8	6–8	6–8	6–8	6–8	6–8	6–8		
Athericidae				2	2	2	2	2	2	2	2	
Asilidae												
Lasiopogon				2	2	2	2	2				
Leptogaster					2	2	2	2	2	2		
Laphria				6–8	6–8	6–8	6–8	6–8				
Empididae												
several genera					2	2	2	2	2	2	2	
several genera				2	2	2	2	2	2	2	2	
Syrphidae	2			2	2	2	2	2	2			
Ephydridae (*Ephydra*)				2	2	2	2	2	2	2	2	
Muscidae												
Limnophora					2	2	2	2	2	2	2	
Graphomya					2	2	2	2	2	2		

always called prolegs which occur on the prothorax and the terminal segment.

Prolegs are typically round or oval fleshy tubercles usually located in pairs ventrally on the prothorax and terminal segment, on the terminal segment alone, or on one or more of the intermediate abdominal segments (Figs. 9.3, 10.7, 23.10, 29.114–116). In all cases they bear one or more curved locomotory spinules near their apices. In those cases where more than one pair of prolegs occur on the abdominal segments, the additional pairs are situated on the dorsal, lateral, and ventrolateral aspects (Figs. 31.51–52). The number and distribution of prolegs among the Diptera are shown in the accompanying table. The prolegs are sometimes modified from the typical form. In *Dasyhelea* (Ceratopogonidae) (Fig. 28.132) the terminal proleg comprises paired, sublateral clusters of a few curved spinules. These spinules are capable of complete retraction within the apex of the terminal segment, together with the anal papillae (*see* "Anus, Anal Papillae, and Tracheal Gills"). Prothoracic and terminal prolegs of larvae of the Thaumaleidae and the Simuliidae appear to be unpaired. This condition probably represents a fusion of paired prolegs. The proleg on the terminal segment of larvae of the Simuliidae appears as numerous concentric rows of spinules encircling the apex of the segment (Figs. 27.89–92).

The locomotory spinules of the prolegs are varied in form. They are sometimes very small, showing little organization on the apex of the proleg; the only pattern evident is that most of the spinules are commonly inclined posteriorly, with only a few spinules on the anterior margin of the proleg directed anteriorly. The spinules are often in the form of relatively large, strongly hooked crochets arranged in one or more partially or completely encircling rows at the apex of the proleg, as in *Atrichopogon* (Ceratopogonidae), the Chironomidae, and *Atherix* (Athericidae) (Figs. 28.131, 29.136, 32.7). The crochets on the prothoracic proleg of the Thaumaleidae are arranged in a linear transverse row (Fig. 26.4). Different kinds of locomotory spinules may be combined on a proleg. Only a single, hooked spinule occurs on each abdominal proleg of the Ptychopteridae (Figs. 22.5–6), the spinule being much larger in *Bittacomorpha* than in *Ptychoptera*.

Creeping welts are typically transverse swollen ridges on the anterior ventral margins and sometimes the anterior dorsal margins of usually the first seven abdominal segments (Figs. 5.59, 5.72, 7.74, 7.82, 14.97). They are most common among larvae of the Schizophora but are also present in some larvae of the Nematocera and orthorrhaphous Brachycera, e.g. Tipulidae, Mycetophilidae, Rhagionidae, Xylophagidae, Empididae, and Dolichopodidae. Creeping welts normally bear spinules that are commonly arranged in transverse rows. The spinules in a few of the anterior rows may be inclined anteriorly, but most of the spinules covering the remainder of the creeping welt are inclined posteriorly (Fig. 5.102). When the welt involves the posterior portion of the preceding segment, the anteriorly inclined spinules are usually on this portion. Sometimes spinules are present laterally and dorsally on the abdominal segments, even though raised welts are not evident; such spinules may partially or completely encircle the anterior margins of the thoracic segments (Figs. 5.59, 5.76, 5.98). Spinules may be present on both dorsal and ventral anterior segmental margins without evident ridges, as in *Synneuron* (Synneuridae) (Fig. 21.6). Raised welts or ridges that lack spinules as are present in *Cramptonomyia* (Pachyneuridae) and *Lutzomyia* (Psychodidae) (Figs. 12.5, 17.16) probably have some use in locomotion. A locomotory function can also be attributed to other body tubercles of some larvae, even if only acting as an anchor against backward slippage.

A third very different type of foot-like structure, the suction disc, occurs in larvae of the Blephariceridae and some Psychodidae (e.g. *Maruina*). Suction discs are adaptations used by the larva for maintaining its position in swiftly flowing water. Suction discs have been thought to be modified prolegs (Hora 1933); however, this suggestion appears unlikely. Tonnoir (1933) has shown rather convincingly how these structures may have evolved in the Psychodidae and by analogy also in the Blephariceridae. Furthermore, larvae of the Blephariceridae have musculated lateral conical projections on the abdominal segments (Fig. 8.8), quite separate from the suction discs, which are believed to be homologous with the prolegs (Hinton 1955). The suction disc has a fleshy rim bearing marginal hairs. A hole in the center of this rim opens into a large internal chamber. Muscles are inserted in the roof of this chamber which contract to elevate the roof and increase the volume of the chamber. When the fleshy rim is closely applied to a smooth substrate such as a rock, the increased volume of the chamber creates a negative pressure within, which holds the larva firmly in position.

Other body parts also may assist in larval movement. The mandibles are important in this regard, especially in brachycerous larvae. They are used to provide an anchoring point against which contraction of the larval body results in forward motion. Transverse rows of backwardly directed setae called ambulatory combs (Fig. 23.10) are present on the venter of abdominal segments five to seven in larvae of the Dixidae. Preanal and postanal ridges on many brachycerous larvae appear to function in the same way as creeping welts. They sometimes bear spinules similar to those on the creeping welts, e.g. Micropezidae and Milichiidae (Figs. 5.70, 5.91). In *Ephydra* (Ephydridae), these spinules take the form of nearly typical crochets (Fig. 5.63). A single, rather large spicule is present on the preanal ridge of *Canace macateei* Malloch (Canacidae) (Fig. 5.37).

RESPIRATORY SYSTEM

The respiratory system includes the internal system of tracheae and the external spiracles. Although no discussion of internal anatomy has been given here, except for the head, comparative studies of the tracheal system of Diptera larvae (Keilin 1944; Whitten 1955, 1960, 1963; Tatchell 1960) are highly significant in larval systematics and must be at least briefly discussed.

Internal tracheal system. The general plan of the structure of the tracheal system of Diptera larvae, as given by Whitten (1955), is shown in Fig. 15. There are two dorsal and two lateral ***longitudinal trunks***. The dorsal trunks are united by ten segmental ***anastomoses*** (*sing.* ***anastomosis***). Eight ***transverse connectives*** join the dorsal and lateral trunks on each side. Two dorsal and two ventral ***cervical tracheae*** and two ***supraesophageal ganglionic tracheae*** project into the head; the dorsal cervical tracheae and the ganglionic tracheae are united by a ***cervical anastomosis***. A series of ***ventral ganglionic tracheae*** and ***visceral tracheae*** project from the lateral trunks, and the first three ganglionic tracheae form ***midventral anastomoses***. Ten pairs of ***spiracular tracheae*** may be present, although all may not be functional. Although this arrangement is subject to variation in detail, the full complement of tracheae and anastomoses are present in larvae of the Bibionidae, the Psychodidae, the Trichoceridae, the Anisopodidae, and the Brachycera (Whitten 1960). Deviations from this plan by reduction of one or more of the tracheal anastomoses or connectives occur in larvae of at least some Tipulidae, Mycetophilidae, Sciaridae, Cecidomyiidae, Dixidae, Culicidae, Thaumaleidae, Simuliidae, Ceratopogonidae, and Chironomidae. The Scatopsidae follow the general plan but have an extra 11th dorsal anastomosis. The tracheae of larval Blephariceridae also follow the general plan except that the tracheae associated with the eighth abdominal segment (terminal portions of dorsal and ventral longitudinal trunks and the dorsal connectives) are absent (Whitten 1963).

The tracheal system of larvae that live freely in water fulfills a hydrostatic function as well as a respiratory function. The dorsal tracheal trunks of larvae of some Chaoboridae and some Culicidae are widened into tracheal vesicles, which help the larvae maintain their position in the water (Damant 1924, Keilin 1944). Some larvae of *Hybomitra* (Tabanidae) have swollen dorsal tracheal trunks, which allow them to float on the surface of the water where they can move by lashing the terminal portion of the body back and forth.

Number and distribution of spiracles. More important in the systematics of larval Diptera has been the individual characteristics and location of the ***spiracles***. The basic number of spiracles on Diptera larvae is 10 pairs, although this number is present only in the Bibionidae and the Palaearctic genus *Pachyneura* (Pachyneuridae). These paired spiracles are located on the prothorax, the metathorax, and each of eight abdominal segments. The spiracles have often been named after the segment on which they are located.

However, the spiracles on the prothorax are apparently the mesothoracic spiracles that have migrated forward (Hinton 1947). Thus, it is more accurate and convenient to refer to them as the ***anterior spiracles***. Similarly the eighth pair of abdominal spiracles, although usually located on this segment, is situated on the apparent ninth segment in larvae of *Plecia* and *Bibio* (Bibionidae), presumably as a result of backward migration. Therefore, this terminal eighth pair of spiracles is best referred to as the ***posterior spiracles***. The metathoracic spiracles are referred to as the ***posterior thoracic spiracles***, but the intermediate ***abdominal spiracles*** are differentiated by the number of the segment on which they occur.

Various degrees of reduction in the number of spiracles has taken place among Diptera larvae, and a convenient terminology has been devised for the resulting spiracular arrangements. This system is explained diagrammatically in Fig. 16. The ***holopneustic*** system is the basic arrangement discussed above for the Bibionidae and *Pachyneura* (Pachyneuridae). Loss of the posterior thoracic spiracles yields the ***peripneustic*** system, which is characteristic of the larvae of the Pachyneuridae (except *Pachyneura*), the mycetophilid subfamily Ditomyiinae, the Cecidomyiidae, the Scatopsidae, and the Synneuridae. In this system, as in the holopneustic system, the anterior spiracles and the posterior spiracles are normally larger than the intermediate abdominal spiracles. The ***hemipneustic*** system, characterized by the loss of the posterior spiracles, has usually been considered as a variation of the peripneustic system. Representative of this system are the larvae of most Mycetophilidae and Sciaridae. The ***amphipneustic*** spiracular system has only the anterior and posterior spiracles. This type is the most common and is characteristic of larvae of the Tanyderidae, the Axymyiidae, most Psychodidae, the Trichoceridae, the Anisopodidae, the Thaumaleidae, and most Brachycera. The presence of anterior spiracles only, the ***propneustic*** condition, appears to be confined to some Mycetophilidae (*Diadocidia* and some Sciophilinae). The presence of posterior spiracles only, the ***metapneustic*** system, is found in larvae of several families, most of which live in aquatic or semiaquatic habitats, such as the Tipulidae, the Ptychopteridae, the Dixidae, the Culicidae, and the Tabanidae. Larvae of the Tabanidae have anterior spiracles that are extruded just before pupation, but it is not known if they are functional. Finally, spiracles are absent in larvae of some families; such forms are said to be ***apneustic***. All apneustic larvae are aquatic and include the Blephariceridae, the Deuterophlebiidae, the Nymphomyiidae, some Chaoboridae (e.g. *Chaoborus*), the Simuliidae, the Ceratopogonidae, most Chironomidae, the Athericidae, some Empididae, and representatives of several other families. Although they have no spiracles, they all have well-developed tracheae.

The spiracular system may change from one larval instar to another. For example, in the Mycetophilidae first-stage larvae are metapneustic, with the posterior spiracles occurring on the eighth abdominal segment; second- and third-stage larvae are propneustic; and fourth-stage larvae are hemipneustic (the eighth pair of abdominal spiracles are not regained) or peripneustic (Madwar 1937). First-stage larvae of the Muscomorpha are metapneustic, whereas the second- and third-stage larvae are usually amphipneustic.

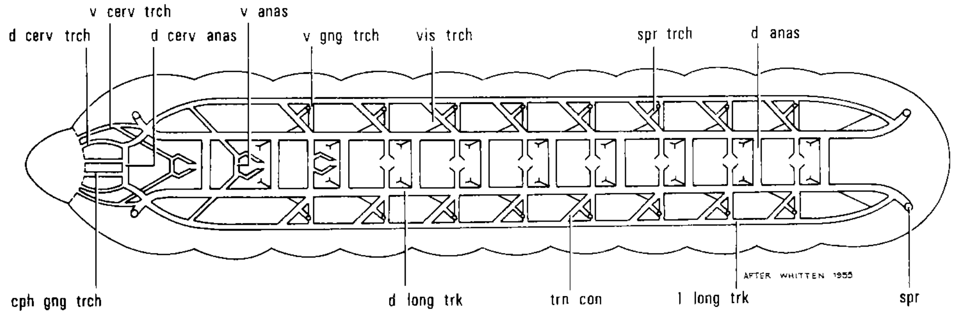
When spiracles are absent, remnants of the spiracular tracheae remain in the form of internal ***spiracular filaments*** that connect the tracheal trunks to the integument where the spiracle would normally occur. Although external evidence of the attachment of the spiracular filaments is usually not apparent, vestigial, nonfunctional spiracles can be seen in larvae of the Culicidae, the Simuliidae, the Mydidae, and the Asilidae (Figs. 27.76, 40.28, 42.76–77).

All spiracles are most commonly located laterally in the holopneustic, peripneustic, and hemipneustic systems. Only in a few Cecidomyiidae and the Scatopsidae are the posterior spiracles situated posteriorly. However, in larvae having the amphipneustic and metapneustic spiracular systems, the posterior spiracles most commonly assume a posterior or dorsal position. Often the posterior face of the terminal segment which bears the spiracles is flattened and is referred to as the ***spiracular disc*** (spiracular field). Of those larvae with the amphipneustic and metapneustic spiracular systems, only in the Tanyderidae, *Phlebotomus* and *Trichomyia* (Psychodidae), *Olbiogaster* (Anisopodidae), the Therevidae, the Scenopinidae, the Mydidae, and the Asilidae are the terminal spiracles situated laterally. The anterior spiracles are usually situated laterally, but they are in a subdorsal position in the Agromyzidae.

Structures of spiracles. The structure of larval spiracles is diverse. This diversity is exhibited not only among species but between the instars of species and between spiracles on the same larva. The anterior spiracles often differ from the abdominal spiracles, sometimes quite markedly; likewise the posterior spiracles may differ from others on the abdomen. Common to all spiracles of Diptera larvae is the absence of an internal mechanical closing device.

The variations of Diptera larval spiracles have been discussed by Keilin (1944) and Krivosheina (1969). Their discussions and that given here are based almost exclusively on mature larvae. There is an acute lack of detailed information on earlier instars. However, spiracles of the earlier stages that are presently known conform in most respects to the following description with the exception of the number of ***spiracular openings*** in each spiracle, which normally increases with maturity of the larva.

Keilin (1944) differentiated three types of spiracles based on the molting process of the spiracle. In spiracles of type I (Fig. 17), as seen in the Culicidae, the opening



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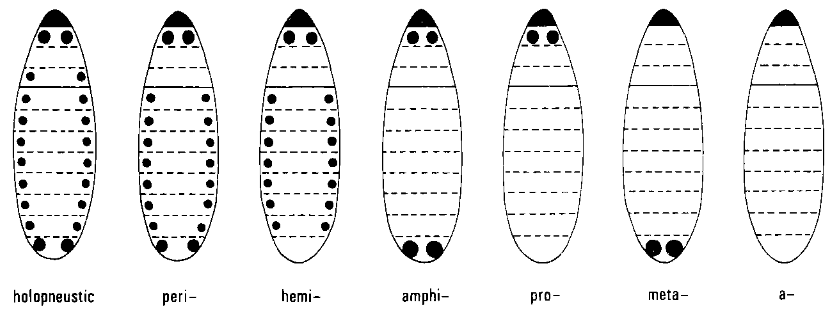

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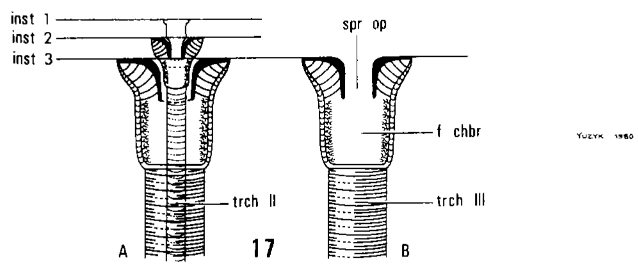

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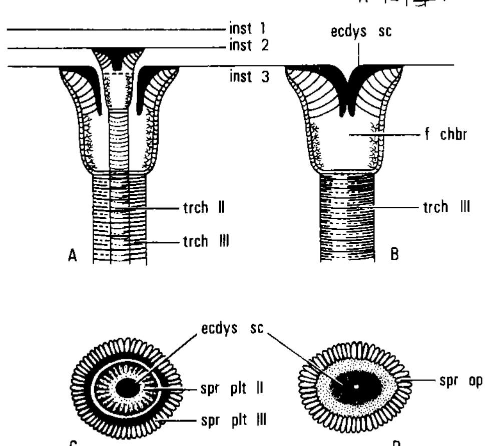

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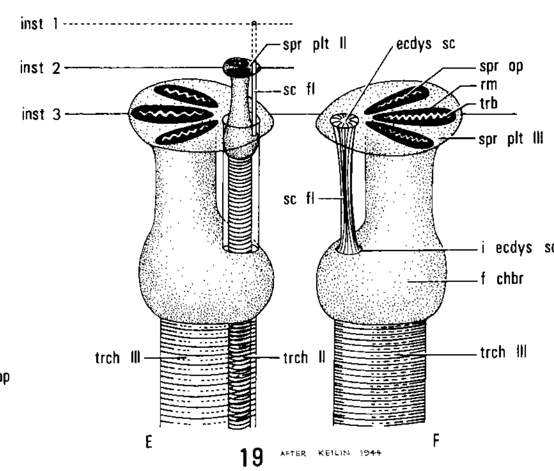

19

Figs. 3.15–19. Respiratory features of Diptera larvae: (15) diagrammatic dorsal view of generalized tracheal system; (16) diagrammatic representation of spiracular systems; (17–19) three basic types of spiracles—*A* before ecdysis, *B* after ecdysis, *C* and *D* anterior view before and after ecdysis.

Abbreviations: cph gng trch, cephalic ganglionic trachea; d anas, dorsal anastomosis; d cerv anas, dorsal cervical anastomosis; d cerv trch, dorsal cervical trachea; d long trk, dorsal longitudinal trunk; ecdys sc, ecdysial scar; f chbr, felt chamber; i ecdys sc, inner ecdysial scar; inst, instar; l long trk, lateral longitudinal trunk; rm, rima; sc fl, scar filament; spr, spiracle; spr op, spiracular opening; spr plt, spiracular plate; spr trch, spiracular trachea; st, sternite; trb, trabecula; trch, trachea; trn con, transverse connective; v anas, ventral anastomosis; v cerv trch, ventral cervical trachea; v gng trch, ventral ganglionic trachea; vis trch, visceral trachea.

through which the spiracular trachea of the previous instar is withdrawn becomes the spiracular opening (air inlet) of the next instar. The posterior spiracles of the Tabanidae are apparently also of this type. The spiracular opening in larvae of the Tabanidae is not associated with the exposed, vertically linear element of the spiracle (Fig. 31.55) homologous to that found in other larvae on which are located the spiracular openings; rather, the spiracular openings are situated on either side of these elements beneath a loose fold of integument, and they communicate with simple lateral apertures in the tracheal trunks (Teskey 1969). In the type II spiracle (Fig. 18), found in most Nematocera and the orthorrhaphous Brachycera, the ecdysial opening is closed and forms a central ***ecdysial scar***. Perforated oval or linear areas providing new means of air intake are usually arranged around this scar more or less radially. The spiracular openings and ecdysial scar are located on a more or less well-defined ***spiracular plate***. But of greatest significance in type II as well as in type I spiracles is the fact that the ***felt chamber*** of successive larval instars is developed around the felt chamber of the previous instars. The felt chamber lies between the spiracular plate and the trachea. The chamber may bear on its walls various filamentous outgrowths that sometimes ramify to form a maze of passages. The chamber functions as a filter. The type III spiracle (Fig. 19), characteristic of the Muscomorpha, has the ecdysial scar situated near the margin of the spiracular plate. The number of spiracular openings are usually greatly reduced, commonly to only three on each of the posterior spiracles. The ecdysial scar is displaced because the felt chamber develops beside, not around, the felt chamber of the previous instar. The trachea of the previous instar is withdrawn through a hole at the base of the newly developed felt chamber.

In Diptera larvae, Krivosheina (1969) distinguished two types of spiracles, radially symmetric and asymmetric. This distinction appears to coincide with Keilin's observations in that he emphasized the symmetry of the encircling arrangement of the spiracular openings and the central position of the ecdysial scar on the type II spiracle. The type III spiracle is asymmetric. However, the spiracles of several families of lower Diptera are decidedly asymmetric, as in the Mycetophilidae, the Sciaridae, the Anisopodidae, the Thaumaleidae, the Therevidae, the Scenopinidae, and the Asilidae, with the spiracular openings only partially encircling the spiracular plate (Figs. 19.21–22, 38.13–14). The intermediate abdominal spiracles of some Mycetophilidae have only one spiracular opening. Yet there is little doubt that the spiracles of these larvae are of type II. Keilin (1944) showed this to be the case in larvae of *Thereva* (Therevidae) and *Laphria* (Asilidae). Madwar (1937) illustrated the central position of the ecdysial scar filament within the felt chambers of several species of Mycetophilidae and Sciaridae.

The symmetry of the arrangement of the spiracular openings on the type II spiracle is greater than that of the type III spiracle, particularly in relation to the terminal spiracles. In nearly all type II spiracles a uniform, linear, semicircular or circular arrangement of the spiracular openings occurs, and the spiracular openings usually number more than three. If more than three spiracular openings occur in the type III spiracles, they are rarely, or never, similar in shape or symmetrically organized.

The spiracular openings are associated with a few to many variously shaped (oval, linear, lenticular, curved, serpentine), sometimes elevated areas (Figs. 5.8–10, 5.13, 5.16, 5.18, 5.20–30, 5.34–35, 7.86, 13.15–17, 21.8). The longer spiracular openings each sometimes bear a marginal supporting sclerotization called a ***rima*** (*pl.* ***rimae***); the rima on each side of the spiracular opening may be further strengthened by cross struts or serrations called ***trabeculae*** (*sing.* ***trabecula***) (Figs. 18; 5.80). The margin of the spiracular plate itself, called the ***peritreme***, is also usually sclerotized. Hypodermic ***spiracular glands*** that secrete a hydrofuge substance open on the surface of the spiracular plate. These glands can normally be detected only under special circumstances. In most larvae of the Schizophora the glands are associated with variously branched ***spiracular hairs***. Normally four such hairs are located near the outer end of each spiracular opening (Figs. 5.39, 5.104). In larvae of the Coelopidae a fringe of spiracular hairs encircles the spiracle inside the peritreme (Fig. 5.85). An area or areas of scar tissue marking the point of withdrawal of the spiracle and trachea of the previous instar is prominent on most spiracular plates. Normally only one such ecdysial scar is present, but in *Bibio* and *Dilophus* (Bibionidae) two and three scars, respectively, are present (Figs. 13.16–17). Major branching of tracheae occurring at the spiracle has resulted in these multiple scars.

The spiracles are usually sessile in larvae of the Nematocera, whereas they are commonly more or less elevated above the body surface on short supporting structures in larvae of the Brachycera. However, in the Scatopsidae each posterior spiracle occurs at the end of a sclerotized cylinder that is at least three times longer than its diameter (Fig. 20.24). Any greater elevation of the posterior spiracles than this is apparently an adaptation to living in liquid media. In these cases the posterior spiracles occur together at the end of a ***respiratory siphon***. Such siphons may be relatively short as in representatives of the Psychodidae, the Culicidae, the Tabanidae, the Stratiomyidae, and the Ephydridae (Figs. 5.62–63, 17.15, 25.28–32, 31.51–52, 36.84), or slender, elongated, and sometimes retractable as in the Axymyiidae, the Ptychopteridae, some Syrphidae, and the Aulacigastridae (Figs. 5.15, 5.64, 11.6, 22.5).

Another adaptation to an aquatic existence is seen in some Stratiomyidae, where the terminal spiracles lie within a ***spiracular atrium*** (Fig. 36.86). The opposing edges of this atrium normally bear fringes of hydrophobic hairs that surround a bubble of air when the larva submerges. Lobes surrounding the posterior spiracles can achieve the same effect as a spiracular atrium, especially when these lobes are fringed with hydrophobic hairs as in the Tipulidae and the Dolichopodidae (Figs. 7.78, 7.81, 7.84, 48.40). The bubble of air may act as a gill (Hennig 1973). Larvae of the Sarcophagidae (Fig. 5.84) have a spiracular atrium that almost certainly offers protection to the posterior spiracles in both wet and dry environments even though it is not fringed and cannot be completely closed. Larvae of *Gasterophilus* (Gasterophilidae), living much of their lives in the stomachs of horses, can completely cover their posterior spiracles with two transverse folds of integument.

The posterior spiracles of some larvae, e.g. some species of *Chrysops*, *Merycomyia*, and *Tabanus* (Tabanidae), *Chrysogaster* (Syrphidae), and *Notiphila* (Ephydridae) (Figs. 5.61–62, 31.58–59), are modified to form a ***respiratory spine***. Hinton (1957) suggested that such spines are used to penetrate the air spaces in aquatic plants. However, the respiratory spines of tabanid larvae do not constitute the point of air intake. Spines or pointed projections having no known function are present on the margin of the spiracular plate of some larvae of the Micropezidae, the Psilidae, the Lonchaeidae, and the Clusiidae (Figs. 5.86–89, 5.91).

In the larvae of the Muscomorpha the anterior spiracles exhibit a widely varied appearance, in most cases quite different from the posterior spiracles. They are almost always elevated or projecting and involve several to many spiracular openings. Among the Aschiza these openings are most commonly sessile on a spiracular stalk. They are either randomly arranged along the sides of the stalk (Fig. 5.64) or arranged in a row near to or at its apex (Figs. 5.16, 5.42). In the Schizophora the openings are most commonly at the ends of papillae of various lengths projecting from the stalk. The branching of these papillae is diagnostically important. This branching may be characterized as fan-like, with the papillae more or less arising from a common point (Figs. 5.68, 5.77, 5.103); semicircular (Figs. 5.92, 5.96); tree-like, with the papillae arising laterally on a central axis (Figs. 5.66, 5.71, 5.93, 5.97); bicornuate, a rather distinctive modification of the fan form that is distinctive of larvae of some Tephritidae, *Tanypeza* (Tanypezidae), and the Scathophagidae (Fig. 5.81); brush-like (Figs. 5.22–23, 5.26); or dendritic, with numerous long, slender filaments having a common point of origin and capable of retraction within the body (Fig. 5.60). Although these are the basic configurations, there are many intergrades between the fan-like and tree-like forms.

Anus, anal papillae, and tracheal gills. The ***anus*** is located ventrally or posteriorly on the terminal body segment. A terminal position is found only among some Nematocera, e.g. *Bibio* (Bibionidae) and Lestremiinae (Cecidomyiidae). The anus may be situated in a transverse or, more commonly, a longitudinal (Figs. 13.12–14, 16.10) cleft. This cleft is usually bordered or surrounded by the ***perianal pad***, an area of distinctive size, shape, and surface contour.

The perianal pad is a prominent feature of many Diptera (Figs. 5.59, 5.70, 5.91, 7.71, 19.19–20). Stoffolano (1970) described some of the variations in the pad, referring to its very thin cuticle and large epidermal cells containing polytene chromosomes; but he provided no evidence as to its function.

Outgrowths of distinctive shape and size, called ***anal papillae*** (Figs. 7.72, 7.75, 11.6, 25.32, 27.90, 29.114), are found arising from the perianal pad or from within the anus in many aquatic or semiaquatic larvae of the Nematocera. The anal papillae are delicate, thin-walled structures, which in the resting state are sometimes retracted within the anus. One to three pairs of anal papillae are normally present, although these are sometimes secondarily branched.

The anal papillae are commonly considered to have a respiratory function. This theory is valid when the papillae are especially well tracheated, for example, in some Culicidae (Lewis 1949); however, they are primarily used as osmoregulatory organs (Wigglesworth 1938, Brindle 1952, Strenzke and Neumann 1960).

The term tracheal gills has sometimes been used for the anal papillae, but because the respiratory function of these structures is of minor importance, this term is inappropriate. However, there are other structures ventrally on the preanal segments in some Chironomidae and Blephariceridae (Figs. 8.8, 29.115) that apparently have only a respiratory function and can rightfully be called ***tracheal gills*** (Harnisch 1954, Whitton 1963).

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KEY TO FAMILIES—ADULTS 4

J. F. McAlpine

This key is designed primarily for Nearctic Diptera and it includes only the 108 families that occur, or are likely to occur, in the Nearctic region. Most, though probably not all, the characters employed are reliable for keying most non-Nearctic members of the same families. For example, if one were keying a Neotropical specimen of the Agromyzidae it would probably key out readily to that family. However, the user should be aware that atypical members of some families from other regions probably do not key out satisfactorily.

A single, continuous key is provided because it is more convenient for most users than are several keys for the two suborders and other main divisions of the order. A synoptic key to the main divisions is given at the beginning to reduce to some degree the necessity of going through the entire key and turning many pages before arriving at the final couplet for keying a particular specimen.

Most of the characters used are illustrated either in this section or in accompanying sections of this volume. A selection of labeled wings (Figs. 1–76), representing most of the Nearctic families, has been assembled for ready reference and comparison. Likewise for convenience, some heads of Nematocera (Figs. 77–84) and orthorrhaphous Brachycera (Figs. 85–96) are reproduced. Because this volume does not include treatments of the 65 families of the Muscomorpha (cyclorrhaphous Brachycera), examples of heads (Figs. 97–122) and habitus figures (Figs. 123–161) prepared for particular sections are repeated in this chapter to illustrate the key. A few special features (Figs. 162–181) are illustrated in this chapter only. The terms and abbreviations used here and throughout the Manual are defined in Chapter 2.

The first couplet, which attempts to separate fully winged forms from those whose wings are reduced or absent (Figs. 182–194), may give trouble to those who are unfamiliar with Diptera. However, doubtful forms are accommodated in both parts of the key and key out satisfactorily regardless of which way they are taken. Users are also cautioned that wing venation, employed so frequently throughout the key, is sometimes hard to see and interpret. The extent of the costa (whether it continues around the wing or not) and the development of the subcosta (whether it is complete or not) are among the most difficult features to ascertain. These and other venational characters are best seen by using transmitted, rather than reflected, light over a white background.

In many cases new characters are used to distinguish groups of families as well as individual families. For example, the Calyptratae is separated from the remaining Schizophora primarily by means of a well-developed greater ampulla (couplet 58). This character is easily seen and is much more dependable than those previously used for this purpose, namely a dorsal seam on the pedicel (second antennal segment), enlarged lower calypter, and the allegedly complete transverse scutal suture. Similarly, a new venational character is used for separating the families Bombyliidae and Therevidae (couplet 48), because the characters used in previous keys are inadequate for accurate separation of all members of these two families.

Some families, e.g. Thaumaleidae, are brought out in several places in the key, and portions of some families, e.g. Cecidomyiidae, are brought out separately. This duplication is desirable for several reasons. Sometimes the real or apparent conditions of characters used in certain forms are such that they may be taken either way in a particular couplet; for example, the family Thaumaleidae, in which the antennal flagellum is unusually short and consolidated for a nematocerous fly (couplets C and 3), is taken out in couplet 41, as well as in couplet 13. In other cases both alternatives of the characters used in a particular couplet sometimes occur within a single family; for example, in the Cecidomyiidae the ocelli may be present (Lestremiinae) or they may be absent (Cecidomyiinae and Porricondylinae) and the first tarsomere may be normal (Lestremiinae) or it may be reduced and fused with the second tarsomere (Cecidomyiinae and Porricondylinae). Therefore, most of the Cecidomyiidae keys out in couplet 11, and a lesser part in couplet 12. In a few cases common but distinctive members of a family are removed separately; for example, it seemed preferable to take *Pollenia* out in a separate couplet (couplet 63) on the basis of obvious characters rather than to carry it along with difficulty to a couplet that removes the remainder of the family.

Synoptic key to main divisions

A. Wing greatly reduced or absent (Figs. 182–194) 130
  Wing well-developed .... B

B. Wing extremely narrow, with greatly reduced venation and extraordinarily long fringes (Fig. 5). Flagellum with an elongate annulated stalk and inflated knob (Figs. 182; 10.3). Very small aquatic flies less than 2 mm long, unusually slender, pale, and weakly sclerotized (Fig. 182) ....aberrant NEMATOCERA....**Nymphomyiidae** (Ch. 10)

Wing broader, with more complete venation and shorter fringes. Not agreeing in other characters C

C. Antennal flagellum with four or more freely articulated flagellomeres (Figs. 2.12–21), typically with apical ones not consolidated into a stylus or arista. Palpus usually with three to five segments (Figs. 77–84) ....NEMATOCERA....4

Antennal flagellum usually consolidated into a single compound segment, typically bearing a terminal to dorsal stylus or arista (Figs. 2.22–45). Palpus with not more than two segments (Figs. 87, 88, 103–105) ....BRACHYCERA....D

D. Ptilinal fissure and lunule absent (Figs. 85–96). CuA_2 usually long, often reaching wing margin or joining A_1 near its apex (Figs. 27–52) ....ORTHORRHAPHOUS BRACHYCERA and MUSCOMORPHA, ASCHIZA....30

Ptilinal fissure and lunule present (Figs. 2.8; 97–122). CuA_2 usually short, usually joining A_1 near wing base (Figs. 53–76) ....MUSCOMORPHA, SCHIZOPHORA....E

E. Thorax usually strongly flattened, with venter greatly broadened and widely separating mid and hind coxae medially (Figs. 160, 161, 171). Claws strongly recurved and toothed (Fig. 179). Adult ectoparasitic on birds and mammals ....CALYPTRATAE, HIPPOBOSCOIDEA....56

Thorax not unduly flattened, with venter narrow and with mid and hind coxae close together medially. Claws not strongly recurved and toothed (Figs. 2.77–78). Adult not ectoparasitic on vertebrates ....F

F. Greater ampulla present as a distinct bulbous swelling below wing base (Fig. 2.66). Vibrissa usually present (Figs. 2.8–10, 2.66;as in Figs. 114–122). Pedicel always with a complete dorsal seam (Figs. 2.43–45) ....CALYPTRATAE, OESTROIDEA and MUSCOIDEA....58

Greater ampulla usually absent, but if present (Tephritidae, Psilidae, Ropalomeridae, and Periscelididae), then vibrissa absent. Pedicel usually with dorsal seam absent or incomplete ....ACALYPTRATAE....72

Complete key to families

1. Wing well-developed, longer than thorax 2

Wing absent or greatly reduced (usually shorter than thorax) (Figs. 182–194) 130

2. Wing extremely narrow, with greatly reduced venation and extraordinarily long fringes (Fig. 5). Flagellum with an elongate annulated stalk and inflated knob (Figs. 182; 10.3). Compound eyes joined on ventral surface of head behind vestigial mouthparts (Fig. 10.9). Very small aquatic flies less than 2 mm long, unusually slender, pale, and weakly sclerotized (Fig. 182) ......aberrant NEMATOCERA....**Nymphomyiidae** (Ch.10)

Wing broader, with more complete venation and shorter fringes. Not agreeing in other characters 3

3. Antennal flagellum usually with four or more freely articulated flagellomeres (Figs. 2.12–21), with apical segments usually not consolidated into a stylus or arista. Palpus usually with three to five segments (Figs. 77–84) ....NEMATOCERA....4

Antennal flagellum usually consolidated into a single compound segment typically bearing a terminal to dorsal stylus or arista (Figs. 2.22–45). Palpus with not more than two segments (Figs. 87, 88, 103–105) ....BRACHYCERA....29

4. Wing with a network of fine crease-like lines between the true veins, and with the number of main veins more or less reduced; anal lobe strongly projecting (Figs. 3, 4) 5

Wing without a network of crease-like lines between the main veins, and not agreeing with above in other respects 6

5. Wing unusually broad and fan-like (Fig. 4). Flagellum with four flagellomeres, the terminal one excessively lengthened in male (Fig. 9.1) ....**Deuterophlebiidae** (Ch. 9)

Wing longer and narrower than above (Fig. 3). Flagellum with 11–13 flagellomeres, the terminal one not lengthened (Fig. 8.1) .... **Blephariceridae** (Ch. 8)

6. Halter with a basal appendage, the prehalter (Figs. 2.71, 22.1) ...... **Ptychopteridae** (Ch. 22)

Halter without a prehalter (Figs. 2.70, 2.72) 7

7. Wing with two strong anal veins, A_1 and A_2, reaching wing margin (Figs. 6, 8). Legs long and slender (Figs. 7.1, 18.1) 8

Wing with at least A_2 absent or fading out before reaching wing margin (Figs. 9–26). Legs variable 9

8. Scutum with a complete V-shaped suture (Fig. 7.1). Ocelli absent or rudimentary (Fig. 7.2). A_2 usually more than half as long as A_1 and relatively straight (Fig. 6) .... **Tipulidae** (Ch. 7)

Scutum with V-shaped suture incompletely developed in middle. Ocelli present (Fig. 18.1). A_2 much less than half as long as A_1, and strongly curved at apex (Fig. 8) .... **Trichoceridae** (Ch. 18)

9. R with five free branches reaching wing margin; cell d present; anal lobe well-developed (Fig. 1) .... **Tanyderidae** (Ch. 6)

R usually with fewer than five free branches (Figs. 7, 9–26), but if five free radial branches present (some Psychodidae), then cell d absent and anal lobe undeveloped (Fig. 2) 10

10. C continuing around wing, though weaker along hind margin (Figs. 2, 11–14, 17, 22) 11

C ending just beyond insertion of last branch of R, usually near wing tip (Figs. 7–10, 13, 15, 16, 18–26); if this character indistinct (*Cramptonomyia*), then R with three branches and with a supernumerary crossvein, crossvein r-r, forming a closed cell br_3 between R_{2+3} and R_{4+5} (Fig. 7) 17

11. First tarsomere much shorter than second and both tarsomeres more or less fused; each tarsus thus appearing to be, at most, four-segmented (Fig. 16.81). Ocelli absent. C usually with a break just beyond insertion of R_{4+5} (Fig. 22). Small fragile midges with weakly veined wings (Fig. 16.1) .... **Cecidomyiidae** (**Cecidomyiinae** and **Porricondylinae**) (Ch. 16)

First tarsomere longer than the second (Fig. 16.80); each tarsus clearly five-segmented. Other characters variable 12

12. Ocelli usually present, but if not (females of some *Conarete*), then C with a break just beyond insertion of R_{4+5} (Fig. 22). Small fragile midges with weakly veined wings (Fig. 16.1) .... **Cecidomyiidae** (**Lestremiinae**) (Ch. 16)

Ocelli absent. C without a break just beyond insertion of R_{4+5}. Small to relatively large midges and gnats 13

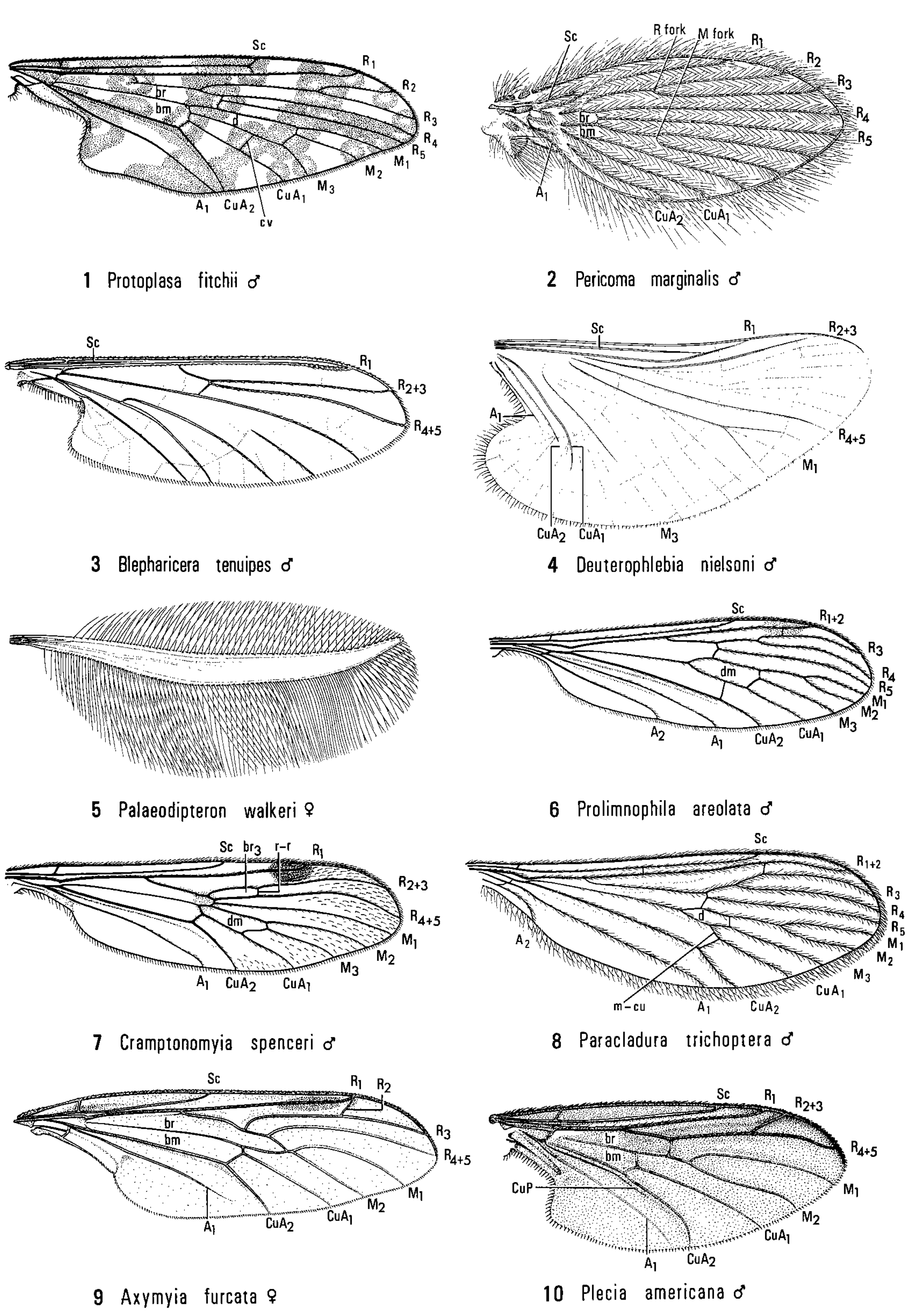
13. Antenna short, about as long as head; flagellum unusually short and slender for Nematocera, with two or three outstanding bristles at apex of terminal flagellomere (Fig. 2.19). Wing with six or seven veins reaching margin (Figs. 17; 26.2–3) .... **Thaumaleidae** (Ch. 26)

Antenna at least twice as long as head; flagellum not unusually reduced, usually with whorls of long hairs on all flagellomeres. Wing with 9–11 veins reaching margin 14

14. Sc incomplete or ending in C or R_1 before middle of wing; therefore one long vein (R_1) reaching C in apical half of wing in front of first forked vein (R_2 and R_3); M with three branches; cells bm and br, if present, not more than half as long as wing (Fig. 2). Pedicel usually smaller than scape and not cup-shaped (Figs. 17.2–9). Very hairy moth-like flies (Fig. 17.1) .... **Psychodidae** (Ch. 17)

Sc complete, ending in C at or beyond middle of wing; therefore two long veins (Sc and R_1) reaching C in apical half of wing in front of first forked vein (R_2 and R_3); M with two branches; cells br and bm usually more than half as long as wing (Figs. 11, 12, 14). Pedicel usually larger than scape and cup-shaped (Figs. 2.12–14). Sparsely to moderately hairy mosquito-like flies 15

15. Scales present on wing veins (Fig. 14), head, and legs and usually on other parts of body (Figs. 25.2–20). Proboscis long, extending far beyond clypeus (Fig. 82) .... **Culicidae** (Ch. 25)



Figs. 4.1–10. Wings of Nematocera: (1) *Protoplasa fitchii* Osten Sacken (Tanyderidae); (2) *Pericoma marginalis* (Banks) (Psychodidae); (3) *Blephariceratenuipes* (Walker) (Blephariceridae); (4) *Deuterophlebia nielsoni* Kennedy (Deuterophlebiidae); (5) *Palaeodipteron walkeri* Ide (Nymphomyiidae); (6) *Prolimnophila areolata* (Osten Sacken) (Tipulidae); (7) *Cramptonomyia spenceri* Alexander (Pachyneuridae); (8) *Paracladura trichoptera* (Osten Sacken) (Trichoceridae); (9) *Axymyia furcata* McAtee (Axymyiidae); (10) *Plecia americana* Hardy (Bibionidae) (*continued*).

Abbreviation: cv, crossvein.

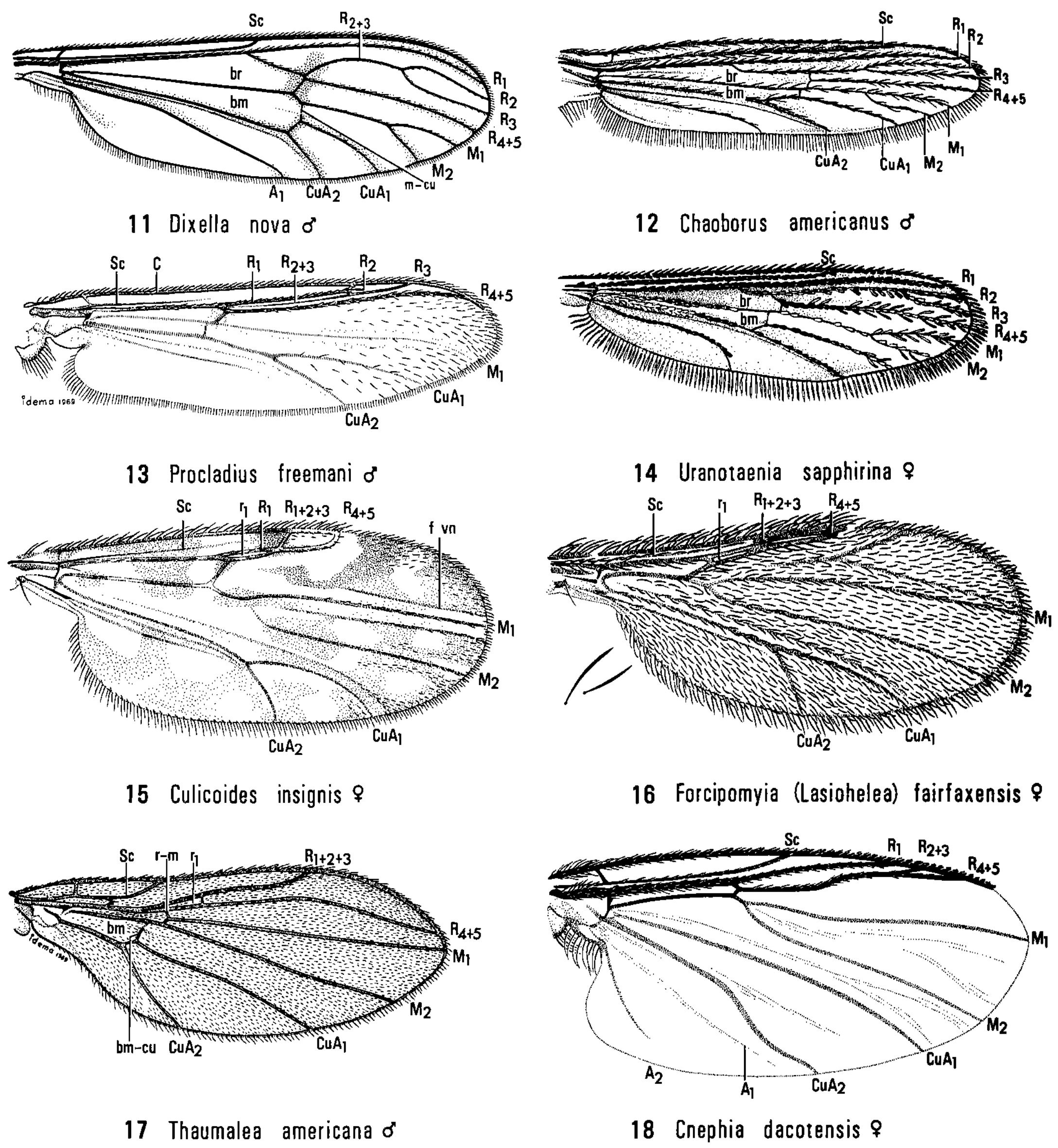
Scales absent from wing veins and other parts of body, though conspicuous hairs frequently present. Proboscis short, barely extending beyond clypeus (Fig. 84) 16

16. Wing veins with very short relatively sparse inconspicuous hairs; stem of R_{2+3} strongly forwardly arched (Fig. 11). Antenna with relatively short sparse indistinctly arranged hairs (Fig. 2.12) .... **Dixidae** (Ch. 23)

Wing veins with long dense conspicuous hairs; stem of R_{2+3} nearly straight (Fig. 12). Antenna with abundant long hairs in distinct whorls (Figs. 24.1, 24.4) .... **Chaoboridae** (Ch. 24)

17(10). Ocelli absent 18

Ocelli present, except in *Hesperodes* (Mycetophilidae) 20

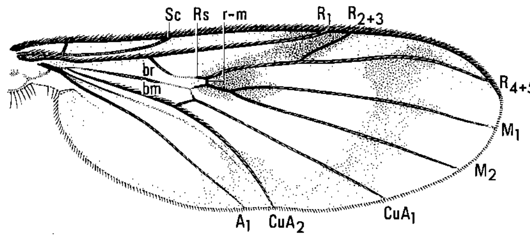


Figs. 4.11–18. Wings of Nematocera (*continued*): (11) *Dixella nova* (Walker) (Dixidae); (12) *Chaoborus americanus* (Johannsen) (Chaoboridae); (13) *Procladius freemani* Sublette (Chironomidae); (14) *Uranotaenia sapphirina* (Osten Sacken) (Culicidae); (15) *Culicoides insignis* Lutz (Ceratopogonidae); (16) *Forcipomyia* (*Lasiohelea*) *fairfaxensis* Wirth (Ceratopogonidae); (17) *Thaumalea americana* Bezzi (Thaumaleidae); (18) *Cnephia dacotensis* (Dyar & Shannon) (Simuliidae) (*continued*).
Abbreviation: f vn, false vein.

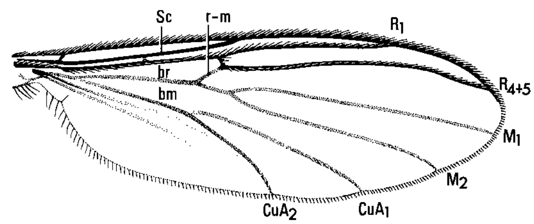
18. Antenna short, about as long as head; flagellum shortly setulose in both sexes (Fig. 81). Wing broad, with posterior veins weak (Fig. 18) .... **Simuliidae** (Ch. 27)

Antenna much longer than head, and distinctly hairy, typically more so in male than in female (Figs. 2.13–14). Wing usually narrow, with posterior veins usually strong (Figs. 13, 15–16) 19

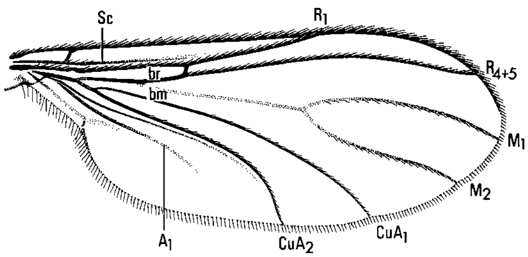
19. Two branches of M present; M_2 usually distinct, sometimes weakened at base, rarely obsolescent; never more than two branches of R reaching wing margin; R_{2+3}, if present, crossvein-like and forming a closed cell r_1 (first radial cell) (Figs. 15, 16). Anterior thoracic spiracle nearly round, separated (sometimes narrowly) from postspiracular membrane by dorsal extension of anepisternum, and situated nearly level with lower



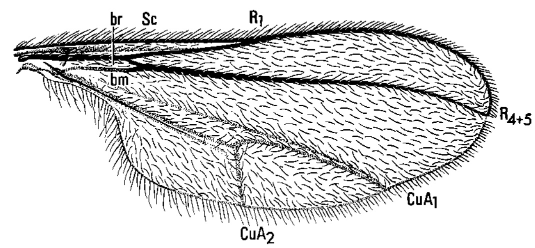
19 Paleoplatyura johnsoni ♂



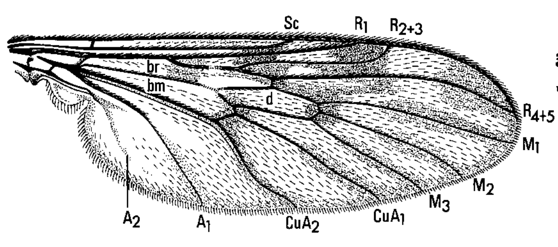
20 Boletina sp. ♂



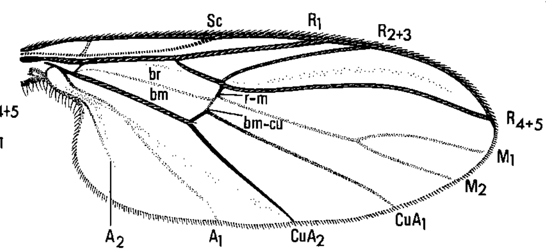
21 Sciara sp. ♂



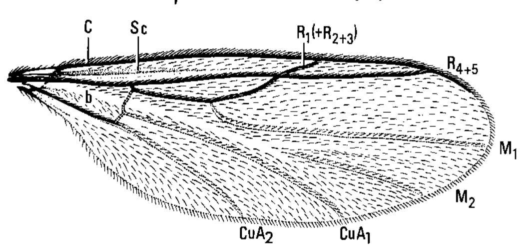
22 Cecidomyia resinicola ♂



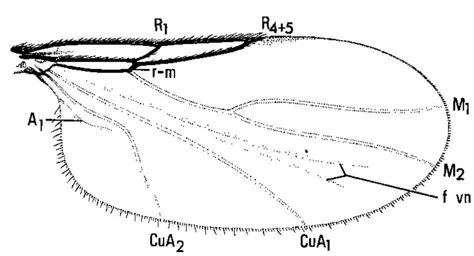
23 Sylvicola fenestralis ♂



24 Mycetobia divergens ♀



25 Synneuron decipiens ♀



26 Coboldia fuscipes ♂

Figs. 4.19–26. Wings of Nematocera (*concluded*): (19) *Paleoplatyura johnsoni* Johannsen (Mycetophilidae); (20) *Boletina* sp. (Mycetophilidae); (21) *Sciara* sp. (Sciaridae); (22) *Cecidomyia resinicola* (Osten Sacken) (Cecidomyiidae); (23) *Sylvicola fenestralis* (Scopoli) (Anisopodidae); (24) *Mycetobia divergens* Walker (Anisopodidae); (25) *Synneuron decipiens* Hutson (Synneuridae); (26) *Coboldia fuscipes* (Meigen) (Scatopsidae).

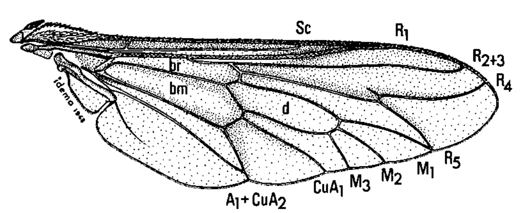
Abbreviation: f vn, false vein.

margin of paratergite (Figs. 28.2, 28.12–15). Mouthparts of female with blade-like mandibles usually present (Fig. 80). Postnotum usually without a longitudinal groove .... **Ceratopogonidae** (Ch. 28)

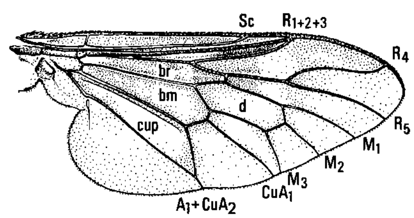
One branch of M present; M_2 never apparent; usually three branches of R reaching wing margin; R_{2+3}, if present, ending in wing margin (Fig. 13). Anterior thoracic spiracle distinctly oval, open posteriorly to postspiracular membrane, and situated well below level of lower margin of paratergite (Figs. 29.38–48). Mouthparts of both sexes lacking functional mandibles (Fig. 83). Postnotum usually with a longitudinal groove (Figs. 29.26–29) .... **Chironomidae** (Ch. 29)

20. Wing with cell d (Fig. 29), and with both cells m_3 and cu*p* closed before wing margin (Fig. 34.2). Antennal flagellum strikingly pectinate (Fig. 89) .... aberrant ORTHORRHAPHOUS BRACHYCERA .... **Xylophagidae (*Rachicerus*)** (Ch. 34)

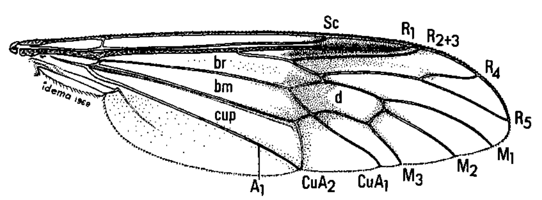
Wing with (Figs. 7, 23) or without (Figs. 9, 10, 19–22, 24–26) cell d or dm, but with both cells m_3 and cu*p* open to wing margin. Antennal flagellum variable, but not as above..21



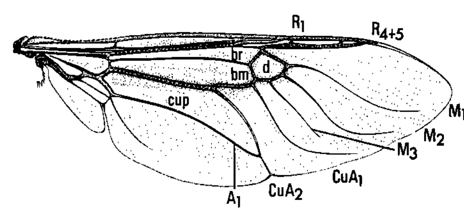
27 Esenbeckia delta ♂



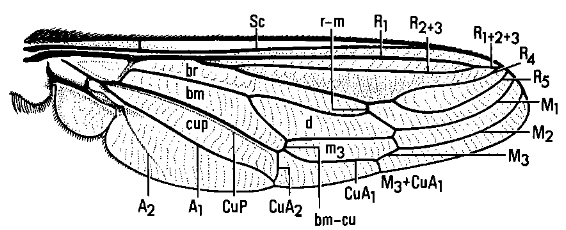
28 Atherix variegata ♀



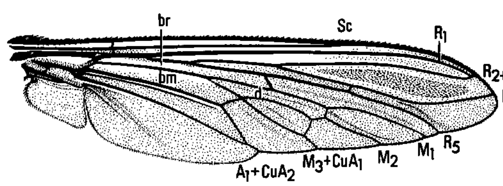
29 Xylophagus abdominalis ♀



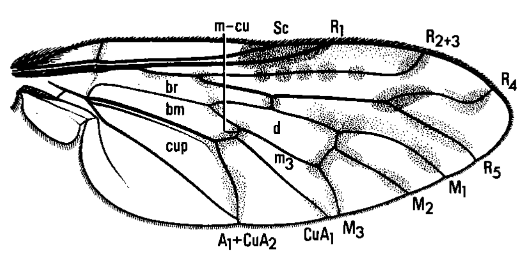
30 Anoplodonta nigrirostris ♀



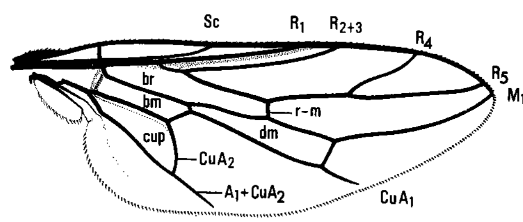
31 Rhaphiomidas acton ♂



32 Promachus bastardii ♂



33 Megalilinga insignata ♂



34 Scenopinus fenestralis ♀

Figs. 4.27–34. Wings of orthorrhaphous Brachycera: (27) *Esenbeckia delta* (Hine) (Tabanidae); (28) *Atherix variegata* Walker (Athericidae); (29) *Xylophagus abdominalis* Loew (Xylophagidae); (30) *Anoplodonta nigrirostris* (Loew) (Stratiomyidae); (31) *Rhaphiomidas acton* Coquillett (Apioceridae); (32) *Promachus bastardii* (Macquart) (Asilidae); (33) *Megalinga insignata* Irwin & Lyneborg (Therevidae); (34) *Scenopinus fenestralis* (Linnaeus) (Scenopinidae) (*continued*).

21. Wing with R three-branched and with a supernumerary crossvein (crossvein r-r) forming cell br_3 between R_{2+3} and R_{4+5}; cell dm usually closed; M three-branched; A_1 complete (Fig. 7) .... **Pachyneuridae (*Cramptonomyia*)** (Ch. 12)

Wing with R sometimes having three branches, but never with a supernumerary crossvein or a closed cell between R_{2+3} and R_{4+5} (Figs. 10, 19, 23, 24); cell d present (Fig. 23) or absent (Figs. 9, 10, 19–22, 24–26); M with two (Figs. 9, 10, 19–21, 24–26) or three branches (Fig. 23); A_1 complete (Figs. 19, 23, 25) or incomplete (Figs. 9, 10, 20, 21, 25, 26) 22

22. Wing with cell d present; M with three branches (Fig. 23) .... **Anisopodidae (Anisopodinae)** (Ch. 19)

Wing with cell d absent; M never with more than two free branches 23

23. Wing with cells br and bm confluent and with six veins arising from the composite basal cell; Sc and A_1 complete (Fig. 24) .... **Anisopodidae (*Mycetobia*)** (Ch. 19)

Wing venation differing from above in one or more respects; if cells br and bm confluent, then with at most five veins arising from composite basal cell (Figs. 19, 25). Sc and A_1 complete or incomplete (Figs. 9, 19, 25) 24

24. R with four branches; R_2 and R_3 occurring as two separate veins; R_2 short oblique and joining R_1 close to wing margin (Fig. 9). Scutum with a pair of shiny oval spots near middle. Tibiae without apical spurs (Fig. 11.1) .... **Axymyiidae** (Ch. 11)

R with three or fewer branches; R_2 and R_3 never occurring as two separate veins (Figs. 10, 19–21, 25, 26). Scutum without shiny spots. Tibiae with (Figs. 174, 176) or without spurs 25

25. Wing with two closed basal cells, that is, with cells br and bm separate and closed distally (Fig. 10). Pulvilli and empodium strongly and equally developed; acropod with three relatively similar pads (Fig. 13.1) .... **Bibionidae** (Ch. 13)

Wing with only one closed basal cell, that is, either with cells br and bm confluent (Fig. 25) or with cell bm open to wing margin (Figs. 20, 21, 26), except in a few Mycetophilidae (*Paleoplatyura*, Fig. 19, and *Platyura*). Pulvilli at most weakly developed; acropod never with three similar pads 26

26. Eyes nearly meeting below antennae, and holoptic above (Fig. 79). Small scatopsid-like flies (Fig. 21.1) .... **Synneuridae** (Ch. 21)

Eyes widely separated below antennae, with (Fig. 77) or without (Fig. 78) a narrow eye bridge above antennae. Size and form variable 27

27. Tibiae without apical spurs (Fig. 20.1). Wing with C ending far before wing apex, and usually with only C and R darkly pigmented (Fig. 26) .... **Scatopsidae** (Ch. 20)

Tibiae with apical spurs (Figs. 174, 176). Wing with C ending at or near wing apex, and usually with all veins darkly pigmented (Figs. 19, 20) 28

28. Eyes meeting in a narrow eye bridge above antennae (Fig. 77) (except in *Pnyxia* in which eyes are reduced in both sexes and wings and halteres are lacking in female, see couplet 136). Wing (Fig. 21) with stem and fork of M subequal in length, and with fork distinctly bell-shaped. All mesothoracic pleural sclerites bare (Figs. 15.12–13) .... **Sciaridae** (Ch. 15)

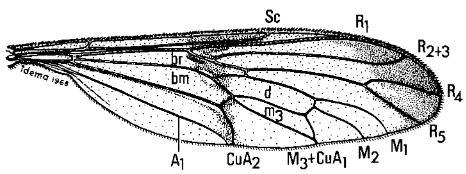
Eyes never meeting above antennae (Fig. 78). Wing (Figs. 19, 20) usually with fork of M much longer than stem, and lanceolate rather than bell-shaped. Usually some mesothoracic pleural sclerites at least weakly haired .... **Mycetophilidae** (Ch. 14)

29(3). Ptilinal fissure and lunule absent (Figs. 85–96). CuA_2 usually long, often reaching wing margin or joining A_1 near its apex (Figs. 27–52) .... ORTHORRHAPHOUS BRACHYCERA and MUSCOMORPHA, ASCHIZA....30

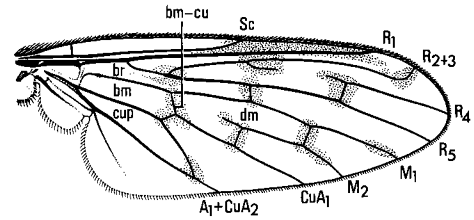
Ptilinal fissure and lunule present (Figs. 2.8; 97–122). CuA_2 usually short, usually joining A_1 near wing base (Figs. 53–76).......... MUSCOMORPHA, SCHIZOPHORA....56

30. Empodia pulvilliform; each acropod with three similar flattened pads below tarsal claws (Fig. 2.75). CuA_2 free (Figs. 35, 37, 39) or meeting A_1 in an acute angle near wing margin (Figs. 27–34) 31

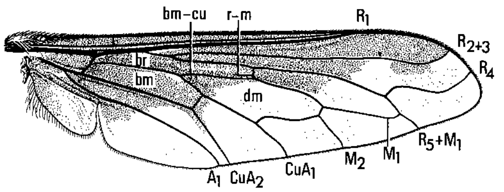
Empodia usually setiform or absent (Fig. 2.77); if acropod with three pads then empodium much narrower and more tapered than pulvilli; if empodia somewhat pulvilliform (some water-striding Empididae and Dolichopodidae), then CuA_2 joining A_1 at an obtuse angle far from wing margin (Figs. 41, 43, 45, 46) 41



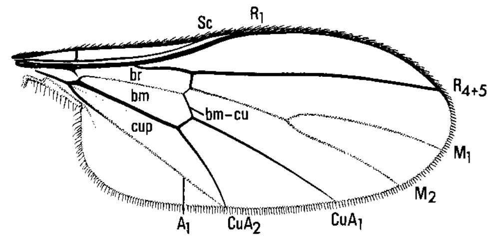
35 Vermileo tibialis ♂



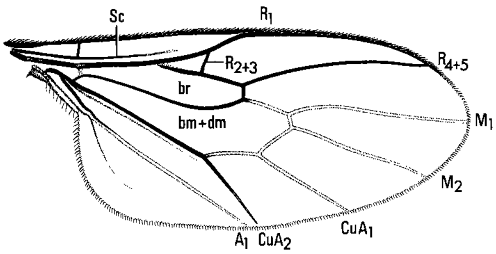
36 Phthiria sp. ♀



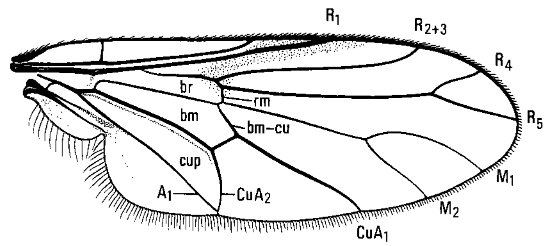
37 Bombylius major ♂



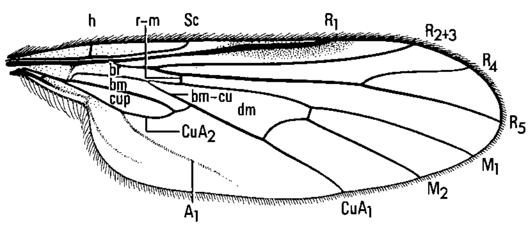
38 Empidideicus humeralis ♀



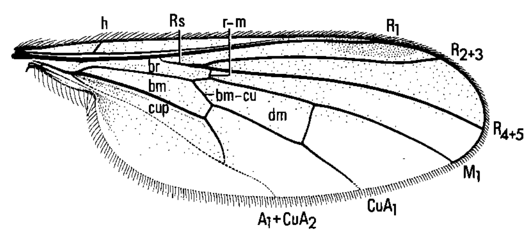
39 Glabellula crassicornis ♀



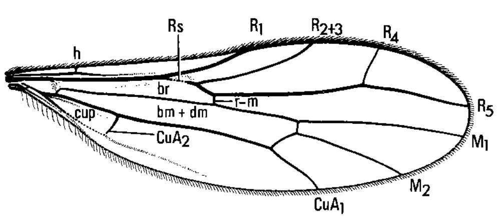
40 Hilarimorpha ditissa ♂



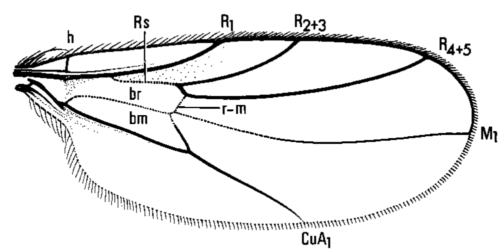
41 Hilara femorata ♂



42 Hybos reversus ♀



43 Neoplasta scapularis ♂



44 Microempis testacea ♀

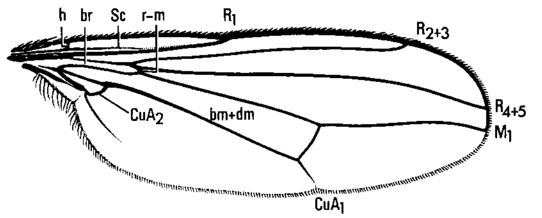
Figs. 4.35–44. Wings of orthorrhaphous Brachycera (*concluded*): (35) *Vermileo tibialis* (Walker) (Vermileonidae); (36) *Phthiria* sp. (Bombyliidae); (37) *Bombylius major* Linnaeus (Bombyliidae); (38) *Empidideicus humeralis* Melander (Bombyliidae); (39) *Glabellula crassicornis* (Greene) (Bombyliidae); (40) *Hilarimorpha ditissa* Webb (Hilarimorphidae); (41) *Hilara femorata* Loew (Empididae); (42) *Hybos reversus* Walker (Empididae); (43) *Neoplasta scapularis* (Loew) (Empididae); (44) *Micrempis testacea* Melander (Empididae).

31. Head unusually small, rarely more than half as wide as thorax; eyes holoptic or nearly so in both sexes. Lower lobe of calypter extremely large, wider than head (Figs. 43.1–2) .... **Acroceridae** (Ch. 43)

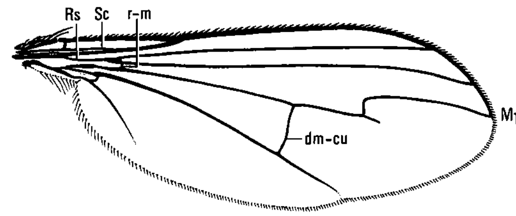
Head more than half as wide as thorax; eyes never holoptic in female. Lower lobe of calypter smaller, not as wide as head 32

32. Venation peculiar: branches of R and M more or less converging to apex of wing; branches of M curving forward and ending before or scarcely behind apex of wing, and with a composite 'diagonal vein' running from distal end of cell br to posterior margin of wing (Fig. 44.1) .... **Nemestrinidae** (Ch. 44)

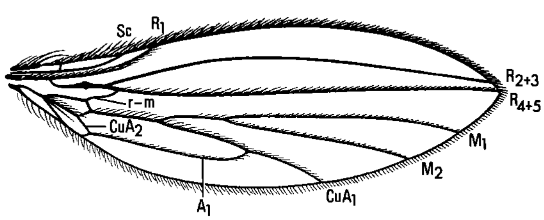
Venation more normal than above; branches of R and M diverging to apical wing margin; branches of M joining margin far behind apex of wing and without a composite 'diagonal vein' (Figs. 27–30) 33



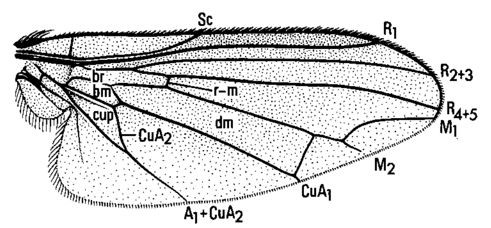
45 Hydrophorus intentus ♂



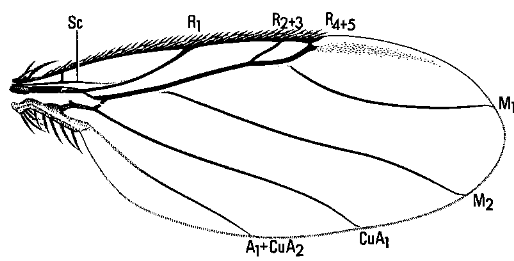
46 Dolichopus cuprinus ♂



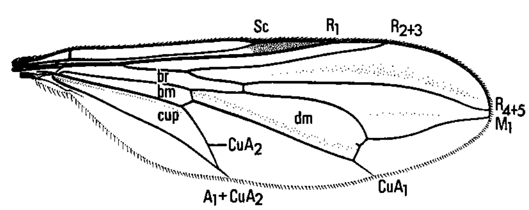
47 Lonchoptera furcata ♀



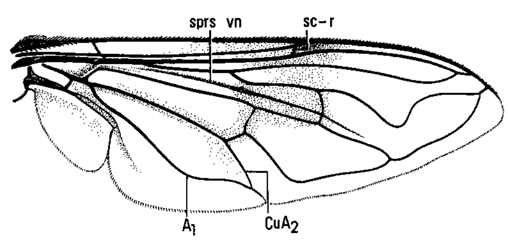
48 Platypeza consobrina ♂



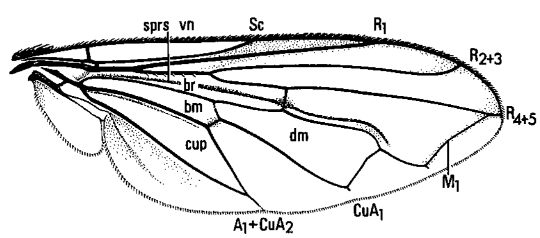
49 Lecanocerus compressiceps ♂



50 Pipunculus fuscus ♂



51 Eristalis tenax ♂



52 Brachyopa notata ♂

Figs. 4.45–52. Wings of Dolichopodidae and aschizous Muscomorpha: (45) *Hydrophorus intentus* Aldrich (Dolichopodidae); (46) *Dolichopus cuprinus* Wiedemann (Dolichopodidae); (47) *Lonchoptera furcata* (Fallén) (Lonchopteridae); (48) *Platypeza consobrina* Zetterstedt (not Nearctic) (Platypezidae); (49) *Lecanocerus compressiceps* Borgmeier (Phoridae); (50) *Pipunculus fuscus* Loew (Pipunculidae); (51) *Eristalis tenax* (Linnaeus) (Syrphidae); (52) *Brachyopa notata* Osten Sacken (Syrphidae).
Abbreviation: sprs vn, spurious vein.

33. C ending near apex of wing (Figs. 29, 30) 34
C continuing around wing, though usually weaker along posterior margin (Figs. 27, 28) .. 36

34. C usually ending well before, rarely nearly at, wing apex; branches of R more or less crowded anteriorly, and all ending in margin well before wing apex; cell d (or dm) short, usually little longer than wide (Fig. 30). Tibial spurs usually absent .... **Stratiomyidae** (Ch. 36)
C extending beyond wing apex; branches of R not crowded anteriorly, with R_5 ending at or beyond wing apex; cell d at least two times as long as broad (Fig. 29). Tibial spurs present on at least mid and hind tibiae 35

35. Fore tibia with a ventral apical spur (Fig. 34.1). Precoxal bridge absent (Fig. 165) .... **Xylophagidae (*Rachicerus*, some *Xylophagus*)** (Ch. 34)
Fore tibia without a ventral apical spur (Fig. 35.1). Precoxal bridge present (Fig. 162) .... **Xylomyidae** (Ch. 35)

36. Subscutellum strongly developed; posterior thoracic spiracle with a scale-like elevation immediately behind it (Fig. 168) (reduced in *Glutops*) 37
Subscutellum absent or very weakly developed; posterior thoracic spiracle never with a scale-like elevation immediately behind it 39

37. Flagellum with a slender nonannulated arista (Fig. 87). Wing with cell r_1 closed by vein R_{2+3} meeting C at end of R_1 (Fig. 28) .... **Athericidae** (Ch. 32)
Flagellum with a coarse annulated stylus (Figs. 85, 86). Wing with cell r_1 open, and with vein R_{2+3} meeting C far beyond end of R_1 (Fig. 27) 38

38. Both upper and lower calypteres large, subequal in size (Fig. 168). First abdominal tergite deeply notched in middle of posterior margin, and with a median suture (Fig. 170). .... **Tabanidae** (Ch. 31)
Upper calypter moderately large; lower one scarcely developed. First abdominal tergite without a median notch or suture .... **Pelecorhynchidae** (Ch. 30)

39. Wing with anal lobe and alula undeveloped, and with C in this area strong; alular incision absent (Fig. 35). Scutellum small, with flat bare disc (Fig. 39.1) .... **Vermileonidae** (Ch. 39)
Wing usually with anal lobe and alula well-developed, but if not (*Xylophagus*), C in this area weak or absent; alular incision present (weak in *Xylophagus*) (Fig. 29). Scutellum large, with convex hairy disc (Figs. 33.1, 34.1) 40

40. Clypeus exposed and strongly convex (Fig. 85), in profile with anterior surface bulging beyond parafacial (Figs. 33.2–3), and usually reaching dorsally to bases of antennae. Flagellum usually with not more than seven flagellomeres, and with distal ones frequently forming a slender stylus or arista (Figs. 33.2–8) .... **Rhagionidae** (Ch. 33)
Clypeus recessed in a deep facial groove and more or less flattened (Fig. 88), in profile with anterior surface depressed below level of parafacial (Figs. 34.5–7), and not reaching dorsally to bases of antennae. Flagellum usually with at least eight gradually smaller flagellomeres, and with apical ones not forming a slender stylus or arista (Figs. 34.4–8), except in *Dialysis* (Fig. 34.10) .... **Xylophagidae** (Ch. 34)

41(30). Palpus with five segments. Flagellum with 10 flagellomeres; terminal flagellomere with two or three outstanding bristles at apex (Fig. 2.19). Wing with six (Fig. 26.3) or seven veins reaching wing margin (Fig. 17). Pulvilli absent. Nematocera with short slender antennae (Fig. 26.1) .... **Thaumaleidae** (Ch. 26)
Palpus with at most two segments. Flagellum with three or four flagellomeres (Figs. 2.22–45); terminal flagellomere not as above. Wing venation otherwise. Pulvilli usually present (Figs. 2.75–78) 42

42. CuA_2 reaching wing margin near A_1 (Figs. 37–39) or joining A_1 near wing margin (Figs. 31–33, 36, 40, 50–52); if joining A_1, then CuA_2 at least 1.5 times longer than apical section of A_1, except in a few Bombyliidae (Figs. 45.29, 45.33) 43
CuA_2 absent (Figs. 44, 49) or vestigial (Fig. 43), or joining A_1 far from wing margin (Figs. 34, 41–43, 48); if joining A_1, then CuA_2 not or scarcely longer than apical section of A_1, except in a few Empididae (Fig. 47.22) and Platypezidae (*Polyporivora* spp.) 50

43. Branches of M peculiarly curved forward, more or less parallel to posterior wing margin; at least M_1 ending freely in wing margin before wing apex (Fig. 31). Large asilid-like flies 44

Branches of M not curved as above, but if forwardly bent then not ending freely in wing margin (Figs. 51, 52). Size and form variable 45

44. Flagellum unusually long, with a slender stalk-like base and strongly clubbed apex; stalk at least two times as long as combined length of scape and pedicel (Figs. 90; 40.1–10). A single ocellus present (Fig. 90) .... **Mydidae** (Ch. 40)

Flagellum shorter than head, without a stalk-like base; entire flagellum not much longer than combined length of scape and pedicel (Figs. 41.1, 41.4). Three ocelli present (Figs. 41.1, 41.4) .... **Apioceridae** (Ch. 41)

45. Spurious vein evident as a strong vein-like fold between Rs and M; M_1 curved forward more or less in line with crossvein dm-cu and joining unbranched R_{4+5} in a crossvein-like manner (Figs. 51, 52, 126) .... **Syrphidae** (Ch. 52)

Spurious vein undeveloped; M_1 usually not curved forward in a crossvein-like manner, but if so (some Bombyliidae) then joining a furcate R_{4+5} (Fig. 37) 46

46. Head strongly hemispherical, with compound eyes unusually large and almost meeting on midline both above and below antenna (Fig. 127). Flagellum with a dorsal arista (Fig. 127). R_{4+5} unbranched; C ending at wing apex (Fig. 50) .... **Pipunculidae** (Ch. 53)

Head usually not hemispherical, but if so (some Bombyliidae, Figs. 45.1–9), then flagellum without a dorsal arista (Figs. 45.1–7). R_{4+5} usually furcate; C usually continuing around wing (Figs. 32, 33, 36–40) 47

47. Vertex usually distinctly excavated between eyes; ocellar tubercle below dorsal level of eyes; eyes never holoptic (Fig. 91). Face relatively long, with a cluster or row of long bristles called the mystax (Fig. 91). Proboscis stout, polished; labella reduced and inconspicuous; hypopharynx protrusible, strongly developed for piercing (Fig. 2.54) .... **Asilidae** (Ch. 42)

Vertex not or only slightly concave; ocellar tubercle usually elevated above dorsal level of eyes (Fig. 92); eyes usually holoptic in male (Figs. 45.1, 46.1). Face relatively short, sometimes hairy, but without a mystax. Proboscis short and stout (Fig. 46.1) to long and slender (Fig. 45.1), usually dull pruinose; labella usually well-developed and conspicuous; hypopharynx not protrusible, not developed for piercing 48

48. Wing with cell bm truncate distally and with four corners from which arise four separate veins, namely M_{1+2}, M_3, CuA_1, and CuA_2; base of cell m_3 truncate (Fig. 33) .... **Therevidae** (Ch. 37)

Wing with cell bm, when present, pointed distally and with three corners from which arise three separate veins, namely M_{1+2}, $M_3 + CuA_1$, and CuA_2 (Figs. 36–40); base of cell m_3, when present, pointed (as in Fig. 35) 49

49. Wing with cell dm absent, and with R_{4+5} and M_{1+2} rather similarly forked, each fork not longer than its stem (Fig. 40). Small blackish empidid-like flies, 3–5 mm long, with dusky wings .... **Hilarimorphidae** (Ch. 46)

Wing with cell dm usually present (Figs. 36, 37), but if not (Figs. 38, 39), then R_{4+5} and M_{1+2} not similarly forked. Small to large yellowish to blackish flies, with marked or unmarked wings .... **Bombyliidae** (Ch. 45)

50(42). Flagellum with a minute stylus concealed in a subapical pit (Figs. 2.32, 38.6–10). Crossvein r-m at or beyond middle of wing; M unbranched and curved forward, joining R_{4+5} or closely approaching it in wing margin (Fig. 34) .... **Scenopinidae** (Ch. 38)

Flagellum usually with an elongate, fully exposed stylus or arista (Figs. 2.33–37) (absent in empidid *Allanthalia*, Fig. 47.45). Crossvein r-m well before middle of wing (Figs. 41–48) or absent (Fig. 49); M branched (Figs. 41, 43, 46–48) or unbranched (Figs. 42, 44, 45), sometimes curved forward but not as above 51

51. Wing pointed at apex, and with peculiar linear venation; main veins except Sc and R_3 with black setulae above (Fig. 47). Flagellum rounded, with a terminal arista. Slender brownish or yellowish flies, 2–5 mm long (Fig. 123) .... **Lonchopteridae** (Ch. 49)

Wing rounded at apex, and with radiating venation; veins at least in posterior half of wing not setose. Flagellum, body size, and color variable 52

52. Wing with branches of R strongly thickened and crowded into anterior base, and with four other weak and peculiarly aligned veins in remainder of wing blade; C ending near middle of anterior margin (Fig. 49). Small humpbacked flies, 1–4 mm long (Fig. 125) .... **Phoridae** (Ch. 51)

Wing with branches of R not strongly thickened and crowded anterobasally, and with other veins normal; C extending at least to wing apex 53

53. Antenna with pedicel much longer than flagellum; flagellum with a dorsal three-segmented arista (Fig. 104). Mid coxal prong strongly developed (Fig. 2.66) .... SCHIZOPHORA (lacking a ptilinum).... **Sciomyzidae** (*Sepedon*) (Ch. 84)

Antenna with pedicel not or scarcely as long as flagellum (Figs. 2.34–36); if arista three-segmented (Platypezidae), then terminally situated. Mid coxal prong absent...... 54

54. Wing with both A_1 and Sc reaching wing margin, and with cell *cup* acute at posterior apex (Fig. 48). Hind tarsus, at least in male, with one or more basal tarsomeres expanded and flattened. Arista three-segmented, terminally situated (Fig. 124) .... **Platypezidae** (Ch. 50)

Wing rarely with A_1 reaching wing margin (some Empididae, Figs. 47.31, 47.33), but if so either Sc incomplete or cell *cup* obtuse or rounded at posterior apex. Hind tarsus not modified as above. Arista or stylus two-segmented, terminally or dorsally situated (absent in empidid genus *Allanthalia*, Fig. 47.45) 55

55. Rs orginating at or near level of crossvein h, distal to crossvein h by, at most, length of crossvein h; crossvein r-m in basal fourth of wing; cells bm and dm confluent, that is, crossvein bm-cu absent; Sc usually abruptly curved posteriorly and fused with R_1 (Fig. 46), except in Hydrophorinae (Fig. 45) .... **Dolichopodidae** (Ch. 48)

Rs originating well distal to level of crossvein h, usually distal to it by more than length of crossvein h; crossvein r-m distal to basal fourth of wing; cell bm usually separated from cell dm (when cell dm present) by crossvein bm-cu; Sc usually joining C or ending freely, never abruptly joining R_1 (Figs. 41–44) .... **Empididae** (Ch. 47)

56(29). Body flattened (Figs. 160, 161), with thoracic venter greatly broadened and widely separating mid and hind coxae medially (Fig. 171). Claws strongly recurved and toothed (Fig. 179). Adults ectoparasitic on birds and mammals .... CALYPTRATAE, HIPPOBOSCOIDEA.... 57

Thorax not so flattened, with venter narrow and with mid and hind coxae close together medially. Claws not strongly recurved and toothed (Figs. 2.77–78). Adults not ectoparasitic 58

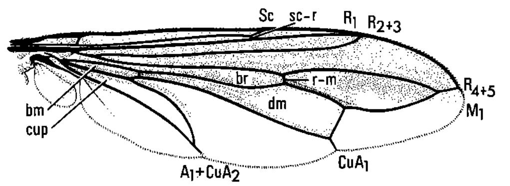
57. Compound eye large, horizontally oval, at least three-fourths as high as head, with at least 100 very small facets (Fig. 161). Posterior wing veins weaker, less crowded, and more divergent than anterior ones (Fig. 76). Ectoparasitic on birds and mammals other than bats .... **Hippoboscidae** (Ch. 111)

Compound eye small or absent, but if present, round, never more than half as high as head, and with less than 40 relatively large bead-like facets (Fig. 160). Wing veins relatively uniform in strength, dispersal, and arrangement (Fig. 160). Ectoparasitic on bats .... **Streblidae** (Ch. 113)

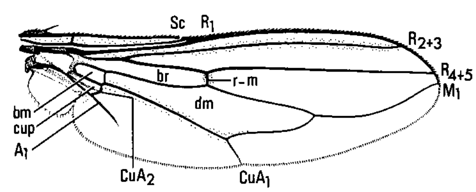
58. Greater ampulla present as a bulbous swelling below wing base (Fig. 2.66). Vibrissa usually present (Figs. 2.8–10, 2.66). Antennal pedicel always with a complete dorsal seam (Figs. 2.43–45) .... CALYPTRATAE, MUSCOIDEA and OESTROIDEA.... 59

Greater ampulla usually absent, but if present (Tephritidae, Psilidae, Ropalomeridae, and Periscelididae), then vibrissa absent. Antennal pedicel usually without a complete dorsal seam .... ACALYPTRATAE.... 72

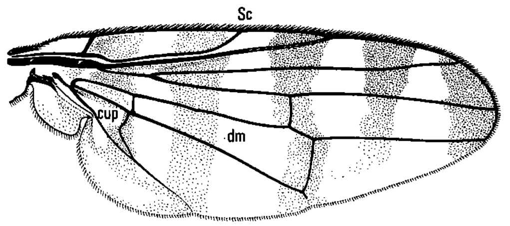
59. Large heavy-bodied hairy but bristleless flies, 9–25 mm long, resembling honeybees, carpenter bees, or bumblebees (Fig. 158). Head inflated, with reduced or atrophied mouthparts, no vibrissae, and small sunken antennae. Meron (Fig. 2.66) usually with a



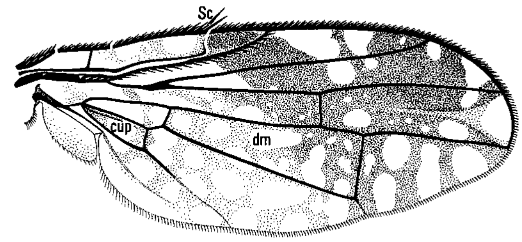
53 Physocephala texana ♀



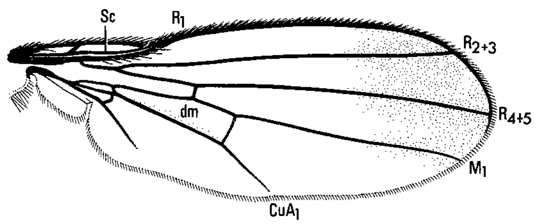
54 Odontoloxozus longicornis ♂



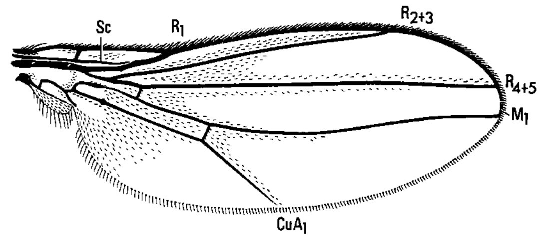
55 Pseudotephritis cribellum ♀



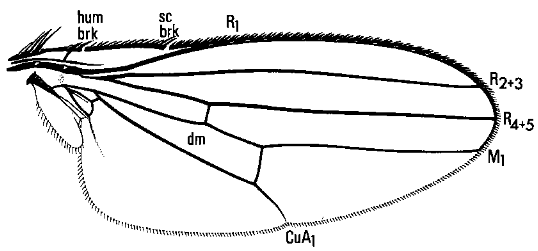
56 Tephritis subpura ♀



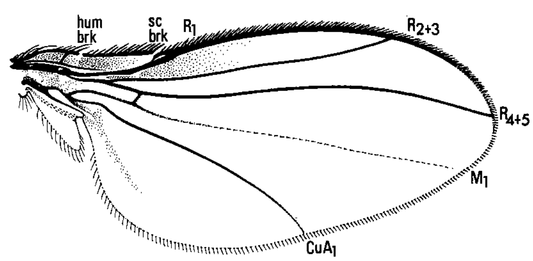
57 Chaetoclusia bakeri ♂



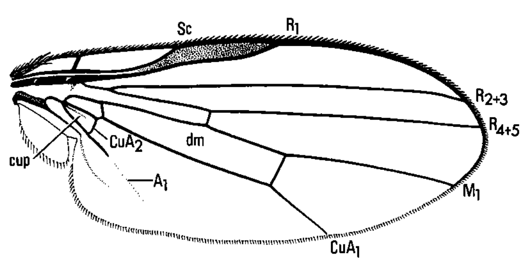
58 Leiomyza laevigata ♀



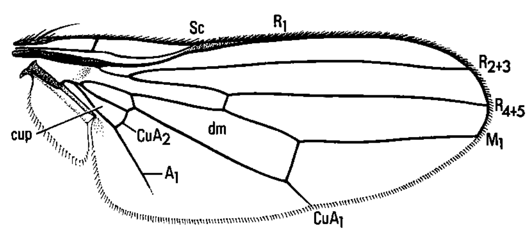
59 Madiza glabra ♂



60 Carnus hemapterus ♀



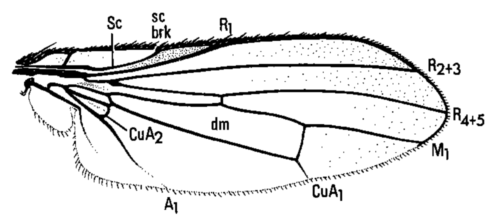
61 Cremifania nigrocellulata ♀



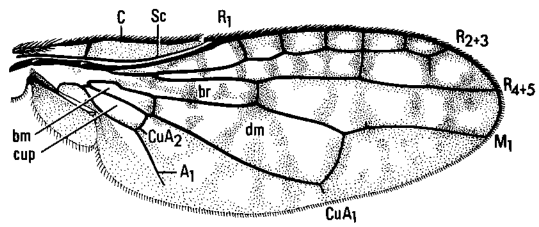
62 Paraleucopis corvina ♀

Figs. 4.53–62. Wings of acalyptrate Muscomorpha: (53) *Physocephala texana* (Williston) (Conopidae); (54) *Odontoloxozus longicornis* (Coquillett) (Neriidae); (55) *Pseudotephritis cribellum* (Loew) (Otitidae); (56) *Tephritis subpura* (Johnson) (Tephritidae); (57) *Chaetoclusia bakeri* Coquillett (not Nearctic) (Clusiidae); (58) *Leiomyza laevigata* (Meigen) (Asteiidae); (59) *Madiza glabra* Fallén (Milichiidae); (60) *Carnus hemapterus* Nitzsch (Carnidae); (61) *Cremifania nigrocellulata* Czerny (Chamaemyiidae); (62) *Paraleucopis corvina* Malloch (Chamaemyiidae).

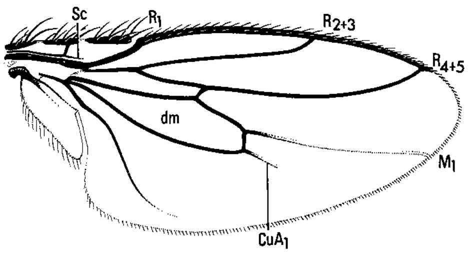
Abbreviations: hum brk, humeral break; sc brk, subcostal break.



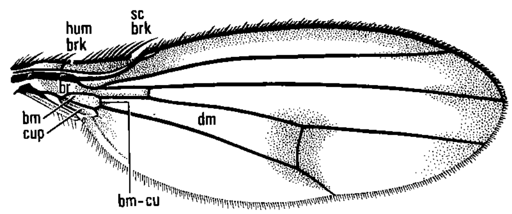
63 Tephrochlamys rufiventris ♀



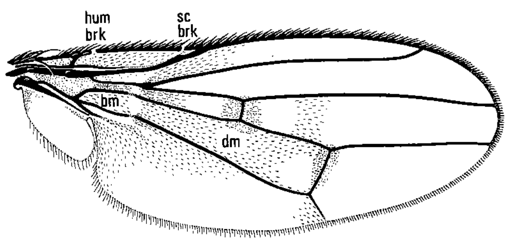
64 Neorhinotora diversa ♂



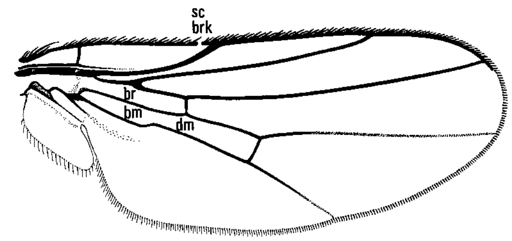
65 Leptocera fontinalis ♀



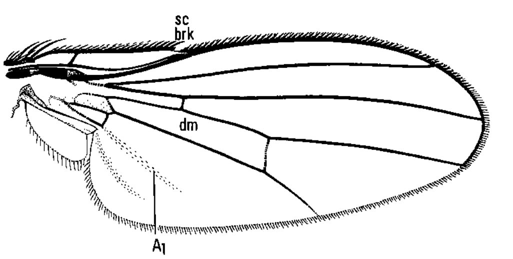
66 Diastata vagans ♂



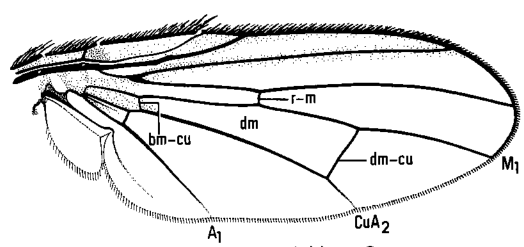
67 Parydra aquila ♀



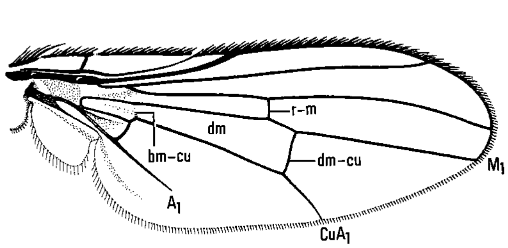
68 Chlorops certimus ♀



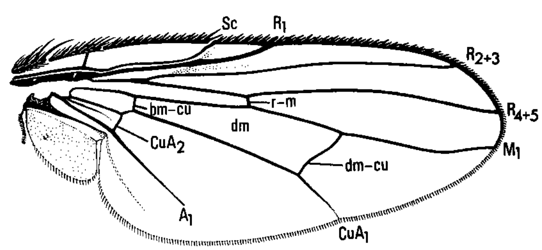
69 Tethina horripilans ♂



70 Botanophila spinidens ♀



71 Acridomyia canadensis ♂



72 Muscina assimilis ♀

Figs. 4.63–72. Wings of acalyptrate and calyptrate Muscomorpha: (63) *Tephrochlamys rufiventris* (Meigen) (Heleomyzidae); (64) *Neorhinotora diversa* (Giglio-Tos) (Rhinotoridae); (65) *Leptocera fontinalis* (Fallén) (Sphaeroceridae); (66) *Diastata vagans* Loew (Diastatidae); (67) *Parydra aquila* (Fallén) (Ephydridae); (68) *Chlorops certimus* Adams (Chloropidae); (69) *Tethina horripilans* (Melander) (Tethinidae); (70) *Botanophila spinidens* (Malloch) (Anthomyiidae); (71) *Acridomyia canadensis* Snyder (Anthomyiidae); (72) *Muscina assimilis* (Fallén) (Muscidae).

Abbreviations: hum brk, humeral break; sc brk, subcostal break.

cluster of long hairs. Larvae exclusively obligate parasites of mammals .... **Oestridae** (Ch. 107)

Usually smaller trimmer ordinarily bristled flies, 1–15 mm long. Head almost always with well-developed mouthparts, vibrissae, and antennae. Meron bare or with a row of bristles, sometimes with scattered fine hairs in addition to bristles. Larvae rarely obligate parasites of mammals 60

60. Meron with a row of bristles, and sometimes with additional hairs (Fig. 2.66) 61

Meron without bristles 68

61. Subscutellum strongly developed, prominently and evenly convex in profile (Fig. 2.66) .... **Tachinidae** (Ch. 110)

Subscutellum absent or weakly developed (Fig. 169), but if weakly developed (Rhinophoridae), upper half more or less membranous and concave in profile 62

62. Abdomen and usually thorax with a distinct metallic blue or green luster. Palpus usually orange yellow .... **most Calliphoridae** (Ch. 106)

Abdomen usually mostly dull, variegated gray, brown, or black; sometimes shining black, but never metallic blue or green. Palpus blackish to yellowish 63

63. Thorax with silky wavy yellowish hairs in addition to normal black bristles and hairs .... **Calliphoridae (*Pollenia*)** (Ch. 106)

Thorax without silky yellowish hairs 64

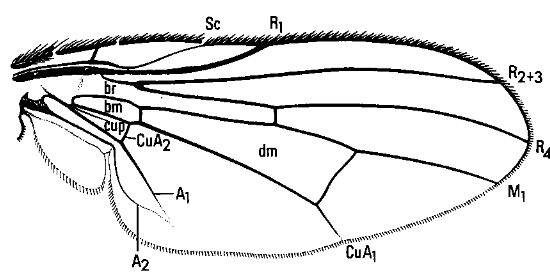
64. Scutum usually with three conspicuous black stripes on a gray background (Fig. 159). Notopleuron (Fig. 2.66) usually with three or four bristles. Hind coxa usually with hairs on posterior surface. Arista usually plumose (Fig. 159) .... **Sarcophagidae (most Sarcophaginae)**(Ch. 108)

Scutum with or without black stripes; notopleuron always with only two bristles (Fig. 2.66). Hind coxa always without hairs on posterior surface. Arista bare to plumose 65

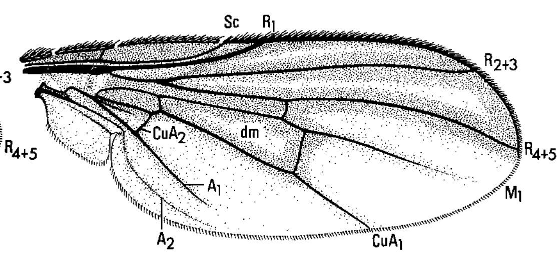
65. Coxopleural streak absent .... **Calliphoridae (Opsodexiinae)** (Ch. 106)

Coxopleural streak present (Fig. 2.66) 66

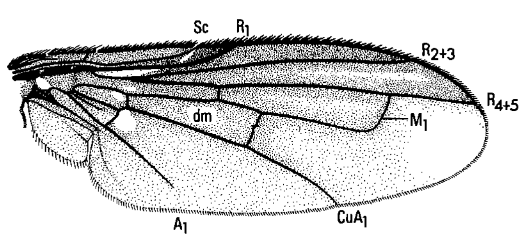
66. Second abdominal sternite overlapping margins of second abdominal tergite (Fig. 180). Lower calypter with inner base expanded, impinging on scutellum (Fig. 173) .... **Sarcophagidae (Miltogramminae)** (Ch. 108)



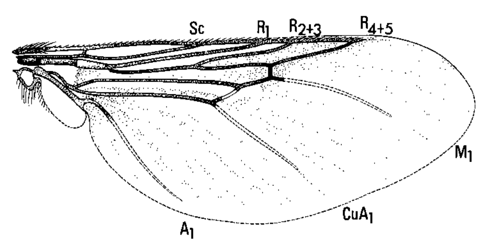
73 Fannia canicularis ♀



74 Bezzimyia sp. ♀



75 Melanophora roralis ♀



76 Hippobosca longipennis ♀

Figs. 4.73–76. Wings of Calyptratae: (73) *Fannia canicularis* (Linnaeus) (Muscidae); (74) *Bezzimyia* sp. (Tachinidae); (75) *Melanophora roralis* (Linnaeus) (Rhinophoridae); (76) *Hippobosca longipennis* Fabricius (Hippoboscidae).

Second abdominal sternite not overlapping margins of second abdominal tergite (Fig. 181). Lower calypter with inner base not expanded, widely removed from the scutellum (Fig. 172) 67

67. M complete and joining R_{4+5} (Fig. 75) .... **Rhinophoridae** (Ch. 109)

Apical portion of M atrophied (Fig. 74) .... **Tachinidae** (***Bezzimyia***) (Ch. 110)

68. A_2 curved forward beyond apex of A_1, with course of A_1 (if extended) intersecting A_2 before wing margin; Sc always nearly straight on apical two-thirds (Fig. 73). Hind tibia always with a strong bristle near middle of dorsal surface in addition to preapical dorsal bristle (Fig. 177) .... **Muscidae (Fanniinae)** (Ch. 105)

A_2 not curved as above, with course of A_1 not intersecting A_2 before wing margin; Sc usually distinctly curved forward on apical half or less (Figs. 70–72). Hind tibia rarely with a strong bristle near middle of dorsal surface (though a similar bristle called the calcar sometimes present on posterodorsal surface) 69

69. Palpus absent. Crossveins r-m and dm-cu separated by a distance not or scarcely greater than length of crossvein dm-cu; crossvein bm-cu partially atrophied (Fig. 71) .... **Anthomyiidae** (***Acridomyia***) (Ch. 104)

Palpus present. Crossveins r-m and dm-cu usually more widely separated; crossvein bm-cu usually complete (Figs. 70, 72) 70

70. A_1 never attaining wing margin even as a fold (Fig. 72). Lower calypter broad, never linear[1] .... **most Muscidae** (Ch. 105)

A_1 usually traceable to wing margin at least as a crease-like fold (Fig. 70), but if not (some Scathophagidae), then lower calypter linear 71

71. Scutellum usually with fine pale hairs on apicoventral surface (Fig. 169), and frons usually narrower in male than in female (Figs. 2.8, 2.10); if scutellum bare on ventral surface and frons wide in male (Fucelliinae, some Myopinini), then frons with strong interfrontal bristles (Fig. 2.8). Occiput never with fine pale hairs, with coarse black bristles and hairs only. Katepisternum usually with two to four bristles. Lower calypter linear to broadly expanded .... **Anthomyiidae** (Ch. 104)

Scutellum bare on ventral surface; frons wide in both sexes, and without interfrontal bristles. Occiput almost always with rather numerous fine pale hairs, sometimes interspersed with additional black bristles and hairs. Katepisternum usually with one bristle. Lower calypter always linear .... **Scathophagidae** (Ch. 103)

72(58). Proboscis usually very long and slender, frequently two or more times longer than head; pedicel usually longer than first flagellomere (Fig. 128). Crossvein sc-r present or cell cu*p* distinctly longer than cell bm, or with both characters present simultaneously; M joining R_{4+5} or closely approaching it (Fig. 53) .... **Conopidae** (Ch. 54)

Proboscis usually shorter and stouter, not longer than head except in some Milichiidae where it is elbowed (Fig. 143). Pedicel usually shorter than first flagellomere, but if longer (some Neriidae, Fig. 131, most Sciomyzidae, Fig. 104, and some Piophilidae, e.g. males of *Prochyliza*), then crossvein sc-r absent and cell cu*p* shorter than cell bm; M approaching R_{4+5} or not (Figs. 54–69) 73

73. Ocelli absent in Nearctic members. Medium to large flies, with heavily marked wings (Fig. 138) .... **Pyrgotidae** (Ch. 65)

Ocelli present. Size variable, with wings marked or unmarked 74

74. Eye at end of a stout stalk. Antennae widely displaced laterally. Scutellum with only two subapical bristles, each arising from an elongate process (Fig. 132) .... **Diopsidae** (Ch. 61)

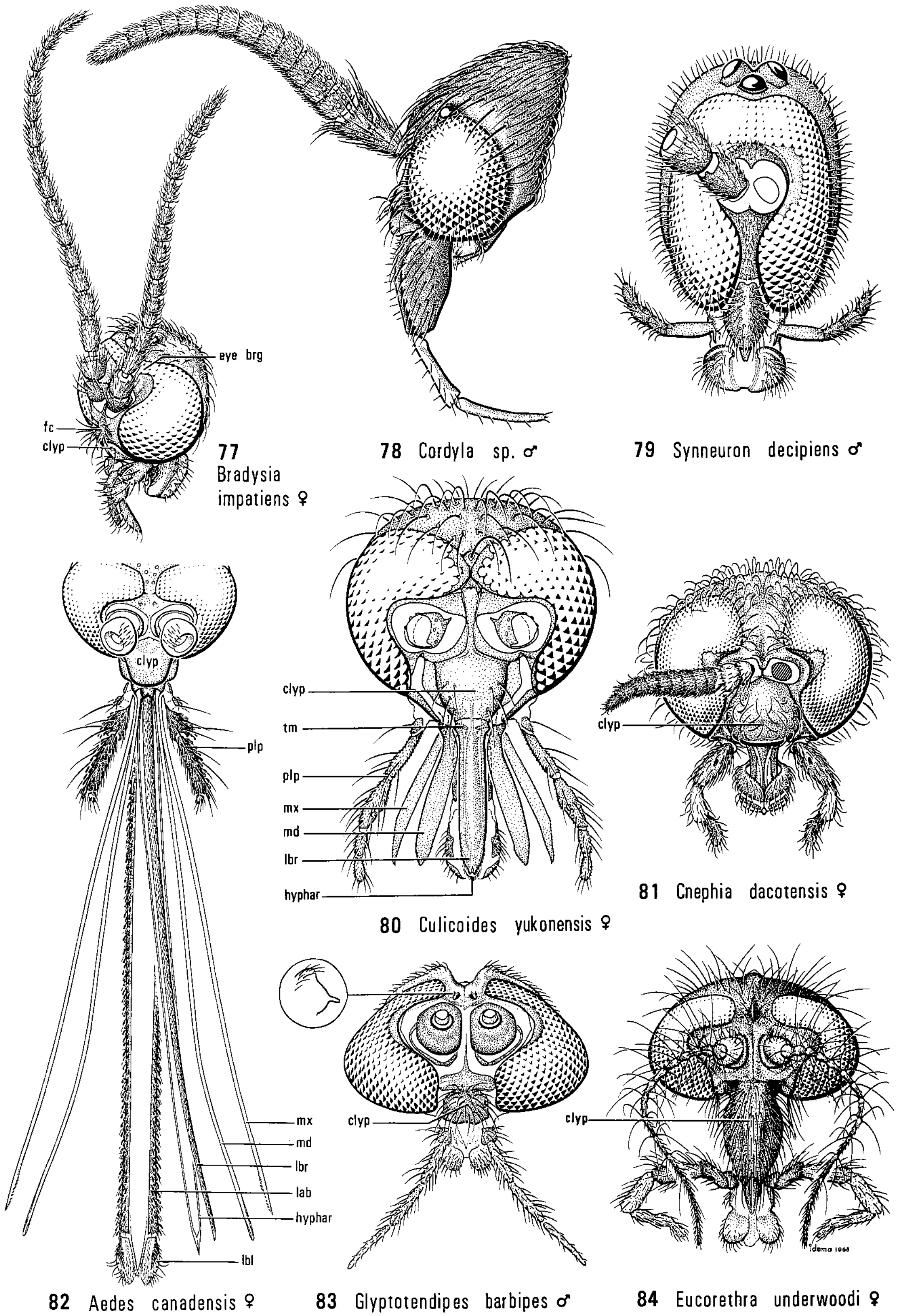
Eye not on a stalk. Antennae not displaced. Scutellum usually with four bristles not arising from elongate processes 75

75. Arista minute, situated apically on a very large first flagellomere. Compound eye very large and pubescent. Scutellum large, convex, uniformly setose (Fig. 157) .... **Cryptochetidae** (Ch. 100)

Arista well-developed. Compound eye and scutellum variable 76

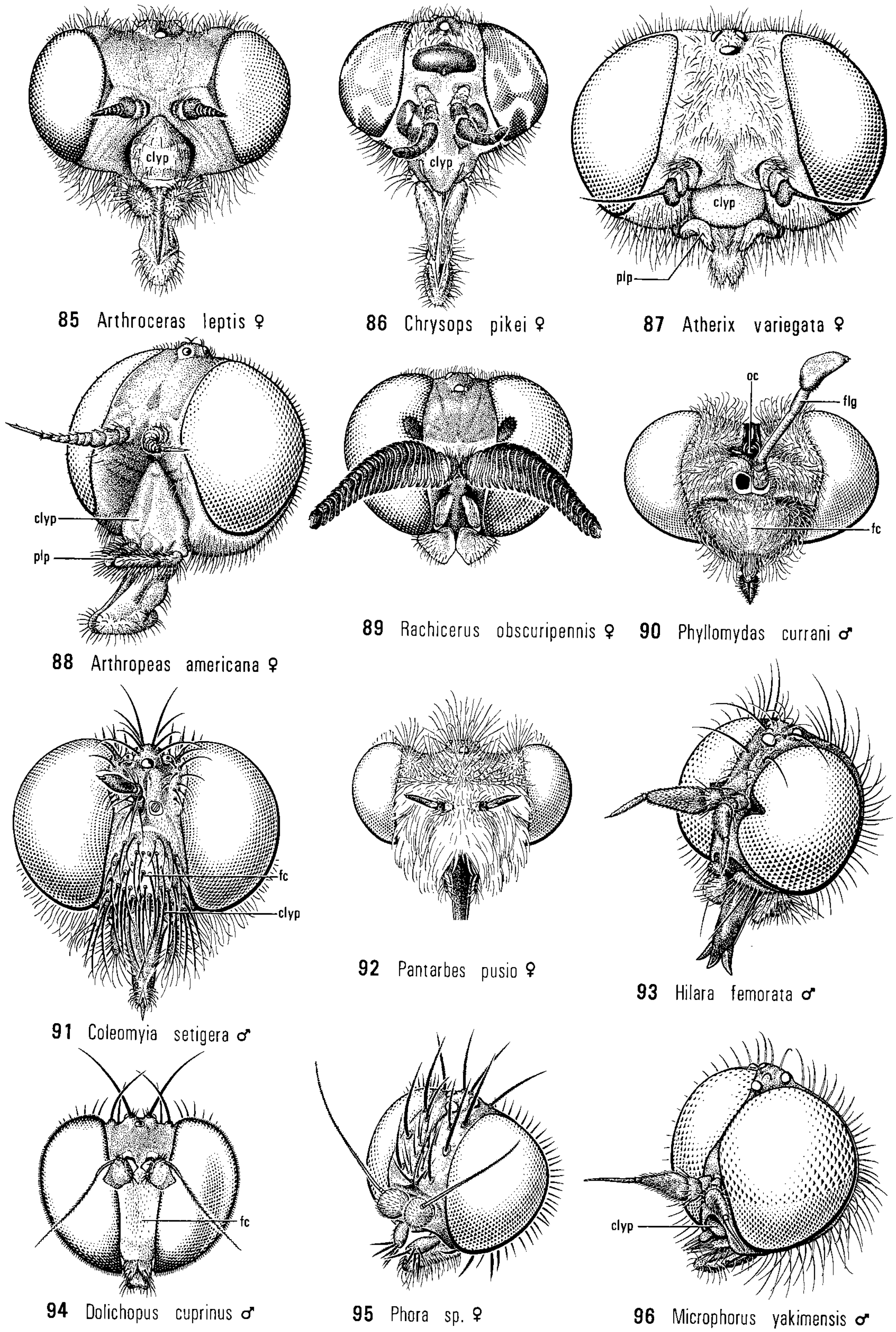
(continued on p. 109)

[1] *Coenosopsia prima* Malloch (Anthomyiidae), from Florida and Texas, keys here; it differs from Muscidae in having an outstanding seta at lower base of first tarsomere of hindleg, and two spiracles on the sixth abdominal segment of the female.

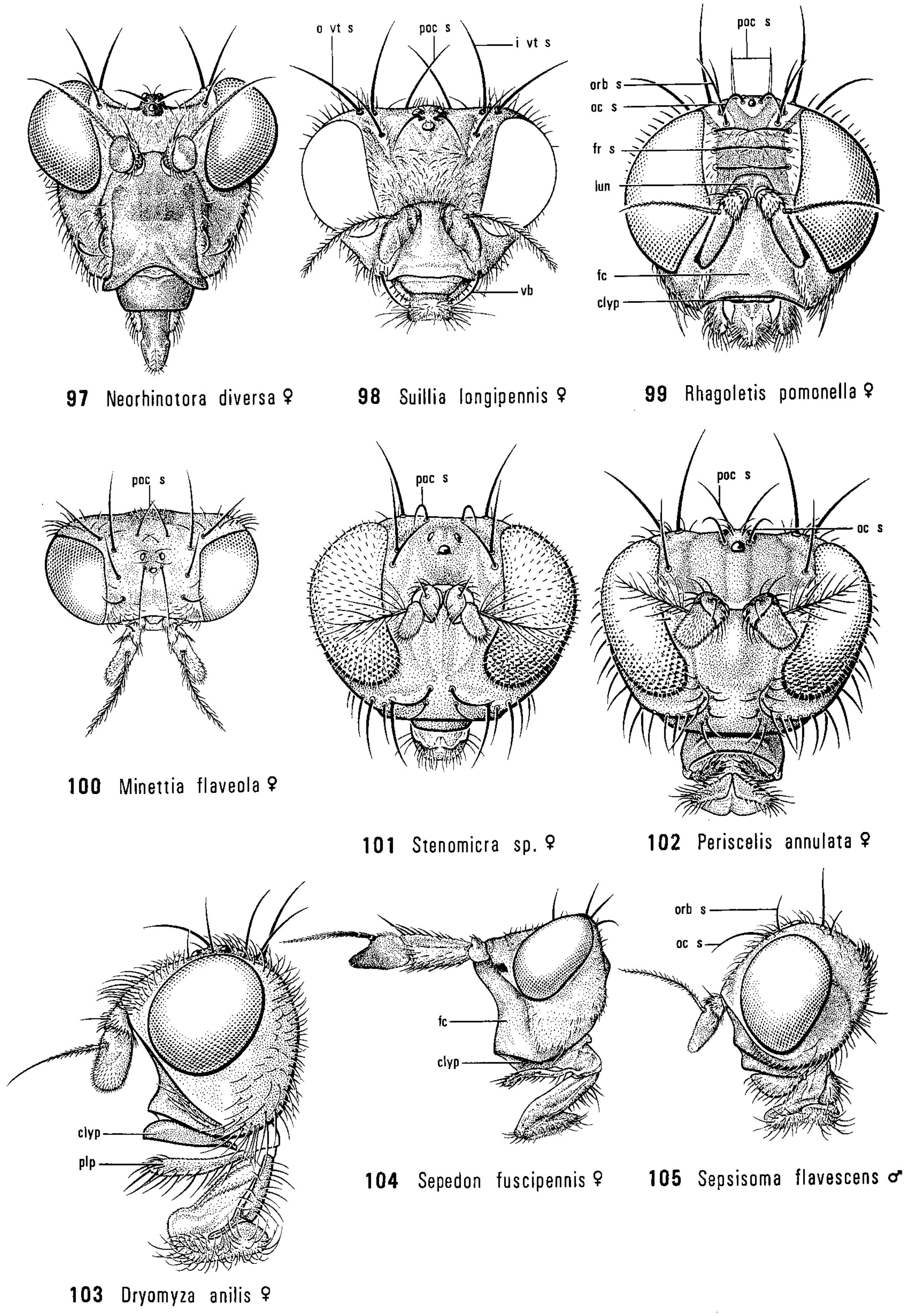


Figs. 4.77–84. Heads of Nematocera: (77) *Bradysia impatiens* (Johannsen) (Sciaridae); (78) *Cordyla* sp. (Mycetophilidae); (79) *Synneuron decipiens* Hutson (Synneuridae); (80) *Culicoides yukonensis* Hoffman (Ceratopogonidae); (81) *Cnephia dacotensis* (Dyar & Shannon) (Simuliidae); (82) *Aedes canadensis* (Theobald) (Culicidae); (83) *Glyptotendipes barbipes* (Staeger) (Chironomidae); (84) *Eucorethra underwoodi* Underwood (Chaoboridae).

Abbreviations: clyp, clypeus; eye brg, eye bridge; fc, face; hyphar, hypopharynx; lab, labium; lbl, labella; lbr, labrum; md, mandible; mx, maxilla; plp, palpus; tm, torma.



Figs. 4.85–96. Heads of orthorrhaphous Brachycera: (85) *Arthroceras leptis* (Osten Sacken) (Rhagionidae); (86) *Chrysops pikei* Whitney (Tabanidae); (87) *Atherix variegata* Walker (Athericidae); (88) *Arthropeas americana* Loew (Xylophagidae); (89) *Rachicerus obscuripennis* Loew (Xylophagidae); (90) *Phyllomydas currani* Hardy (Mydidae); (91) *Coleomyia setigera* (Cole) (Asilidae); (92) *Pantarbes pusio* Osten Sacken (Bombyliidae); (93) *Hilara femorata* Loew (Empididae); (94) *Dolichopus cuprinus* Wiedemann (Dolichopodidae); (95) *Phora* sp. (Phoridae); (96) *Microphorus yakimensis* Melander (Empididae).
Abbreviations: clyp, clypeus; fc, face; flg, flagellum; oc, ocellus; plp, palpus.

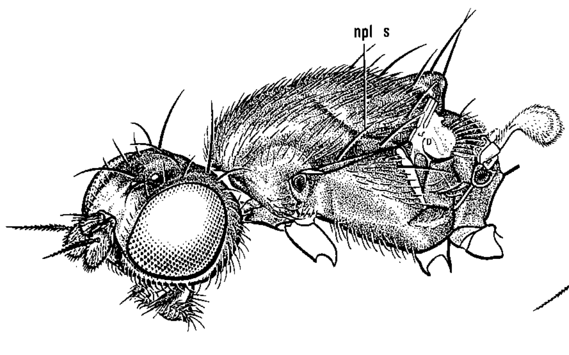


Figs. 4.97–105. Heads of acalyptrate Muscomorpha: (97) *Neorhinotora diversa* (Giglio-Tos) (Rhinotoridae), (98) *Suillia longipennis* (Loew) (Heleomyzidae), and (99) *Rhagoletis pomonella* (Walsh) (Tephritidae), anterior view; (100) *Minettia flaveola* (Coquillett) (Lauxaniidae), dorsal view; (101) *Stenomicra* sp. (Aulacigastridae) and (102) *Periscelis annulata* (Fallén) (Periscelididae), anterior view; (103) *Dryomyza anilis* Fallén (Dryomyzidae), (104) *Sepedon fuscipennis* Loew (Sciomyzidae), and (105) *Sepsisoma flavescens* Johnson (Richardiidae), left lateral view (*continued*).

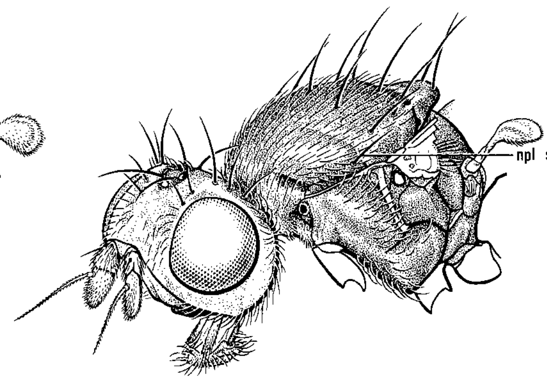
Abbreviations: clyp, clypeus; fc, face; fr s, frontal seta; i vt s, inner vertical seta; lun, lunule; oc s, ocellar seta; orb s, orbital seta; o vt s, outer vertical seta; plp, palpus; poc s, postocellar seta; vb, vibrissa.

76. Hind tarsus with first tarsomere distinctly swollen and usually shorter than second tarsomere (Fig. 149). Sc always incomplete; CuA_1 usually incomplete (Fig. 65) .... **Sphaeroceridae** (Ch. 93)

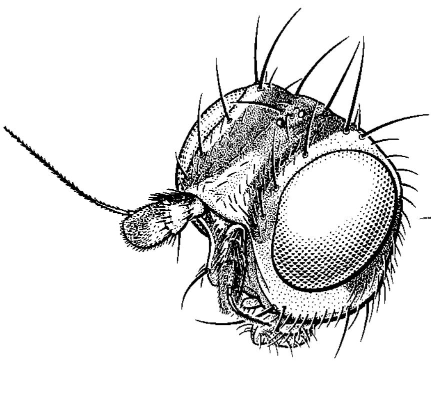
Hind tarsus with first tarsomere not swollen and longer than second tarsomere. Sc complete or incomplete; CuA_1 usually complete 77



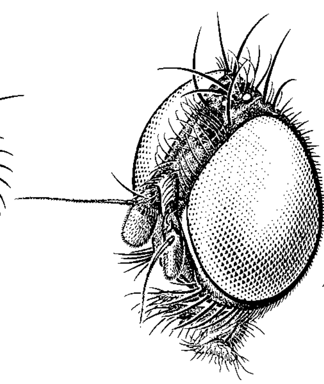
106 Strongylophthalmyia angustipennis ♀



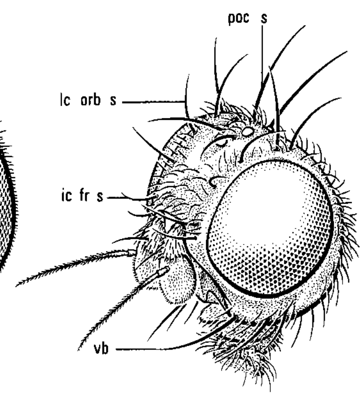
107 Psila rosae ♀



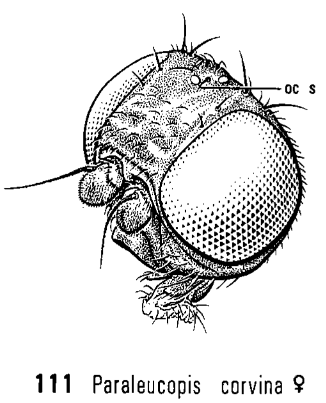
108 Latheticomyia tricolor ♀



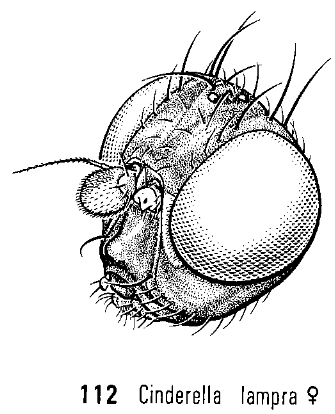
109 Dasiops alveofrons ♂



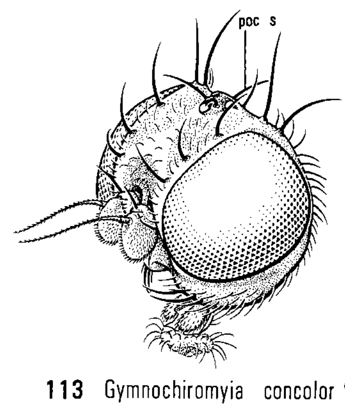
110 Actenoptera hilarella ♂



111 Paraleucopis corvina ♀



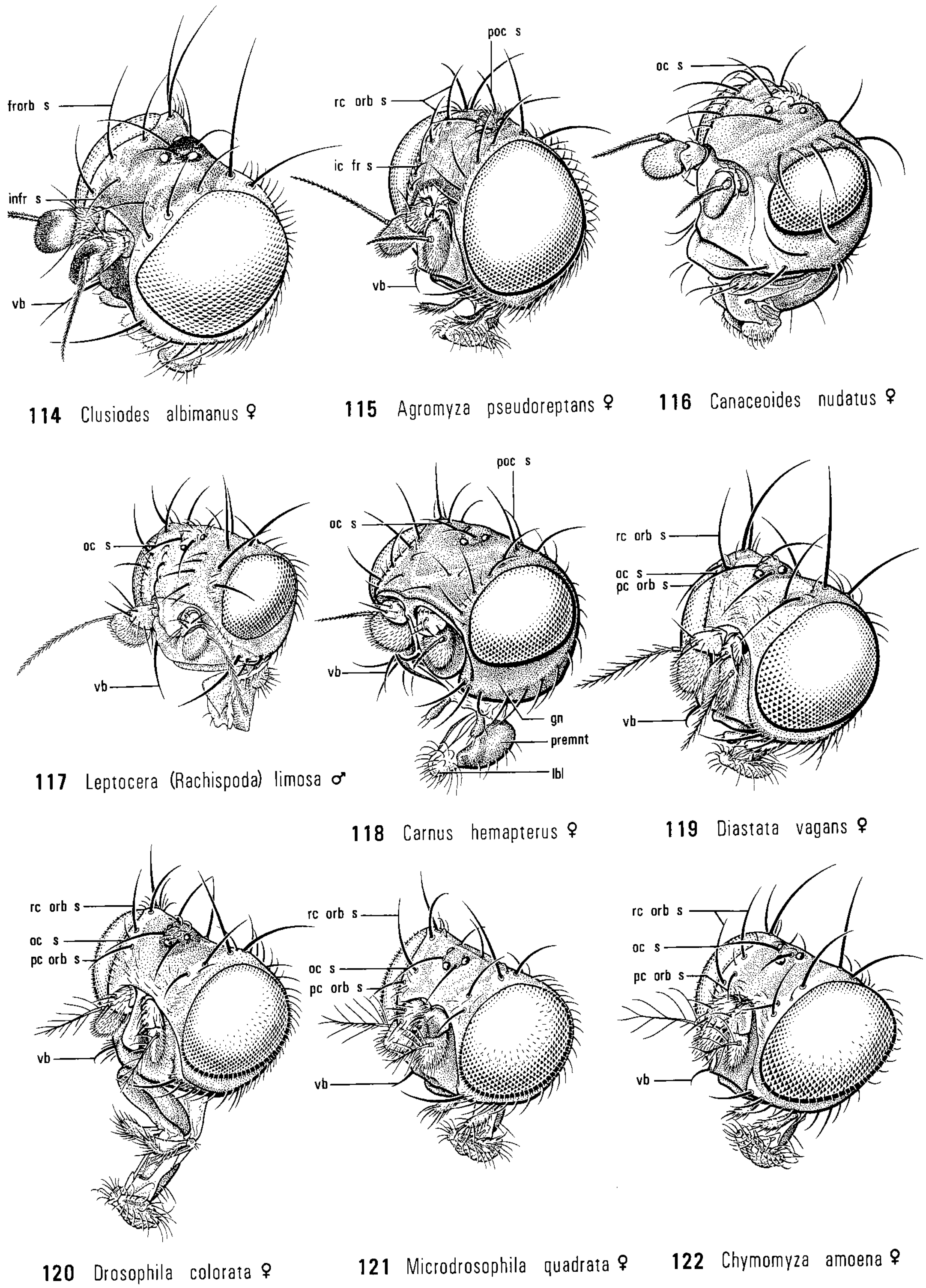
112 Cinderella lampra ♀



113 Gymnochiromyia concolor ♀

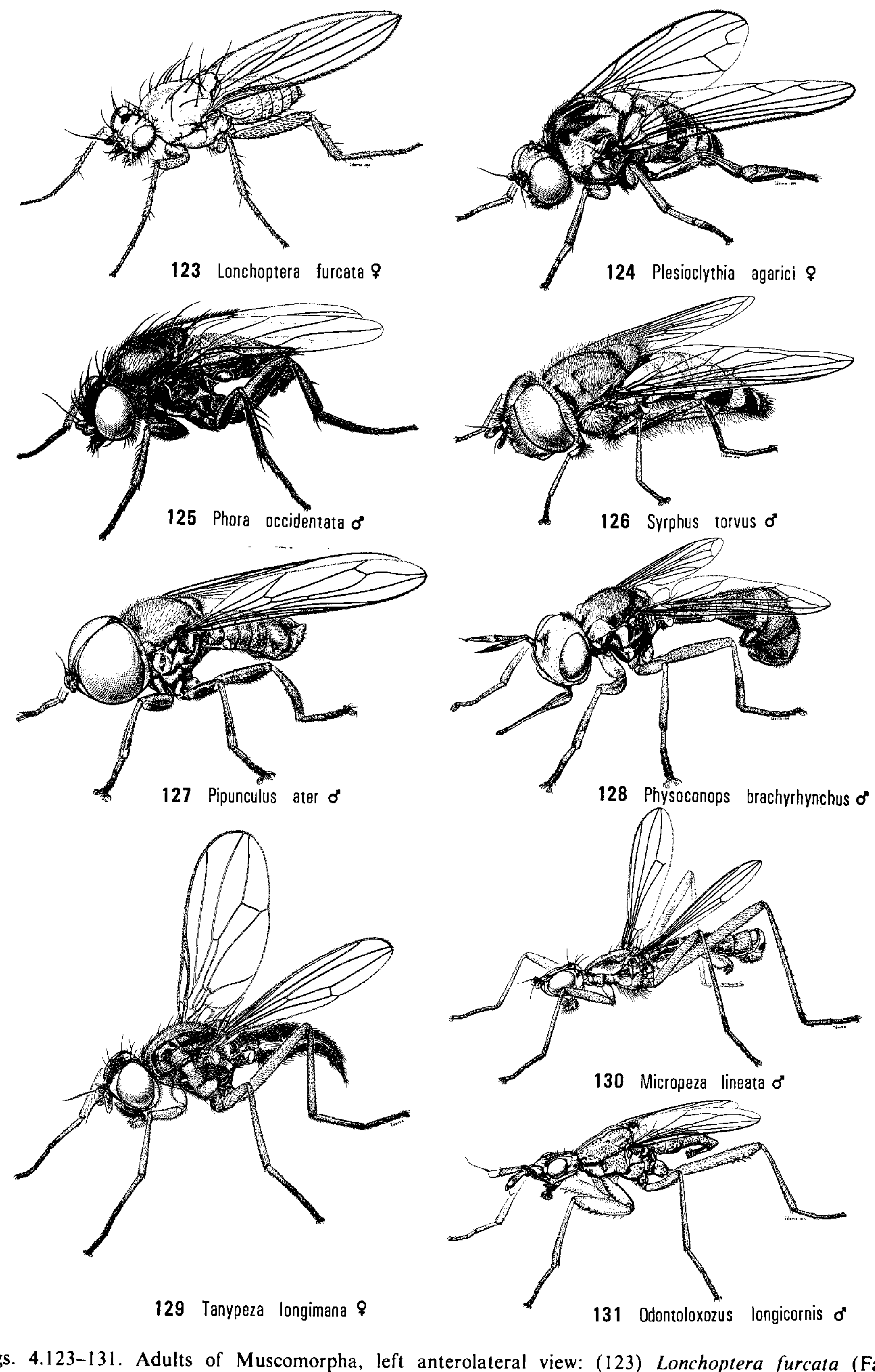
Figs. 4.106–113. Heads (and thoraces in Figs. 106 and 107) of acalyptrate Muscomorpha, left anterolateral view (*continued*): (106) *Strongylophthalmyia angustipennis* Melander (Strongylophthalmyiidae); (107) *Psila rosae* (Fabricius) (Psilidae); (108) *Latheticomyia tricolor* Wheeler (Cypselosomatidae); (109) *Dasiops alveofrons* McAlpine (Lonchaeidae); (110) *Actenoptera hilarella* (Zetterstedt) (Piophilidae); (111) *Paraleucopis corvina* Malloch (Chamaemyiidae); (112) *Cinderella lampra* Steyskal (Heleomyzidae); (113) *Gymnochiromyia concolor* (Malloch) (Chyromyidae).

Abbreviations: ic fr s, inclinate frontal seta; lc orb s, lateroclinate orbital seta; npl s, notopleural seta; oc s, ocellar seta; orb s, orbital seta; poc s, postocellar seta; vb, vibrissa.

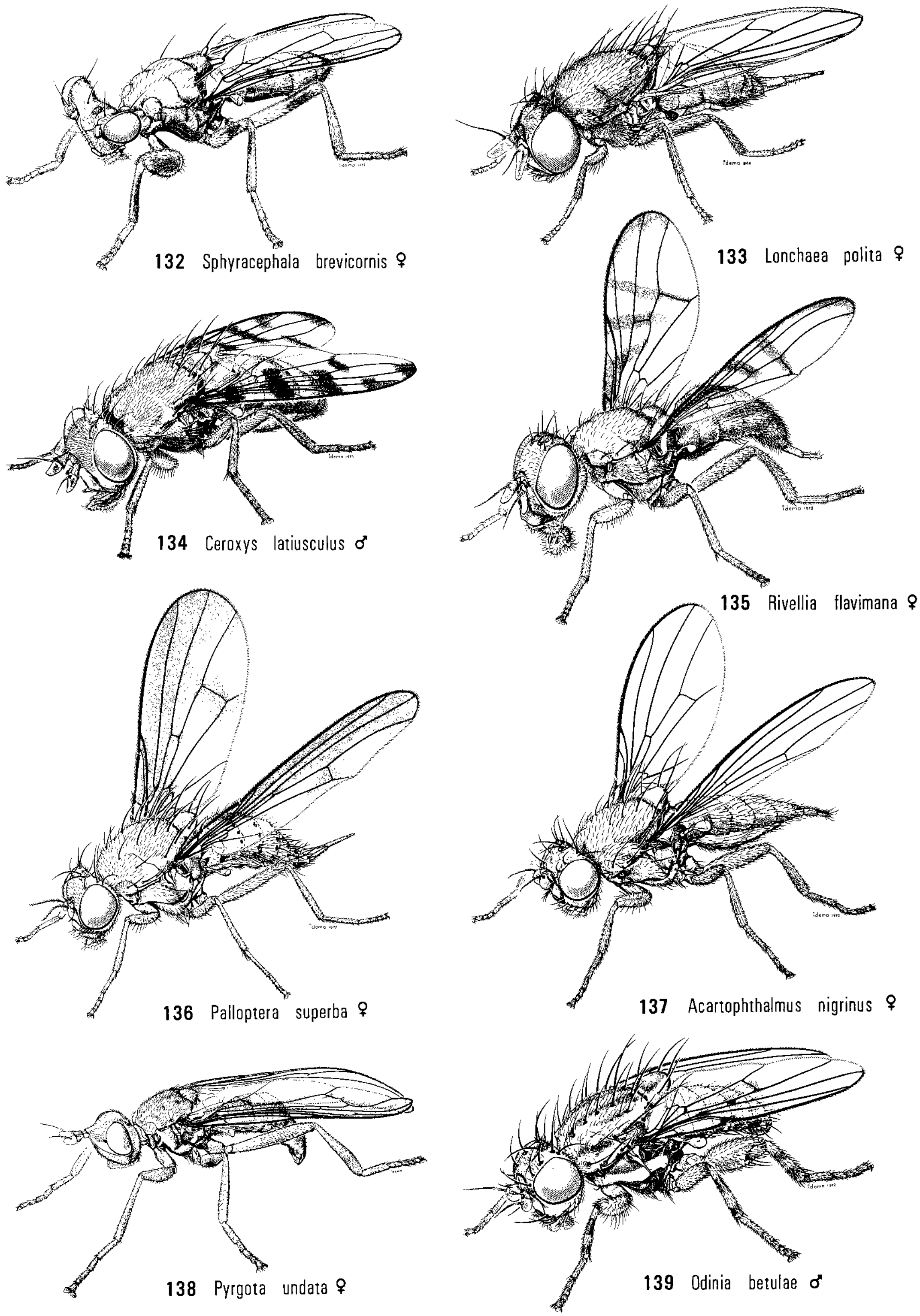


Figs. 4.114–122. Heads of acalyptrate Muscomorpha, left anterolateral view (*concluded*): (114) *Clusiodes albimanus* (Meigen) (Clusiidae); (115) *Agromyza pseudoreptans* Nowak (Agromyzidae); (116) *Canaceoides nudatus* (Cresson) (Canacidae); (117) *Leptocera* (*Rachispoda*) *limosa* (Fallén) (Sphaeroceridae); (118) *Carnus hemapterus* Nitzsch (Carnidae); (119) *Diastata vagans* Loew (Diastatidae); (120) *Drosophila colorata* Walker (Drosophilidae); (121) *Microdrosophila quadrata* (Sturtevant) (Drosophilidae); (122) *Chymomyza amoena* (Loew) (Drosophilidae).

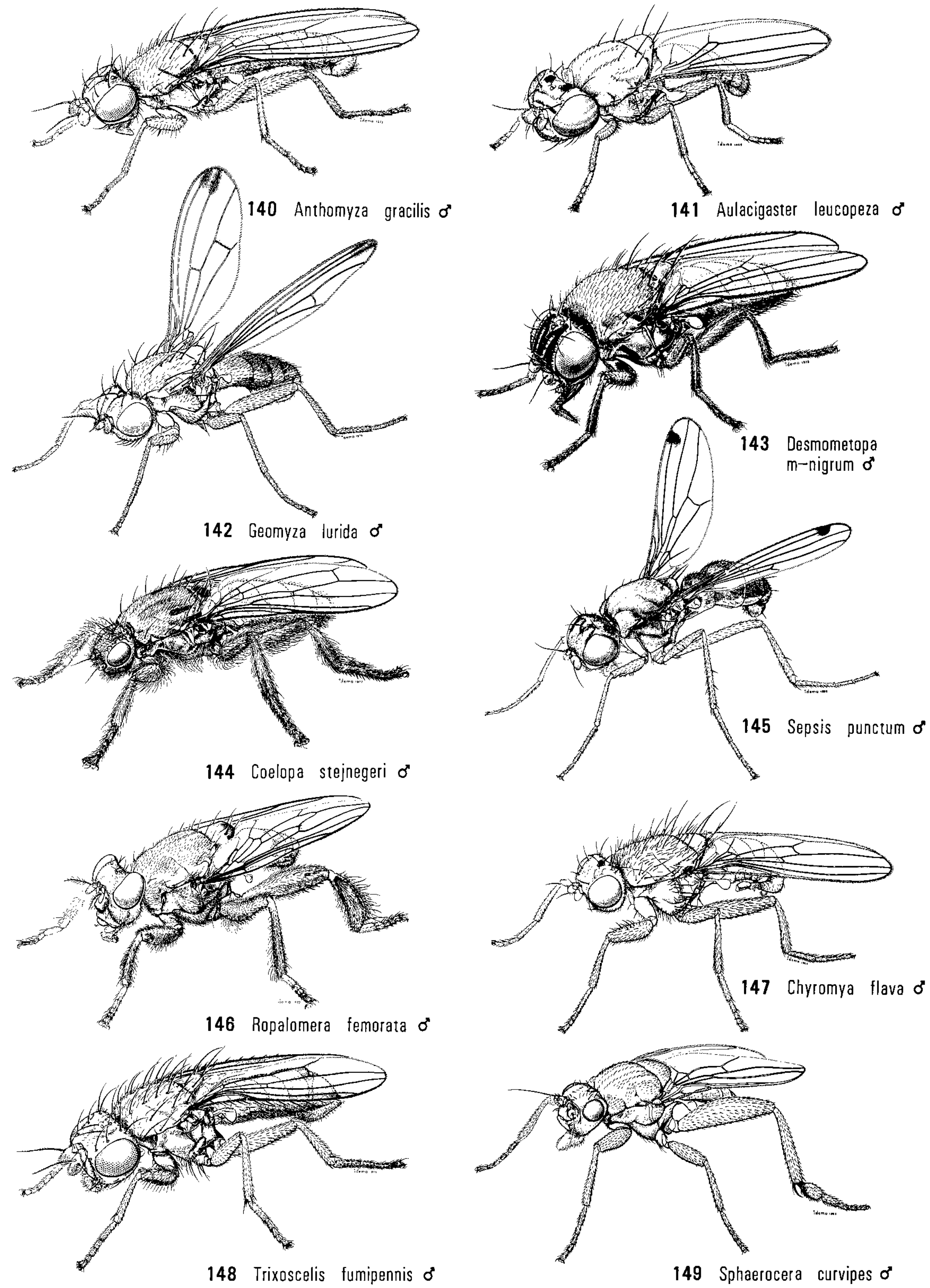
Abbreviations: frorb s, fronto-orbital seta; gn, gena; ic fr s, inclinate frontal seta; infr s, interfrontal seta; lbl, labella; lun, lunule; oc s, ocellar seta; pc orb s, proclinate orbital seta; poc s, postocellar seta; premnt, prementum; rc orb s, reclinate orbital seta; vb, vibrissa.



Figs. 4.123–131. Adults of Muscomorpha, left anterolateral view: (123) *Lonchoptera furcata* (Fallén) (Lonchopteridae); (124) *Plesioclythia agarici* (Willard) (Platypezidae); (125) *Phora occidentata* Malloch (Phoridae); (126) *Syrphus torvus* Osten Sacken (Syrphidae); (127) *Pipunculus ater* Meigen (Pipunculidae); (128) *Physoconops brachyrhynchus* (Macquart) (Conopidae); (129) *Tanypeza longimana* Fallén (Tanypezidae); (130) *Micropeza lineata* Van Duzee (Micropezidae); (131) *Odontoloxozus longicornis* (Coquillett) (Neriidae).



Figs. 4.132–139. Adults of acalyptrate Muscomorpha, left anterolateral view: (132) *Sphyracephala brevicornis* (Say) (Diopsidae); (133) *Lonchaea polita* Say (Lonchaeidae); (134) *Ceroxys latiusculus* (Loew) (Otitidae); (135) *Rivellia flavimana* Loew (Platystomatidae); (136) *Palloptera superba* Loew (Pallopteridae); (137) *Acartophthalmus nigrinus* (Zetterstedt) (Acartophthalmidae); (138) *Pyrgota undata* Wiedemann (Pyrgotidae); (139) *Odinia betulae* Sabrosky (Odiniidae) (*continued*).



Figs. 4.140–149. Adults of acalyptrate Muscomorpha, left anterolateral view (*continued*): (140) *Anthomyza gracilis* Fallén (Anthomyzidae); (141) *Aulacigaster leucopeza* (Meigen) (Aulacigastridae); (142) *Geomyza lurida* (Loew) (Opomyzidae); (143) *Desmometopa m-nigrum* (Zetterstedt) (Milichiidae); (144) *Coelopa stejnegeri* Aldrich (Coelopidae); (145) *Sepsis punctum* (Fabricius) (Sepsidae); (146) *Ropalomera femorata* (Fabricius) (Ropalomeridae); (147) *Chyromya flava* (Linnaeus) (Chyromyidae); (148) *Trixoscelis fumipennis* Melander (Trixoscelididae); (149) *Sphaerocera curvipes* Latreille (Sphaeroceridae) (*continued*).

77. Sc abruptly bent forward at nearly 90°, weakened beyond the bend and ending at subcostal break; wing almost always with markings (Fig. 56). Pedicel with a dorsal cleft. Vibrissae absent (Fig. 99). Greater ampulla usually weakly distinguishable (as in Fig. 2.66). Anepimeron always with bristles or hairs or with both (as in Fig. 2.66) .... **Tephritidae** (Ch. 66)

Sc less abruptly bent. Disagreeing with above in one or more of remaining characters 78

78. Slender-bodied flies, with long slender legs (Figs. 129–131). R_{4+5} and M meeting or strongly converging at wing margin; Sc always complete (Figs. 54, 129–131) 79

Usually stouter flies, with shorter more robust legs. R_{4+5} and M usually subparallel or divergent at wing margin, but if these veins converging (Ropalomeridae, Fig. 146), then legs not long and slender; Sc complete or incomplete 81

79. Eyes very large, distinctly higher than long, and closer together in male than in female. Ocellar bristles present. R_1 setose above. Katepisternum evenly pilose, but without outstanding bristles or hairs (Fig. 129) .... **Tanypezidae** (Ch. 58)

Eyes smaller than above, not much higher than long, and equidistant in both sexes. Ocellar bristles absent. R_1 not setose. Katepisternum never evenly pilose, always with one to many outstanding bristles or hairs 80

80. Arista apical (Fig. 131) .... **Neriidae** (Ch. 57)

Arista arising on basal half of dorsal surface (Fig. 130) .... **Micropezidae** (Ch. 56)

81. Sc complete or nearly so, ending in C or just short of it and free from R_1 distally (Figs. 63, 64) 82

Sc incomplete, not reaching C, often fusing with R_1 distally (Figs. 65, 67–68) 108

82. C without a subcostal break (Figs. 55, 58, 61, 62) 83

C with a subcostal break (Figs. 63–69) 93

83. Vertex usually strongly excavated. Apical section of M bent sharply forward in line with crossvein dm-cu, and ending near R_{4+5} before wing apex (Fig. 146) .... **Ropalomeridae** (Ch. 85)

Vertex convex or shallowly concave. Apical section of M not bent or only gently forwardly curved, always ending behind wing apex 84

84. Posterior thoracic spiracle with one or more fine bristles on lower margin. Form usually ant-like; head subspherical; palpus vestigial (except in *Orygma*); abdomen usually elongate and basally constricted (Fig. 145) .... **Sepsidae** (Ch. 86)

Posterior thoracic spiracle without bristles or outstanding hairs. Form usually not ant-like; palpus usually well-developed 85

85. Metepisternum setose below posterior thoracic spiracle; thorax distinctly flattened. Squatty and strongly bristled flies (Fig. 144) .... **Coelopidae** (Ch. 82)

Metepisternum bare; thorax not very flattened. Form and bristling variable 86

86. Face broadly membranous and sunken in middle; vibrissa present (Fig. 114) 87

Face uniformly sclerotized and convex in middle; vibrissa absent (Figs. 103, 104) 88

87. Arista subapical; frons with a pair of cruciate interfrontal bristles (Fig. 114). C without humeral break (Fig. 57). All tibiae with a preapical dorsal bristle (Fig. 175) .... **Clusiidae (some *Clusiodes*)** (Ch. 70)

Arista dorsobasal. Frons without cruciate interfrontal bristles. C with humeral break (Fig. 137). All tibiae without a preapical dorsal bristle (Fig. 137) .... **Acartophthalmidae** (Ch. 71)

88. Some or all tibiae with a preapical dorsal bristle (Fig. 175) 89

All tibiae without a preapical dorsal bristle 91

89. Postocellar bristles distinctly convergent (Fig. 100) .... **Lauxaniidae** (Ch. 87)

Postocellar bristles almost parallel (Fig. 99), divergent (Fig. 110), or absent (Fig. 116)....90

90. Clypeus large and prominent, in profile distinctly bulging beyond lower margin of face (Fig. 103). Pedicel always short (Fig. 103) .... **Dryomyzidae** (Ch. 83)

Clypeus small and withdrawn, in profile more or less concealed under lower margin of face (Fig. 104). Pedicel usually elongate (Fig. 104) .... **Sciomyzidae** (Ch. 84)

91. Costal section between apices of Sc and R_1 as long as cell c; adjacent membrane entirely blackish; remainder of wing whitish hyaline (Fig. 61). Small flies, 3 mm long. Female with membranous tubular ovipositor .... **Chamaemyiidae** (***Cremifania***) (Ch. 88)

Costal section between apices of Sc and R_1 shorter than cell c; adjacent membrane usually not entirely blackish; if this area blackish then remainder of wing with additional markings. Usually larger flies. Female with rigid shaft-like ovipositor 92

92. Postocellar bristles distinctly developed, divergent (Fig. 134). Katepisternal bristle present (except in *Myrmecothea*, a strikingly ant-like genus with two scutellar setae) .... **Otitidae**, in part (Ch. 63)

Postocellar bristles absent or very weakly developed. Katepisternal bristles absent, though hair or pile commonly present. Form never especially ant-like, always with four scutellar setae (Fig. 135) .... **Platystomatidae** (Ch. 64)

93(82). Vertex strongly excavated (Fig. 97). Wing with one to many supernumerary crossveins between C and R_{2+3} (Fig. 64) .... **Rhinotoridae** (Ch. 92)

Vertex not or only slightly excavated. Wing without supernumerary crossveins between C and R_{2+3} 94

94. Subcranial cavity unusually large. Gena with one to several strong upcurved bristles immediately below compound eye. Frons unusually broad, with three to five pairs of lateroclinate fronto-orbital bristles (Fig. 116) .... **Canacidae** (Ch. 102)

Subcranial cavity not unusually large. Gena without strong upcurved bristles immediately below compound eye. Frons not unusually broad, with fewer than three lateroclinate fronto-orbital bristles 95

95. Vibrissa present (Figs. 98, 110, 114, 115, 117–122), but sometimes weak in Tethinidae (Fig. 156) 96

Vibrissa absent (Figs. 102, 111), but subvibrissal bristles sometimes vibrissa-like, e.g. Chyromyidae (Fig. 113) and Lonchaeidae (Fig. 109) 104

96. C with a distinct humeral break in addition to subcostal break (Figs. 59, 60) 97

C without humeral break, with subcostal break only (Figs. 63, 69) 99

97. Arista broadly plumose (as in Fig. 2.41). C extensively and strongly spinose in Nearctic species. All tibiae with a strong preapical dorsal bristle. Medium-sized yellowish flies, with strongly arched scutum (Fig. 150) .... **Curtonotidae** (Ch. 94)

Arista bare or shortly haired. C not spinose. Tibiae without a preapical dorsal bristle. Small to very small mostly shining black flies, with normally arched scutum 98

98. Gena broad, and with a row of bristles in middle. Proboscis with stout bulbous prementum and short inconspicuous labella (Fig. 118) .... **Carnidae**, in part (Ch. 80)

Gena usually narrow, but if broad, bristles confined to lower margin. Proboscis with slender prementum and long conspicuous labella folded back along prementum (Fig. 143) .... **Milichiidae**, in part (Ch. 79)

99. Pedicel with an angular though sometimes weak projection on outer side. Arista subapical. Frons with two to five strong more or less equally spaced mostly reclinate fronto-orbital bristles, with at most only the lowest one inclinate (Fig. 114) .... **Clusiidae** (Ch. 70)

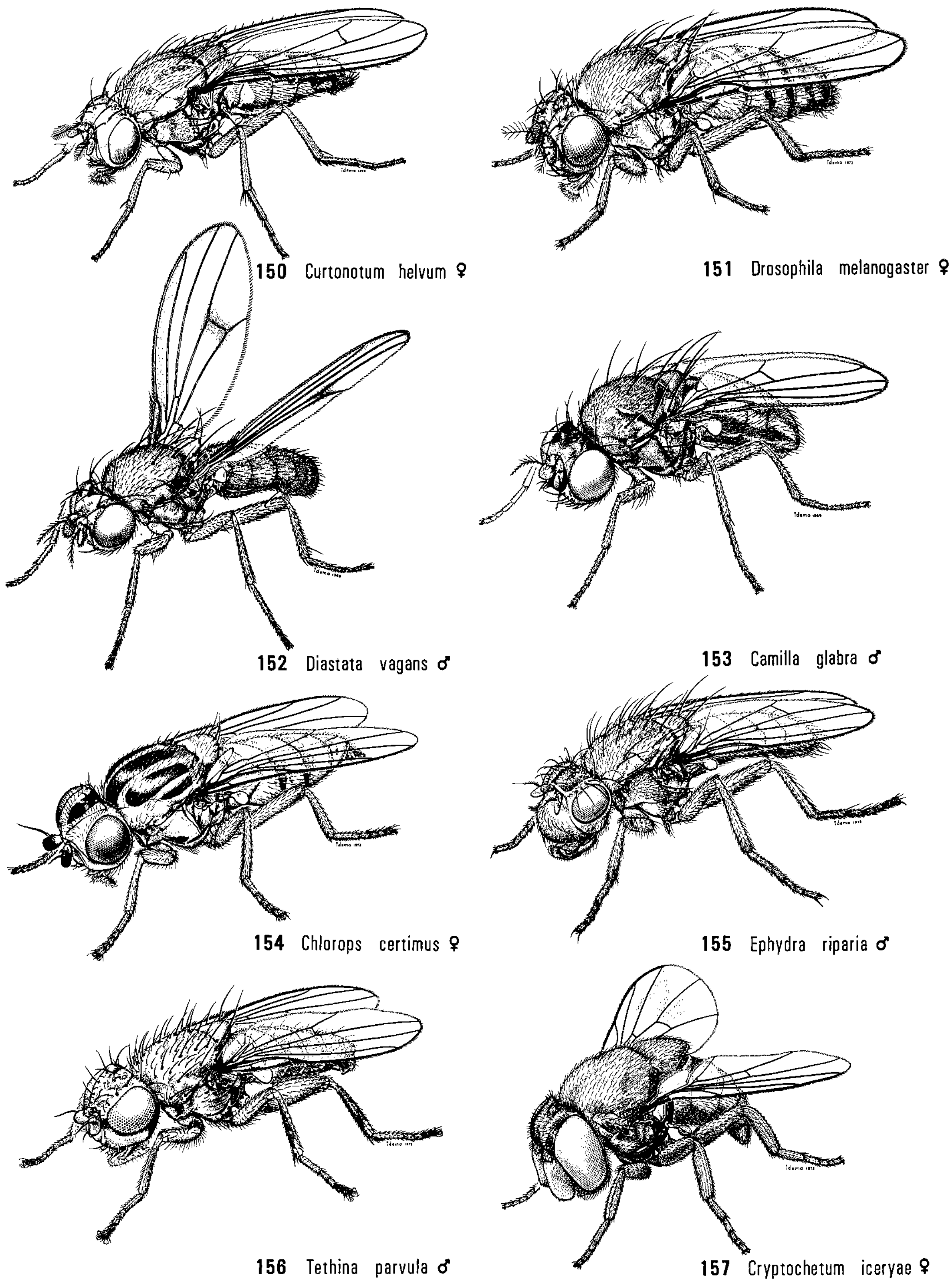
Pedicel without an angular projection. Arista dorsobasal. Frons usually with fewer or less equally spaced fronto-orbital bristles, but if with two to five (Agromyzidae, some Otitidae), then two or three of the lower ones are strongly inclinate (Fig. 115) 100

100. Postocellar bristles divergent (Figs. 110, 115) 101

Postocellar bristles convergent (Fig. 98) or absent 102

101. Frons always with three to five strong inclinate frontal bristles that are relatively similar to the two reclinate orbital bristles in size and spacing (Fig. 115) .... **Agromyzidae**, in part (Ch. 73)

Frons seldom with any strong inclinate frontal bristles, but if one or two present (*Actenoptera*), then these positioned distant from and inclined oppositely to the two lateroclinate orbital bristles (Fig. 110) .... **Piophilidae** (Ch. 69)



Figs. 4.150–157. Adults of acalyptrate Muscomorpha, left anterolateral view (*concluded*): (150) ***Curtonotum helvum*** (Loew) (Curtonotidae); (151) ***Drosophila melanogaster*** Meigen (Drosophilidae); (152) ***Diastata vagans*** Loew (Diastatidae); (153) ***Camilla glabra*** (Fallén) (Camillidae); (154) ***Chlorops certimus*** Adams (Chloropidae); (155) ***Ephydra riparia*** Fallén (Ephydridae); (156) ***Tethina parvula*** (Loew) (Tethinidae); (157) ***Cryptochetum iceryae*** (Williston) (Cryptochetidae).

102. All tibiae without a preapical dorsal bristle. C not spinose; A_1 fading out on apical third or more, never traceable to wing margin (Fig. 69). Vibrissa and postocellar bristles weakly differentiated to virtually absent (Fig. 156) .... **Tethinidae**, in part (Ch. 101)

All tibiae with a preapical dorsal bristle (Fig. 175). C spinose, except in some Heleomyzidae (*Borboropsis* and *Oldenbergiella*) in which A_1 is traceable to wing margin (Fig. 63). Vibrissa and postocellar bristles strong (Fig. 98) 103

103. Ocellar bristles arising on ocellar triangle above anterior ocellus (Fig. 98) .... **Heleomyzidae** (Ch. 89)

Ocellar bristles arising just outside ocellar triangle beside or slightly below anterior ocellus (Fig. 148) .... **Trixoscelididae** (Ch. 90)

104(95). Halter black. Anepisternum with a row of strong bristles posteriorly. Frons, face, thorax, abdomen, and legs (exclusive of tarsi) black, usually with metallic reflections. Stout bristly flies with broad flat abdomen; female with lance-like ovipositor (Fig. 133) .... **Lonchaeidae** (Ch. 62)

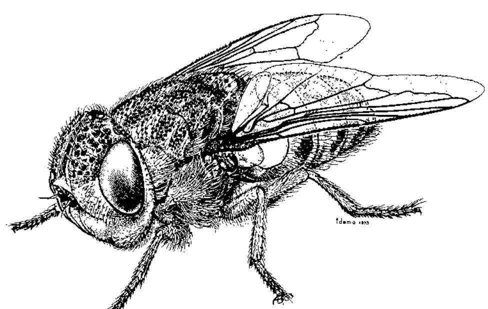
Halter usually whitish, but if halter blackish, then anepisternum without a row of strong bristles, and/or head, thorax, abdomen, and legs not as extensively black. Form variable 105

105. Postocellar bristles convergent (Figs. 113, 147) .... **Chyromyidae** (Ch. 91)

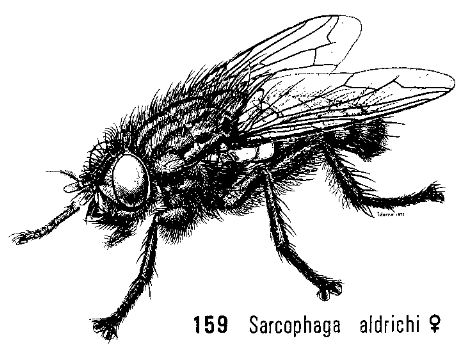
Postocellar bristles divergent or absent 106

106. Scutum with one or more presutural dorsocentral bristles (Fig. 136) [except in some specimens of *Temnosira subarcuata* (Johnson)]. Cell cu*p* without an angular extension at posterior apex (Fig. 136). Disc of proepisternum always bare (Fig. 163) .... **Pallopteridae** (Ch. 68)

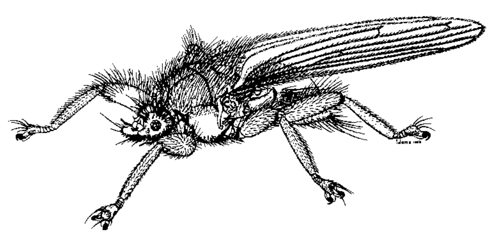
Scutum usually without presutural dorsocentral bristles (Fig. 134), but if these bristles present, then cell cu*p* with an angular extension at posterior apex (Fig. 55) or disc of proepisternum setose (Fig. 164), or both 107



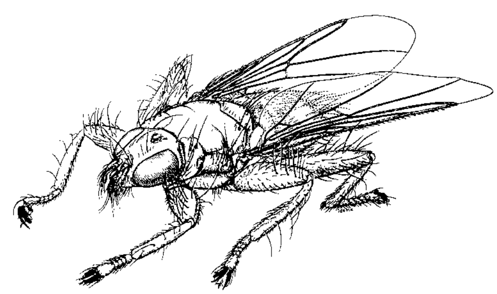
158 Oestrus ovis ♀



159 Sarcophaga aldrichi ♀

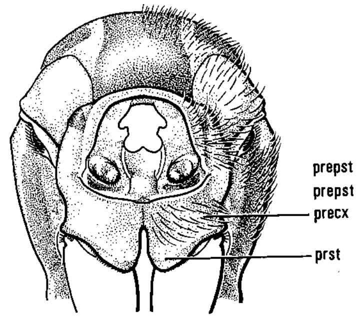


160 Trichobius corynorhini ♀

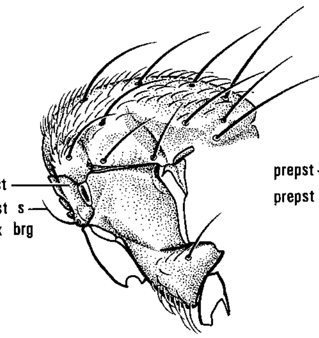


161 Ornithomya anchineuria ♀

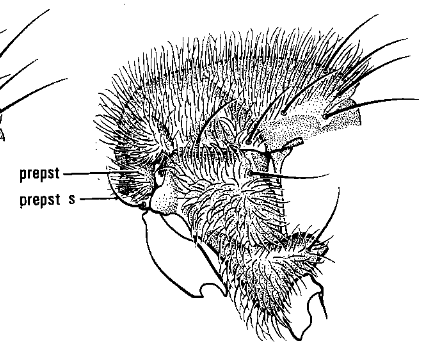
Figs. 4.158–161. Adults of calyptrate Muscomorpha, left anterolateral view: (158) *Oestrus ovis* Linnaeus (Oestridae); (159) *Sarcophaga aldrichi* Parker (Sarcophagidae); (160) *Trichobius corynorhini* Cockerell (Streblidae); (161) *Ornithomya anchineuria* Speiser (Hippoboscidae).



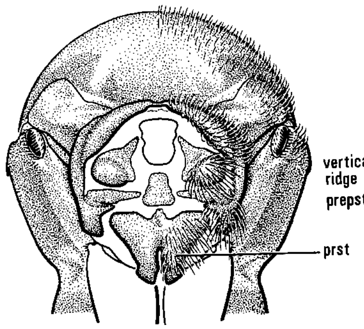
162 Xylomya americana ♂



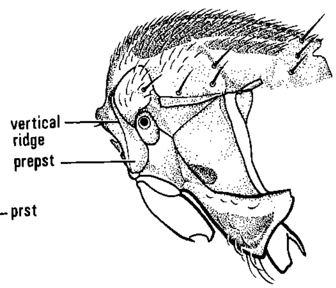
163 Palloptera claripennis ♂



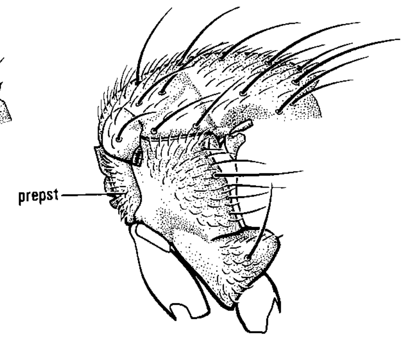
164 Omomyia regularis ♂



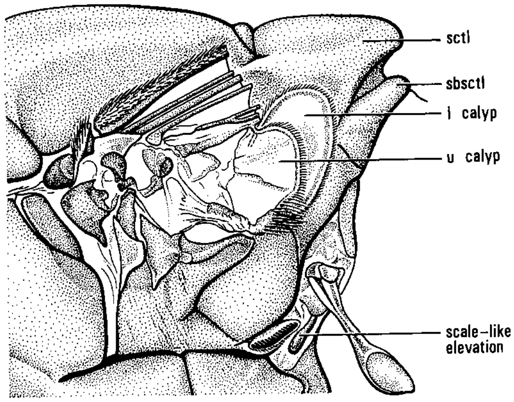
165 Xylophagus abdominalis ♀



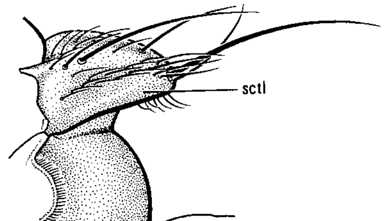
166 Chlorops certimus ♀



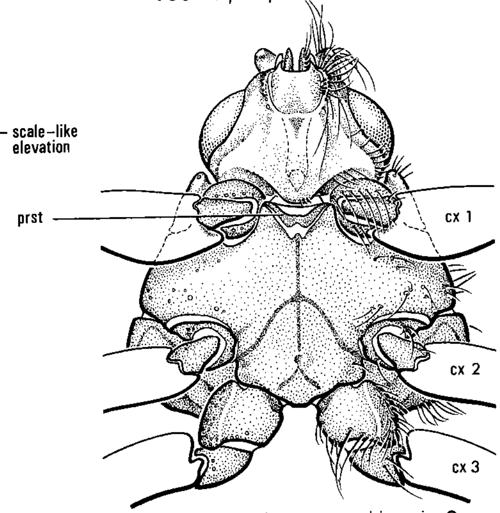
167 Ephydra riparia ♀

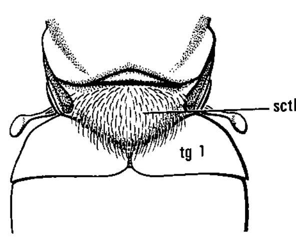


168 Tabanus sulcifrons ♀



169 Hylemya alcathoe ♂





170 Tabanus sulcifrons ♀

171 Ornithomya anchineuria ♀

107. Cell cu*p* without an angular extension at posterior apex. Frons normally with a single orbital bristle (Fig. 105), but this bristle sometimes duplicated in male of *Omomyia hirsuta* Coquillett .... **Richardiidae** (Ch. 67)

Cell cu*p* usually with an angular extension at posterior apex (Fig. 55), but if this extension lacking, then frons with two orbital bristles (Fig. 134) .... **Otitidae**, in part (Ch. 63)

108(81). C without subcostal or humeral break (Figs. 58, 62) 109

C with at least subcostal break present (Figs. 59, 60) 112

109. Ocellar bristles absent (Fig. 101) .... **Aulacigastridae** (***Stenomicra***) (Ch. 76)

Ocellar bristles present, though sometimes weakly so (Figs. 102, 111) 110

110. CuA_2 and A_1 strong; cell cu*p* complete (Fig. 62). Arista bare or micropubescent (Fig. 111) .... **Chamaemyiidae** (***Paraleucopis***) (Ch. 88)

CuA_2 and A_1 atrophied; cell cu*p* incomplete or absent (Fig. 58). Arista bare to plumose 111

111. R_1 joining C in basal third of wing; R_{4+5} and M distinctly convergent distally (Fig. 58). Postocellar setae weak or absent .... **Asteiidae** (Ch. 78)

R_1 joining C near middle of wing; R_{4+5} and M not convergent. Postocellar setae strong (Fig. 102) .... **Periscelididae** (Ch. 77)

112. CuA_2 and A_1 absent or vestigial, never forming a closed cell cu*p*; crossvein bm-cu absent, making cells bm and dm confluent (Figs. 67, 68) 113

CuA_2 and A_1 present, always forming a closed cell cu*p*; crossvein bm-cu usually present, making cells bm and dm usually separate (Fig. 66) 116

113. C with subcostal break only, without humeral break; CuA_1 usually with a kink marking position of atrophied crossvein bm-cu (Fig. 68). Arista bare or micropubescent, never plumose (Fig. 154) .... **Chloropidae** (Ch. 99)

C with both subcostal and humeral breaks; CuA_1 without a kink (Fig. 67). Arista bare to long plumose 114

114. Face strongly convex; subcranial cavity usually very large. Postocellar bristles, if present, divergent (Fig. 155) .... **Ephydridae** (Ch. 98)

Face concave; subcranial cavity normal. Postocellar bristles convergent or subparallel 115

115. Arista plumose. M_1 strong and normally pigmented. Mid tibia with a preapical dorsal bristle (Fig. 153) .... **Camillidae** (Ch. 97)

Arista micropubescent (Fig. 118). M_1 weak and unpigmented (Fig. 60). Mid tibia without a preapical dorsal bristle .... **Carnidae** (***Carnus, Meoneura***) (Ch. 80)

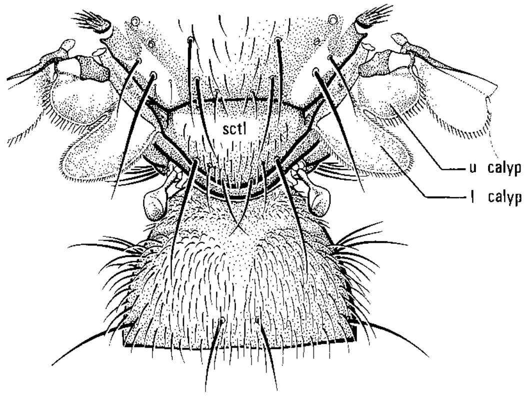
116. Vibrissa absent and gena without a vibrissa-like bristle (Figs. 106, 107). Katepisternum without an outstanding bristle, though frequently setulose (Figs. 106, 107). Mostly slender rather fragile flies, with elongate wings 117

Vibrissa present (Figs. 119–122) or gena with a vibrissa-like bristle (Fig. 113). In either case, katepisternum always with one or more outstanding bristles. Form variable 118

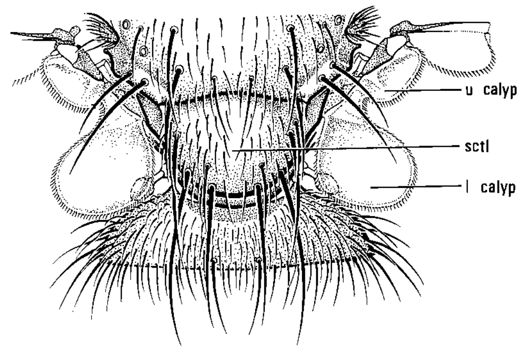
117. Notopleuron usually with two bristles; anepisternum with an outstanding bristle, in addition to fine hairs (Fig. 106). Ocelli situated far forward, with the anterior one about midway between vertex and antennae (Fig. 106) .... **Strongylophthalmyiidae** (Ch. 59)

Figs. 4.162–171. Special characters of Diptera: prosternum and adjoining areas of (162) *Xylomya americana* (Wiedemann) (Xylomyidae) and (165) *Xylophagus abdominalis* Loew (Xylophagidae), ventral view; propleuron and adjoining areas of (163) *Palloptera claripennis* Malloch (Pallopteridae), (164) *Omomyia regularis* Curran (Richardiidae), (166) *Chlorops certimus* Adams (Chloropidae), and (167) *Ephydra riparia* Fallén (Ephydridae), left lateral view; (168, 170) details of calypteres and posterior thoracic spiracle of *Tabanus sulcifrons* Macquart (Tabanidae), left lateral view; (169) scutellum of *Hylemya alcathoe* (Walker) (Anthomyiidae), left lateral view; (171) thoracic venter of *Ornithomya anchineuria* Speiser (Hippoboscidae), ventral view (*continued*).

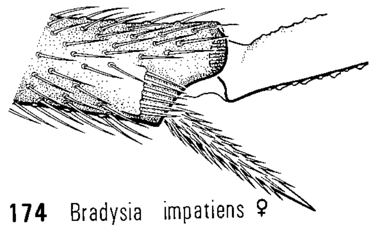
Abbreviations: cx, coxa; l calyp, lower calypter; precx brg, precoxal bridge; prepst, proepisternum; prepst s, proepisternal seta; prst, prosternum; sbsctl, subscutellum; sctl, scutellum; tg, tergite; u calyp, upper calypter.



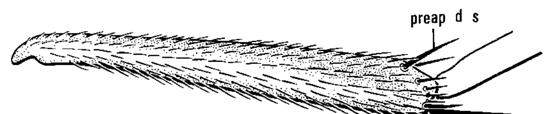
172 Melanophora roralis ♂



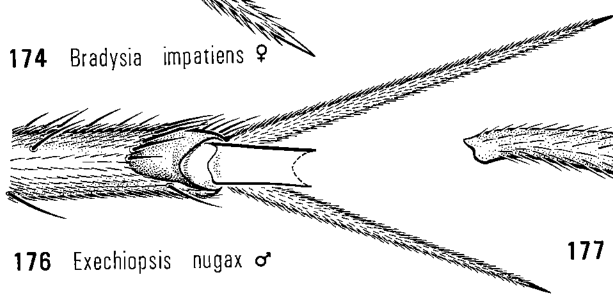
173 Anicia campestris ♀



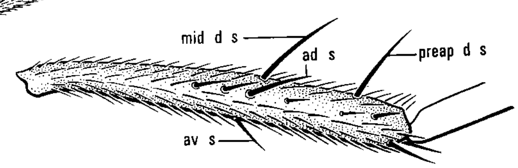
174 Bradysia impatiens ♀



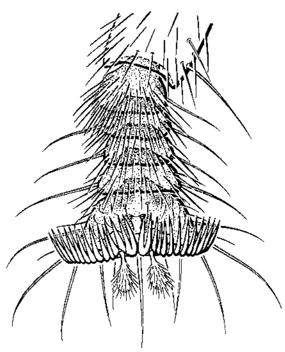
175 Clusiodes sp. ♀



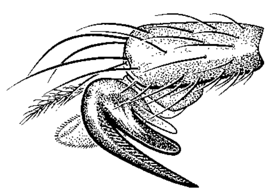
176 Exechiopsis nugax ♂



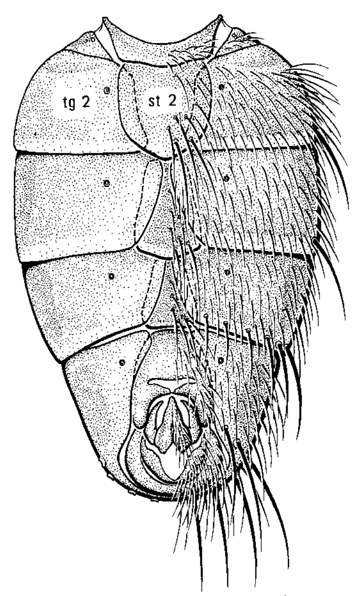
177 Fannia canicularis ♂



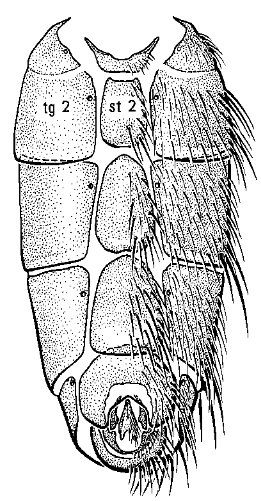
178 Braula coeca ♀



179 Icosta americana ♂



180 Anicia campestris ♂



181 Melanophora roralis ♂

Notopleuron with one bristle, the posterior one; anepisternum without a bristle, with fine hairs only (Fig. 107). Ocelli situated near vertex, with the anterior one on dorsal third of frons (Fig. 107) .... **Psilidae** (Ch. 60)

118. Ocellar bristles absent (Fig. 101) or extremely weak, but if these bristles minutely present (*Aulacigaster*), then frons with a bright orange band near anterior margin (Fig. 141) .... **Aulacigastridae** (Ch. 76)

Ocellar bristles present and usually strong (Figs. 119–122). Frons never with a bright orange band 119

119. C with both a humeral and subcostal break (Figs. 59, 60, 66) 120

C without a humeral break, with a subcostal break only (Fig. 69) 125

120. Long axis of antenna strongly elbowed, with flagellum distinctly decumbent; arista frequently long plumose (Figs. 2.41; 119–122) 121

Long axis of antenna nearly straight, with flagellum more or less porrect. Arista bare or shortly pubescent (Figs. 108, 112) 122

121. C with small evenly spaced erect spinules beyond subcostal break (Fig. 66). Proclinate orbital bristle arising dorsolaterally to lowermost reclinate orbital bristle (Figs. 119, 152) .... **Diastatidae** (Ch. 96)

C without erect spinules, with ordinary reclinate setulae only. Proclinate orbital bristle usually arising ventromedially to reclinate orbital bristle (Fig. 120); if arising above reclinate orbital bristle (*Chymomyza*, Fig. 122), then dorsomedially to it; if arising laterally to it (*Microdrosophila*, Fig. 121), then ventrolaterally to it .... **Drosophilidae** (Ch. 95)

122. Face tuberculate (Fig. 112). Mid tibia with a preapical dorsal bristle (as in Fig. 175) .... **Heleomyzidae** (***Cinderella***) (Ch. 89)

Face not tuberculate. All tibiae lacking a distinct preapical dorsal bristle 123

123. All fronto-orbital bristles uniformly oriented, essentially reclinate; interfrontal bristles weak and scattered; middle of face membranous and sunken, bearing some fine setulae on upper portion in Nearctic species (Fig. 108) .... **Cypselosomatidae** (Ch. 55)

Fronto-orbital bristles not uniformly directed, usually with some inclinate, some lateroclinate, some proclinate and some reclinate; interfrontal bristles usually stronger and serially arranged; middle of face sclerotized and raised, usually bare (Fig. 118) 124

124. Gena broad, with a row of bristles in middle. Proboscis with stout bulbous prementum and short inconspicuous labella (Fig. 118) .... **Carnidae**, in part (Ch. 80)

Gena usually narrow, but if broad, then bristles confined to lower margin. Proboscis with slender prementum and long conspicuous labella folded back along prementum (Fig.143) .... **Milichiidae**, in part (Ch. 79)

125(119). All tibiae with a preapical dorsal bristle. Frons with two reclinate orbital bristles above and one inclinate frontal bristle below (Fig. 139) .... **Odiniidae** (Ch. 72)

All tibiae without a preapical dorsal bristle. Fronto-orbital bristles not as above 126

126. Anepimeron setulose. Frons with a single orbital bristle (Fig. 142) .... **Opomyzidae** (Ch. 74)

Anepimeron usually bare, but if setulose, then frons with more than one orbital bristle .. 127

Figs. 4.172–181. Special characters of Diptera (*concluded*): relative position of calypteres of (172) *Melanophora roralis* (Linnaeus) (Rhinophoridae) and (173) *Anicia campestris* (Fallén) (Sarcophagidae); (174) apical spine of left fore tibia of *Bradysia impatiens* (Johannsen) (Sciaridae), anterior view; (175) preapical dorsal and apical ventral bristles of left mid tibia of *Clusiodes* sp. (Clusiidae), anterior view; (176) apical spines of left hind tibia of *Exechiopsis nugax* (Johannsen) (Mycetophilidae), dorsal view; (177) bristles of left hind tibia of *Fannia canicularis* (Linnaeus) (Muscidae), anterior view; (178) right hind claws of *Braula coeca* Nitzsch (Braulidae), ventral view; (179) right fore claws of *Icosta americana* (Leach) (Hippoboscidae), anterior view; relative position of second abdominal sternite and tergite in (180) *Anicia campestris* (Sarcophagidae) and (181) *Melanophora roralis* (Rhinophoridae), ventral view.

Abbreviations: ad s, anterodorsal seta; av s, anteroventral seta; l calyp, lower calypter; mid d s, mid dorsal seta; preap d s, preapical dorsal seta; sctl, scutellum; st, sternite; tg, tergite; u calyp, upper calypter.

127. Postocellar bristles divergent (Fig. 115), always present .... **Agromyzidae**, in part (Ch. 73)
Postocellar bristles convergent or absent 128

128. Anepisternum bare. Fore femur usually with a strongly developed ctenidial spine (Fig. 140) .... **Anthomyzidae** (Ch. 75)
Anepisternum setulose (Figs. 147, 156). Fore femur usually without a distinct ctenidial spine 129

129. Proepisternal and proepimeral bristles present (Fig. 156) .... **Tethinidae**, in part (Ch. 101)
Proepisternal bristle always absent; proepimeral bristle absent, except in some *Aphaniosoma* (Fig. 147) .... **Chyromyidae** (Ch. 92)

130(1). Flagellum with two or more distinctly separate flagellomeres, exclusive of stylus or arista (Figs. 2.12–21) 131
Flagellum with a single consolidated segment, exclusive of stylus or arista (Figs. 2.22–45) 137

131. Ocelli absent 132
One ocellus, at least, present 134

132. Mesoscutum with complete V-shaped suture (Fig. 7.1) ...... **Tipulidae (eight genera)** (Ch. 7)
Mesoscutum without a complete V-shaped suture 133

133. Eye minute. Wing and halter absent (Fig. 185) .... **Cecidomyiidae (*Baeonotus*)** (Ch. 16)
Eye well-developed. Vestiges of wing and halter present .... **Chironomidae (*Clunio, Eretmoptera*)** (Ch. 29)

134. Tibiae without apical spurs .... **Cecidomyiidae (several genera)** (Ch. 16)
Tibiae with apical spurs, these sometimes very short (Figs. 174, 176) 135

135. Eye bridge present (Fig. 77) .. **Sciaridae (some females of *Bradysia* and *Epidapus*)** (Ch. 15)
Eye bridge absent (Fig. 78) 136

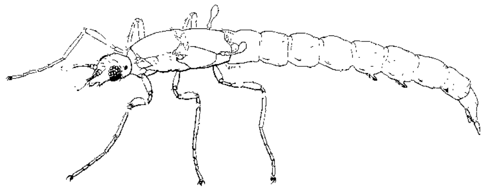
136. Palpus one-segmented. Body about 2 mm long .... **Sciaridae (female of *Pnyxia scabiei*)** (Ch. 15)
Palpus with three or more segments. Body at least 4 mm long .... **Mycetophilidae (females of *Baeopterogyna* and some *Boletina*)** (Ch. 14)

137(130). Body less than 2 mm long. Flagellum with an elongate annulated stalk and inflated knob. Compound eyes joined on ventral surface of head behind vestigial mouthparts. Very small aquatic flies, less than 2 mm long, unusually slender, pale, and weakly sclerotized (Fig. 182) .... **Nymphomyiidae (*Palaeodipteron walkeri*)** (Ch. 10)
Body more than 2 mm long. Flagellum without an elongate annulated stalk. Compound eyes not meeting on ventral surface of head. Stouter, darker, more strongly sclerotized flies 138

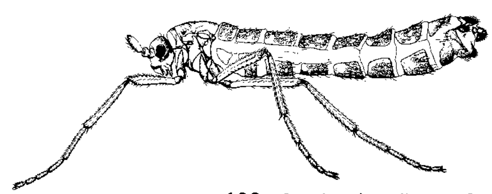
138. Pedicel swollen; flagellum at least twice as long as broad and with a minute apical seta. Remnant of larval eye strongly apparent. Abdomen about three times as long as remainder of body (Fig. 183) .... **Chironomidae (*Oreadomyia albertae*)** (Ch. 29)
Pedicel not swollen; flagellum less than twice as long as broad, and usually with an elongate stylus or arista. Remnant of larval eye not apparent. Abdomen less than twice as long as remainder of body 139

139. Thorax unusually short (in dorsal view less than half as long as head), and closely adjoining and rather similar in shape to abdominal tergite 1 + 2 (Fig. 184). Tarsi without claws, but bearing an inflexed comb of many microscopic teeth (Fig. 178). Associated with the honeybee .... **Braulidae (*Braula coeca*)** (Ch. 81)
Thorax at least as long as head, strongly separated from abdominal tergite 1 + 2 and differing greatly from it in shape. Each tarsus with two claws 140

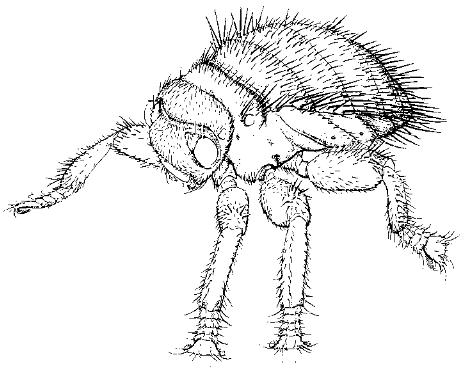
140. Mid and hind coxae widely separated ventromedially (Fig. 171); tarsal claws strongly recurved and toothed (Fig. 179). Ectoparasites of bats, birds, or mammals 141
Coxae not widely separated ventromedially; tarsal claws simple. Usually not ectoparasites of bats or mammals, sometimes associated with nestling birds (Carnidae) 143



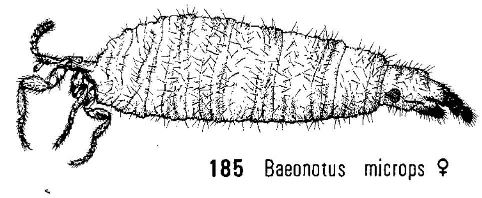
182 Palaeodipteron walkeri ♂



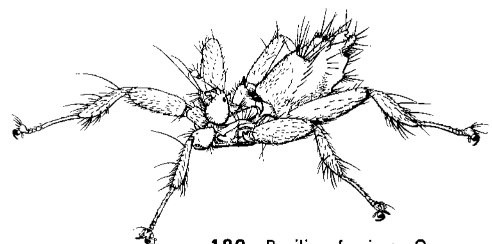
183 Oreadomyia albertae ♀



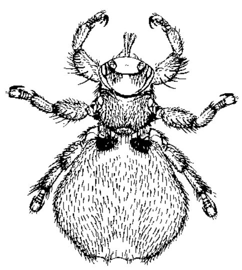
184 Braula coeca ♀



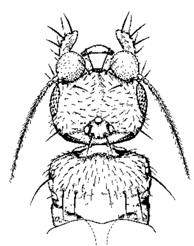
185 Baeonotus microps ♀



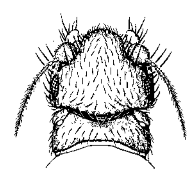
186 Basilia forcipata ♀



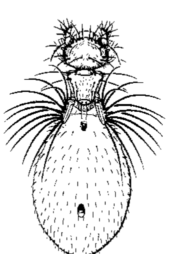
187 Melophagus ovinus ♀



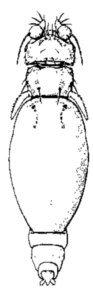
188 Puliciphora occidentalis ♀



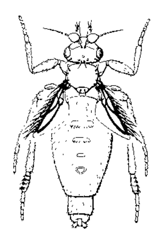
189 Chonocephalus sp. ♀



190 Acontistoptera brasiliensis ♀

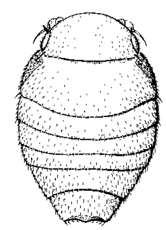


191 Ecitomyia wheeleri ♀



192 Commoptera solenopsidis ♀

193 Trophodeinus pygmaeus ♀



194 Aenigmatias eurynotus ♀

Figs. 4.182–194. Diptera with wings absent or greatly reduced: (182) *Palaeodipteron walkeri* Ide (Nymphomyiidae), left dorsolateral view; (183) *Oreadomyia albertae* Kevan & Cutten-Ali-Khan (Chironomidae), left lateral view; (184) *Braula coeca* Nitzsch (Braulidae), left dorsolateral view; (185) *Baeonotus microps* Byers (Cecidomyiidae), left lateral view; (186) *Basilia forcipata* Ferris (Nycteribiidae), left dorsolateral view; (187) *Melophagus ovinus* (Linnaeus) (Hippoboscidae), dorsal view; head and thorax, dorsal view, of (188) *Puliciphora occidentalis* (Melander & Brues) and (189) *Chonocephalus* sp. (Phoridae); body, dorsal view, of (190) *Acontistoptera brasiliensis* Schmitz (species not Nearctic), (191) *Ecitomyia wheeleri* Brues, (192) *Commoptera solenopsidis* Brues, (193) *Trophodeinus pygmaeus* Borgmeier, and (194) *Aenigmatias eurynotus* (Brues) (Phoridae).

141. Head vertically oriented, folded back into groove on mesoscutum. First tarsomere of each tarsus very elongate, at least as long as remainder of tarsus (Fig. 186). Ectoparasites of bats .... **Nycteribiidae (*Basilia*)** (Ch. 112)

Head horizontally oriented, not folded back. First tarsomere of each tarsus short, subequal to second tarsomere. Parasites of bats, birds, or mammals 142

142. Compound eye always present and relatively large, vertically oval, at least three-fourths as high as head, with at least 100 very small facets (Figs. 161, 187). Ectoparasites of birds and mammals other than bats .... **Hippoboscidae (*Melophagus*** and **females of *Lipoptena*)** (Ch. 111)

Compound eye sometimes absent, but if present, small and round, never more than half as high as head, with less than 40 relatively large bead-like facets (Fig. 160). Ectoparasites of bats .... **Streblidae (several genera)** (Ch. 113)

143. Lunule absent (Figs. 93–96) 144

Lunule present (Figs. 117–122) 146

144. Arista with three aristomeres (Figs. 2.37; 188–194) .... **Phoridae (females of several genera)** (Ch. 51)

Arista with two aristomeres (Figs. 2.34, 2.36) 145

145. Proboscis short and retracted. Vertex excavated. Compound eye pubescent (Fig. 94) .... **Dolichopodidae (females of some *Campsicnemus*)** (Ch. 48)

Proboscis elongate and projecting. Vertex convex. Compound eye bare .... **Empididae (*Chersodromia*)** (Ch. 47)

146. First tarsomere of hindleg swollen, shorter than second tarsomere (Fig. 149) .... **Sphaeroceridae (*Carolinaptera*, some *Leptocera*)** (Ch. 93)

First tarsomere of hindleg not swollen, longer than second tarsomere 147

147. Propleuron with a vertical ridge (Fig. 166) .... **Chloropidae (some *Conioscinella*)** (Ch. 99)

Propleuron without a vertical ridge (Fig. 167) 148

148. Face strongly convex; subcranial cavity unusually large (Fig. 155) .... **Ephydridae (females of some *Hyadina*** and ***Nostima*)** (Ch. 98)

Face concave; subcranial cavity normal (Fig. 118) 149

149. Postocellar bristles absent; frons with a single, reclinate orbital bristle. Reduced wing with an apical spot (Fig. 142) .... **Opomyzidae (some *Geomyza*)** (Ch. 74)

Postocellar bristles present; frons with at least two orbital bristles (Fig. 118). Reduced wing, if present, without an apical spot 150

150. Postocellar bristles subparallel; gena with a row of strong bristles in middle (Fig. 118). Associated with nestling birds .... **Carnidae (*Carnus hemapterus*)** (Ch. 80)

Postocellar bristles convergent; gena without a row of bristles in middle (Figs. 98, 120–121). Not associated with birds 151

151. All tibiae without a preapical dorsal bristle; fore femur with a strong ctenidial bristle (Fig. 140). Frons with two strong reclinate fronto-orbital bristles on lower half .... **Anthomyzidae (some *Anthomyza*)** (Ch. 75)

Some or all tibiae with a preapical dorsal bristle; fore femur without a ctenidial bristle. Frons without strong fronto-orbital bristles on lower half (Figs. 98, 120) 152

152. Frons with a proclinate orbital bristle (Fig. 120). Arista plumose (Fig. 120) .... **Drosophilidae (mutant *Drosophila*)** (Ch. 95)

Frons without a proclinate fronto-orbital bristle (Fig. 98). Arista bare or micropubescent (as in Figs. 114–118) .... **Heleomyzidae (some *Lutomyia*)** (Ch. 89)

KEY TO FAMILIES—LARVAE 5

H. J. TESKEY

Discretion is needed in using this key, particularly when dealing with families of the Muscomorpha. In that infraorder, larvae of fewer than 5% of the Nearctic species representing only perhaps 10–15% of the genera have been described in enough detail for diagnosis. Therefore in many families of the Muscomorpha, including several with abundant species, the larvae of the few that are known may be atypical of the family. In other families of the Muscomorpha the variation is so great that some repetition was needed in constructing the key. Larval identification of families is easier, however, for the Nematocera and orthorrhaphous Brachycera than for the Muscomorpha. In these groups larvae of approximately 10% of the species representing 40% of the genera have been described, and each of the families or their natural subdivisions are comparatively homogeneous.

Larvae of the following families have not been described: Acartophthalmidae, Asteiidae, Camillidae, Chyromyidae, Diastatidae, Hilarimorphidae, Neriidae, Rhinotoridae, Richardiidae, Ropalomeridae, Strongylophthalmyiidae, Tethinidae, and Trixoscelididae.

Because the posterior spiracles are frequently closely associated and are sometimes even borne on a single base, they are usually referred to here in the plural sense. The anterior spiracles, however, are widely separated and are always referred to in the singular.

Key

1. Sclerotized head skeleton not apparent. Respiratory system peripneustic. Terminal abdominal segment with large upwardly curved horn-like tubercles (Fig. 21.6). Larva living in decaying wood .... NEMATOCERA, in part.... **Synneuridae** (Ch. 21)

   Head capsule or internal cephalopharyngeal skeleton usually conspicuous. Respiratory system usually not as above, but if peripneustic, then terminal segment lacking large curved horn-like tubercles of type shown in Fig. 21.6 2

2. Larva small, often yellow to reddish. A small postcephalic segment present between prothorax and head capsule in addition to three thoracic and nine abdominal segments (Figs. 16.7–9, 16.11). Head capsule very small, lightly sclerotized, and rounded or only slightly longer than broad; mouthparts indistinctly differentiated; antenna two- or three-segmented; paired cephalic bars projecting posteriorly from lateral margins (Fig. 16.5). Prothorax usually with a variously shaped sternal spatula ventrally (Fig. 16.7). Respiratory system peripneustic or apneustic. Larva inhabiting plant galls but also free-living in a variety of habitats .... NEMATOCERA, in part.... **Cecidomyiidae** (Ch. 16)

   Size and color various. Postcephalic segment usually not distinguishable. Head capsule or internal cephalopharyngeal skeleton with well-differentiated mouthparts; paired cephalic bars lacking. Prothorax without sternal spatula. Respiratory system variable 3

3. Mandibles normally moving against one another in a horizontal or oblique plane, usually with two or more apical teeth, rarely hook-like or sickle-shaped. Head capsule usually complete and permanently exserted (eucephalic), but if partially retracted within thorax and incomplete as a result of excisions in the capsule posteriorly (Tipulidae, couplet 4), then lacking tentorial arms .... most NEMATOCERA.... 4

   Mandibles moving parallel to one another in a vertical plane, usually hook-like or sickle-shaped and without secondary apical teeth (Figs. 31.56, 33.22, 34.15). Head capsule variously reduced posteriorly and partially or almost entirely retracted within thorax (hemicephalic) or replaced by an internal cephalopharyngeal skeleton (Figs. 3.5, 5.3, 5.50–51, 40.29, 45.59–60, 47.58), but if appearing complete and permanently exserted, then with a slender metacephalic rod extending into prothorax (Fig. 37.24) .... BRACHYCERA.... 28

4. Head capsule longitudinally excised dorsally to varying degrees, in extreme cases reduced to several slender rods; capsule capable of partial or complete retraction within thorax (Figs. 7.67, 7.76–77, 7.83, 7.87–88). Respiratory system usually metapneustic, only rarely apneustic. Larva found mostly in wet earth or decaying wood .... **Tipulidae** (Ch. 7)

   Head capsule complete and incapable of retraction within thorax. Respiratory system usually not as above 5

5. Head, thorax, and first abdominal segment fused into a compound body division; a suctorial disc present ventromedially on compound segment and on each of the five segments following (Figs. 8.7–8). Attached to objects in a stream bed .... **Blephariceridae** (Ch. 8)

Head, thorax, and first abdominal segment distinctly separated; suctorial discs present or absent 6

6. A pair of prolegs, each bearing apical crochets, present on each of seven or eight abdominal segments (Figs. 9.2–3, 10.6–7). In streams clinging to stones 7

Characters not as above 8

7. Eight pairs of slender prolegs present ventrally on abdominal segments. Antenna shorter than head (Fig.10.7) .... **Nymphomyiidae** (Ch. 10)

Seven pairs of rather stout prolegs present laterally on abdominal segments. Antenna longer than head, forked near middle (Figs. 9.2–3) .... **Deuterophlebiidae** (Ch. 9)

8. Respiratory system holopneustic or peripneustic, with eight pairs of abdominal spiracles; posterior spiracles usually conspicuously larger than other seven pairs of abdominal spiracles 9

Respiratory system not as above; if hemipneustic, with only seven pairs of abdominal spiracles, then all abdominal spiracles of equal size (Fig. 14.9) 12

9. Respiratory system holopneustic. All segments usually with tuberculous or spinous processes (Figs. 13.12–14). Feeding on plant roots and decaying organic matter .... **Bibionidae** (Ch. 13)

Respiratory system peripneustic. Only terminal abdominal segment sometimes having tuberculous or spinous processes, although other segments sometimes with broad tumid swellings associated with creeping welts 10

10. Mandibles moving in an oblique downward direction; labrum slender and somewhat laterally compressed, with a dense brush of short setae on its ventral apex and epipharyngeal surface. Terminal abdominal segment with a pair of dorsally sclerotized lobes or a broad sclerotized shelf below posteriorly directed spiracles and behind anus. Posterior spiracles either sessile or each at apex of a sclerotized tubular process (Fig. 20.24). In excrement and decaying matter .... **Scatopsidae** (Ch. 20)

Mandibles moving horizontally; labrum broad, with sparse setae especially toward apex. Terminal abdominal segment lacking sclerotized areas. Posterior spiracles sessile and situated laterally on penultimate abdominal segment or associated with spinous processes dorsally on terminal abdominal segment. In decaying wood 11

11. Body hairs conspicuous, the longest approximately half width of segment (Fig. 12.5) .... **Pachyneuridae** (Ch. 12)

Body hairs inconspicuous, much shorter than half width of segment (Fig. 14.103) .... **Mycetophilidae (Ditomyiinae)** (Ch. 14)

12. Respiratory system hemipneustic, rarely propneustic or apneustic. Mandible or maxilla or both flattened or lamellate, with a serrate inner margin (Figs. 14.98–99). Associated with fungi 13

Respiratory system amphipneustic, metapneustic, or apneustic. Mandible and maxilla not flattened, without a serrate inner margin 14

13. Posterior tentorial bridge complete or nearly complete (Fig. 15.33) (usually visible beneath integument within occipital cavity in preserved specimens without special treatment). Abdominal creeping welts without sclerotized spicules (Fig. 15.35) .... **Sciaridae** (Ch. 15)

Posterior tentorial bridge absent (Fig. 100) or if bridge partially formed, abdominal creeping welts with sclerotized spicules (Fig. 14.97) .... **Mycetophilidae**, in part (Ch. 14)

14. Posterior spiracles mounted at end of a slender respiratory siphon that is nearly or fully as long as the body when completely extended 15

Posterior spiracles mounted on no more than a very short siphon, much shorter than body, or spiracles absent 16

15. Integument smooth, shiny, white. Respiratory siphon nonretractile. Anal papillae large, pinnately branched (Fig. 11.6). Burrowing in wet decaying logs .... **Axymyiidae** (Ch. 11)

Integument with numerous hairs, warts, or tubercles. Respiratory siphon retractile. Anal papillae small, unbranched (Figs. 22.5–6). Found in saturated soil .... **Ptychopteridae** (Ch. 22)

16. Thoracic segments fused and indistinctly differentiated, forming a round or somewhat flattened compound segment that is wider than any of the abdominal segments (Figs. 24.10, 25.33–34). A preanal fan-like ventral brush of setae present on terminal abdominal segment (Figs. 24.14, 25.30–32). Lateral tufts of long setae often present on body segments 17

Thoracic segments usually individually distinguishable, and about equal in diameter to or narrower than widest of the abdominal segments. Ventral brush of setae on terminal abdominal segment absent. Setae untufted on thoracic and abdominal segments 18

17. Prominent brush of setae on either side of labrum (Figs. 25.23, 25.26–27, 25.33–34). Antenna of moderate length, usually with short apical setae .... **Culicidae** (Ch. 25)

Labral setae absent or few in number, and not divided into two groups on either side of labrum (Figs. 24.9–10). Antenna sometimes prehensile, with long apical setae .... **Chaoboridae** (Ch. 24)

18. Paired crochet-bearing prolegs present ventrally on first and usually second abdominal segments. Abdomen with two flattened posterolateral processes behind the posterior spiracles having setose margins that project above a conical dorsally sclerotized process bearing the anus and anal papillae ventrally (Fig. 23.10) .... **Dixidae** (Ch. 23)

Prolegs lacking on abdominal segments 1 and 2. Abdomen without posterior flattened fringed postspiracular processes, and without a conical dorsally sclerotized anal process 19

19. Prothorax with one proleg or a pair of prolegs ventrally (Figs. 26.4, 27.77, 28.130–131, 29.114–116) 20

Prothorax lacking prolegs 23

20. Head capsule usually with a pair of conspicuous folding labral fans dorsolaterally. Abdomen swollen apically; terminal segment ending in a ring or circlet of numerous radiating rows of minute hooked spines (Fig. 27.77). Inhabiting flowing water .... **Simuliidae** (Ch. 27)

Head capsule lacking labral fans. Abdomen not conspicuously swollen apically; terminal segment without radiating rows of hooked spines posteriorly, but sometimes with one or two anal prolegs bearing crochets 21

21. Respiratory system amphipneustic; anterior spiracle on a short stalk; posterior spiracles opening into a transverse cleft between finger-like processes on abdominal segment 8. Prothoracic and terminal prolegs unpaired (Fig. 26.4). On rocks washed by a film of water .... **Thaumaleidae** (Ch. 26)

Respiratory system apneustic. Prothoracic or terminal prolegs usually paired even if distinction is only a slight separation of the apical spines or crochets 22

22. All body segments with prominent tubercles or setae or both (Figs. 28.130–131) .... **Ceratopogonidae (Forcipomyiinae)** (Ch. 28)

Body segments, except sometimes the terminal one, lacking prominent tubercles and setae (Figs. 29.114, 29.116) .... **Chironomidae** (Ch. 29)

23. Abdominal segment 8 with a pair of long filamentous processes arising laterally behind spiracles; abdominal segment 9 with similar paired processes arising dorsolaterally and from near apex of two elongate cylindrical posteroventrally projecting prolegs (Fig. 6.4). In saturated sandy gravel bordering streams .... **Tanyderidae** (Ch. 6)

Posterior abdominal segments without long filamentous processes, and without prolegs or with only a single terminal proleg 24

24. Respiratory system apneustic. Larva slender, smooth, with uniform bead-like segments; long setae present only on terminal abdominal segment (Figs. 28.132–134) .... **Ceratopogonidae**, in part (Ch. 28)

Respiratory system amphipneustic or metapneustic. Larva usually somewhat wrinkled, with secondarily divided segments; distinctive setation or sclerotized plaques present on most segments 25

25. Secondary segmentation of prothorax and abdominal segments evident, with these segments having a distinct narrow annulus anteriorly (Fig. 19.19). Posterior spiracles sessile on surface of terminal abdominal segment and placed either laterally or apically, with apically positioned spiracles surrounded by five small lobes (Figs. 19.20–22). In decaying organic material .... **Anisopodidae** (Ch. 19)

Secondary segmentation either not apparent, or usually with thoracic and first abdominal segments subdivided into two sections and remaining abdominal segments subdivided into three elementary sections. Posterior spiracles either mounted on a respiratory siphon or as above, but if sessile and apical in position then surrounded by only four lobes 26

26. Posterior spiracles and a pair of fan-like setal brushes borne dorsally at caudal margin of a sclerotized plate on terminal abdominal segment or at apex of a short respiratory siphon projecting posterodorsally from terminal abdominal segment. A sclerotized plaque or plaques evident dorsally on one or more of the secondary segmental divisions (Figs. 17.14–15). In aquatic or semiaquatic habitats or in decaying organic material .... **Psychodidae (Psychodinae)** (Ch. 17)

Posterior spiracles not borne on a respiratory siphon. Sclerotized plaques absent 27

27. Posterior spiracles situated laterally on terminal or penultimate abdominal segment. Either setae on integument prominent and systematically arranged with clavate forms evident and with some very long setae on dorsum of terminal segment (Fig. 17.16) (Phlebotominae), or setae short and unmodified or absent (Fig. 17.17) (Trichomyiinae) .... **Psychodidae**, in part (Ch. 17)

Posterior spiracles situated on apex of terminal abdominal segment and surrounded by four fleshy lobes (Fig. 18.7). Setae variable. In decaying vegetable matter .... **Trichoceridae** (Ch. 18)

28. Sclerotized portions of cranium always present and usually partially exposed externally (Figs. 31.56, 33.15, 34.11, 37.24, 44.5, 45.59, 48.44). Labrum, mandibles, or maxillae readily recognizable .... ORTHORRHAPHOUS BRACHYCERA....29

External sclerotized portions of cranium completely lacking; only a membranous pseudocephalic segment anterior to prothorax remaining, normally bearing two pairs of papilla-like projections considered to be vestiges of antennae and palpi; characteristically shaped cephalopharyngeal skeleton retracted completely within prothorax or almost entirely absent in some, usually parasitic, species (Figs. 3.12; 45, 79). Homologs of labrum, mandibles, and maxillae not clearly definable .... MUSCOMORPHA....46

29. Sclerotized plates present dorsally on one or more thoracic segments or on terminal abdominal segment or on both; sclerotized plate on terminal abdominal segment obliquely truncate, with projecting processes, and bearing posterior spiracles. Exposed portion of head capsule darkly sclerotized and conical, with mouthparts very small and projecting at tip of cone (Figs. 34.11–13). In soil or under bark of decaying trees .... **Xylophagidae** (Ch. 34)

Sclerotized plates usually lacking on thoracic and terminal abdominal segments but if a plate present on terminal segment it does not bear spiracles. Exposed portion of head capsule not uniformly conical, and mouthparts relatively larger 30

30. Body dorsoventrally compressed. Integument hardened by calcareous deposits accumulated in small roundish or hexagonal facets that impart a shagreened appearance. Head capsule permanently partially exposed and capable of only slight independent movement (Figs. 35.6–7, 36.71–75, 36.84) 31

Body of various form. Integument not hardened and not faceted with calcium deposits, sometimes tough and leathery. Head capsule capable of much independent movement 32

31. Prothoracic and mesothoracic segments with a smooth field on dorsum. Anus bordered anteriorly by a transverse row of strong posteriorly directed teeth (Figs. 35.6–7) .... **Xylomyidae** (Ch. 35)

Prothoracic and mesothoracic segments with normal shagreened pattern on dorsum. Anus not bordered anteriorly by teeth .... **Stratiomyidae** (Ch. 36)

32. Body long and slender, eel-like, with 20 apparent segments. Posterior spiracles situated laterally on fourth segment from end (Fig. 38.11). Head capsule appearing to be complete and permanently exserted, flexibly articulated posteriorly with a slender or spatulate metacephalic rod lying within thorax (Figs. 37.24, 37.26, 38.12) 33

Body not eel-like, with no more than 12 apparent segments. Posterior spiracles on terminal or penultimate abdominal segment. Head capsule more or less reduced, especially posteroventrally, and partially retracted within thorax, with or without a single broad or nonspatulate metacephalic rod lying within thorax, or with two such rods present 34

33. Metacephalic rod expanded apically (Fig. 37.24). Antenna minute and peg-like. Setae on each side of thoracic segments shorter than diameter of segments and situated ventrolaterally (Fig. 37.23). Predacious in soil and decaying wood .... **Therevidae** (Ch. 37)

Metacephalic rod slender throughout (Fig. 38.12). Antenna long and filamentous. Setae on each side of thoracic segments as long as diameter of segments, and mesothoracic seta situated higher on segment than prothoracic and metathoracic setae (Fig. 38.11). Predacious on insects in the household, in stored foods and in wood .... **Scenopinidae** (Ch. 38)

34. Larva parasitic on other Arthropoda. Body plump and grub-like. Head usually small, almost completely retracted within thorax, with only mandibles or maxillae and at least a vestige of labrum visible externally 35

Larva free-living. Body usually elongate, slender. Portions of dorsal plate of head capsule and mouthparts visible externally 37

35. Body robust, tough, leathery. Terminal abdominal segment with posterior dorsal margin scalloped by blunt projections (Fig. 44.4). Maxilla large and shovel-shaped; mandible absent (Fig. 44.5). Parasitic on grasshoppers and beetle larvae .... **Nemestrinidae** (Ch. 44)

Body whitish, with thin transparent integument (Fig. 43.28). Terminal abdominal segment otherwise. Mandible slender and pointed, often smaller than maxilla (Figs. 45.59–60) 36

36. Body pear-shaped, with enlarged abdomen (Fig. 43.28). Internal parasites of spiders .... **Acroceridae** (Ch. 43)

Body moderately crescentic in shape, tapered front and back. Parasitic on insects .... **Bombyliidae** (Ch. 45)

37. Body with terminal segments distinctly enlarged; integument wrinkled and warty. Abdominal segment 1 with a ventral proleg. Abdominal segment 7 with a dorsal row of spine-like tubercles along posterior margin. Posterior spiracles situated dorsally on abdominal segment 8 (Fig. 39.5). Constructs pitfall traps in sandy soil for capturing prey .... **Vermileonidae** (Ch. 39)

Body usually cylindrical and relatively smooth-skinned. Prolegs, if present, situated on several segments. Abdominal segment 7 lacking dorsal row of tubercles. Posterior spiracles, if present, situated caudally on terminal segment or dorsolaterally on penultimate or terminal segment 38

38. A brush of retrorse spines situated above base of each mandible and attached to mandible such that when it strikes downward the brush of spines is pulled forward from beneath a semitransparent membranous covering and the spines are erected (Figs. 3.7, 31.56, 33.22). Portion of cranium lying within thorax continuous with anterior exposed portion without apparent break, although desclerotization may suggest bilateral division (Fig. 33.15). Tentorial arms solidly connected with tentorial phragmata, except in *Rhagio* (Fig. 33.22) .. 39

Such a brush of spines associated with mandibles absent. Posterior portion of cranium (metacephalic rod or rods) lying within thorax separated from anterior exposed portion by a clear seam allowing independent flexibility between the two portions (Figs. 40.29, 42.78–79, 47.58, 48.41, 48.43). Tentorial arms also flexibly attached to tentorial phragmata 42

39. Respiratory system apneustic. Living in stream beds 40

Respiratory system metapneustic or amphipneustic 41

40. Larva slightly flattened dorsoventrally. Slender tubercles of progressively increasing size situated laterally and dorsolaterally on abdominal segments 1–7; two longer caudal tubercles, fringed with hairs, on terminal segment. All abdominal segments with a ventral pair of prolegs bearing crochets (Fig. 32.7) .... **Athericidae** (Ch. 32)

Larva cylindrical, with smooth shiny integument and with segmentation bead-like, lacking tubercles and prolegs (Fig. 30.4) .... **Pelecorhynchidae** (Ch. 30)

41. Posterior spiracles lying within fissures to either side of a pair of abutting vertically linear bars (Fig. 31.55) or a retractable laterally compressed spine (Figs. 31.58–59); spiracles situated at apex of a short respiratory siphon or a comparable slightly domed area delimited caudally on terminal segment. Tracheal trunks closely approximated within terminal segment and siphon (Fig. 31.58). Terminal segment lacking tubercles. Several or all of anterior seven abdominal segments with an encircling row of projections sometimes bearing apical spicules and functioning as prolegs (Figs. 31.51–54). Submentum present (Fig. 31.56) .... **Tabanidae**(Ch. 31)

Posterior spiracular openings exposed; spiracle circular or oval; tracheal trunks distinctly separated caudally. Terminal segment either deeply cleft caudally to form two or four lip-like lobes, or bearing a pair of sclerotized horn-like processes dorsally and a pair of rounded lobes ventrally (Figs. 33.16–21); posterior spiracles on caudal face of dorsal lobes. First seven abdominal segments with ventral creeping welts. Submentum absent .... **Rhagionidae** (Ch. 33)

42. Head with a single relatively narrow or broader metacephalic rod that is sometimes split almost to base; sclerotized submentum present ventrally on head capsule; maxilla large and heavily sclerotized, more prominent than slender mandible (Figs. 40.29, 42.78–79). Nine abdominal segments present. Respiratory system functionally amphipneustic, although remnants of spiracles forming a holopneustic system usually visible; posterior spiracles situated laterally on abdominal segment 8 (Figs. 40.28, 42.76–77). Larva usually large at maturity 43

Head skeletonized in appearance, with two slender metacephalic rods and two tentorial arms the most prominent of features (Figs. 47.58, 48.41, 48.43); submentum absent; maxilla sometimes appearing to be absent, and never heavily sclerotized nor more prominent than mandible. Eight abdominal segments present; posterior spiracles, when present, located caudally on terminal segment. Respiratory system amphipneustic, metapneustic, or apneustic. Larva usually small 45

43. Maxillae laterally compressed, tending to cup mandibles, and similar in length to mandibles; maxillary palpus situated apically (Fig. 40.29). Habitat terrestrial .... **Mydidae** (Ch. 40)

Maxillae more or less dorsoventrally compressed, often toothed apically and concave ventrally to form gouge-like digging structures, usually much longer than mandibles; maxillary palpus situated laterally (Figs. 42.78–79) 44

44. Abdominal segment 8 about twice as long as wide; posterior spiracles lying laterally near anterior margin of this eighth segment. Habitat terrestrial .... **Apioceridae** (Ch. 41)

Abdominal segment 8 no longer than half its diameter; posterior spiracles situated dorsolaterally in posterior half of eighth segment (Figs. 42.76–77). Habitat terrestrial ...... **Asilidae** (Ch. 42)

45. Metacephalic rods moderately expanded to spatulate apically (Figs. 48.41, 48.43). Terminal abdominal segment either with four (or rarely two ventral) primary lobes surrounding posterior spiracles (Figs. 48.40, 48.44), or evenly rounded as in plant-mining forms; one pair of abdominal prolegs (in *Systenus*) and either six or seven abdominal creeping welts present .... **Dolichopodidae** (Ch. 48)

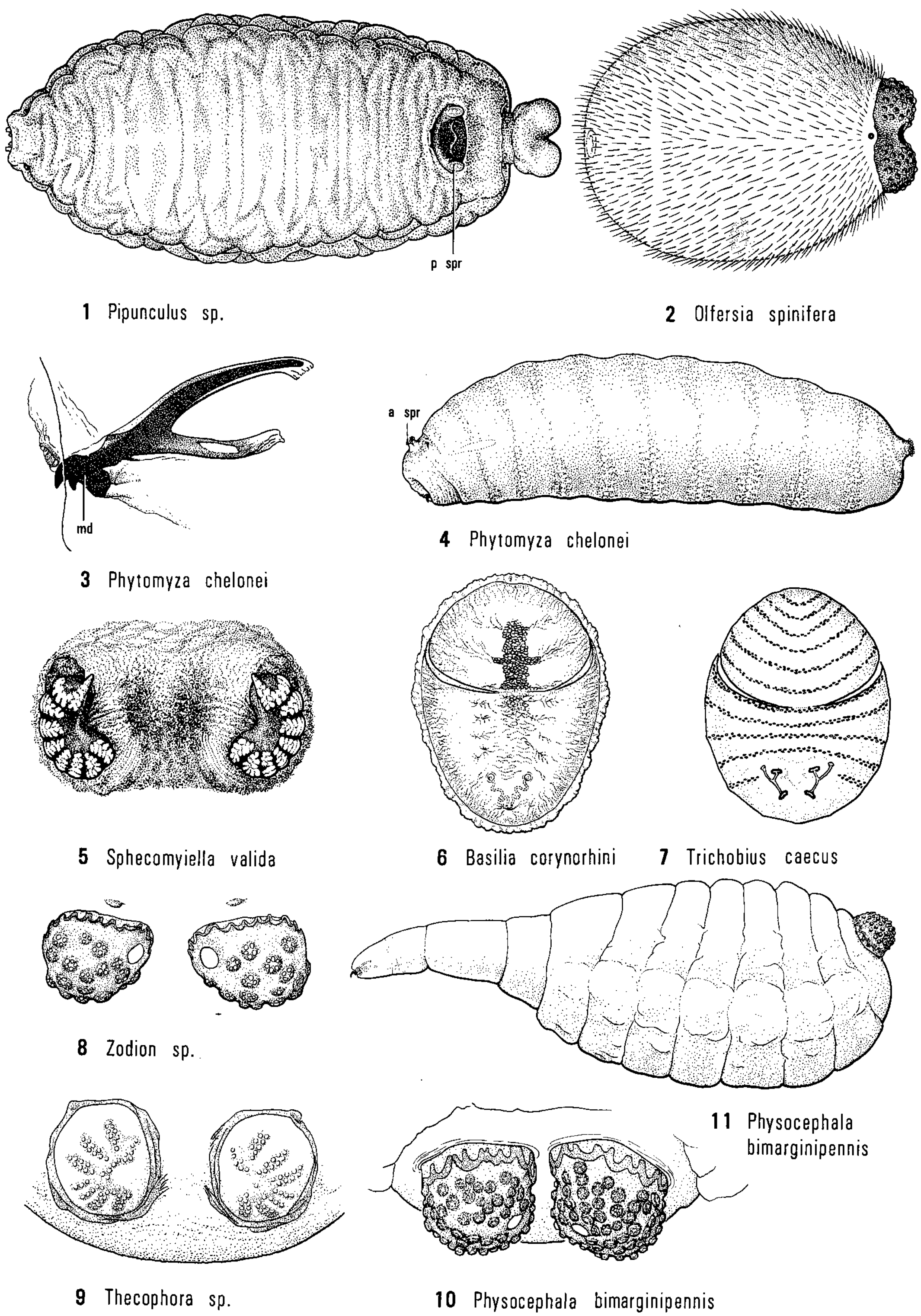
Metacephalic rods slender throughout (Fig. 47.58). Terminal abdominal segment either bearing a single median protuberance below posterior spiracles (Figs. 47.57, 47.63), or if more than one terminal lobe present, then respiratory system often apneustic and seven or eight pairs of abdominal prolegs with apical hook-like crochets present (Figs. 47.56, 47.59–60) .... **Empididae** (Ch. 47)

46. Posterior spiracles on a common very characteristically formed sclerotized plate (Fig. 1). Parasitic on Homoptera .... **Pipunculidae** (Ch. 53)

Posterior spiracles not on a common sclerotized plate of the form shown 47

47. Anterior spiracles near one another on dorsal surface of prothorax (Fig. 4). Mandible with longitudinal axis at oblique or right angles to remainder of cephalopharyngeal skeleton, and usually bearing two or more pairs of equal-sized anteriorly directed teeth (Fig. 3). Phytophagous, mostly leaf miners .... **Agromyzidae** (Ch. 73)

Anterior spiracles situated laterally. Mandible usually on same plane as remainder of cephalopharyngeal skeleton, and either bearing less than two pairs of teeth or bearing two or more pairs of teeth of unequal size 48



Figs. 5.1–11. Larval characters of Muscomorpha: (1) larva of *Pipunculus* sp. (Pipunculidae), dorsal view; (2) puparium of *Olfersia spinifera* (Leach) (Hippoboscidae), dorsal view; (3) cephalopharyngeal skeleton of *Phytomyza chelonei* Spencer (Agromyzidae); (4) larva of *P. chelonei*, lateral view; (5) posterior spiracles of *Sphecomyiella valida* (Harris) (Pyrgotidae); dorsal view of puparium of (6) *Basilia corynorhini* (Ferris) (Nycteribiidae) and (7) *Trichobius caecus* Edwards (Streblidae); posterior spiracles of (8) *Zodion* sp. (Conopidae), (9) *Thecophora* sp. (Conopidae), and (10) *Physocephala bimarginipennis* Karsch (Conopidae); (11) larva of *P. bimarginipennis*, lateral view.

Abbreviations: a spr, anterior spiracle; md, mandible; p spr, posterior spiracle.

48. Larva up to 2 mm long, oval to globular in shape. Either two pairs of posterior spiracles present, or the more posterior pair united into one plate; spiracles on each side usually visibly joined by slender convoluted branches of the felt chamber (Figs. 6, 7). Cephalopharyngeal skeleton lacking. Associated with bats on which adults are ectoparasitic 49

Larva of variable length and shape. No more than one pair of posterior spiracles present. Cephalopharyngeal skeleton usually present 50

49. Posterior spiracles represented by simple circular pore-like spiracular openings (Fig. 6) ....**Nycteribiidae** (Ch. 112)

Posterior spiracles oval, crescent-shaped, or with numerous spiracular openings placed circularly on margin, or otherwise modified (Fig. 7) ....**Streblidae** (Ch. 113)

50. Posterior spiracles elevated on structures ranging from a single short prominence to a very long and retractile respiratory tube (Figs. 14, 15, 17, 19); spiracular plates united along median margin (Figs. 13, 18, 20). Body with dense pubescence or systematically arranged spicules or tubercles (Figs. 12, 14, 15, 17, 19)..**Syrphidae** (Ch. 52)

Posterior spiracles either sessile or elevated above surface of terminal abdominal segment; spiracular plates normally well-separated, but if appearing fused, then body lacking dense pubescence, prominent spicules, and tubercles 51

51. Posterior spiracles each with numerous roundish, oval, or short slit-like spiracular openings; these openings randomly arranged, or situated along margin of spiracular plate, or associated with intricately convoluted coral-like or serpentine bands resembling a maze (Figs. 2, 5, 8, 10, 21, 24, 35, 36). Body usually with many tumid wrinkles, or otherwise rather swollen and roundish to pear-shaped 52

Posterior spiracles thorn-like (Fig. 38), or each spiracle with three isolated oval or slit-like relatively large and sometimes sinuous spiracular openings (Fig. 69), rarely with four to six such openings (Figs. 28, 49). Body usually rather slender and subcylindrical or flattened....59

52. Larva deposited as a smooth and generally featureless oval to round prepupa with a darkly sclerotized spiracular plate that is often large enough to cap end of body (Fig. 2) and with integumentary setae on some species. Associated with birds and mammals on which adults are ectoparasitic..**Hippoboscidae** (Ch. 111)

Larva not as above 53

53. Spiracular openings oval, arrayed in a circle on margin of spiracular plate. Parasitic on grasshoppers..**Anthomyiidae** (***Acridomyia***) (Ch. 104)

Spiracular openings distributed rather evenly over spiracular plate 54

54. Posterior spiracular plates kidney-shaped, each comprising a series of curvilinear bands with 8–14 yellowish to orange clusters of round or oval to short bar-like spiracular openings in each band, and with uppermost cluster extended into a short spine (Fig. 5). Parasitic on Scarabaeidae..**Pyrgotidae** (Ch. 65)

Posterior spiracular plates not as above 55

55. Posterior spiracular plates dome-shaped, either with circular wart-like protuberances each bearing several pale spiracular openings (Figs. 8–11) or with linear clusters of pores radiating from ecdysial scar. Parasitic on bees and wasps ....**Conopidae** (Ch. 54)

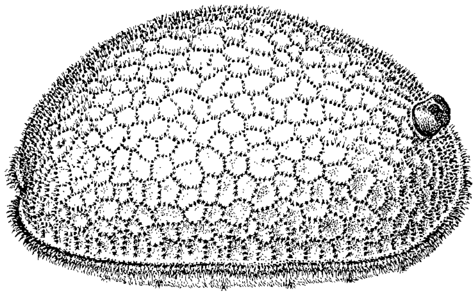
Posterior spiracular plates not dome-shaped, without wart-like protuberances. Parasitic on other insects and mammals 56

56. Posterior spiracles each with numerous openings elevated on a coral-like sculpturing of the spiracular plate; spiracular plate usually more or less clearly tripartite (Figs. 21, 24). Parasitic on various insects and chilopods ....**Tachinidae**, in part (Ch. 110)

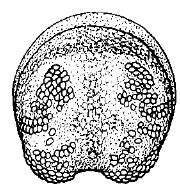
Posterior spiracles differing from above. Endoparasitic on mammals..57

57. Posterior spiracles with many short intricately serpentine lines resembling a maze, and clearly arranged on each spiracular plate into three groups (Fig. 35). Integument mostly covered with scale-like spines ....**Oestridae (Cuterebrinae)** (Ch. 107)

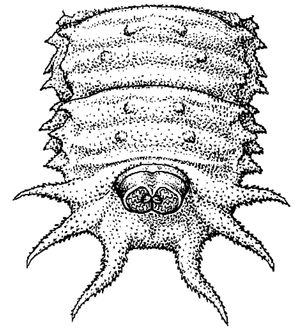
Posterior spiracles with oval to round spiracular openings arranged into more than three groups. Integument with spines restricted to margins of segment or to ventral surface; spines often not scale-like 58



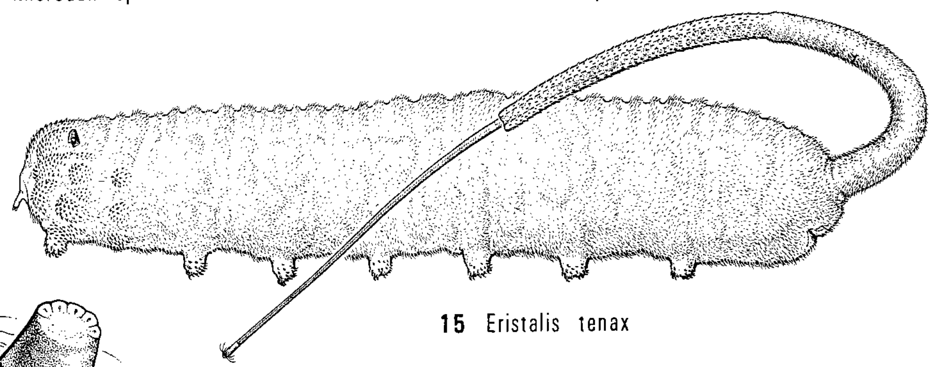
12 Microdon sp.



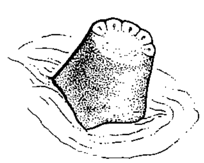
13 Microdon sp.



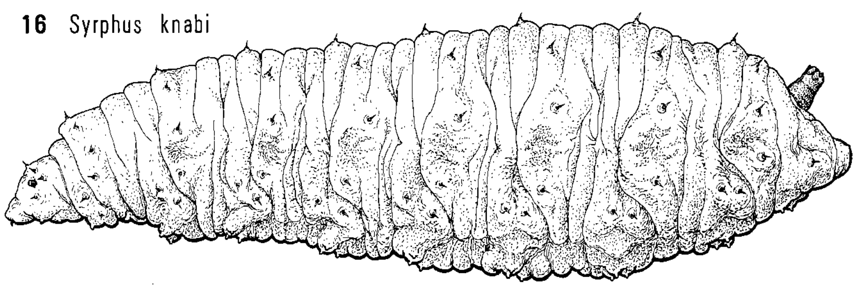
14 Volucella bombylans



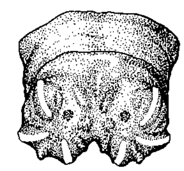
15 Eristalis tenax



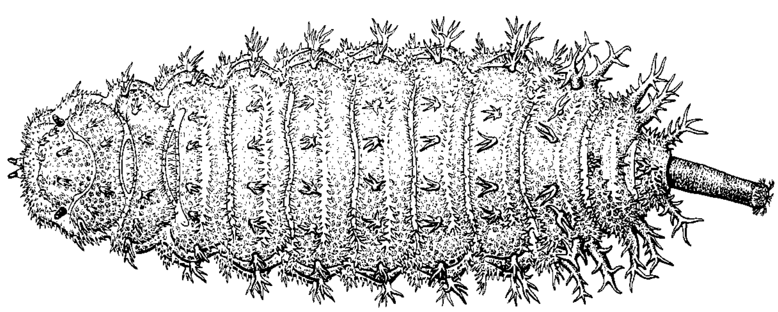
16 Syrphus knabi



17 Syrphus knabi



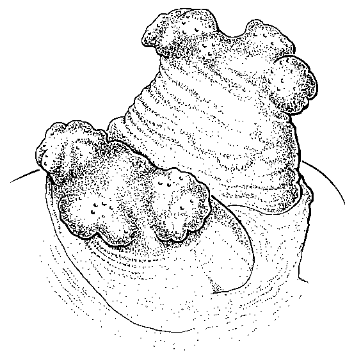
18 Syrphus knabi



19 Brachyopa sp.

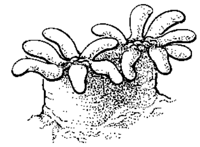
20 Brachyopa sp.

Figs. 5.12–20. Larval characters of Syrphidae: (12) larva of *Microdon* sp., dorsolateral view; (13) posterior spiracles of *Microdon* sp.; (14) terminal segments of *Volucella bombylans* (Linnaeus), dorsal view; (15) larva of *Eristalis tenax* (Linnaeus), lateral view; (16) anterior spiracle of *Syrphus knabi* Shannon; (17) larva of *S. knabi*, lateral view; (18) posterior spiracles of *S. knabi*; (19) larva of *Brachyopa* sp., dorsal view; (20) posterior spiracles of *Brachyopa* sp.

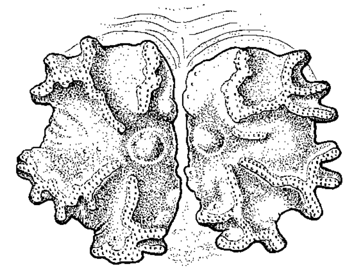


21 Ceracia dentata

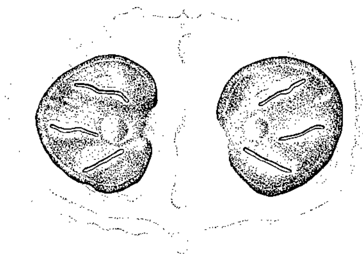
22 Ceracia dentata



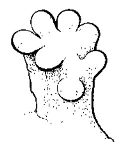
23 Cleonice sp.



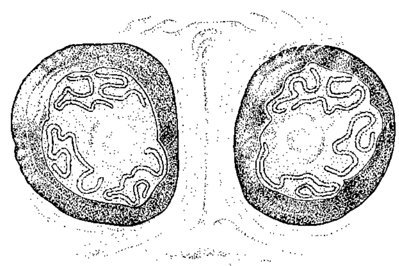
24 Blepharomyia sp.



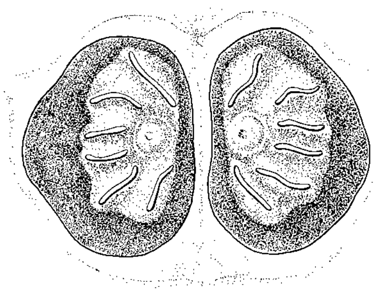
25 Lypha fumipennis



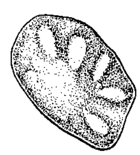
26 Lypha fumipennis



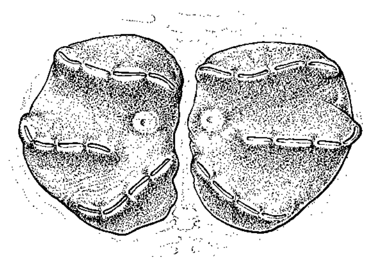
27 Lespesia callosomae



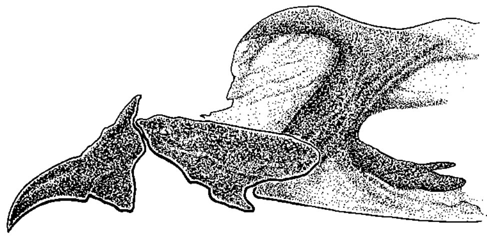
28 Zaira sp.



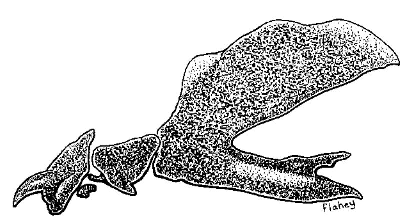
29 Zaira sp.



30 Uramya halisidotae



31 Uramya halisidotae



32 Zaira sp.

Figs. 5.21–32. Larval characters of Tachinidae: (21) posterior spiracles of *Ceracia dentata* (Coquillett); (22) anterior spiracle of *C. dentata*; (23) anterior spiracle of *Cleonice* sp.; (24) posterior spiracle of *Blepharomyia* sp.; (25) posterior spiracles and (26) anterior spiracle of *Lypha fumipennis* Brooks; posterior spiracles of (27) *Lespesia callosomae* Beneway and (28) *Zaira* sp.; (29) anterior spiracle of *Zaira* sp.; (30) posterior spiracles and (31) cephalopharyngeal skeleton of *Uramya halisidotae* (Townsend); (32) cephalopharyngeal skeleton of *Zaira* sp.

58. Posterior spiracles placed on dorsal surface of a transverse cleft of terminal abdominal segment, and capable of being occluded within the cavity when opposing surfaces are brought together (Fig. 36) .... **Oestridae (Oestrinae)** (Ch. 107)

Posterior spiracles placed on evenly rounded terminal extremity of body where they are unprotected .... **Oestridae (Hypodermatinae)** (Ch. 107)

59. Body stout, blunt posteriorly, strongly tapered anteriorly, with one or two rows of stout spines partially or entirely encircling most segments (Fig. 33). Posterior spiracles capable of being occluded within a cavity of terminal abdominal segment; spiracular plate with three parallel vertically oriented bands (Fig. 34). Endoparasitic on horses .... **Oestridae (Gasterophilinae)** (Ch. 107)

Characteristics not as above 60

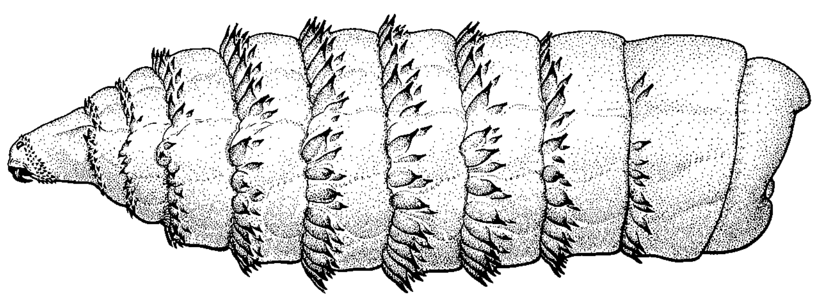
60. Posterior spiracles on a short telescopic respiratory tube that is not forked terminally; spiracles separated only by a slight depression (Figs. 37, 39) .... **Canacidae** (Ch. 102)

Posterior spiracles either not on a telescopic respiratory tube, or on a telescopic tube that is conspicuously forked terminally 61

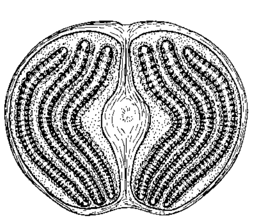
61. Terminal abdominal segment with a pair of slender filaments at least as long as body. Posterior spiracles thorn-like, situated dorsally (Fig. 38). Parasitic on coccids .... **Cryptochetidae** (Ch. 100)

Terminal abdominal segment lacking long filaments. Posterior spiracles not as above 62

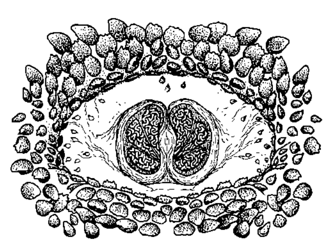
62. Body cylindrical, tapered anteriorly, bluntly rounded posteriorly; terminal segment often with abundant minute spicules but lacking symmetrically placed papillae or tubercles on any segment. Anterior spiracle sometimes absent, when present simple, with one to many randomly arranged papillate openings situated either at apex of a short stalk or nearly sessile on surface of prothorax (Figs. 22, 23, 26, 29). Posterior spiracles often heavily sclerotized, usually at least slightly elevated above plane of segment; each spiracle with three to several short to long spiracular openings that are serpentine, bowed, or variously bent, but



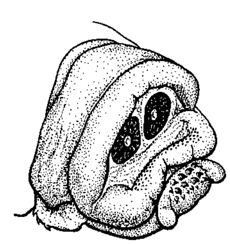
33 Gasterophilus intestinalis



34 Gasterophilus intestinalis



35 Cuterebra emasculator



36 Oestrus ovis

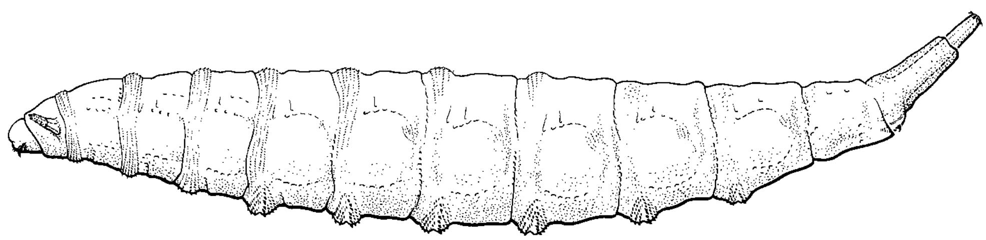
Figs. 5.33–36. Larval characters of Oestridae: (33) larva of *Gasterophilus intestinalis* (De Geer), lateral view; (34) posterior spiracles of *G. intestinalis*; (35) posterior spiracles of *Cuterebra emasculator* Fitch; (36) terminal segments of *Oestrus ovis* Linnaeus, oblique posterior view.

occasionally straight and often following distinct ridges on the spiracular plate; spiracular openings arranged more or less radially around ecdysial scar but almost never in a predominately vertical axis (Figs. 25, 27, 28, 30). Cephalopharyngeal skeleton strong and thickset, lacking parastomal bars (Figs. 31, 32). Parasitic on insects and isopods .... **Rhinophoridae** (Ch. 109)
Tachinidae, in part (Ch. 110)

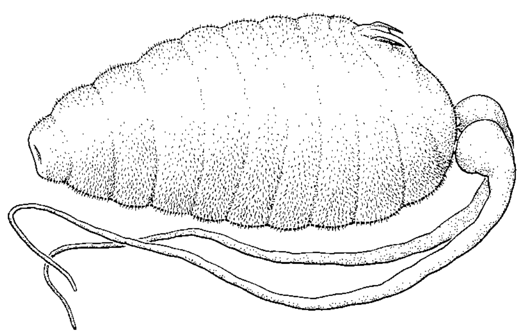
Generally differing from above. If spiracular openings of posterior spiracles serpentine, then cephalopharyngeal skeleton with accessory oral sclerites 63

63. Body distinctly flattened dorsoventrally, with thin striated lateral margins on tergal plates of all segments. Long filamentous processes present on terminal abdominal segment and first two thoracic segments (Fig. 40) .... **Lonchopteridae** (Ch. 49)

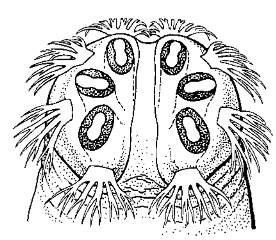
Body often not dorsoventrally flattened, but if so, then lacking thin striated lateral margins on tergal plates of all segments. Long filamentous processes, when present, not restricted to terminal abdominal segment and first two thoracic segments 64



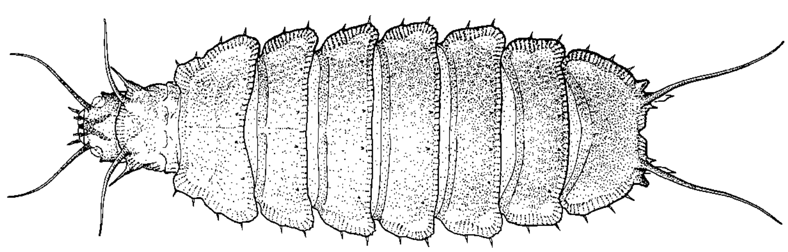
37 Canace macateei



38 Cryptochetum yokohama

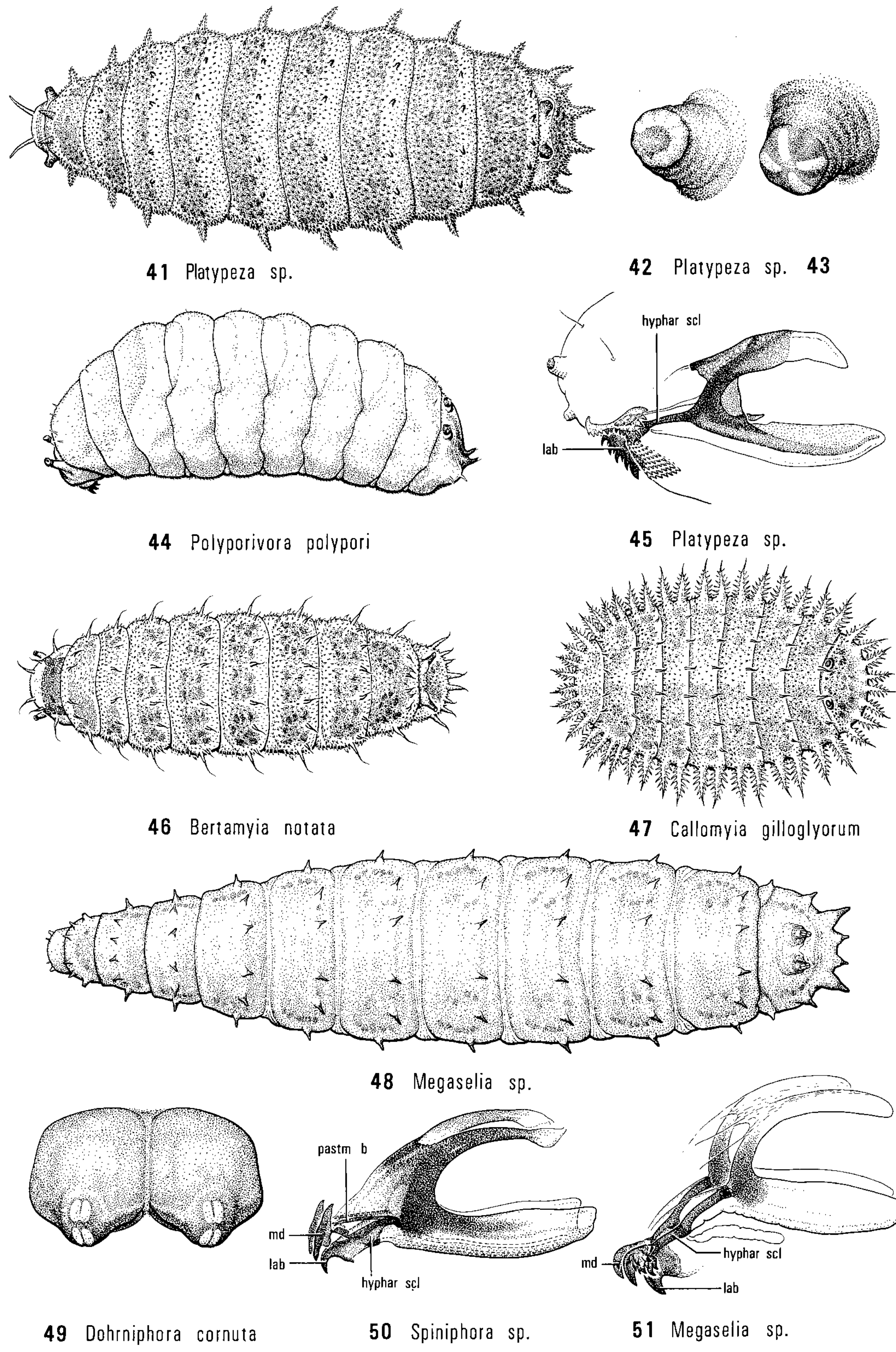


39 Canace macateei



40 Lonchoptera sp.

Figs. 5.37–40. Larval characters of Muscomorpha: (37) larva of *Canace macateei* Malloch (Canacidae), lateral view; (38) larva of *Cryptochetum yokohama* (Kuwana) (Cryptochetidae) (not Nearctic), lateral view; (39) posterior spiracles of *Canace macateei*; (40) larva of *Lonchoptera* sp. (Lonchopteridae), dorsal view.



Figs. 5.41–51. Larval characters of Muscomorpha: (41) larva of *Platypeza* sp. (Platypezidae), dorsal view; (42) anterior and (43) posterior spiracle of *Platypeza* sp.; (44) larva of *Polyporivora polypori* (Willard) (Platypezidae), lateral view; (45) cephalopharyngeal skeleton of *Platypeza* sp.; (46) dorsal view of larva of *Bertamyia notata* (Loew) (Platypezidae), (47) *Callomyia gilloglyorum* Kessel (Platypezidae), and (48) *Megaselia* sp. (Phoridae); (49) posterior spiracles of *Dohrniphora cornuta* (Bigot) (Phoridae); (50) cephalopharyngeal skeleton of *Spiniphora* sp. (Phoridae) and (51) *Megaselia* sp.

Abbreviations: hyphar scl, hypopharyngeal sclerite; lab, labium; md, mandible; pastm b, parastomal bar.

64. Anterior spiracle simple, each with one to several sessile spiracular openings arrayed peripherally at apex of a short tubular or conical projection (Fig. 42). Body often somewhat dorsoventrally flattened. All body segments usually bearing several systematically arranged spicules or tubercles, usually with those situated laterally most prominent (Figs. 41, 44, 46, 47, 48). Tentoropharyngeal and hypopharyngeal sclerites finely constructed and fused together; hypopharyngeal sclerite usually continuous anteriorly with a single or multitoothed median labial sclerite, or with paired mandibles, or with both structures (Figs. 45, 50, 51) 65

Anterior spiracle either absent, or bearing two or more short papillae or long filaments branching from apex of a spiracular stalk. Tentoropharyngeal and hypopharyngeal sclerites often more strongly constructed than above and distinctly separated; hypopharyngeal sclerite fused to hook-like labial sclerite only in first instar larva of some species 66

65. Posterior spiracles each on short conical apically sclerotized spiracular supports, with four spiracular openings on each spiracle arranged radially around ecdysial scar (Fig. 43)........ ....**Platypezidae** (Ch. 50)

Posterior spiracles variously supported, each with spiracular openings arranged in two pairs placed one behind the other (Fig. 49) ....**Phoridae** (Ch. 51)

66. First four body segments and terminal abdominal segment with encircling rows of small strobiliform tubercles (Fig. 52). Respiratory system metapneustic; posterior spiracles sessile. Tentoropharyngeal and hypopharyngeal sclerites fused. Mining wax walls of bee combs ....**Braulidae** (Ch. 81)

If tubercular processes present on thoracic segments, then also present on most abdominal segments. Respiratory system usually amphipneustic with posterior spiracles elevated and tentoropharyngeal and hypopharyngeal sclerites usually separate 67

67. Spiculate or setiferous tubercles present on several body segments preceding terminal one (Figs. 53, 55) 68

Tubercles entirely absent, or situated only on terminal abdominal segment 70

68. Tubercles present only on abdominal segments. Body cylindrical ....**Drosophilidae** (***Drosophila***), in part (Ch. 95)
Ephydridae (***Discomyza***) (Ch. 98)

Tubercles present on both thoracic and abdominal segments. Body dorsoventrally flattened 69

69. Posterior spiracles each on a short nonsetiferous tuberculate process situated dorsally near anterior margin of last abdominal segment; process terminating in three lobes each bearing a spiracular opening. Body tubercles pinnately setiferous (Fig. 53) ....**Muscidae** (***Fannia***) (Ch. 105)

Posterior spiracles each on a long slender spiculate tuberculate process arising caudally on terminal abdominal segment. Other spiculate tubercles on body differing from spiracular tubercle only in being longer (Fig. 55) ....**Periscelididae** (Ch. 77)

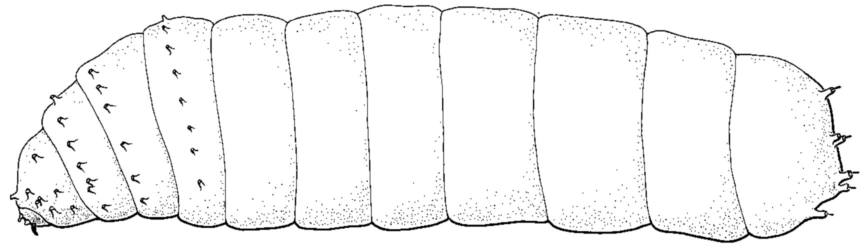
70. One or more body segments densely clothed with minute setulae or spicules, or terminal abdominal segment attenuated into a respiratory tube (Figs. 56, 63–65, 73); or terminal abdominal segment bearing a characteristic complement of one or more pairs of symmetrically placed papillae or tubercles (Figs. 59, 69, 70, 72, 76, 82, 84) 71

Body segments lacking abundant setulae, spicules, papillae, or tubercles, and generally featureless with exception of spicules on creeping welts that may occasionally encircle anterior margins of a few segments 86

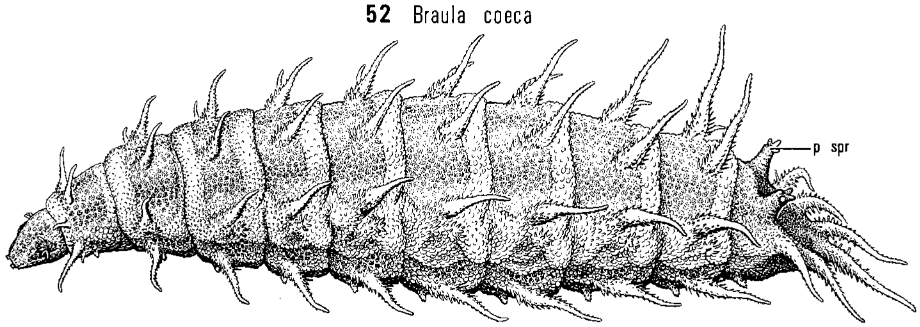
71. Cephalopharyngeal skeleton with a ventral arch below base of anteriorly toothed or serrated mandibles (Figs. 57, 58). Larva predacious or parasitic on freshwater snails ....**Sciomyzidae** (Ch. 84)

Cephalopharyngeal skeleton lacking a ventral arch below mandibles 72

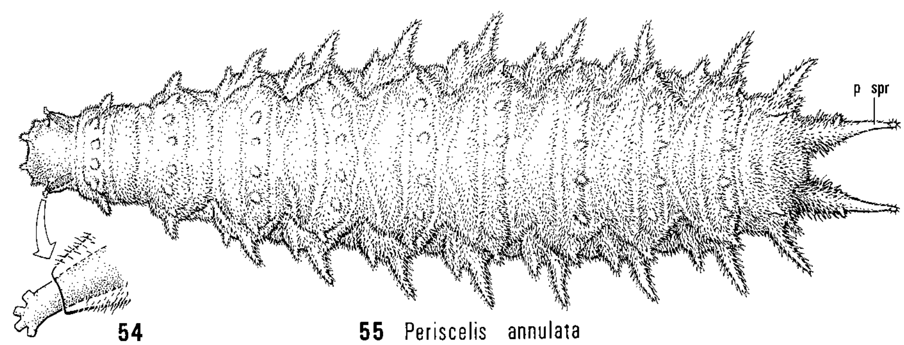
72. Either terminal abdominal segment more or less tapered posteriorly because of close proximity or basal union of conical spiracular prominences (Figs. 59, 65, 67, 70), or the basal union sometimes attenuated into a respiratory tube (Figs. 62–64); shorter spiracular prominences, when not in form of a respiratory tube, usually each with a tubercle present dorsally or dorsolaterally at base (Figs. 59, 65). Spicules or setulae often extensively covering integument of one or more segments 73



52 Braula coeca

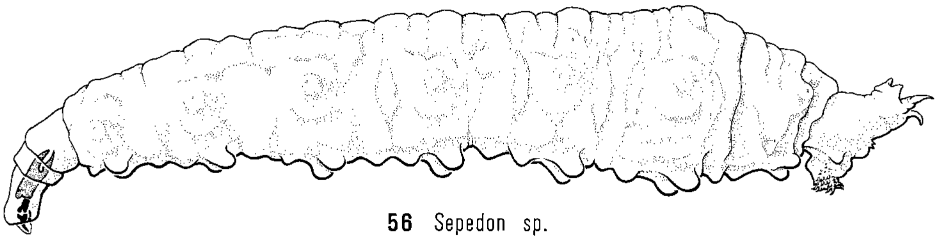


53 Fannia canicularis

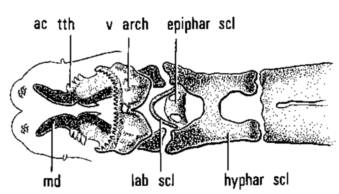


54

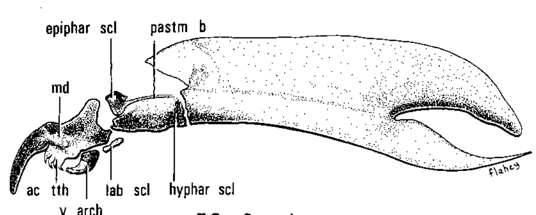
55 Periscelis annulata



56 Sepedon sp.



57 Sepedon sp.

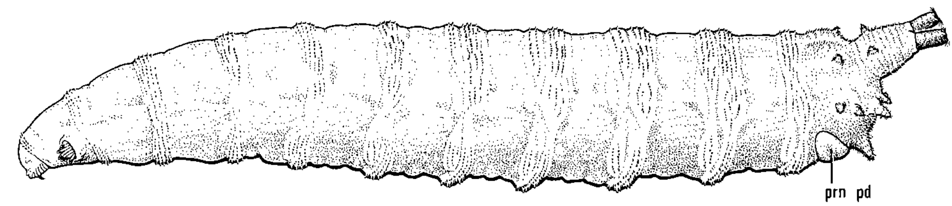


58 Sepedon sp.

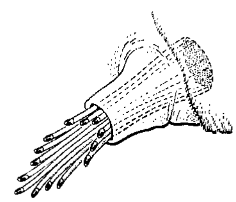
Figs. 5.52–58. Larval characters of Muscomorpha: (52) larva of *Braula coeca* Nitzsch (Braulidae), lateral view; (53) larva of *Fannia canicularis* (Linnaeus) (Muscidae), dorsolateral view; (54) anterior spiracle of *Periscelis annulata* (Fallén) (Periscelididae); (55) larva of *P. annulata*, dorsal view; (56) larva of *Sepedon* sp. (Sciomyzidae), lateral view; cephalopharyngeal skeleton of *Sepedon* sp., (57) in ventral view and (58) in lateral view.

Abbreviations: ac tth, accessory teeth; epiphar scl, epipharyngeal sclerite; hyphar scl, hypopharyngeal sclerite; lab scl, labial sclerite; md, mandible; pastm b, parastomal bar; p spr, posterior spiracle; v arch, ventral arch.

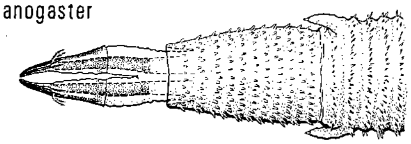
Terminal abdominal segment rather truncate; posterior spiracular prominences sometimes elongate, but distinctly separate and lacking tubercles on the base of each prominence. Spicules or setae usually present only on margins of segments (Fig. 72) 79



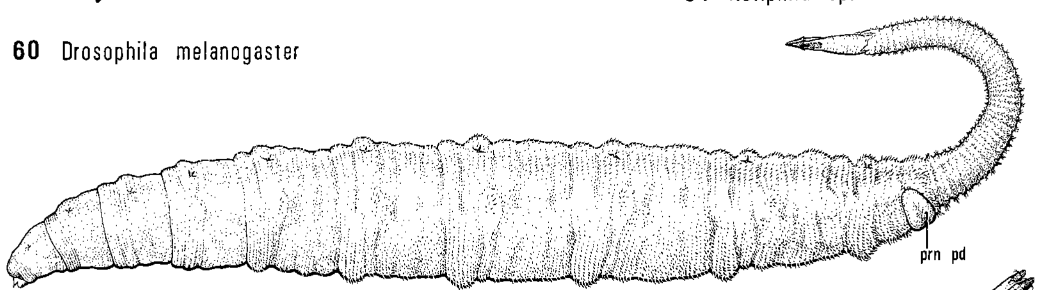
59 Drosophila melanogaster



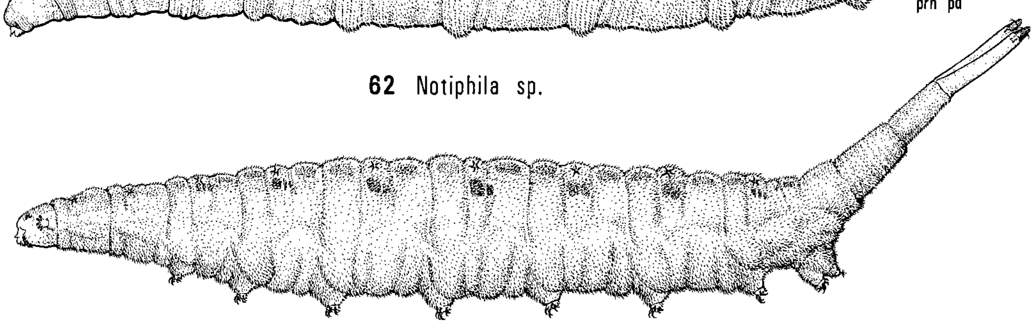
60 Drosophila melanogaster



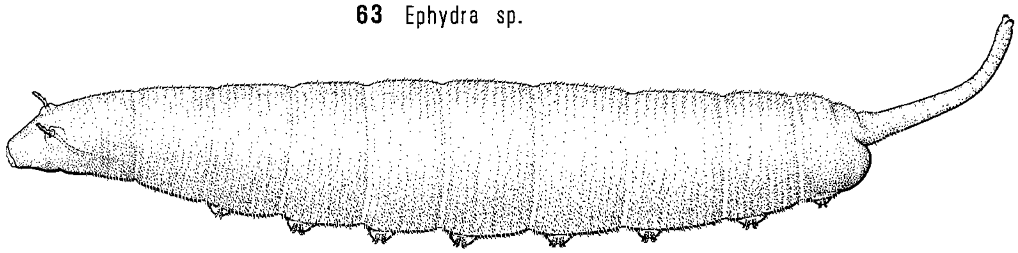
61 Notiphila sp.



62 Notiphila sp.



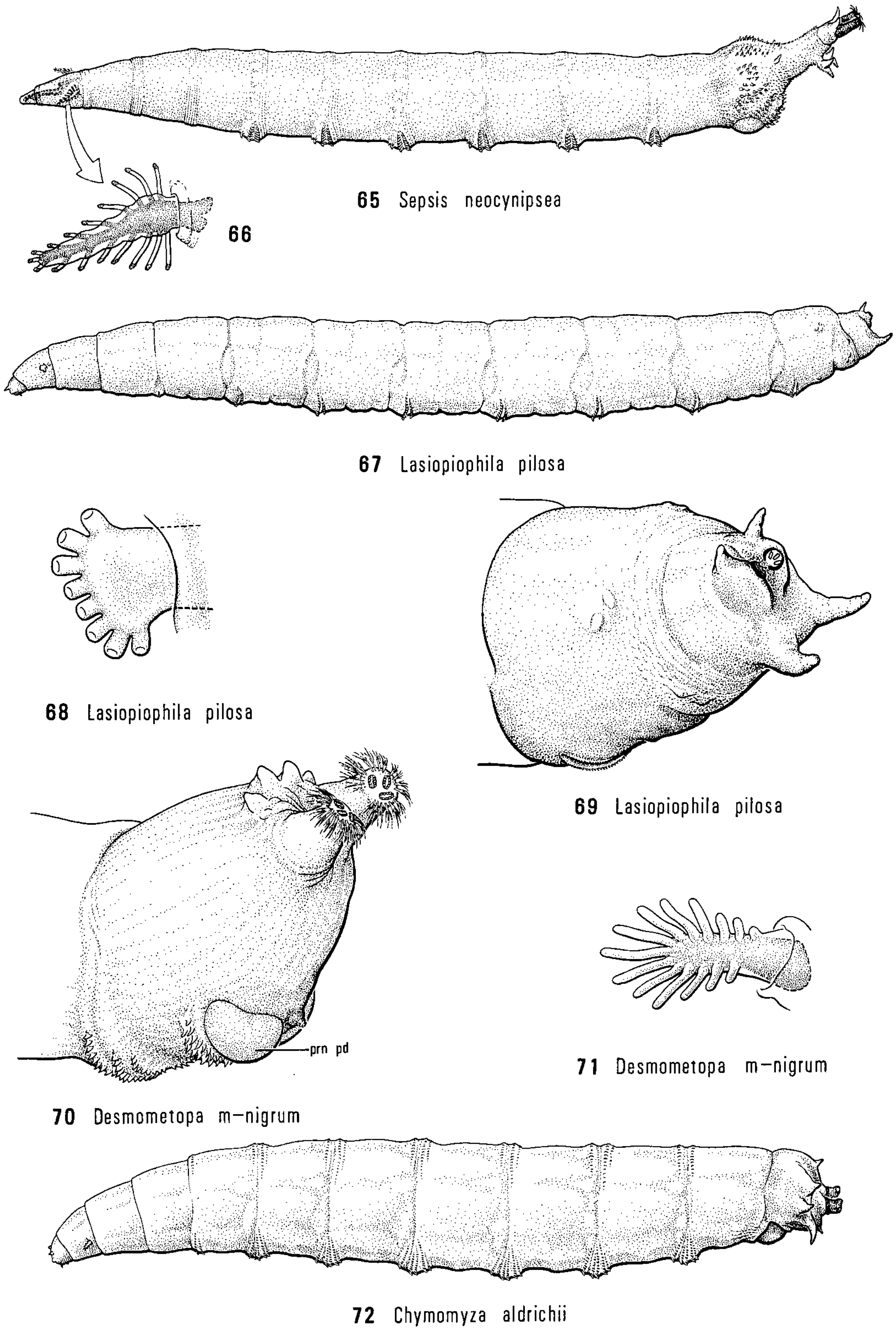
63 Ephydra sp.



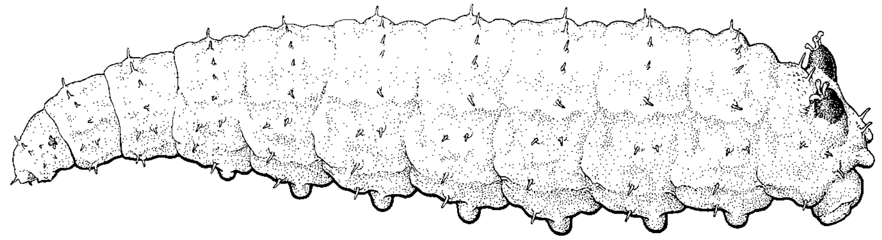
64 Aulacigaster leucopeza

Figs. 5.59–64. Larval characters of Muscomorpha: (59) larva of *Drosophila melanogaster* Meigen (Drosophilidae), dorsolateral view; (60) anterior spiracle of *D. melanogaster*; (61) apex of respiratory siphon of *Notiphila* sp. (Ephydridae); (62) larva of *Notiphila* sp., lateral view; (63) larva of *Ephydra* sp. (Ephydridae), lateral view; (64) larva of *Aulacigaster leucopeza* (Meigen) (Aulacigastridae), dorsolateral view.

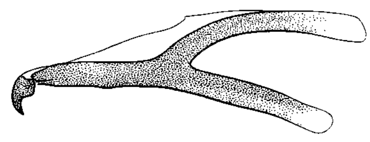
Abbreviation: prn pd, perianal pad.



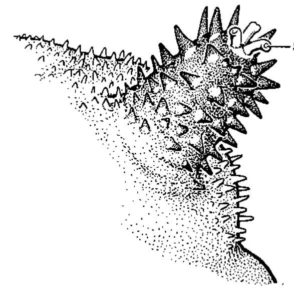
Figs. 5.65–72. Larval characters of Muscomorpha: (65) larva of *Sepsis neocynipsea* Melander & Spuler (Sepsidae), dorsolateral view; (66) anterior spiracle of *S. neocynipsea*; (67) larva of *Lasiopiophila pilosa* (Staeger) (Piophilidae), lateral view; (68) anterior spiracle of *L. pilosa*; (69) oblique posterior view of terminal segment of *L. pilosa* and (70) *Desmometopa m-nigrum* (Zetterstedt) (Milichiidae); (71) anterior spiracle of *D. m-nigrum*; (72) larva of *Chymomyza aldrichii* Sturtevant (Drosophilidae), lateral view.
Abbreviation: prn pd, perianal pad.



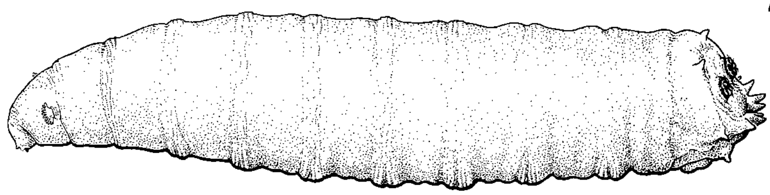
73 Leucopis simplex



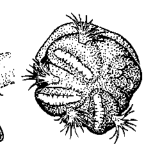
74 Leucopis simplex



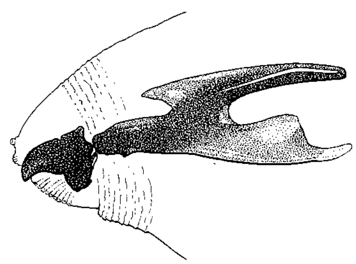
75 Leucopis sp.



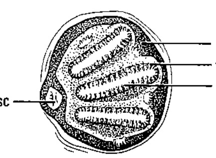
76 Hylemya brassicae



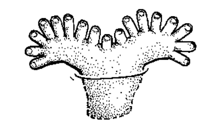
77 Hylemya brassicae **78**



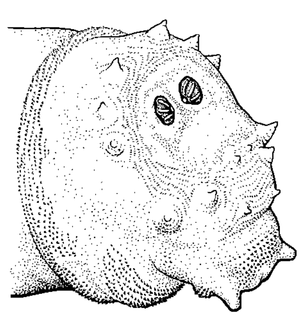
79 Hylemya brassicae



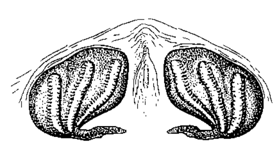
80 Cynomyopsis cadaverina



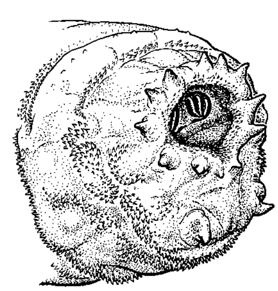
81 Scathophaga stercoraria



82 Cynomyopsis cadaverina



83 Ravinia querula



84 Ravinia querula

Figs. 5.73–84. Larval characters of Muscomorpha: (73) larva of *Leucopis simplex* Loew (Chamaemyiidae), lateral view; (74) cephalopharyngeal skeleton of *L. simplex*; (75) posterior spiracular prominence of *Leucopis* sp.; (76) larva of *Hylemya brassicae* (Bouché) (Anthomyiidae), dorsolateral view; (77) anterior and (78) posterior spiracle of *H. brassicae*; (79) cephalopharyngeal skeleton of *H. brassicae*; (80) posterior spiracle of *Cynomyopsis cadaverina* (Robineau-Desvoidy) (Calliphoridae); (81) anterior spiracle of *Scathophaga stercoraria* (Linnaeus) (Scathophagidae); (82) terminal segment of *C. cadaverina*, oblique posterior view; (83) posterior spiracles of *Ravinia querula* (Walker) (Sarcophagidae); (84) terminal segment of *R. querula*, oblique posterior view.

Abbreviations: ecdys sc, ecdysial scar; perit, peritreme; rm, rima; spr ppl, spiracular papilla; trb, trabecula.

73. Anterior spiracle with a basal stalk terminating in many long filamentous processes (Fig. 60), and capable of being entirely retracted within the body .... **Drosophilidae (Drosophilinae)** (Ch. 95)

Anterior spiracle absent or constructed differently than above, but if in form of an elongate stalk that can be retracted within the body, then apically bearing short serially arranged lateral buds (Fig. 64) 74

74. Posterior spiracles each prolonged as a hollow spine (Figs. 61, 62) (*Scaptomyza* of Drosophilidae also with such spiracles, keyed in previous couplet) .... **Ephydridae (Notiphilinae)** (Ch. 98)

Posterior spiracles not spine-like 75

75. Terminal abdominal segment attenuated posteriorly into a more or less elongate respiratory tube lacking tubercles dorsally and usually capable of some invagination. Spicules or setae entirely covering all abdominal segments (Figs. 63, 64) 76

Terminal abdominal segment tapered, either with a very short respiratory tube, or with closely placed or basally fused conical spiracular prominences; spiracular prominences each with a tubercle present dorsally at or near base. Spicules or setulae not covering all aspects of every abdominal segment (Fig. 65) 77

76. Posterior respiratory tube long, with a very short and unsclerotized terminal fork, and with length of each branch about equal to its diameter (Fig. 64) .... **Aulacigastridae** (Ch. 76)

Posterior respiratory tube of variable length, but with terminal fork usually apically sclerotized, and with length of each branch greater than its diameter (Fig. 63) .... **Ephydridae**, in part (Ch. 98)

77. Spicules and pubescence extensively covering terminal abdominal segment only (Fig. 65). Posterior spiracles usually with well-developed spiracular setae (in *Orygma* resembling *Coelopa*, Fig. 85); anterior spiracle with buds projecting to either side of a more or less elongate central axis (Fig. 66) .... **Sepsidae** (Ch. 86)

Spicules present only at segmental margins of terminal abdominal segment, or extensively covering other segments besides the terminal one. Posterior spiracles with spiracular setae inconspicuous or absent; anterior spiracle with buds projecting fan-like (except in some Lauxaniidae) (Fig. 68) 78

78. Posterior spiracles situated on median sloping faces of spiracular prominences and appearing capable of retraction on one another (Fig. 69). Segments immaculate except for tubercles on terminal segment and spicules on anterior ventral creeping welts of abdominal segments (Figs. 67, 69) .... **Piophilidae** (Ch. 69)

Posterior spiracles situated squarely on apices of spiracular prominences. Spicules on abdominal segments normally much more extensive than above .... **Lauxaniidae** (Ch. 87)

79. Posterior spiracular openings arranged with longitudinal axes aligned such that two openings are nearly parallel to each other and the third is nearly at a right angle (Fig. 70); each spiracular opening often isolated on its own papilla-like projection. Terminal segment often with transverse ridge of three or four small tubercles on dorsum near base of spiracular prominences (Fig. 70) .... **Milichiidae**, in part (Ch. 79)

Posterior spiracular openings normally rather symmetrically radiating from an ecdysial scar. Anal segment lacking a ridge of tubercles at base of spiracular prominences 80

80. Integument of all segments clothed with fine pubescence or spicules (Fig. 73) 81

Integument of all but perhaps terminal segment free from pubescence or spicules except on anterior margins associated with creeping welts 82

81. Posterior spiracular openings each on a digitate papilla-like projection from spiracular plate (Figs. 73, 75). Cephalopharyngeal skeleton with hypopharyngeal and tentoropharyngeal sclerites fused (Fig. 74). Predators and parasites of aphids, adelgids, and coccids .... **Chamaemyiidae** (Ch. 88)

Posterior spiracular openings sessile on surface of spiracular plate. Hypopharyngeal and tentoropharyngeal sclerites separate .... **Drosophilidae (Steganinae)**, in part (Ch. 95)

82. Posterior spiracles sessile on surface of anal segment (Figs. 82, 84), and either lacking a sclerotized peritreme or with spiracular openings slit-like and positioned vertically or on a ventral median incline (Figs. 80, 83) 83

Posterior spiracles more or less distinctly elevated above plane of terminal segment (Fig. 76), and usually differing in other of above characters 85

83. Posterior spiracles each lacking a sclerotized peritreme, and each with an ecdysial scar situated medially or mediodorsally to spiracular openings (Fig. 105). Cephalopharyngeal skeleton with greatly contrasting degrees of pigmentation.................**Tephritidae**, in part (Ch. 66)

Posterior spiracles each with a distinctly sclerotized peritreme; ecdysial scar, or the place where the spiracular openings converge if the scar is not visible, situated ventrally or ventromedially (Figs. 80, 83). Cephalopharyngeal skeleton relatively uniformly pigmented 84

84. Posterior spiracles in a deep spiracular cavity (Fig. 84); spiracular openings inclined more or less vertically; ecdysial scar usually not visible; peritreme incompletely encircling spiracular plate (Fig. 83) ....**Sarcophagidae** (Ch. 108)

Posterior spiracles exposed at apex of terminal abdominal segment (Fig. 82); spiracular openings obliquely inclined; ecdysial scar present; peritreme completely encircling spiracular plate (Fig. 80) ....**Calliphoridae** (Ch. 106)

85. Anterior spiracle bicornuate, with buds arranged on two more or less distinct diverging arms (Fig. 81). Cephalopharyngeal skeleton lacking parastomal bars (as in Fig. 79) ....
....................**Scathophagidae**, in part (Ch. 103)

Anterior spiracle fan-shaped or tree-like (Figs. 77, 93), or parastomal bars present in cephalopharyngeal skeleton, or both features present ....**Heleomyzidae**, in part (Ch. 89)

Sphaeroceridae, in part (Ch. 93)

Curtonotidae (Ch. 94)

Drosophilidae (**Steganinae**), in part (Ch. 95)

Anthomyiidae (Ch. 104)

86. Posterior spiracles sessile on surface of terminal segment (Fig. 104) 87

Posterior spiracles distinctly elevated on short supporting structures (Figs. 87–89, 91, 102)......88

87. Spiracular peritreme unpigmented (Fig. 105) ....**Tephritidae**, in part (Ch. 66)

Spiracular peritreme distinctly pigmented (Fig. 90) ....**Otitidae**, in part (Ch. 63)

Chloropidae, in part (Ch. 99)

88. Spiracular setae prominent, arising as a continuous fringe along border of posterior spiracular plates; spiracular openings usually band- or slit-like and distinctly bowed or abruptly bent (Fig. 85) ....**Coelopidae** (Ch. 82)

Spiracular setae, if visible, not arising as a complete fringe but arranged in three or four groups of setae or individual branched setae (Figs. 86, 104); spiracular openings not as above........89

89. Posterior spiracular plate with one or more bordering spines or lobes, or with a sharp ridge along the dorsal margin (Figs. 86–89, 91) 90

Posterior spiracular plate without lobes, spines, or ridges along the margin 92

90. Cephalopharyngeal skeleton degenerate, with all portions except small mandibles unpigmented ..
....................**Clusiidae** (Ch. 70)

Cephalopharyngeal skeleton of normal size, and darkly pigmented 91

91. Posterior spiracular openings short and oval, aligned at almost right angles to one another (Figs. 86, 87) ....**Psilidae** (Ch. 60)

Lonchaeidae, in part (Ch. 62)

Dryomyzidae (***Helcomyza***) (Ch. 83)

Posterior spiracular openings radiating from ecdysial scar at distinctly less than right angles, or irregularly or peripherally arranged (Figs. 88, 91) ....**Micropezidae** (Ch. 56)

Otitidae (***Tetanops***) (Ch. 63)

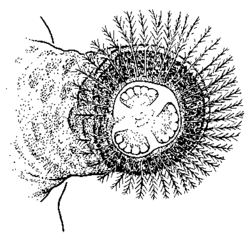
Scathophagidae (***Hydromyza***) (Ch. 103)

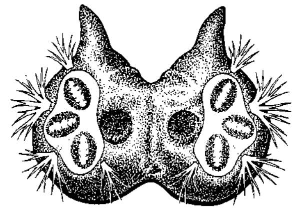
92. Anterior spiracle bicornuate (as in Fig. 81) ....**Tanypezidae** (***Tanypeza***) (Ch. 58)

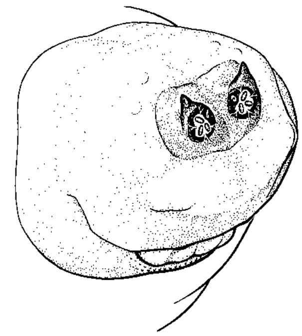
Anterior spiracle otherwise 93

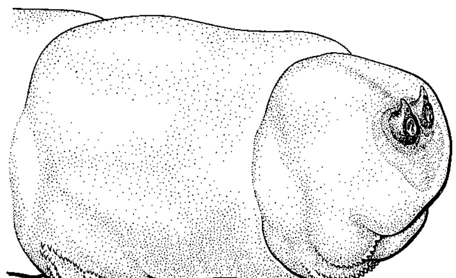
93. Anterior spiracle with buds projecting semicircularly (Figs. 92, 96) or tree-like (Figs. 93, 97)......
....................94

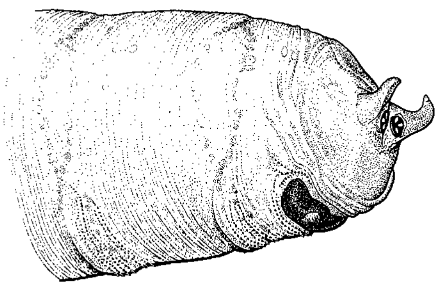
Anterior spiracle otherwise 95

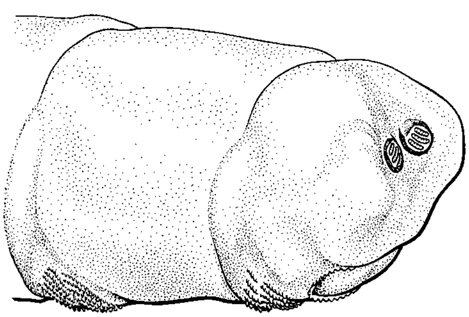

85 Coelopa frigida

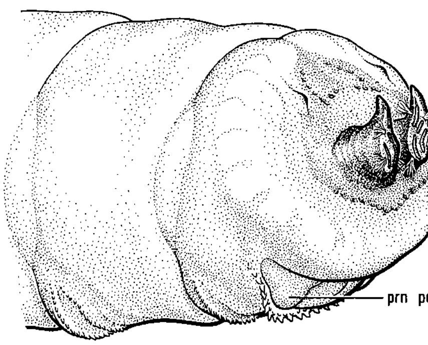

86 Loxocera cylindrica


87 Lonchaea corticis

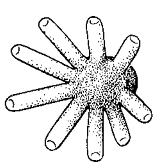

88 Tetanops (Eurycephalomyia) myopaeformis

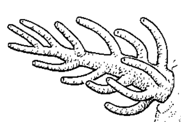

89 Clusia sp.

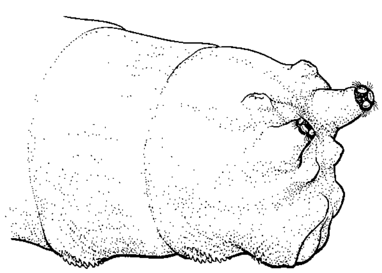

90 Pseudotephritis corticalis

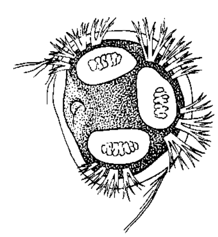


91 Compsobata univitta


92 Leptocera (Thoracochaeta) zosterae

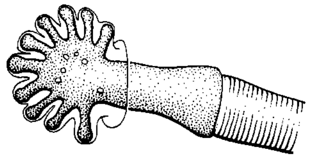

93 Leptocera sp.


94 Leptocera sp.

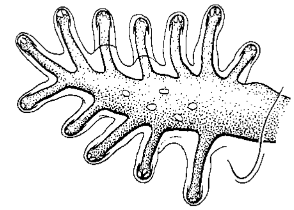

95 Leptocera sp.

Figs. 5.85–95. Larval characters of Muscomorpha: (85) posterior spiracle of *Coelopa frigida* (Fabricius) (Coelopidae); (86) posterior spiracles of *Loxocera cylindrica* Say (Psilidae); (87) terminal segment of *Lonchaea corticis* Taylor (Lonchaeidae), oblique posterior view; oblique posterior view of terminal segments of (88) *Tetanops* (*Eurycephalomyia*) *myopaeformis* (Röder) (Otitidae), (89) *Clusia* sp. (Clusiidae), (90) *Pseudotephritis corticalis* (Loew) (Otitidae), and (91) *Compsobata univitta* (Walker) (Micropezidae); (92) anterior spiracle of *Leptocera* (*Thoracochaeta*) *zosterae* Haliday (Sphaeroceridae) and (93) *Leptocera* sp.; (94) terminal segments of *Leptocera* sp.; (95) posterior spiracle of *Leptocera* sp.

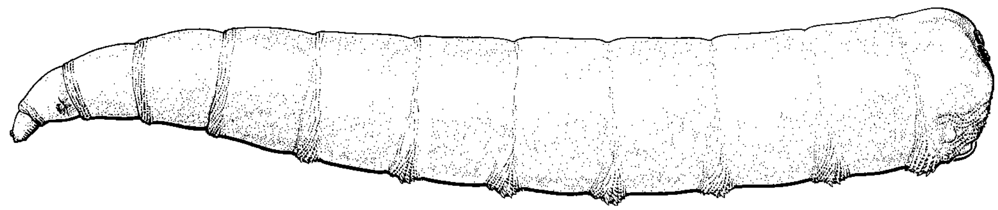
Abbreviation: prn pd, perianal pad.



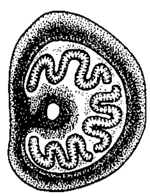
96 Opomyza petrei



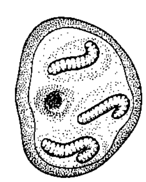
97 Geomyza balachowskyi

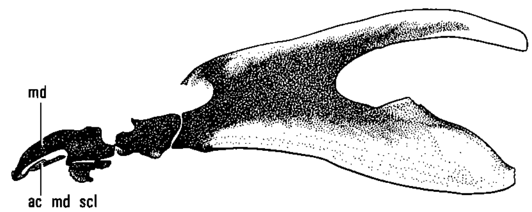


98 Dendrophaonia sp.

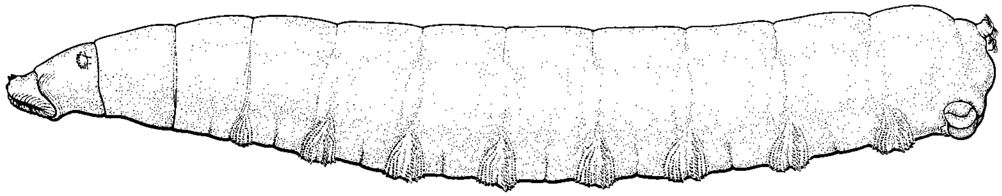


99 Musca domestica

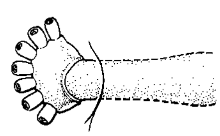




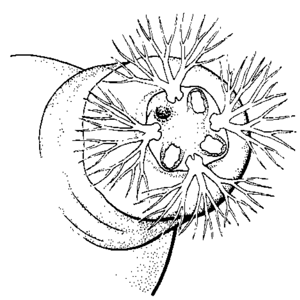
100 Dendrophaonia sp. **101**



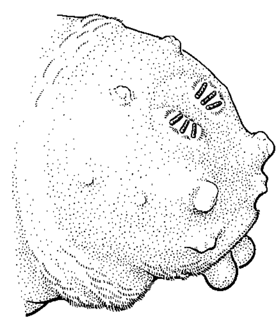
102 Elachiptera sp.



103 Elachiptera sp.



104 Elachiptera sp.



105 Rhagoletis pomonella

Figs. 5.96–105. Larval characters of Muscomorpha: (96) anterior spiracle of *Opomyza petrei* Mesnil (Opomyzidae) and (97) *Geomyza balachowskyi* Mesnil (Opomyzidae); (98) larva of *Dendrophaonia* sp. (Muscidae), lateral view; (99) posterior spiracle of *Musca domestica* Linnaeus (Muscidae) and (100) *Dendrophaonia* sp.; (101) cephalopharyngeal skeleton of *Dendrophaonia* sp.; (102) larva of *Elachiptera* sp. (Chloropidae), ventrolateral view; (103) anterior and (104) posterior spiracle of *Elachiptera* sp.; (105) posterior spiracles of *Rhagoletis pomonella* (Walsh) (Tephritidae).

Abbreviations: ac md scl, accessory mandibular sclerite; md, mandible.

94. Posterior spiracles usually on a cylindrical support two or three times longer than diameter of spiracular plate; three short oval spiracular openings arranged more or less circularly around margin of plate (Figs. 94, 95), or asymmetrically positioned in relation to both margins of spiracular plate or ecdysial scar .... **Sphaeroceridae**, in part (Ch. 93)

Posterior spiracles barely elevated to a height of less than one diameter of the spiracular plate; spiracular openings radiating from ecdysial scar at approximately 90° to nearest neighbor (as in Figs. 86, 87) .... **Opomyzidae** (Ch. 74)

95. Cephalopharyngeal skeleton with accessory oral sclerites (Fig. 101), or posterior spiracles either with serpentine spiracular openings or openings distinctly angled (Figs. 99, 100), or both features present .... **Muscidae**, in part (Ch. 105)

Neither of these characteristics evident .... **Cypselosomatidae** (Ch. 55)
Diopsidae (Ch. 61)
Lonchaeidae, in part (Ch. 62)
Otitidae, in part (Ch. 63)
Platystomatidae (Ch. 64)
Pallopteridae (Ch. 68)
Odiniidae (Ch. 72)
Anthomyzidae (Ch. 75)
Milichiidae, in part (Ch. 79)
Carnidae (Ch. 80)
Dryomyzidae, in part (Ch. 83)
Heleomyzidae, in part (Ch. 89)
Chloropidae, in part (Ch. 99)

TANYDERIDAE 6

C. P. Alexander

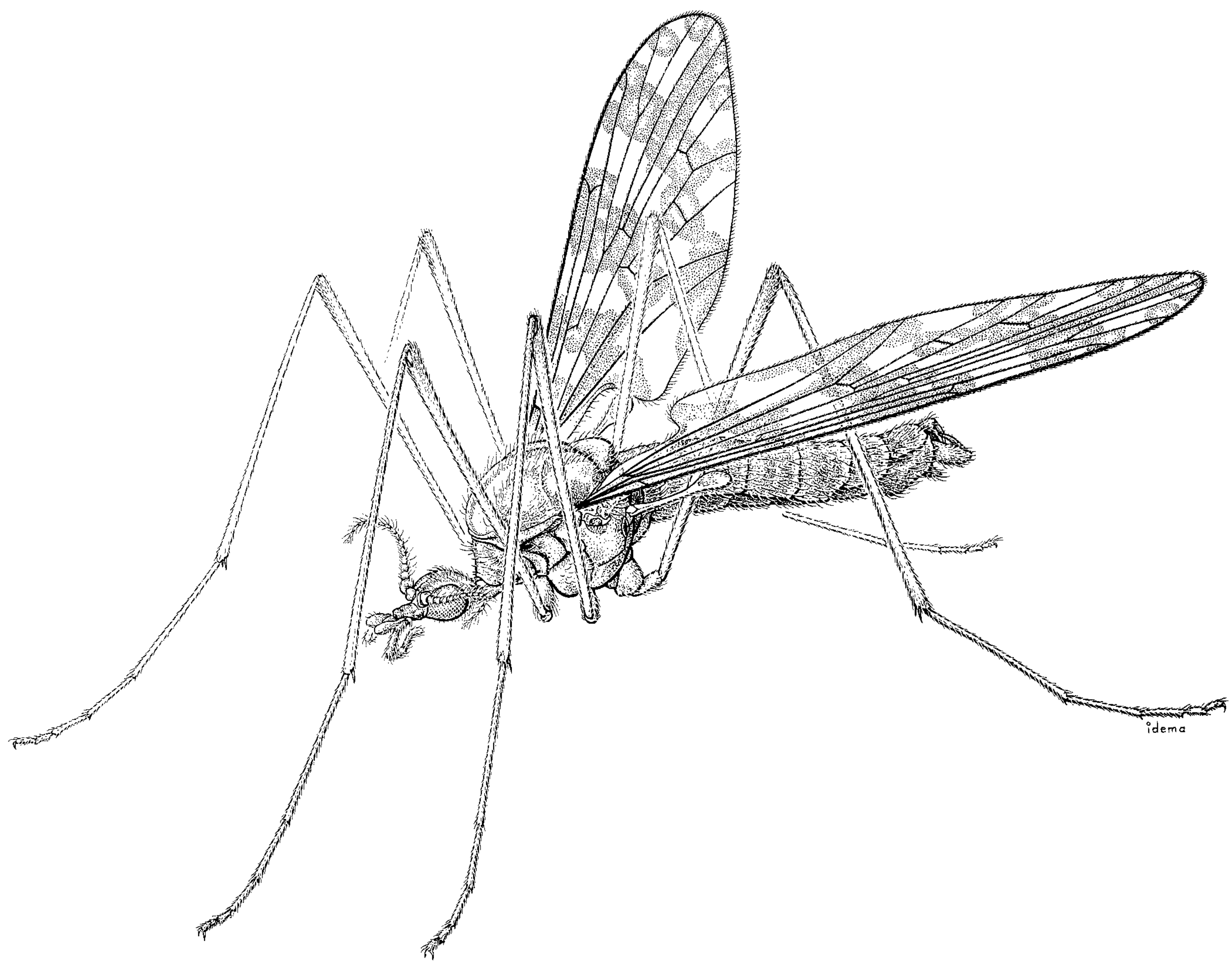


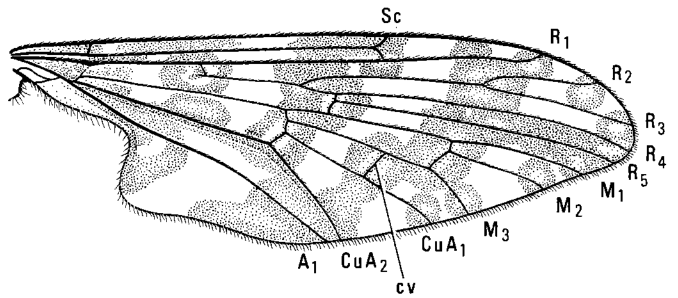
Fig. 6.1. Male of *Protoplasa fitchii* Osten Sacken.

Medium-sized flies, with a handsomely banded wing pattern in regional genera (Fig. 1).

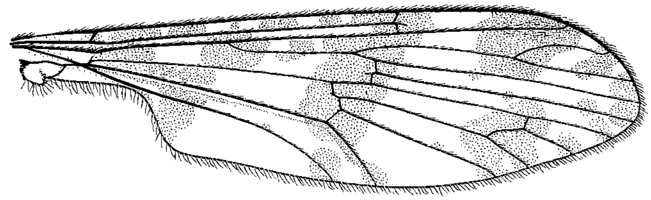
Adult. Head: mouthparts moderately produced; palpus long. Antenna with 15–25 segments, but usually with 16 in Nearctic genera; flagellomeres simple, cylindrical; terminal flagellomere shorter than penultimate. Compound eye with erect hairs between the ommatidia; ocelli lacking.

Thorax: cervical sclerites (the so-called neck) commonly lengthened, shorter in Nearctic species. Wing with five branches of R attaining the margin; one or two supernumerary crossveins in wing cells in most genera, present in *Protoplasa* Osten Sacken (Fig. 2, cv) but lacking in Nearctic species of *Protanyderus* Handlirsch (Fig. 3).

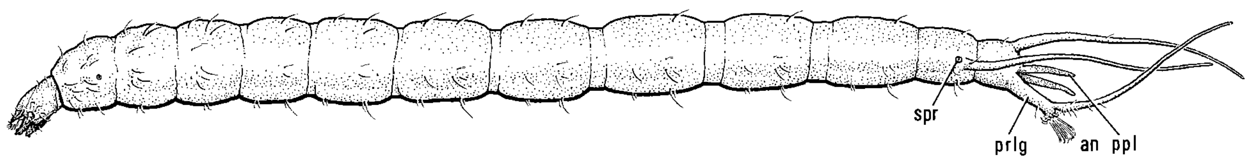
Abdomen: male terminalia gradually rotated 180° through segments 8 and 9; hypandrium, or sternite 9,



2 Protoplasa fitchii ♂



3 Protanyderus margarita ♂



4 Protoplasa fitchii

Figs. 6.2–4. Wings and larva: wing of (2) *Protoplasa fitchii* Osten Sacken and (3) *Protanyderus margarita* Alexander; (4) larva of *Protoplasa fitchii*.
Abbreviations: an ppl, anal papilla; cv, crossvein; prlg, proleg; spr, spiracle.

reduced to a narrow strap-shaped sclerite lying in front of gonocoxites; gonocoxites extended and fused with each other ventrally; gonostylus prominently forked; aedeagus trifid.

Detailed accounts of adult morphology found in Crampton (1925, 1926*b*), Peus (1958), and Williams (1933).

Larva. Eucephalic, terete, amphipneustic (Fig. 4). Creeping welts lacking. Terminal end of abdomen with six long filaments; one pair borne near caudal ends of two elongate anal prolegs; prolegs each terminating in a circlet of short outer crochets and a central group of long slender crochets. Four simple anal papillae.

Pupa. Head surmounted by a high bispinous crest. Pronotal respiratory horns fairly small, smooth, equal in size. Leg sheaths lying side by side; fore pair shortest; hind pair longest. Venation showing clearly on wing pads. Abdominal segments with a tuberculate armature chiefly near posterior margins of segments.

Biology and behavior. Immature stages occur in sandy soil at margins of large streams. The larvae are aquatic or nearly so. References to regional species include Alexander (1930), Crampton (1930*a*, 1930*b*), Knight (1963, 1964), and Rose (1963); for the extralimital genus *Eutanyderus* Alexander, refer to Hinton (1966) and Colless and McAlpine (1970); for *Peringueyomyina* Alexander, see Wood (1952). The larvae of *Eutanyderus* occur in the outer layers of submerged, rotting logs in alpine streams in eastern Australia. Exner and Craig (1976) have recently published some excellent photographs of the larva of *Protanyderus margarita* Alexander, some specimens of which had been captured and kept alive.

Classification and distribution. There are 37 recent species of Tanyderidae distributed among 11 genera, as well as the fossil genus *Macrochile* Loew [discussed by Crampton (1926*a*)] found in Baltic amber, from the lower Oligocene. Two genera with four species are known from North America. Most of the remaining groups are Australasian.

Key to genera

1. Wing with a supernumerary crossvein in cell m_3 (Fig. 2) .... ***Protoplasa*** Osten Sacken
   1 sp., *fitchii* Osten Sacken; eastern; Alexander 1942
   Wing without supernumerary crossvein (Fig. 3) .... ***Protanyderus*** Handlirsch
   3 spp.; western; Alexander 1967

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TIPULIDAE 7

C. P. ALEXANDER AND GEORGE W. BYERS[1]

Fig. 7.1. Male of *Tipula trivittata* Say.

[1] Material dealing with adult forms was prepared by C. P. Alexander, and that dealing with immature stages by George W. Byers.

Typically slender-bodied flies (Fig. 1), with V-shaped transverse mesonotal suture. Wing elongate, rather narrow. Legs very long and slender, breaking readily at suture between trochanter and femur. Ocelli absent. Length up to 60 mm; size varying from tiny species of *Tasiocera* Skuse with wing length of about 2 mm, to large species of *Holorusia* Loew with wing often 40 mm long and of *Leptotarsus* Guérin-Méneville (*Longurio* Loew) with body length often 60 mm.

Adult. Head: rostrum small and inconspicuous in Limoniinae, commonly more conspicuous and often extended into a small projection called the ***nasus*** in Tipulinae (Fig. 2), sometimes greatly elongated in *Limonia* (*Geranomyia* Haliday) to about half as long as head and thorax combined and even longer in *Elephantomyia* Osten Sacken and *Toxorhina* Loew; mouthparts usually proportional in size to rostrum; palpus normally four-segmented, but sometimes reduced to a single element; lengthened labrum, hypopharynx, and labella comprising rostrum in *Limonia* (*Geranomyia*); greatly lengthened frons and clypeus comprising rostrum in *Elephantomyia* and *Toxorhina*, with very reduced palpi, labrum, and other mouthparts situated at extreme apex. Antenna varying greatly among groups (Figs. 8–14), usually short or moderate in length, but occasionally extremely long in male of some species, sometimes reaching three or four times body length as in some *Megistocera* Wiedemann, *Leptotarsus*, *Hexatoma* Latreille, and *Rhabdomastix* Skuse; segments numbering between five (some species of *Chionea* Dalman) and 39 (some species of exotic *Gynoplistia* Westwood), but generally numbering 13 in Tipulinae and 14–16 in Limoniinae; flagellomeres usually simple and unmodified, ranging in shape from nearly globular to oval and cylindrical, very elongated in species having long antennae, occasionally branched in male and only rarely branched in both sexes (*Ctenophora* Meigen); scape and pedicel normally similar throughout Tipulidae; one or more flagellomeres occasionally fused together to reduce the number of antennal segments from the usual 16 to as few as five (*Chionea*). Compound eyes large, usually widely separated to display a broad posterior vertex but sometimes holoptic to reduce posterior vertex to a capillary strip or to eliminate it completely (*Limonia* spp.); eyes usually glabrous, but in Pediciini with short erect hairs located between ommatidia; ommatidia numerous; ocelli absent.

Thorax: pronotum usually well-developed, sometimes elongate (*Limonia* spp., *Toxorhina* spp.), jutting anteriorly over prescutum; small paired impressions (tuberculate pits) often present on anterior half of prescutum; other impressed areas or prescutal pits sometimes large and conspicuous, present in postpronotal region. Legs with coxae well-developed; trochanters usually short, but longer in *Atarba* Osten Sacken and *Rhabdomastix*; tibiae with or without two terminal spurs; tarsal claws simple or variously toothed (some species of *Limonia* and *Tipula* Linnaeus).

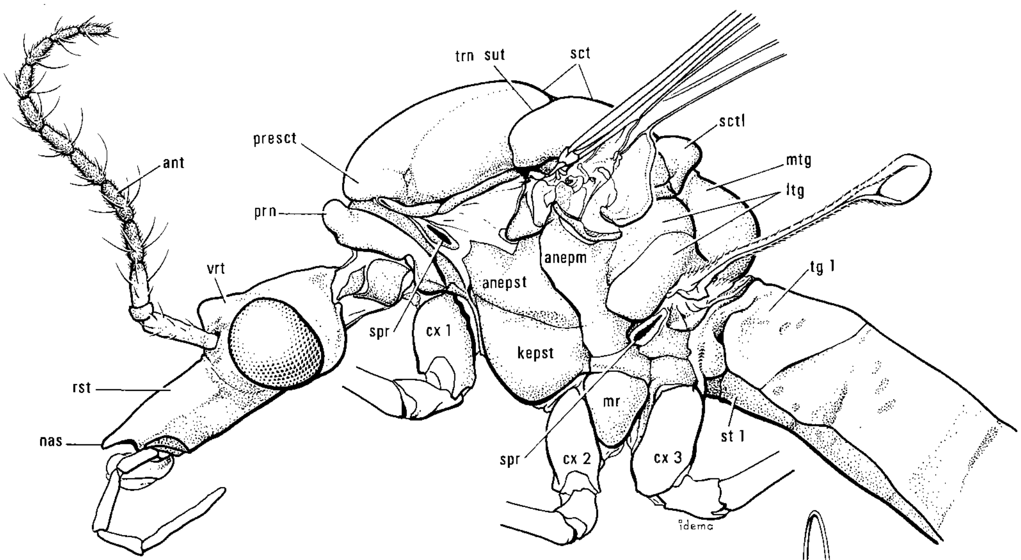
Halter long to very long in all Nearctic species. Wing normally present, but reduced or lost by atrophy in a few groups, sometimes in both sexes (*Chionea*) and sometimes only in female; venation correspondingly modified. Wing venation greatly variable within family and extremely important in taxonomy, generally characterized by two complete anal veins, 9–12 veins reaching wing margin, basal cells at least half length of wing, and a distinctive region near apical third of wing, called the ***cord***, where branching of Rs, M, and CuA frequently occurs in an almost linear transverse line; venational nomenclature of Comstock and Needham as modified by Alexander (1918, 1927, 1929) for the branching of R and Sc used in adult key.[2]

Abdomen: long to very long. Male terminalia (Figs. 3–6) with tergite 9 usually separate but sometimes fused with sternite 9 and gonocoxite to form a continuous ring; gonocoxite variously modified, usually with a ventromedial lobe or extension called the aedeagal guide (adminiculum), and sometimes with a modified structure or ***interbase*** also present medially which is especially characteristic of the Pediciini, primitive Hexatomini, and certain other groups; gonostylus partially to completely divided, variously modified, providing important characters for separating genera and species. Ovipositor of female variously modified, but usually including two pairs of elongate sclerotized valves (Fig. 7); paired cerci situated dorsally, usually lengthened, gently upcurved to the tips; hypogynial valves (hypovalvae) situated ventrally, shorter, obtuse; in Cylindrotominae and eriopterine *Cryptolabis* Osten Sacken, cerci and hypogynial

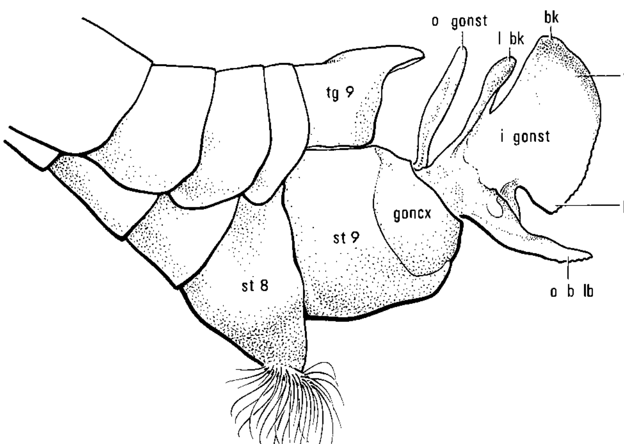
[2] Dr. Alexander's agreement with Tillyard's interpretation of CuA as being unbranched and the vein preceding it therefore being M_4 is not followed here. Instead CuA is interpreted as having two branches, CuA_1 and CuA_2, the former comprising crossvein m-cu and M_4 of Tillyard (see Chapter 2 for a thorough explanation).

Figs. 7.2–6. Head, thorax, and male terminalia: (2) head and thorax of *Tipula trivittata* Say, lateral view; male terminalia of (3) *Tipula* (*Lunatipula*) *monticola* Alexander in lateral view, (4) *Tipula* (*Yamatotipula*) *eluta* Loew in posteroventral view, and (5) *Limonia* (*Rhipidia*) *lecontei* Alexander and (6) *Rhabdomastix subfascigera* Alexander in dorsal view.

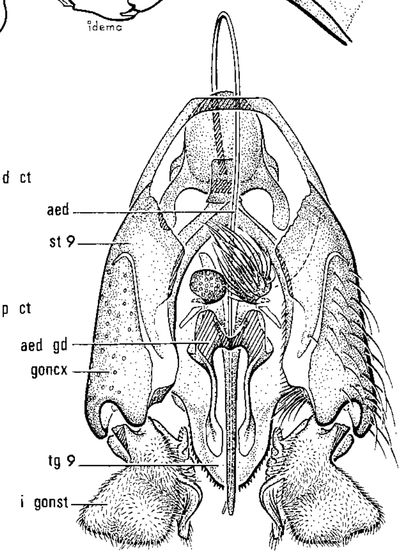
Abbreviations: aed, aedeagus; aed gd, aedeagal guide; anepm, anepimeron; anepst, anepisternum; ant, antenna; bk, beak; cx, coxa; d ct, dorsal crest; goncx, gonocoxite; i gonst, inner gonostylus; interb, interbase; kepst, katepisternum; l bk, lower beak; ltg, laterotergite; mr, meron; mtg, mediotergite; nas, nasus; o b lb, outer basal lobe; o gonst, outer gonostylus; p ct, posterior crest; pm, paramere; presct, prescutum; prn, pronotum; rst, rostrum; rst spn, rostral spine; sct, scutum; sctl, scutellum; spr, spiracle; st, sternite; tg, tergite; trn sut, transverse suture; vrt, vertex.



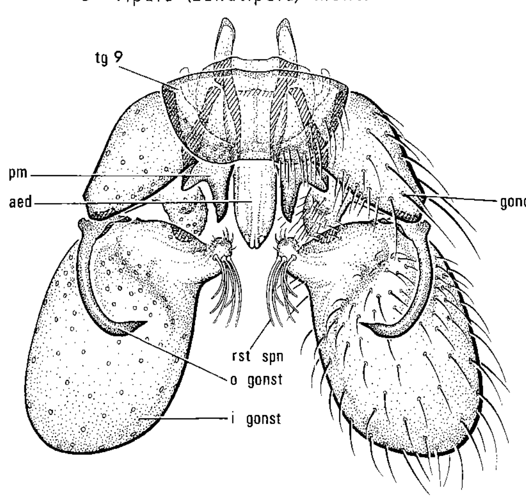
2 Tipula trivittata ♂



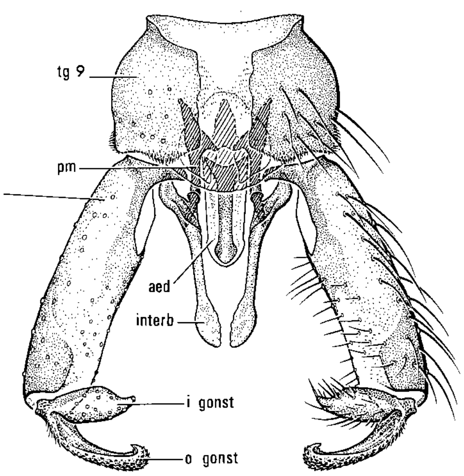
3 Tipula (Lunatipula) monticola ♂



4 Tipula (Yamatotipula) eluta ♂



5 Limonia (Rhipidia) lecontei ♂



6 Rhabdomastix subfascigera ♂

valves reduced and highly modified for a specialized type of oviposition. Detailed descriptions of male and female terminalia found in Byers (1961*b*), Crampton (1941, 1942), Frommer (1963), Rees and Ferris (1939), and Snodgrass (1903, 1904).

Larva. Elongate, usually terete or nearly so, with posterior two-thirds or more of head capsule enclosed within prothoracic segment, usually functionally metapneustic (rarely apneustic), although often with vestigial lateral spiracles. Head capsule distinct, well-sclerotized anteriorly, deeply incised ventrally and often dorsolaterally, retractable within anterior thoracic segments; mandibles opposed or nearly so, moving in horizontal or oblique plane (Figs. 67, 83, 87). Abdominal segments smooth or with transverse rows of fine hairs; transverse creeping welts or, less commonly, fleshy projections sometimes present; terminal segment generally glabrous, often partially sclerotized, bearing posterior spiracles; spiracular disc usually surrounded by lobe-like projections of variable length; anal papillae or membranous anal lobes usually present.

Biology and behavior. The Tipulidae are found from the northernmost lands of the Arctic to lowland equatorial forests, and from the marine intertidal zone to over 5600 m in certain high mountain ranges. Most species are associated with moist, temperate environments; adults are ordinarily found in low, leafy vegetation near streams and lakes in forested areas. However, many species inhabit open meadows, fairly dry rangelands, and even deserts. Because many species of Tipulidae are so abundant, they are extensively preyed upon by birds, mammals, fishes, and other vertebrates, as well as by spiders and predacious insects. The Tipulidae are therefore of tremendous ecological importance. Larvae of a few species that feed on roots of forage crops or on seedling field crops can become economic pests.

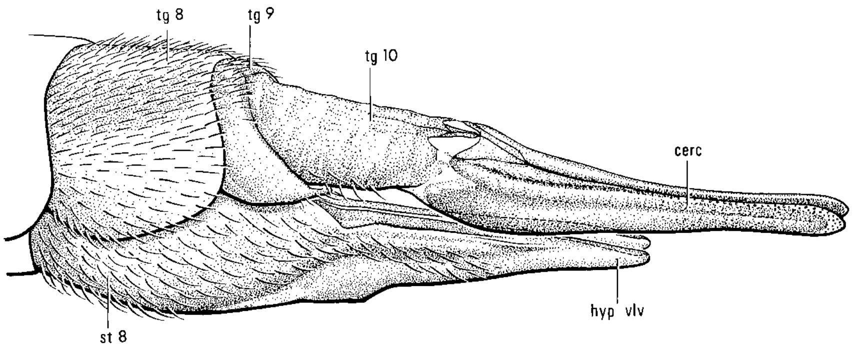
As might be expected in a group of insects as large and varied as the Tipulidae, the immature stages occupy a wide variety of habitats. Habitats ranging from strictly aquatic to completely terrestrial are briefly described here, and examples of the genera that are found in each are given:

- fresh water, especially rapidly flowing streams—*Antocha* Osten Sacken, *Hesperoconopa* Alexander, *Cryptolabis* Osten Sacken
- intertidal zones or brackish water—*Limonia* (*Idioglochina* Alexander) on the Pacific coast, *Limonia* (*Dicranomyia* Stephens) on the Atlantic
- aquatic environment during the larval stage and margins or dryer areas for pupation—*Tipula* Linnaeus, *Limonia* Meigen, *Thaumastoptera* Mik, and many Pediciini, Hexatomini, and Eriopterini
- steep or vertical cliff faces supporting a film or scum of algal growth that is constantly kept wet by slow-flowing or percolating waters or, occasionally, by more rapidly flowing water—some species of *Limonia* Meigen, *Orimarga* Osten Sacken (Vaillant 1950), *Elliptera* Schiner
- moist to wet cushions of mosses or liverworts growing on rocks or earth—Cylindrotominae, various Limoniinae, Tipulinae including *Dolichopeza* Curtis (Byers 1961*b*)
- dry to saturated decaying wood or, occasionally, sodden logs in streams, where larvae commonly feed on fungus mycelia—*Ctenophora* Meigen, *Gnophomyia* Osten Sacken, *Teucholabis* Osten Sacken, *Lipsothrix* Loew
- rich organic earth or mud, as found along margins of streams or lakes or in swamps and marshes; in masses of leaf drift at stream borders; in wet spots in woods where humus is kept saturated—numerous genera and species
- sandy, gravelly, or loamy soils with moderate humus, as found along stream borders—eriopterine groups such as *Gonomyia* Meigen, *Rhabdomastix* Skuse, *Arctoconopa* Alexander, and *Hesperoconopa* Alexander
- decaying plant materials such as masses of leaves, stems, or fruits in various stages of putrefaction—various subgenera and species of *Limonia*
- fungi, both woody and fleshy—*Ula* Haliday, *Limonia* (*Metalimnobia* Matsumura)
- organic matter accumulated in the nests of birds and mammals—chiefly Tipulinae
- leaves of various terrestrial higher plants and mosses—chiefly *Cylindrotoma* Macquart
- dry soil as found in lawns, pastures, or on the ranges of the west—*Nephrotoma* Meigen, *Tipula* Linnaeus, *Dicranoptycha* Osten Sacken.

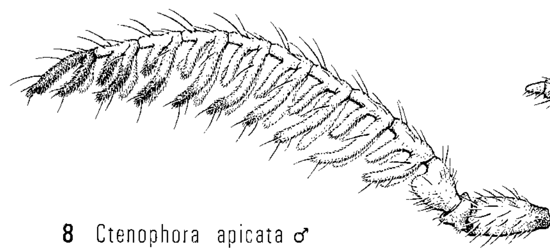
The following papers provide detailed accounts of the immature stages and include bibliographies that may also be consulted for further information: Alexander 1920, 1922, 1931*b*; Bangerter 1928–1934; Brindle 1957–1967; Brodo 1967; Bryce 1956, 1957; Byers 1958–1961*b*; Chiswell 1956; Foote 1963; Hennig 1950; Hynes 1958–1969*c*; Pritchard and Hall 1971; Rogers 1926*a*–1949; Rogers and Byers 1956; Saunders 1928; Savtshenko 1955; Theowald 1957, 1967; Tokunaga 1930; Vaillant 1950.

The life cycle of a crane fly typically consists of a brief egg stage (6–14 days), four larval stages, and a fairly short pupal stage (5–12 days) before emergence of the short-lived adult. Depending on the species and the environmental conditions, especially temperature and humidity, the entire cycle may be as short as 6 wk or as long as 4 yr. Exceptionally long cycles occur in Arctic species. Most species at temperate latitudes or elevations produce one or two generations a year.

Classification and distribution. The family Tipulidae is the single largest family in the Diptera, with approximately 14 000 species; some 1525 of these in 64 genera occur in America north of Mexico. According to

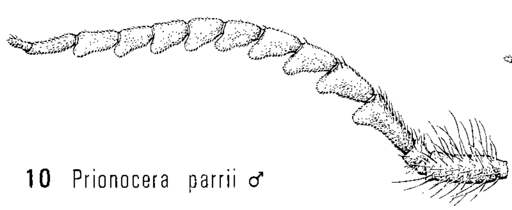


7 Tipula (Yamatotipula) noveboracensis ♀

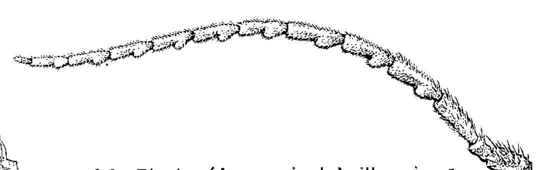


8 Ctenophora apicata ♂

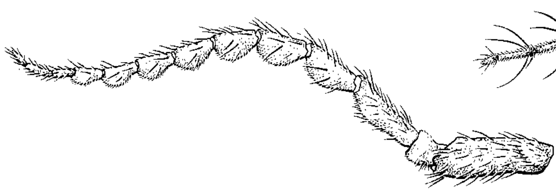
9 Ctenophora apicata ♀



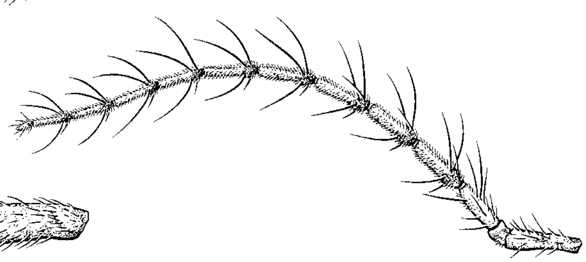
10 Prionocera parrii ♂



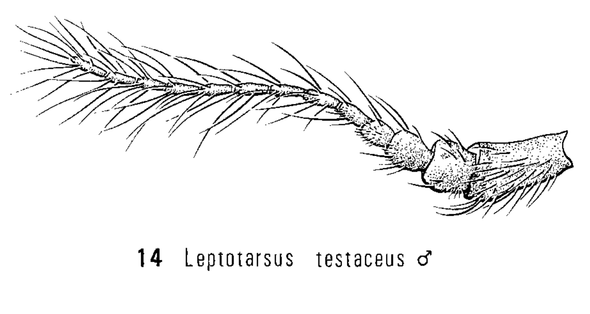
11 Tipula (Angarotipula) illustris ♂



12 Holorusia rubiginosa ♀



13 Tipula (Lunatipula) triplex ♂



14 Leptotarsus testaceus ♂

Figs. 7.7–14. Ovipositor and antennae: (7) ovipositor of *Tipula* (*Yamatotipula*) *noveboracensis* Alexander in lateral view; antennae of (8, 9) *Ctenophora apicata* Osten Sacken, (10) *Prionocera parrii* (Kirby), (11) *Tipula* (*Angarotipula*) *illustris* Doane, (12) *Holorusia rubiginosa* Loew, (13) *Tipula* (*Lunatipula*) *triplex* Walker, and (14) *Leptotarsus testaceus* (Loew).

Abbreviations: cerc, cercus; hyp vlv, hypogynial valve; st, sternite; tg, tergite.

the present interpretation, the family Tipulidae is the sole representative of the superfamily Tipuloidea. Other families that had once been considered members of this superfamily are now assigned to other superfamily groups. The position of these flies in specific superfamilies is still held in question by some students of the order.

Our knowledge of North American tipulid larvae is still fragmentary. The immature forms of probably fewer than 10% of our species have been described. In some genera, even in a few with many species, larvae of only one or a few species are known. Therefore, the limitations of the larval key should be recognized. Some portions of the key are necessarily based on these known but possibly atypical representatives. The genera are not keyed in a phylogenetic sequence because larval characters, particularly the superficial ones utilized in the key, often yield groupings that do not coincide with those based upon adult characteristics. External, more or less readily visible characters are mainly used for identification. All structural details used, however, can be seen with an ordinary dissecting microscope. Diagnostic features include the shape and pigmentation of the spiracular disc on the terminal segment and the characteristics of its peripheral lobes, degree of sclerotization of the dorsal and lateral portions of the head, development of the midventral hypostomal bridge, and presence or absence of raised, often setiferous creeping welts on the abdominal segments. Where possible, the larval habitat is described when each genus is identified. Some genera occasionally appear in two or more places so that generic assignment of species whose larvae are at present unknown might be possible. North American genera for which no larval forms are yet known are *Cheilotrichia* Rossi, *Nasiternella* Wahlgren, *Neocladura* Alexander, *Neolimnophila* Alexander, *Ornithodes* Coquillett, *Phyllolabis* Osten Sacken, *Prolimnophila* Alexander, *Shannonomyia* Alexander, *Tasiocera* Skuse, *Thaumastoptera* Mik, and *Toxorhina* Loew. Although these genera represent 19% of the total, they contain only about 3% of Nearctic tipulid species. The key includes *Cheilotrichia* and *Thaumastoptera* based on characteristics of European species. Probable positions of some other genera are also indicated. The key will undoubtedly need revision as descriptions of newly discovered specimens are published.

The Tipulidae probably evolved from ancestors resembling or perhaps even included in the Architipulidae, a family of primitive Diptera about 140 million years old, known from the Upper Jurassic deposits of Europe. Because fossils of nine families of Nematocera, including one tipulid, have been found in the Cretaceous amber of central Canada (Carpenter 1934), the Tipulidae can be assumed to have become differentiated from related families by middle to late Cretaceous times (about 70 million years ago). Records of Tipulidae from the lower Tertiary period, in contrast, are numerous and are from many parts of the world. Specimens in Baltic amber (Alexander 1931*a*), judged to have been preserved 40–45 million years ago, include representatives of two genera of Tipulinae, both still extant, and 29 genera of Limoniinae, 25 of which are extant. This amber is apparently of upper Eocene or lower Oligocene age. Fossils of approximately equivalent age from Gurnet Bay on the Isle of Wight add a few more genera, especially in the Tipulinae. In North America, the volcanic shales near Florissant, Colo., probably of upper Oligocene or lower Miocene age (perhaps 30 million years old), have yielded representatives of seven genera of Tipulinae, three of which are still extant; one extant genus of Cylindrotominae; and 17 genera of Limoniinae, 10 of which are extant (Scudder 1894). The recently described Chiapas amber from southern Mexico, of approximately the same age as the Florissant beds, includes a few Tipulidae. The older (Eocene) Green River shales of Colorado and various other early to middle Tertiary deposits in North America contain remains of Tipulidae, but these records are generally fragmentary (Scudder 1890, Handlirsch 1910).

The description, classification, and distribution of Nearctic Tipulidae have been dealt with extensively in the literature. Many relevant papers are listed, together with a catalog of species, in the Diptera catalog edited by Stone *et al.* (1965). The papers by Alexander (1966, 1967), Brodo (1967), and Byers (1961*b*) are particularly important because they provide keys to species of major regions of North America. Other useful publications that list species of various political regions and natural areas are those by Alexander, published between 1934 and 1954.

Keys to genera

Adult

1. Fully winged 2
   Subapterous 163
2. Terminal segment of palpus elongate; nasus usually distinct. Flagellum commonly with 11 segments. Sc_1 usually atrophied or incomplete; CuA slightly constricted at branching of CuA_1 and CuA_2 (Figs. 15, 20–25). Size large; wing commonly over 10 mm, usually much larger .... TIPULINAE....4

Terminal segment of palpus short; nasus absent. Flagellum usually with either 12 or 14 segments, but sometimes with fewer segments. Sc_1 complete; CuA straight, not constricted at branching of CuA_1 and CuA_2 (Figs. 16–19, 26–29). Size small or medium, rarely large; wing commonly under 10 mm, usually much smaller 3

3. Tip of R_{1+2} usually atrophied, with R_1 gradually converging toward and fusing with R_3 well before wing margin; R_{1+2}, if present, arising near this point of fusion; free tip of Sc_2 present (Figs. 26–29) .... CYLINDROTOMINAE....49

Tip of R_{1+2} present; R_1 not appearing to converge on collision course with R_3; R_2 commonly present and usually in form of a nearly transverse crossvein between R_1 and R_3; free tip of Sc_2, recognizable by its lack of setae and its angular divergence from R_1, preserved in many species in tribe Limoniini, lacking in all other Nearctic tribes .... LIMONIINAE....53

4. Legs unusually long and slender, filiform. Either R_{1+2} and free ending of Sc_1 atrophied with Sc_2 entering R close to origin of Rs (Fig. 22), or R_{1+2} present with Sc very long and with Sc_1 reaching C very close to free tip of Sc_2 (Figs. 20, 21) 5

Legs long but stouter. R_{1+2} usually preserved, but when atrophied Sc of moderate length and Sc_1 atrophied before fork of Rs with Sc_2 entering R_1 at or near mid length of Rs 9

5. Sc very long; Sc_1 preserved; free tip of Sc_2 at margin close to Sc_1 6

Sc shorter; Sc_1 atrophied .... ***Dolichopeza*** Curtis....7

6. Crossvein r-m originating in Rs; crossvein m-cu present (Fig. 20) .... ***Megistocera*** Wiedemann
1 sp., *longipennis* (Macquart); Texas to Florida

Crossvein r-m originating in R_{4+5}; crossvein m-cu absent; CuA_1 fused with lower border of cell dm for short distance (Fig. 21) .... ***Brachypremna*** Osten Sacken
1 sp., *dispellens* (Walker); southern, eastern

7. Cell dm open by atrophy of basal section of M_3; outer medial field thus appearing pectinate (Fig. 22) .... ***Dolichopeza*** (***Dolichopeza*** Curtis)
2 spp.; temperate, northern

Cell dm closed 8

8. Wing with cells beyond cord having abundant macrotrichia .... ***Dolichopeza*** (***Megistomastix*** Alexander)
tropical (Greater Antilles)

Wing without macrotrichia in cells .... ***Dolichopeza*** (***Oropeza*** Needham)
13 spp.; temperate, lacking in west

9. Antennal flagellum with flagellomeres branched in male and less produced in female of Nearctic species (Figs. 8, 9) .... ***Ctenophora*** Meigen....10

Antennal flagellum with flagellomeres simple or slightly produced to appear serrate 13

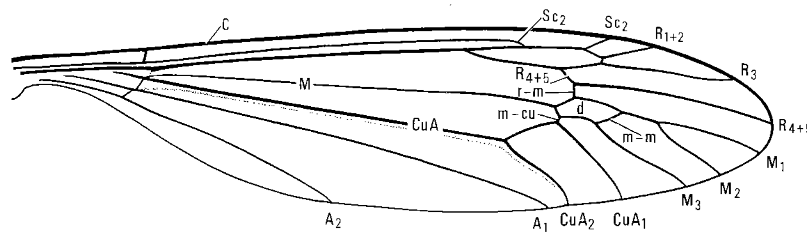
10. Intermediate flagellomeres of male three-branched; flagellomeres 2–10 each with a longer basal pair of branches and a single shorter spur on outer half; each basal branch with a single long seta before mid length; vestiture short; first flagellomere deeply bilobate; terminal flagellomere small, simple. Ovipositor with cerci slender, saber-shaped, much longer than width of head .... ***Ctenophora*** (***Tanyptera*** Latreille)
1 sp., *dorsalis* Walker; central, eastern

Intermediate flagellomeres of male four-branched. Ovipositor with cerci no longer than width of head 11

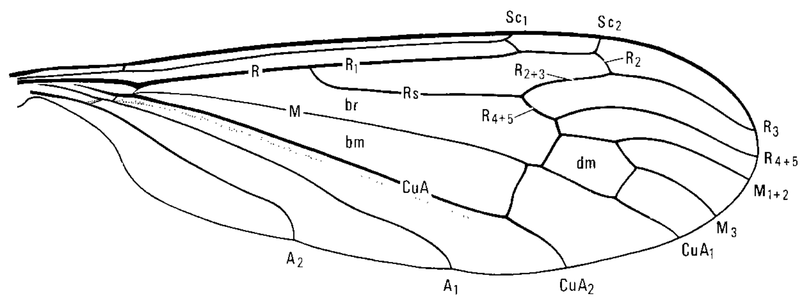
11. First flagellomere of male deeply bilobate and outer lobule weakly emarginate; flagellomeres 2–10 each with four branches arranged in pairs; branches short, subequal in length to flagellomeres; basal pair of branches each with a single strong seta; terminal flagellomere small, simple; flagellar vestiture short .... ***Ctenophora*** (***Phoroctenia*** Coquillett)
1 sp., *vittata angustipennis* Loew; western temperate

First flagellomere of male simple; flagellomeres 2–10 each with four longer branches 12

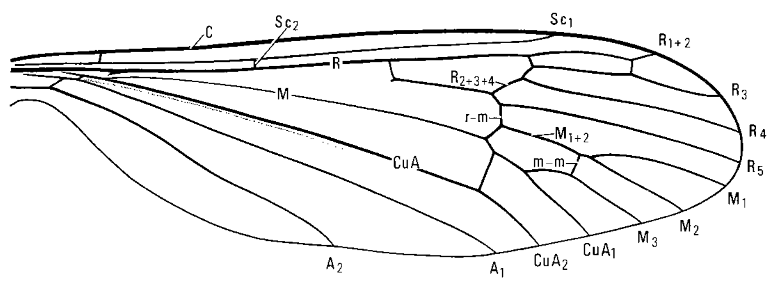
12. Flagellomeres 2–10 each with four moderately long branches; basal pair of branches longer than others; each branch with a long seta before mid length (Fig. 8); flagellar vestiture short and inconspicuous; terminal flagellomere small, simple .... ***Ctenophora*** (***Ctenophora*** Meigen)
2 spp.; temperate



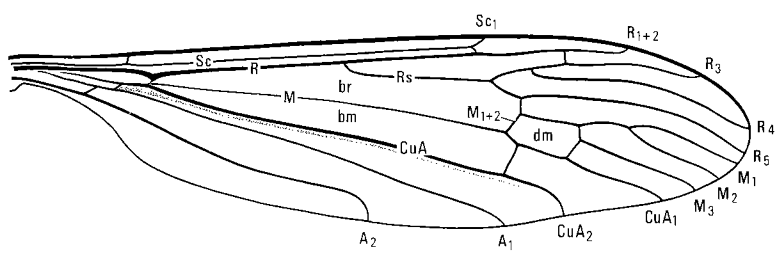
15 Tipula (Yamatotipula) tricolor ♂



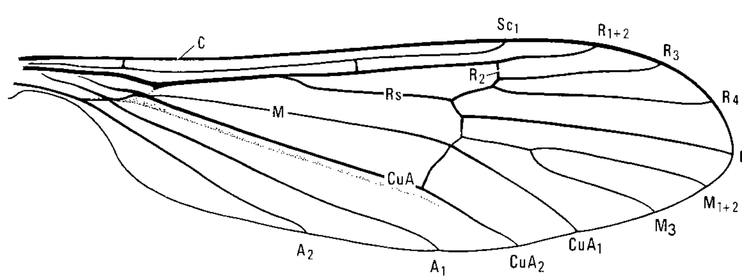
16 Limonia (Metalimnobia) triocellata ♂



17 Dicranota (Eudicranota) pallida ♂



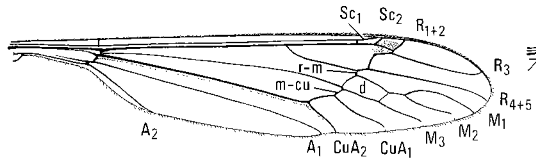
18 Pseudolimnophila inornata ♂



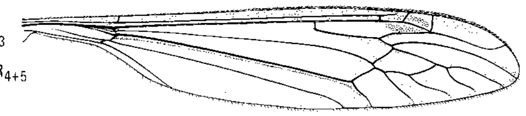
19 Ormosia monticola ♀

Figs. 7.15–19. Wings: (15) *Tipula* (*Yamatotipula*) *tricolor* Fabricius; (16) *Limonia* (*Metalimnobia*) *triocellata* (Osten Sacken); (17) *Dicranota* (*Eudicranota*) *pallida* Alexander; (18) *Pseudolimnophila inornata* (Osten Sacken); (19) *Ormosia monticola* (Osten Sacken) (*continued*).

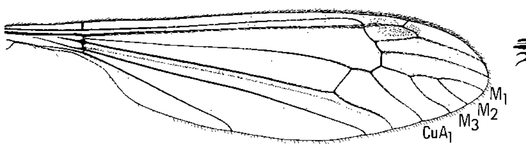
Flagellomeres 2–10 each with four very long branches that exceed length of flagellomeres; vestiture dense, erect; terminal flagellomere elongate, appearing trifid with a pair of subequal basal branches .... ***Ctenophora* (*Pselliophora* Osten Sacken)**
Neotropical, Mexico



20 Megistocera longipennis ♂

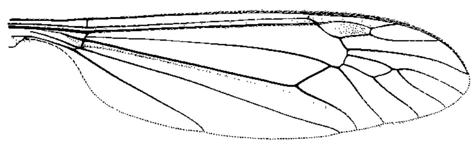


21 Brachypremna dispellens ♀

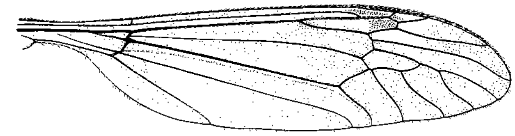


22 Dolichopeza americana ♀

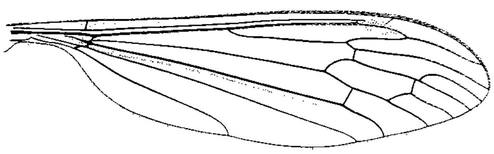
23 Tipula (Yamatotipula) caloptera ♂



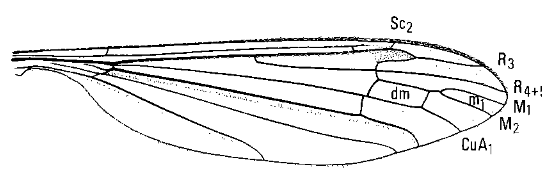
24 Nephrotoma ferruginea ♂



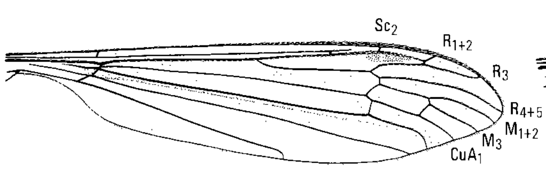
25 Tipula (Lunatipula) dorsimacula ♂



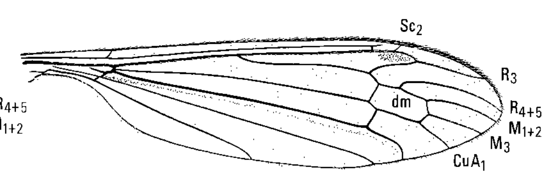
26 Cylindrotoma distinctissima americana ♂



27 Phalacrocera tipulina ♂



28 Phalacrocera replicata ♂



29 Liogma nodicornis ♂

Figs. 7.20–29. Wings (*continued*): (20) *Megistocera longipennis* (Macquart); (21) *Brachypremna dispellens* (Walker); (22) *Dolichopeza americana* Needham; (23) *Tipula* (*Yamatotipula*) *caloptera* Loew; (24) *Nephrotoma ferruginea* (Fabricius); (25) *Tipula* (*Lunatipula*) *dorsimacula* Walker; (26) *Cylindrotoma distinctissima americana* Osten Sacken; (27) *Phalacrocera tipulina* Osten Sacken; (28) *Phalacrocera replicata* (Linnaeus); (29) *Liogma nodicornis* (Osten Sacken) (*continued*).

13. Flagellomeres without conspicuous verticils or elongate setae (Figs. 10, 11) 14
Flagellomeres with distinct verticils or elongate setae (Figs. 12–14) 15

14. Antenna with lower face of flagellomeres slightly produced near outer end, giving organ a serrate appearance (Fig. 10) .... ***Prionocera*** Loew
16 spp.; northern

Flagellomeres either enlarged on basal half (Fig. 11) or uniformly cylindrical .... ***Tipula*** (***Angarotipula*** Savtshenko), in part
2 spp.; widespread

15. Size very large; wing commonly over 25 mm, sometimes 40 mm or more. R_3 near mid length bent strongly caudally, narrowing the cell. Antenna with lower faces of intermediate flagellomeres protuberant, without strong setae; upper surfaces with short verticils; terminal three flagellomeres smaller than the rest (Fig. 12) .... ***Holorusia*** Loew
1 sp., *rubiginosa* Loew, largest in Nearctic region; western

Size smaller; wing less than 30 mm, commonly less than 20 mm. R_3 straight or virtually so. Antenna not as above 16

16. Flagellomeres cylindrical, with short normal setae on proximal ones and long conspicuous setae on outer ones (Fig. 14) .... ***Leptotarsus*** Guérin-Méneville (***Longurio*** Loew)
4 spp.; eastern U.S.A.

Flagellomeres with bases enlarged and with stout verticils, outwardly without conspicuous setae (Fig. 13) 17

17. Sc ending nearly opposite origin of Rs; basal section of Rs short, oblique; cell m_1 sessile or very short–petiolate; CuA_1 uniting with M for short distance before fork of M (Fig. 24). Body coloration highly polished, often black and yellow .... ***Nephrotoma*** Meigen
40 spp.; widespread

Sc longer; Sc_2 meeting R_1 beyond origin of Rs; Rs longer, usually exceeding basal section of CuA_1; cell m_1 long–petiolate; CuA_1 or crossvein m-cu meeting M beyond its fork (Figs. 15, 25). Body coloration usually opaque, pruinose .... ***Tipula*** Linnaeus, in part 18

18. Antennal flagellomeres without verticils (Fig. 11) .... ***Tipula*** (***Angarotipula*** Savtshenko), in part
1 sp., *illustris* Doane; widespread

Antennal flagellomeres with verticils 19

19. Distal wing cells with macrotrichia 20
No macrotrichia in wing cells 22

20. Thorax polished orange or yellow, sometimes with dark or blackened stripes .... ***Tipula*** (***Hesperotipula*** Alexander), in part
18 spp.; western

Thorax opaque yellow, brown, or gray, sometimes with darkened opaque stripes 21

21. Calypter without strong setae .... ***Tipula*** (***Trichotipula*** Alexander), in part
30 spp.; primarily western, 4 spp. eastern

Calypter with setae .... ***Tipula*** (***Setitipula*** Alexander)
3 spp.; western

22. Tarsi creamy white .... ***Tipula*** (***Tipulodinodes*** Alexander)
1 sp., *lacteipes* Alexander; western

Tarsi darkened 23

23. Calypter without strong setae 24

Calypter with setae 38

24. Wing of female with two veins, M_1 and M_3, emanating from cell dm; basal section of CuA_1 before fork of M, as in *Nephrotoma* (insufficiently known, perhaps based on abnormal specimens and perhaps belonging in *Yamatotipula* Matsumura) .... ***Tipula*** (***Nesotipula*** Alexander)
1 sp., *pribilovia* Alexander; Alaska

Wing of female with at least three veins emanating from cell d or dm 25

25. Body coloration polished yellow and black, much as in *Nephrotoma*. Wing veins posterior to R_1 glabrous or virtually so .... ***Tipula*** (***Nobilotipula*** Alexander)
2 spp.; eastern

Body coloration opaque. Wing veins with microtrichia 26

26. Male terminalia with tergite 9 and sternite 9 fused to form a continuous ring 27

Male terminalia with tergite 9 and sternite 9 separated by a suture 28

27. Wing sometimes unpatterned, but commonly with darkened longitudinal stripes along veins and without a strong transverse darkening in cell bm (Fig. 23); basal section of M_3 short, usually subequal to or less than crossvein r-m; crossvein m-cu or basal section of CuA_1 meeting cell d or dm some distance before its mid length. Male terminalia commonly with tergite 9 produced into a simple or emarginate lobe apically bearing small blackened spines; ventral lobes of aedeagal guide appearing as pale spatulate blades (Fig. 4) .... ***Tipula*** (***Yamatotipula*** Matsumura)
51 spp.; widespread

Wing variously patterned with white background and darker costal border, or yellow with a brown cloud at end of A_2; basal section of M_3 longer, from two to three times length of crossvein r-m. Male terminalia with tergite 9 large, notched medially; broad pale lobes with margins roughened or with spine-like projections; lobes of aedeagal guide greatly reduced, not blade-like .... ***Tipula*** (***Platytipula*** Matsumura)
11 spp.; widespread

28. Basal section of Rs short; R_{1+2} present or atrophied. Antenna of male commonly long, one-half length of wing or more. Male terminalia with tergite 9 shallowly to deeply emarginate; lobes covered with coarse setae; gonostylus very irregular in conformation; gonocoxite commonly with a blackened corrugated lobe on median face .... ***Tipula*** (***Microtipula*** Alexander)
large varied Neotropical group, with some species bordering Nearctic portions of Mexico

Wing, antenna, and terminalia not as above 29

29. Basal section of Rs long; R_{1+2} present, usually with darkened mottled pattern. Antenna commonly long, or very long; extreme bases of flagellomeres each with a knob-like enlargement to present a bead-like appearance. Male terminalia commonly with a variously modified lobe on posterior border of sternite 8 .... ***Tipula*** (***Eumicrotipula*** Alexander)
widespread in tropics, sparsely represented in southwestern Nearctic

Wing, antenna, and terminalia not as above 30

30. Wing variously patterned with darker coloration 31

Wing without darker markings other than pterostigma 37

31. Wing with white or grayish background, with sparse brown clouds in distal ends of cells bm, cu*p*, and a_1; distal cells having central streaks; cell cua_1 long and narrow .... ***Tipula*** (***Trichotipula*** Alexander), in part
see couplet 21

Wing with darkened pattern heavier and differently arranged; cell cua_1 broader 32

32. Male terminalia with tergite 9 variously trilobate; posterior margin of sternite 8 variously produced, commonly with a median bispinous plate .... ***Tipula*** (***Lindneria*** Mannheims)
6 spp.; widespread

Male terminalia with tergite 9 and sternite 8 differently constructed 33

33. Male terminalia with outer basal division of inner gonostylus produced backward as a tail-like extension that bears one or more blackened points, and commonly terminating in a pale membranous blade .... ***Tipula*** (***Beringotipula*** Savtshenko)
22 spp.; widespread

Male terminalia not as above 34

34. Tergite 9 of male terminalia commonly forming a shallowly concave sclerotized saucer. Female ovipositor with cerci strongly constructed; cercus lying transversely, with outer margin serrate .... ***Tipula*** (***Vestiplex*** Bezzi)
17 spp.; chiefly northern or alpine

Male terminalia and female ovipositor not as above 35

35. Tergite 9 of male terminalia commonly with a narrow median emargination and broad lobes; sternite 8 usually with lateral lobes that bear modified setae .... ***Tipula*** (***Pterelachisus*** Rondani), in part
39 spp.; widespread

Tergite 9 of male terminalia not as above; sternite 8 simple, without lateral lobes 36

36. Tergite 9 of male terminalia virtually glabrous, without points or spicules on margin; outer division of gonostylus forming a simple pale fleshy lobe; upper and lower beaks of inner division of gonostylus large, blackened, obtuse; outer basal lobe of inner division of gonostylus large and pale, with abundant strong setae; aedeagus stout .... ***Tipula*** (***Serratipula*** Alexander), in part
5 spp.; California

Tergite 9 of male terminalia provided with microscopic blackened spinoid setae on margin; outer division of gonostylus with a blackened flange at base of upper margin; lower beak of inner division of gonostylus reduced or obsolete; outer basal lobe of inner division of gonostylus a small sessile cushion with sparse spinoid setae; aedeagus slender .... ***Tipula*** (***Savtshenkia*** Mannheims)
9 spp.; primarily northeastern with 1 sp. in California

37. Antenna of male longer than thorax. Abdomen of female much longer than that of male. Male with sternite 8 produced caudally into a broad pale fleshy lobe. Female ovipositor with cerci short and strong, modified for deep boring in soil .... ***Tipula*** (***Odonatisca*** Savtshenko)
5 spp.; northern, western

Antenna of male no longer than thorax. Abdomen of nearly equal length in both sexes. Male sternite 8 without a fleshy lobe. Ovipositor not so modified .... ***Tipula*** (***Arctotipula*** Alexander), in part
17 spp.; western, northern

38. Outer gonostylus of male terminalia large and broad; outer basal lobe of inner gonostylus bearing two arms, with a slender curved spine on posterior one. Antenna 14-segmented .... ***Tipula*** (***Tipula*** Linnaeus)
1 sp., *paludosa* Meigen; Holarctic, on east and west coasts

Male terminalia not as above. Antenna 13-segmented 39

39. Rs short, subequal to or shorter than basal section of CuA_1 40

Rs longer than basal section of CuA_1 41

40. Wing with darkened pattern conspicuously mottled, with a marginal whitened spot on outer cells; wing veins unusually glabrous; branches of M without macrotrichia. Size large; wing in Nearctic species about 20 mm. Male with sternite 8 unarmed .. ***Tipula*** (***Bellardina*** Edwards)
5 spp.; southwestern

Wing with darkened pattern not mottled, without a white marginal spot on distal cells; wing veins with macrotrichia, including all distal medial veins. Size small or medium; wing less than 15 mm. Male terminalia with sternite 8 variously produced or armed .... ***Tipula*** (***Schummelia*** Edwards)
7 spp.; widespread

41. Aedeagal guide (adminiculum) of male terminalia distinctive, T-shaped or Y-shaped with a slender stem and two divergent arms near apex ...... ***Tipula*** (***Triplicitipula*** Alexander), in part
23 spp.; widespread

Aedeagal guide of male terminalia not as above 42

42. Wing patterned and with characteristic venation; crossvein r-m at or close to fork of Rs; R_{4+5} in direct alignment with Rs; M_3 long; CuA_1 confluent with M_3 for short distance. Size large; wing over 20 mm, commonly 25 mm or more .... ***Tipula (Nippotipula*** Matsumura)
1 sp., *abdominalis* (Say); eastern

Wing not patterned; venation not as described; crossvein r-m on R_{4+5} some distance beyond base; M_3 short; crossvein m-cu usually present, or if absent, CuA_1 meeting M_3 at a point. Size usually smaller 43

43. Wing with a conspicuous mottled pattern, with alternating dark and pale areas that are more or less zigzag on basal cells; distal veins with a blackish marginal spot .... ***Tipula*** (***Sinotipula*** Alexander)
17 spp.; western

Wing pattern, when heavy and conspicuous, not mottled or patterned as described above 44

44. Gonocoxite of male terminalia produced into a long strong arm that exceeds gonostylus in length 45

Gonocoxite of male terminalia not produced, or if so only slightly produced and not exceeding gonostylus 46

45. Arm of gonocoxite stout, widened outwardly; apex obtuse or bispinous. Body generally opaque brownish gray ....***Tipula*** (***Labiotipula*** Alexander)
3 spp.; northern

Arm of gonocoxite slender, more or less twisted, narrowed to an acute or subacute tip. Body generally polished orange or yellow ....***Tipula*** (***Hesperotipula*** Alexander), in part
see couplet 20

46. Male terminalia with tergite 9 small and with a median subtergal process situated slightly more ventral than lateral lobes; outer division of gonostylus narrowed outwardly; outer basal lobe of inner division of gonostylus produced backward ....***Tipula*** (***Eremotipula*** Alexander)
25 spp.; western

Male terminalia not as above 47

47. Body usually polished yellow or orange. Ovipositor with cerci short and obtuse ....***Tipula*** (***Hesperotipula*** Alexander), in part
see couplet 20

Body usually not polished yellow or orange. If so, ovipositor with elongate cerci 48

48. Wing veins unusually glabrous; M without macrotrichia. Outer gonostylus of male terminalia large, broad; inner gonostylus unusually simple, without lower beak and outer basal lobe ....***Tipula*** (***Arctotipula*** Alexander), in part
see couplet 37

Wing with macrotrichia on M. Outer gonostylus of male terminalia fairly small; inner gonostylus more complex, with either a lower beak or an outer basal lobe present, usually with both present (Fig. 3) ....***Tipula*** (***Lunatipula*** Edwards)
160 spp.; widespread

49. Head and intervals of mesonotal prescutum with numerous deep punctures; a deep median groove on prescutum ....***Triogma*** Schiner
1 sp., *exsculpta* Osten Sacken; eastern

Head and intervals of mesonotal prescutum smooth; no median prescutal groove 50

50. Three branches of R reaching margin (Fig. 28); R_{1+2} preserved as a distinct element ....***Phalacrocera*** Schiner, in part
4 spp.; 2 spp. eastern, 2 spp. western

Two branches of R reaching margin; R_{1+2} atrophied, giving appearance of a long backward fusion of R_1 and anterior branch of Rs 51

51. Three branches of M reaching margin (Fig. 26) ....***Cylindrotoma*** Macquart
3 spp.; northern

Two branches of M reaching margin; M_3 in *Phalacrocera occidentalis* Alexander usually present as a short spur, not reaching margin 52

52. Crossvein r-m present; distal end of cell dm commonly closed by a single transverse crossvein; cell m_1 present, sessile to short-petiolate; M_3 partially or completely atrophied (Fig. 27). Antennal flagellomeres nearly simple, with lower faces not produced ....***Phalacrocera*** Schiner, in part
see couplet 50

Crossvein r-m usually shortened or obliterated by approximation or fusion of R_{4+5} and M_{1+2}; cell m_1 absent; M_3 complete to margin (Fig. 29). Antennal flagellomeres strongly nodulose, especially in male, with individual flagellomeres subcordate ....***Liogma*** Osten Sacken
1 sp., *nodicornis* (Osten Sacken); eastern to Alberta

53. Eye hairy, with short hairs between ommatidia. Sc_1 very long, exceeding fork of Rs; Sc_2 basal to origin of Rs (Figs. 17, 38, 39) ....PEDICIINI....74

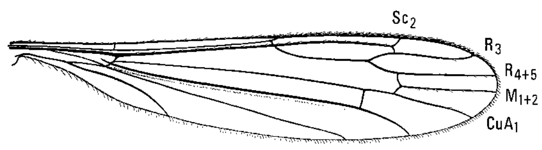
Eye glabrous. Sc_1 short or of moderate length; when Sc_1 longer (some Eriopterini), Sc_2 usually situated distal to origin of Rs; when Sc_2 situated basal to origin of Rs, Sc_1 not exceeding fork of Rs 54

54. Free tip of Sc_2 often present, nearly transversely oriented; R_4 and R_5 fused to margin; only two branches of Rs (R_3 and R_{4+5}) present (Figs. 30–37). Antenna with 12 or 14 flagellomeres ....LIMONIINI....56

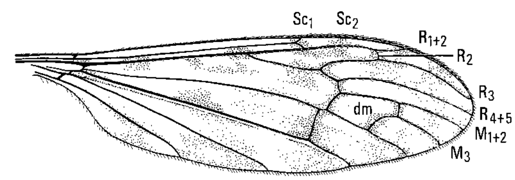
Free tip of Sc_2 lacking; R_4 and R_5 separate; R_4 usually captured by R_{2+3} to form a distinct element R_{2+3+4}; usually three branches of Rs present (exceptions: *Atarba*, *Elephantomyia*, *Teucholabis*, and some *Gonomyia* spp., where R_{2+3} is captured, as above) (Figs. 40–49). Antenna usually with 14 flagellomeres, but with number reduced in *Hexatoma* and a few others 55

55. Tibial spurs present ....HEXATOMINI......86

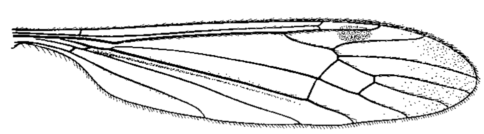
Tibial spurs lacking ....ERIOPTERINI....118



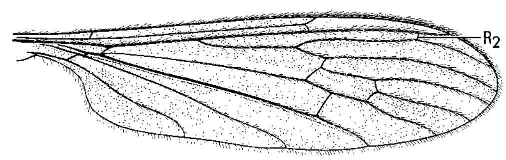
30 Limonia (Alexandriaria) whartoni ♂



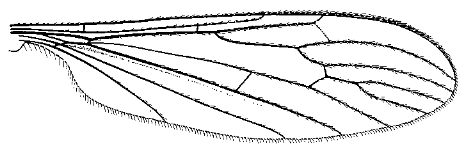
31 Limonia (Metalimnobia) immatura ♀



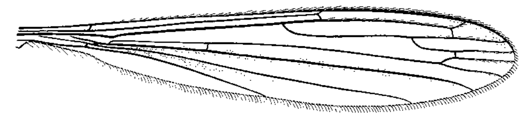
32 Helius flavipes ♂



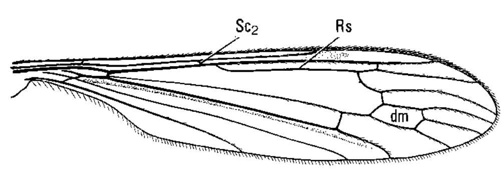
33 Dicranoptycha germana ♀



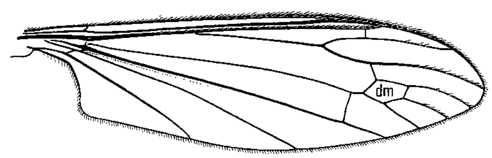
34 Thaumastoptera hynesi ♂



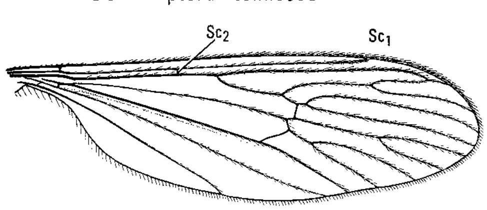
35 Orimarga (Diotrepha) mirabilis ♀



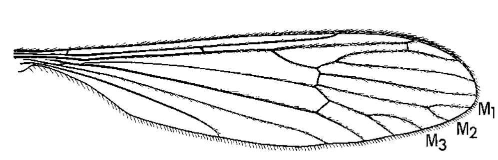
36 Elliptera tennessa ♀



37 Antocha saxicola ♂



38 Pedicia (Tricyphona) protea ♀



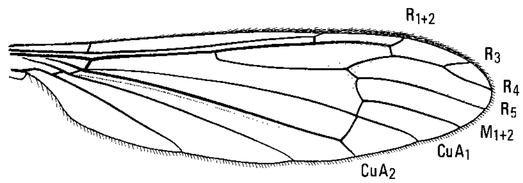
39 Dicranota (Rhaphidolabis) tenuipes ♂

Figs. 7.30–39. Wings (*continued*): (30) *Limonia* (*Alexandriaria*) *whartoni* (Needham); (31) *Limonia* (*Metalimnobia*) *immatura* (Osten Sacken); (32) *Helius flavipes* (Macquart); (33) *Dicranoptycha germana* Osten Sacken; (34) *Thaumastoptera hynesi* Alexander; (35) *Orimarga* (*Diotrepha*) *mirabilis* (Osten Sacken); (36) *Elliptera tennessa* Alexander; (37) *Antocha saxicola* Osten Sacken; (38) *Pedicia* (*Tricyphona*) *protea* (Alexander); (39) *Dicranota* (*Rhaphidolabis*) *tenuipes* (Osten Sacken) (*continued*).

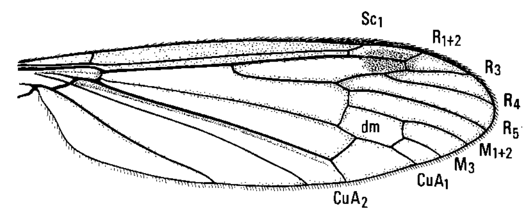
56. Antenna with 12 flagellomeres .... **Limonia** Meigen....57
Antenna with 14 flagellomeres 67

57. One branch of M reaching margin (Fig. 30) .... ***Limonia*** **(*Alexandriaria*** Garrett), in part
3 spp.; 2 spp. western, 1 sp. northeastern
Two branches of M reaching margin (Figs. 31–37) 58

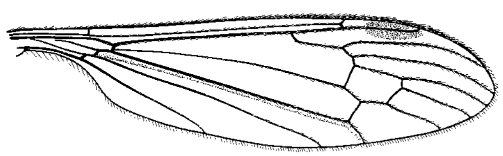
58. Wing with supernumerary crossveins in cells a_1 or r_3 59
Wing without supernumerary crossveins in cells a_1 or r_3, but with a weak vein in cell sc in some species of *Geranomyia* Haliday 60



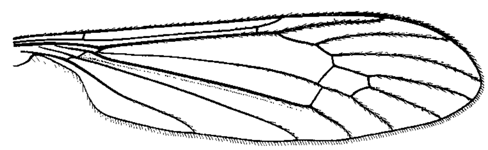
40 Hexatoma megacera ♀



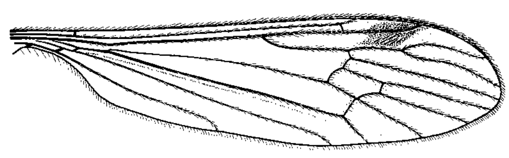
41 Hexatoma (Eriocera) longicornis ♀



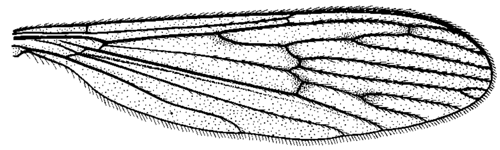
42 Elephantomyia westwoodi ♂



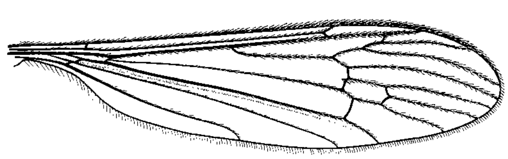
43 Atarba picticornis ♀



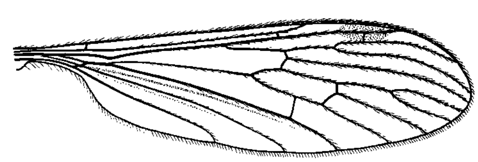
44 Phyllolabis encausta ♀



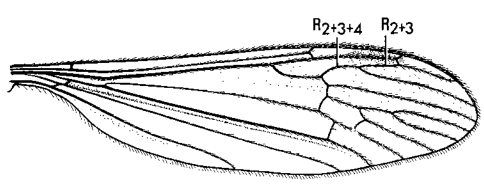
45 Polymera rogersiana ♀



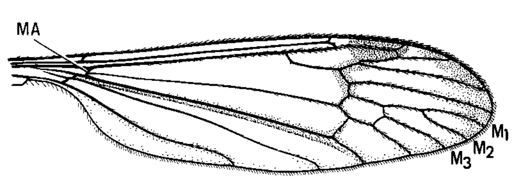
46 Pseudolimnophila noveboracensis ♂



47 Prolimnophila areolata ♂



48 Austrolimnophila toxoneura ♂



49 Limnophila (Phylidorea) adusta ♀

Figs. 7.40–49. Wings (*continued*): (40) *Hexatoma megacera* (Osten Sacken); (41) *Hexatoma* (*Eriocera*) *longicornis* (Walker); (42) *Elephantomyia westwoodi* Osten Sacken; (43) *Atarba picticornis* Osten Sacken; (44) *Phyllolabis encausta* Osten Sacken; (45) *Polymera rogersiana* Alexander; (46) *Pseudolimnophila noveboracensis* (Alexander); (47) *Prolimnophila areolata* (Osten Sacken); (48) *Austrolimnophila toxoneura* (Osten Sacken); (49) *Limnophila* (*Phylidorea*) *adusta* Osten Sacken (*continued*).

59. Supernumerary crossvein in cell a_1 .... ***Limonia*** (***Discobola*** Osten Sacken)
 3 spp.; widespread

 Supernumerary crossvein in cell r_3 .... ***Limonia*** (***Neolimnobia*** Alexander)
 tropical (Antilles)

60. Mouthparts, especially labella, elongate; rostrum about equal in length to combined head and thorax .... ***Limonia*** (***Geranomyia*** Haliday)
 14 spp.; widespread

 Mouthparts shorter than remainder of head 61

61. Flagellomeres of male antenna more or less produced, bipectinate, unipectinate, or subpectinate; flagellomeres in female less-developed, appearing serrated to nearly simple. Male terminalia often with more than two rostral spines, commonly with three to eight in Nearctic species (Fig. 5) .... ***Limonia*** (***Rhipidia*** Meigen)
 8 spp.; widespread

 Flagellomeres of antennae of both sexes ranging from subglobular to oval to elongate, not produced to appear pectinate in male. Male terminalia usually without rostral spines, but sometimes with one or two 62

62. Male terminalia with a simple undivided gonostylus; gonocoxite with simple ventromedial lobe. R_{1+2} longer than R_2 in Nearctic species, shortest in *sociabilis* Osten Sacken .... ***Limonia*** (***Limonia*** Meigen)
 12 spp.; widespread

 Male terminalia with divided gonostylus. Venation not as above 63

63. Ventral division of gonostylus without rostral spines in Nearctic species 64

 Ventral division of gonostylus commonly with two rostral spines, but sometimes with either one or three 65

64. Sc short, ending close to origin of Rs. Proximal flagellomeres oval, with apices abruptly short–pedunculate, and with verticils shorter than flagellomeres .... ***Limonia*** (***Idioglochina*** Alexander)
 1 sp., *marmorata* (Osten Sacken); marine, Pacific ocean

 Sc very long, ending nearly opposite fork of Rs (Fig. 31). Flagellomeres oval, without apical peduncles, and with very long and flexible verticils on proximal flagellomeres. Gonostylus deeply divided, with a third oval lobe at base of ventral division of gonostylus .... ***Limonia*** (***Metalimnobia*** Matsumura)
 9 spp.; widespread

65. Dorsal division of gonostylus of male terminalia in form of a stout club that terminates in several blackened spines; ventral division of gonostylus with two rostral spines placed on a long sinuous prolongation .... ***Limonia*** (***Hesperolimonia*** Alexander)
 1 sp., *infuscata* (Doane); western

 Male terminalia not as above 66

66. Male terminalia with a single stout rostral spine. Body commonly polished black. Anterior vertex of head broad and silvery .... ***Limonia*** (***Melanolimonia*** Alexander)
 4 spp.; widespread, boreal

 Male terminalia with two rostral spines. Coloration not as above .... ***Limonia*** (***Dicranomyia*** Stephens), in part
 70 spp.; widespread

67. R_2 lacking 68

 R_2 present 69

68. Rostrum short and inconspicuous. Sc_2 removed from tip of Sc_1, placed basal to origin of Rs; basal section of Rs long and straight, close to R_1, and in direct alignment with R_{2+3}; crossvein r-m distinct (as in Fig.36) .... ***Elliptera*** Schiner, in part
 6 spp.; widespread

 Rostrum of moderate length, subequal to or longer than remainder of head. Sc_2 at tip of Sc_1, and about opposite the fork of Rs; basal section of Rs short and curved, not in alignment with R_{2+3}; crossvein r-m sometimes shortened or obliterated by approximation of adjoining veins (Fig. 32) .... ***Helius*** Lepeletier & Serville
 2 spp.; widespread

69. R_2 situated beyond level of outer end of cell dm; basal section of CuA_1 joining M_3 beyond fork of M; a conspicuous pale fold in outer end of cell cua_2 (Fig. 33) .... ***Dicranoptycha*** Osten Sacken
23 spp.; widespread

R_2 about opposite crossvein r-m or slightly beyond; basal section of CuA_1 joining M_3 well basal to fork of M; no fold in cell cua_2 70

70. Cell dm absent (Figs. 34, 35) 71

Cell dm present (Figs. 36, 37) 73

71. R_{1+2} equal to or shorter than R_2; R_3 long, decurved, ending at wing tip (Fig. 34) .... ***Thaumastoptera*** Mik
1 sp., *hynesi* Alexander; western

R_{1+2} longer than R_2; R_3 straight, ending before wing tip .... ***Orimarga*** Osten Sacken 72

72. M with two free branches (M_1 and M_3) reaching margin; basal transverse section of CuA_1 uniting with M about opposite origin of Rs or distal to base of Rs, sometimes at or close to fork of M_{1+2} and distal section of CuA_1, but normally near mid length of wing .... ***Orimarga*** (***Orimarga*** Osten Sacken)
4 spp.; southwest to Florida

M with one free branch (M_1) reaching margin; basal transverse section of CuA_1 uniting with M far before fork of M_1 and distal section of CuA_1, at or near one-third to one-fourth the wing length (Fig. 35) .... ***Orimarga*** (***Diotrepha*** Osten Sacken)
1 sp., *mirabilis* (Osten Sacken); southeastern, tropical

73. Anal angle of wing prominent, nearly rectangular; Sc close to R; Sc_2 not evident; basal section of Rs diverging from R_1, in alignment with lengthened R_{4+5}; cell dm present (Fig. 37) .... ***Antocha*** Osten Sacken
7 spp.; mainly eastern

Anal angle of wing less prominent; Sc and R more separated; Sc_2 present; basal section of Rs long and straight, nearly parallel with R_1, in alignment with R_{2+3}; cell dm present (Fig. 36) or absent .... ***Elliptera*** Schiner, in part
see couplet 68

74. Wing membrane with abundant macrotrichia .... ***Ula*** Haliday
3 spp.; eastern

Wing membrane without macrotrichia 75

75. Rostrum produced into a short beak, one-half length of remainder of head or more .... ***Ornithodes*** Coquillett
2 spp.; western, northern

Rostrum inconspicuously developed, at most one-fourth length of remainder of head 76

76. Supernumerary crossvein present in cell bm. Size large; wing of male approximately 10 mm or more. Female subapterous in Nearctic species. Antenna short, with 11 or 12 flagellomeres .... ***Nasiternella*** Wahlgren, in part
1 sp., *hyperborea* (Osten Sacken); northern

Supernumerary crossvein absent. Other characters not as above 77

77. Antenna with either 12 or 14 flagellomeres. Size large; wing 7 mm or more in fully winged species. Wing of some species patterned with darker marking .... **Pedicia** Latreille 78

Antenna with either 11 or 13 flagellomeres. Size small; wing less than 7 mm, usually smaller. Wing commonly unpatterned except for a pterostigmal darkening .... ***Dicranota*** Zetterstedt 80

78. Size large; wing 20 mm or more. Wing with a darkened pattern that forms a triangle involving broad costal and cubital seams that are interconnected across oblique cord. Palpus with terminal segment elongate. M_1 and M_2 commonly separate, but fused in *bellamyana* Alexander .... ***Pedicia*** (***Pedicia*** Latreille)
11 spp.; widespread

Size smaller; wing less than 18 mm, commonly not exceeding about 15 mm. Wing, if patterned, without a triangular darkened area as described; cord of wing transverse or only slightly oblique. Palpus with terminal segment shorter. M_1 and M_2 usually fused 79

79. Inner division of gonostylus of male terminalia terminating in five unequal finger-like lobes .... ***Pedicia*** **(*Pentacyphona*** Alexander)
10 spp.; mostly western
Inner division of gonostylus of male terminalia simple, rarely bilobate .... ***Pedicia*** **(*Tricyphona*** Zetterstedt), in part
40 spp.; widespread

80. Supernumerary crossveins in one or more of cells r_1, r_3, r_4, and bm 81
Supernumerary crossveins lacking 84

81. Supernumerary crossveins in cells r_1, r_3, r_4, and bm .... ***Dicranota*** **(*Polyangaeus*** Doane), in part
3 spp.; western
Supernumerary crossvein in cell r_1 only 82

82. Cell dm present (Fig. 17) .... ***Dicranota*** **(*Eudicranota*** Alexander)
4 spp.; eastern
Cell dm absent 83

83. M_1 and M_2 fused .... ***Dicranota*** **(*Paradicranota*** Alexander)
3 spp.; eastern
M_1 and M_2 separate .... ***Dicranota*** **(*Dicranota*** Zetterstedt)
11 spp.; widespread

84. Cell dm present .... ***Dicranota*** **(*Rhaphidolabina*** Alexander)
1 sp., *flaveola* (Osten Sacken); eastern
Cell dm absent 85

85. M_1 and M_2 fused .... ***Dicranota*** **(*Plectromyia*** Osten Sacken), in part
9 spp.; widespread
M_1 and M_2 separate (Fig. 39) .... ***Dicranota*** **(*Rhaphidolabis*** Osten Sacken)
28 spp.; widespread

86. Antenna sometimes greatly elongated, with 4–10 flagellomeres .... ***Hexatoma*** Latreille 87
Antenna with more than 11 flagellomeres 88

87. Cell dm present; two or three branches of M (M_{1+2} and M_3; or M_1, M_2, and M_3) reaching margin (Fig. 41) .... ***Hexatoma*** **(*Eriocera*** Macquart)
33 spp.; widespread
Cell dm absent; one branch of M (M_{1+2}) reaching margin (Fig. 40) .... ***Hexatoma*** **(*Hexatoma*** Latreille)
2 spp.; eastern

88. Rostrum elongate, exceeding one-half length of remainder of body, with mouthparts at extreme tip. Two branches of Rs reaching margin (Fig. 42) .... ***Elephantomyia*** Osten Sacken
2 spp.; 1 sp. eastern, 1 sp. western
Rostrum short or only of moderate length, not exceeding length of remainder of head. Three branches of Rs present except in *Atarba* 89

89. Two branches of Rs reaching margin (Fig. 43) .... ***Atarba*** Osten Sacken
4 spp.; widespread
Three branches of Rs reaching margin 90

90. Macrotrichia present in some wing cells 91
No macrotrichia in wing cells except in pterostigmal region when latter present 93

91. Macrotrichia in all cells except near wing base. Cell r_3 sessile or very short–petiolate .... ***Ulomorpha*** Osten Sacken
8 spp.; widespread
Macrotrichia sparse, present only in apical cells of wing; cell r_3 petiolate 92

92. M_2 separate or fused with M_1; R_2 usually present but faintly indicated. Antenna short in both sexes. Prescutal tuberculate pits present, removed from anterior border .... ***Paradelphomyia*** Alexander
11 spp.; widespread
M_2 fused with M_1 in Nearctic species; R_2 present. Antenna of male long, subequal to body. Prescutal tuberculate pits lacking .... ***Shannonomyia*** Alexander, in part
3 spp.; widespread

93. Cell c with a supernumerary crossvein; wing patterned with brown transverse bands or with ring-like markings .... ***Epiphragma*** Osten Sacken
4 spp.; widespread

Cell c without a supernumerary crossvein; wing, when patterned, without ring-like markings ..94

94. R_2 lacking; CuA_1 having point contact with M_3 (Fig. 44) .... ***Phyllolabis*** Osten Sacken
12 spp.; chiefly western

R_2 present; CuA_1 fused with M_3 for nearly half its length 95

95. Cell dm absent (Fig. 45). Antenna of male very long; flagellomeres strongly nodulose, appearing bead-like .... ***Polymera*** Wiedemann
2 spp.; southeastern U.S.A.

Cell dm present. Male antenna short, but if longer, flagellomeres not nodulose 96

96. Wing with MA (anterior branch of medius, arculus) lacking (Figs. 47, 48) 97

Wing with MA present (Figs. 46, 49) 101

97. CuA_1 joining M at or close to fork of M .... ***Dactylolabis*** Osten Sacken....98

CuA_1 joining M from one-third to one-half the length of cell dm beyond fork of M 99

98. Apex of gonocoxite produced about one-half length of gonostylus; gonostylus subterminal. Cercus of ovipositor lying transversely, broadly flattened, bearing a strong tooth on lateral or ventral margin; hypogynial valve long, fleshy, with abundant setae .... ***Dactylolabis*** (***Eudactylolabis*** Alexander), in part
2 spp.; western

Gonocoxite not produced; gonostylus terminal. Cercus of ovipositor normally hexatomine, rather slender, without a lateral tooth .... ***Dactylolabis*** (***Dactylolabis*** Osten Sacken)
17 spp.; widespread

99. Cell dm very large, with its proximal end situated far proximal to other elements of cord (Fig. 47) .... ***Prolimnophila*** Alexander
1 sp., *areolata* (Osten Sacken); eastern

Cell dm of normal size, with its proximal end located in approximate alignment with other elements of cord (Fig. 48) .... ***Austrolimnophila*** Alexander....100

100. R_{2+3+4} slightly arcuate, short, at most one-half length of anterior branch of Rs (R_{2+3} + R_3) (Fig. 48). Male with one pair of small weak parameres .... ***Austrolimnophila*** (***Austrolimnophila*** Alexander)
3 spp.; widespread

R_{2+3+4} longer, subequal in length to anterior branch of Rs. Male with two pairs of parameres; outer ones in form of heavy black spines .... ***Austrolimnophila*** (***Archilimnophila*** Alexander)
3 spp.; northern

101. Head strongly narrowed and prolonged posteriorly. Pronotum with sides of anterior margin produced forward. Wing with long and sinuous radial and medial veins beyond cord; R_3 and R_4 usually parallel to one another; M_2 usually separate (Fig. 18), sometimes fused with M_1 (Fig. 46) .... ***Pseudolimnophila*** Alexander
5 spp.; widespread

Head broad, not conspicuously narrowed behind. Distal wing veins beyond cord more nearly straight; cell r_3 widened at margin; M_2 separate or fused with M_1 102

102. Antenna with proximal flagellomeres bearing very long conspicuous verticils that much exceed length of flagellomeres. Wing commonly with pterostigmal macrotrichia .... ***Pilaria*** Sintenis
11 spp.; widespread

Antenna with shorter verticils, not or scarcely exceeding length of flagellomeres. Wing without pterostigmal macrotrichia 103

103. M_2 fused with M_1 in all Nearctic species; R_2 at or close to fork of R_{2+3+4} .... ***Shannonomyia*** Alexander, in part
see couplet 92

M_2 usually separate; R_2 beyond fork of R_{2+3+4} (Fig. 49) .... ***Limnophila*** Macquart....104

104. Supernumerary crossveins in cells r_3, r_5, or bm 105

Supernumerary crossveins absent 108

105. Supernumerary crossvein in cell r_3 .... ***Limnophila*** **(*Dicranophragma*** Osten Sacken)
2 spp.; eastern

No supernumerary crossvein in cell r_3 106

106. Supernumerary crossvein in cell r_5. Size large; wing length over 15 mm .... ***Limnophila*** **(*Eutonia*** Wulp), in part
3 spp.; eastern

Supernumerary crossvein in cell bm. Size smaller; wing length commonly less than 10 mm 107

107. Antenna of male elongate. Rs square and sometimes spurred at origin; wing with a more or less complete crossband .... ***Limnophila*** **(*Idioptera*** Macquart)
2 spp.; northern

Antenna short in both sexes. Rs not or only slightly spurred at origin; wing spotted, very rarely unmarked .... ***Limnophila*** **(*Eloeophila*** Rondani)
19 spp.; widespread

108. Distal wing cells with macrotrichia. Antenna of male very long, with abundant erect elongate setae over entire surface .... ***Limnophila*** **(*Lasiomastix*** Osten Sacken)
3 spp.; eastern

Wing without macrotrichia. Antenna of male not as above 109

109. Size very large; wing length about 18 mm or more .... ***Limnophila*** **(*Eutonia*** Wulp), in part
see couplet 106

Size smaller; wing length not exceeding 15 mm, commonly less 110

110. M_2 fused with M_1 111

M_2 separate (Fig. 49) 113

111. Sc_1 ending some distance before fork of Rs; cell r_3 with a short petiole. Tergite 9 of male terminalia narrow, and with apex deeply emarginate forming two slender lobes. Size small. Coloration yellow with white tarsi .... ***Limnophila*** **(*Dendrolimnophila*** Alexander)
1 sp., *albomanicata* (Alexander); western

Sc longer; Sc_1 opposite fork of Rs; cell r_3 sessile, or virtually so. Tergite 9 of male terminalia not as above. Size larger. Coloration dark with dark tarsi 112

112. Outer division of gonostylus of male terminalia deeply bifid with apices forming two long spines .... ***Limnophila*** **(*Idiolimnophila*** Alexander)
1 sp., *emmelina* Alexander; eastern

Outer division of gonostylus of male terminalia compact, trispinous with outer point longest; aedeagus compressed, reniform .... ***Limnophila*** **(*Prionolabis*** Osten Sacken), in part
21 spp.; widespread

113. Cell m_1 small and short, at most one-third as long as its petiole, rarely lacking. Wing unpatterned. Antenna of male with verticils of proximal flagellomeres long; lower faces of flagellomeres glabrous. Outer division of gonostylus of male terminalia in form of a slender rod, with apex unequally bidentate; aedeagus very small, shorter than subtending horn-like apophyses .... ***Limnophila*** **(*Brachylimnophila*** Alexander)
2 spp.; 1 sp. eastern, 1 sp. western

Cell m_1 long, commonly subequal in length to its petiole or longer (Fig. 49). Other combination of characters not as above 114

114. Base of aedeagus flattened, appearing pod-like or reniform .... ***Limnophila*** **(*Prionolabis*** Osten Sacken), in part
see couplet 112

Aedeagus not as above 115

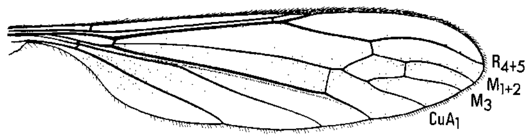
115. Antenna of male elongate, as long as head and thorax; proximal flagellomeres dilated ventrally with both dorsal and ventral verticils; ventral verticils shorter than dorsal ones. Apex of outer division of gonostylus of male terminalia bidentate; aedeagus and parameres elongate; parameres with several spines at apex .... ***Limnophila*** **(*Arctolimnophila*** Alexander)
2 spp.; 1 sp. eastern, 1 sp. western

Antenna and terminalia of male not as above 116

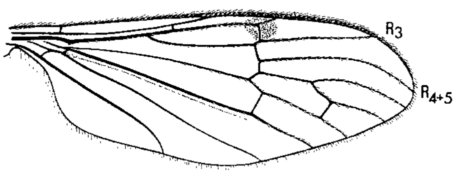
116. Male antenna with normal rather short verticils on both lower and dorsal faces. Aedeagus trifid, sometimes with very long branches .... ***Limnophila* (*Phylidorea* Bigot)**
40 spp.; widespread

Male antenna without ventral verticils, with proximal flagellomeres more or less dilated beneath. Aedeagus simple or trifid, with branches short 117

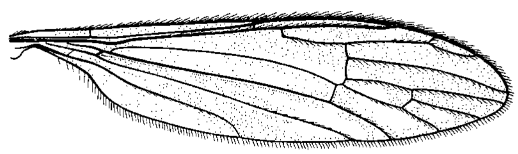
117. Paramere of male terminalia bidentate or tridentate, with tip acute; aedeagus straight, sometimes very short, with apex shallowly notched; outer division of gonostylus in form of a simple glabrous rod with obtuse tip .... ***Limnophila* (*Hesperolimnophila* Alexander)**
3 spp.; western



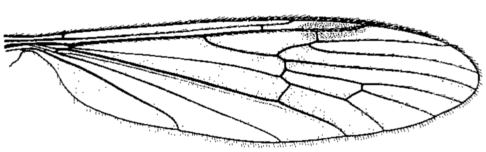
50 Toxorhina magna ♂



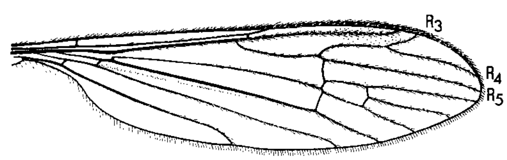
51 Teucholabis complexa ♂



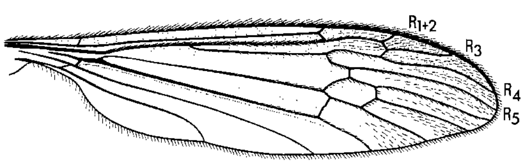
52 Gonomyia (Lipophleps) sulphurella ♀



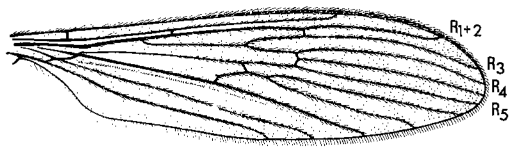
53 Gnophomyia tristissima ♀



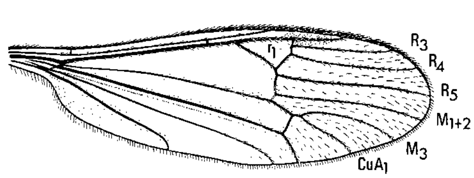
54 Gonomyia (Gonomyia) subcinerea ♀



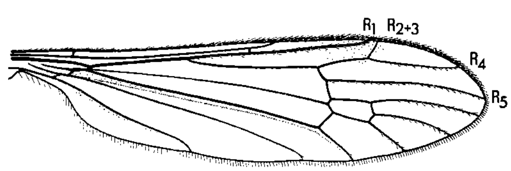
55 Lipsothrix nigrilinea ♀



56 Molophilus (Promolophilus) nitidus ♂



57 Cryptolabis paradoxa ♀



58 Rhabdomastix (Sacandaga) californiensis ♂

Figs. 7.50–58. Wings (*continued*): (50) *Toxorhina magna* Osten Sacken; (51) *Teucholabis complexa* Osten Sacken; (52) *Gonomyia* (*Lipophleps*) *sulphurella* Osten Sacken; (53) *Gnophomyia tristissima* Osten Sacken; (54) *Gonomyia* (*Gonomyia*) *subcinerea* Osten Sacken; (55) *Lipsothrix nigrilinea* (Doane); (56) *Molophilus* (*Promolophilus*) *nitidus* Coquillett; (57) *Cryptolabis paradoxa* Osten Sacken; (58) *Rhabdomastix* (*Sacandaga*) *californiensis* Alexander (*continued*).

Paramere of male terminalia resembling a simple smooth paddle; aedeagus long and slender, gently curved; outer division of gonostylus in form of a simple spine with a small acute point on lower margin before mid length .... ***Limnophila*** (***Afrolimnophila*** Alexander)
2 spp.; 1 sp. eastern, 1 sp. western

118. M_2 separate 119
M_2 fused with M_1 (Figs. 50–58) 121

119. Cell r_3 short, shorter than its petiole; R_2 at or proximal to fork of R_3 and R_4 .... ***Neolimnophila*** Alexander
4 spp.; widespread
Cell r_3 long, about three or four times longer than its petiole; R_2 distal to fork of R_{2+3+4} 120

120. Male terminalia with an undivided gonostylus .... ***Cladura*** Osten Sacken
5 spp.; widespread
Male terminalia with a divided gonostylus. .... ***Neocladura*** Alexander
2 spp.; 1 sp. eastern, 1 sp. western

121. Rostrum very long and slender, at least subequal to combined length of head and thorax, with reduced mouthparts situated at apex. Setae of legs deeply bifid .... ***Toxorhina*** Loew
2 spp.; eastern
Rostrum short, not or scarcely exceeding remainder of head. Setae of legs simple 122

122. Coxae of midleg and hindleg only slightly separated by meral region; meron small, not exceeding coxa in diameter 123
Coxae of midleg and hindleg widely separated by a large meron producing a pot-bellied appearance; meron subequal to or larger than coxa 136

123. Two branches of Rs (R_3 and R_{4+5}) reaching margin (Fig. 51) 124
Three branches of Rs (R_3, R_4, and R_5) reaching margin (Figs. 52, 55, 57) 127

124. Sc_1 ending beyond origin of Rs; basal section of CuA_1 joining cell dm beyond fork of M (Fig. 51) .... ***Teucholabis*** Osten Sacken
7 spp.; predominantly southern
Sc_1 ending before origin of Rs; basal section of CuA_1 joining cell dm at or before fork of M (as in Fig. 52) .... ***Gonomyia*** Meigen, in part.... 125

125. Cell dm absent .... ***Gonomyia*** (***Neolipophleps*** Alexander)
3 spp.; widespread
Cell dm present 126

126. Wing with a conspicuous dark brown pterostigmal spot.... ***Gonomyia*** (***Paralipophleps*** Alexander)
1 sp., *pleuralis* (Williston); southern
Wing with pterostigmal spot lacking or virtually so ...... ***Gonomyia*** (***Lipophleps*** Bergroth), in part
5 spp.; eastern

127. Cell r_3 longer than its petiole (R_{2+3+4}) (Fig. 55) 128
Cell r_3 shorter than its petiole (Fig. 54) .... ***Gonomyia*** Meigen, in part 132

128. R_{1+2} and R_2 short, subequal (Fig. 55) 129
R_{1+2} longer than R_2 (Fig. 53) 130

129. Sc_1 ending before fork of Rs; R_3 oblique, divergent; distal margin of cell r_3 longer than distal margin of cell r_2; cell dm absent. Size small; wing less than 6 mm .... ***Gonomyia*** (***Progonomyia*** Alexander)
4 spp.; southern
Sc_1 ending opposite or beyond fork of Rs; R_3 longitudinal, nearly parallel with R_4; distal margins of cells r_2 and r_3 subequal; cell dm present (Fig. 55). Size large; wing over 8 mm .... ***Lipsothrix*** Loew
6 spp.; western with 1 sp. in east

130. Sc_2 situated near origin of Rs; Sc_1 nearly as long as Rs. Legs with linear scales. Gonostylus of male terminalia terminal; outer division of gonostylus elongate, with a brush of long setae at apex; gonocoxite with a dense brush of setae on median face .... ***Idiognophomyia*** Alexander
2 spp.; western; Byers 1975

Sc_2 situated more distally (Fig. 53); Sc_1 much shorter than Rs. Legs with setae. Male terminalia not as above 131

131. Distal wing cells with macrotrichia; Sc_1 and Sc_2 subequal; cord of wing at near two-thirds length of wing; branches of R rather short and straight. Apex of gonocoxite of male terminalia strongly produced; gonostylus subterminal .... ***Eugnophomyia*** Alexander
2 spp.; southeast to Arizona

Distal wing cells without macrotrichia; Sc_1 longer than Sc_2; cord of wing more basal, shortly beyond mid length; branches of R longer and slightly more curved (Fig. 53). Gonocoxite of male terminalia small, not produced; gonostylus terminal .... ***Gnophomyia*** Osten Sacken
3 spp.; widespread

132. Supernumerary crossvein in cell r_4 .... ***Gonomyia*** (***Euptilostena*** Alexander)
2 spp.; western

Supernumerary crossvein absent in cell r_4 133

133. Sc_1 ending some distance beyond origin of Rs; cell dm absent; basal section of CuA_1 joining M about its own length before fork of M .... ***Gonomyia*** (***Idiocera*** Dale)
17 spp.; widespread

Sc_1 ending opposite or before origin of Rs; cell dm present or absent; basal section of CuA_1 joining M less than its length before fork of M (Fig. 52) 134

134. Cell r_3 very small; R_4 about two-thirds length of R_{2+3+4} .... ***Gonomyia*** (***Lipophleps*** Bergroth), in part
see couplet 126

Cell r_3 larger; R_4 longer than R_{2+3+4} (Fig. 54) 135

135. Antenna with proximal two or three flagellomeres fused. Gonostylus of male terminalia with three simple divisions; gonocoxite not produced at apex; aedeagus very large and complex in structure .... ***Gonomyia*** (***Teuchogonomyia*** Alexander)
4 spp.; western

Antenna with flagellomeres distinct. Gonostylus of male terminalia with two divisions; gonocoxite at apex produced into a small fleshy lobe; aedeagus not greatly modified .... ***Gonomyia*** (***Gonomyia*** Meigen)
25 spp.; widespread

136. Cell r_3 sessile; Rs forking into R_{2+3} and R_{4+5} (Fig. 56) 137

Cell r_3 petiolate; Rs forking into R_{2+3+4} and R_5 (Figs. 57, 58) 139

137. Cell a_2 short and narrow; CuA_1 fusing with M basal to fork of M_3. Gonostylus of male terminalia undivided. Size very small; wing about 2.5 mm or less .... ***Tasiocera*** Skuse (***Dasymolophilus*** Goetghebuer)
5 spp.; widespread

Cell a_2 long and broad; CuA_1 fused with M_3 for short distance distal to fork of M (Fig. 56). Gonostylus of male terminalia with two divisions. Size larger .... ***Molophilus*** Curtis.... 138

138. Male terminalia with a black tergal plate; parameres fused to form an entire black plate or divided into two blades .... ***Molophilus*** (***Promolophilus*** Alexander)
5 spp.; western

Male terminalia without a black tergal plate; parameres forming a simple flattened pale plate .... ***Molophilus*** (***Molophilus*** Curtis)
40 spp.; widespread

139. Gonostylus of male terminalia undivided. Cell dm absent 140

Combination of characters not as above 141

140. Basal section of Rs short; R_{2+3+4} at a right angle to Rs; cell r_1 small and triangular in outline (Fig. 57). Aedeagus of male terminalia stout to massive, darkened, terminating in a single filament. Female with cercus and hypogynial valves of ovipositor short and fleshy .... ***Cryptolabis*** Osten Sacken
11 spp.; mainly western

Basal section of Rs long, arcuate, in longitudinal alignment with R_{2+3+4}; cell r_1 elongate. Gonocoxite of male terminalia bearing a needle-like interbase (as in Fig. 6); aedeagus narrow, divided into three long slender branches. Female terminalia not as above .... ***Phantolabis*** Alexander
1 sp., *lacustris* (Alexander); eastern

141. Cell r_3 shorter than its petiole (R_{2+3+4}) (Fig. 58) 142
Cell r_3 at least as long as its petiole (Figs. 59, 60) 149

142. R_2 lacking. R_3 short, suberect, close to R_1 at margin, longer and more oblique in *neolurida* Alexander; R_3 commonly about one-third length of R_4 or less (Fig. 58). Gonostylus of male terminalia terminal; outer division of gonostylus simple, densely spinose outwardly; interbase long and slender (Fig. 6) .... ***Rhabdomastix*** Skuse.... 143
R_2 present. Other combination of characters not as above 144

143. Antenna of male greatly lengthened, more than three times length of wing .... ***Rhabdomastix*** (***Rhabdomastix*** Skuse)
1 sp., *nuttingi* Alexander; southwestern
Antenna short in both sexes, not exceeding one-half length of wing .... ***Rhabdomastix*** (***Sacandaga*** Alexander), in part
24 spp.; widespread

144. Cell r_3 small; R_4 short, gently curved; Sc_2 absent .... ***Rhabdomastix*** (***Sacandaga*** Alexander), in part
1 sp., *monticola* Alexander; western
Cell r_3 larger; R_4 long, straight; Sc_2 present 145

145. Gonostylus of male terminalia with three divisions .... ***Gonomyodes*** Alexander
4 spp.; western
Gonostylus of male terminalia with either one or two divisions 146

146. Gonostylus of male terminalia undivided .... ***Gonomyopsis*** Alexander
1 sp., *doaneiana* Alexander; western
Gonostylus of male terminalia with two divisions 147

147. Gonostylus of male terminalia subterminal; gonocoxite produced beyond its insertion into a long narrow blade. R_3 oblique, straight .... ***Gonempeda*** Alexander
3 spp.; widespread
Gonostylus of male terminalia terminal; outer division bifurcate except in *exilistyla* (Alexander) where it is simple. R_3 more longitudinal in position .... ***Cheilotrichia*** Rossi.... 148

148. Cell dm present .... ***Cheilotrichia*** (***Cheilotrichia*** Rossi)
1 sp., *alicia* (Alexander); western
Cell dm absent .... ***Cheilotrichia*** (***Empeda*** Osten Sacken)
11 spp.; predominantly western, 1 sp. eastern

149. Wing with abundant macrotrichia in all cells .... ***Ormosia*** Rondani.... 150
Wing usually without such macrotrichia, but when present, restricted to just a few in distal cells or in region of pterostigma 154

150. Cell dm present 151
Cell dm absent 153

151. A_1 and A_2 slightly convergent. Outer division of gonostylus of male terminalia outwardly dilated or slightly bifid; apex of aedeagus divided into two long filaments .... ***Ormosia*** (***Rhypholophus*** Kolenati)
10 spp.; western
A_1 and A_2 divergent. Outer division of gonostylus not dilated outwardly; apex of aedeagus simple 152

152. Outer division of gonostylus of male terminalia oval, with strong spinules on surface; aedeagus very large. Cell dm small; posterior border of cell dm equal to or shorter than following distal section of CuA_1 .... ***Ormosia*** (***Scleroprocta*** Edwards)
3 spp.; 2 spp. eastern, 1 sp. western
Outer division of gonostylus of male terminalia bifid, with strong spines; aedeagus small, slender, with narrow subtending basal plates. Venation not as above .... ***Ormosia*** (***Parormosia*** Alexander)
7 spp.; widespread

153. Medial field comprising M_1 and M_3; M_3 branching from a basal fusion with CuA_1 (as in Fig. 61). Outer division of gonostylus of male terminalia forming a simple curved horn that

narrows to an acute spine; inner division of gonostylus forming a simple yellow blade; paramere simple, rounded, plate-like .... ***Ormosia*** (***Oreophila*** Lackschewitz)
6 spp.; western

Medial field comprising M_1 and M_2; M_3 absent (Fig. 59). Gonostylus of male terminalia variously constructed but not as above; paramere spine-like........ ***Ormosia*** (***Ormosia*** Rondani)
75 spp.; widespread

154. Wing with pterostigmal region dilated and with abundant macrotrichia (Fig. 60). Gonostylus of male terminalia terminal; outer division of gonostylus with an acute spine beyond mid length; aedeagus bilobate .... ***Empedomorpha*** Alexander
1 sp., *empedoides* (Alexander); western

Wing with pterostigmal region normal, without macrotrichia. Male terminalia not as above..155

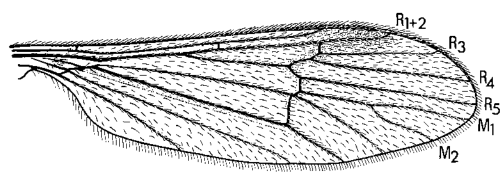
155. Sc_2 usually absent but sometimes preserved; apical section of Sc_1 short, subequal to basal section of CuA_1; distal cells sometimes with sparse macrotrichia (Fig. 61). Outer division of gonostylus of male terminalia gently curved, with a finger-like lobe near mid length................ .... ***Hesperoconopa*** Alexander
5 spp.; western

Sc_2 always present; apical section of Sc_1 long, approximately three times length of basal section of CuA_1; wing cells without macrotrichia (Fig. 62). Male terminalia not as above 156

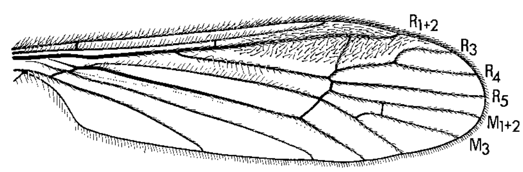
156. Inner division of gonostylus of male terminalia angulate near mid length, with apex slender and bearing small spines; aedeagus forming a slender rod........................... ***Arctoconopa*** Alexander
9 spp.; western

Male terminalia not as above .... ***Erioptera*** Meigen....157

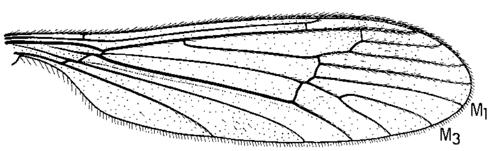
157. Antenna with terminal three flagellomeres smaller than others. Cell dm present. Apical branches of aedeagus of male terminalia short; paramere in form of a simple slender spine; divisions of gonostylus subequal in length, narrow; outer division of gonostylus terminating in a black spine; inner division of gonostylus with tip obtuse .... ***Erioptera*** (***Trimicra*** Osten Sacken)
1 sp., *pilipes* (Fabricius); eastern to Texas



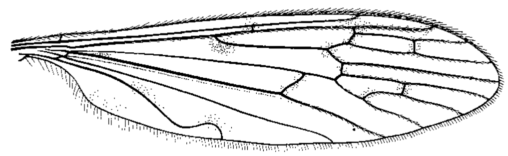
59 Ormosia (Ormosia) manicata ♂



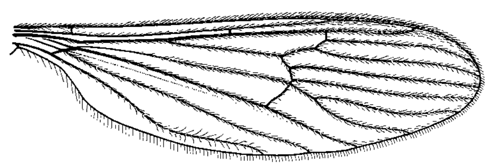
60 Empedomorpha empedoides ♂



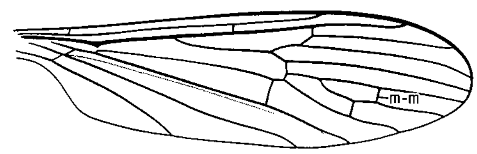
61 Hesperoconopa melanderi ♂



62 Erioptera (Symplecta) cana ♀



63 Erioptera (Erioptera) septemtrionis ♀



64 Erioptera (Hoplolabis) armata ♀

Figs. 7.59–64. Wings (*concluded*): (59) *Ormosia* (*Ormosia*) *manicata* (Doane); (60) *Empedomorpha empedoides* (Alexander); (61) *Hesperoconopa melanderi* (Alexander); (62) *Erioptera* (*Symplecta*) *cana* (Walker); (63) *Erioptera* (*Erioptera*) *septemtrionis* Osten Sacken; (64) *Erioptera* (*Hoplolabis*) *armata* Osten Sacken.

Antenna with outer flagellomeres gradually and progressively smaller. Other combination of characters not as above 158

158. Supernumerary crossvein in cell r_3 usually present (Fig. 62), but lacking in *stictica* Meigen; A_1 and A_2 strongly convergent; A_2 sinuous distally. Gonostylus of male terminalia terminal to slightly subterminal; outer division of gonostylus expanded outwardly, sometimes variously spined; apex of aedeagus deeply forked .... ***Erioptera*** (***Symplecta*** Meigen)
4 spp.; widespread

Supernumerary crossvein lacking in cell r_3. Gonostylus and aedeagus of male terminalia not as above 159

159. Cell dm present (Fig. 64) 160
Cell dm absent (Fig. 63) 162

160. Cell dm divided by a spur running proximally into the cell from basal section of M_3 to M_{1+2} (Fig. 64) .... ***Erioptera*** (***Hoplolabis*** Osten Sacken)
4 spp.; widespread

Cell dm undivided 161

161. Cell dm small, much shorter than veins issuing from it. Male terminalia not as below .... ***Erioptera*** (***Psiloconopa*** Zetterstedt)
30 spp.; widespread

Cell dm large, longer than the veins emanating from it. Male terminalia inverted 180°; outer division of gonostylus unusually large .... ***Erioptera*** (***Ilisia*** Osten Sacken)
5 spp.; eastern

162. Cell dm lost by atrophy of basal section of M_3 (present in *melanderiana* Alexander); A_1 and A_2 divergent; A_2 nearly straight. Gonostylus of male terminalia terminal; outer division of gonostylus deeply divided into two spines; inner division of gonostylus forming a long simple spine .... ***Erioptera*** (***Mesocyphona*** Osten Sacken)
15 spp.; widespread

Cell dm lost by atrophy of crossvein m-m; A_1 and A_2 convergent; A_2 sinuous distally (Fig. 63). Gonostylus of male terminalia not as above .... ***Erioptera*** (***Erioptera*** Meigen)
29 spp.; widespread

163. Body length commonly more than 8–10 mm. Wing usually reduced in female only to about 10 mm, but virtually absent in both sexes of *quaylii* Doane. Head with distinct tubercle on frons, commonly with a nasus; terminal palpal segment long .... TIPULINAE.... ***Tipula*** (***Pterelachisus*** Rondani), in part
see couplets 35, 36, and 41 ***Tipula*** (***Serratipula*** Alexander), in part
Tipula (***Triplicitipula*** Alexander), in part

Body length commonly less than 5 mm, but sometimes larger. Head without tubercle on frons, and without a nasus; terminal palpal segment short .... LIMONIINAE.... 164

164. Eye with hairs between ommatidia .... PEDICIINI.... 165
Eye without hairs .... LIMONIINI, HEXATOMINI, ERIOPTERINI.... 166

165. Body length up to about 10 mm, commonly smaller; wing length up to about 6 mm, but usually smaller .... ***Nasiternella*** Wahlgren, in part
female only, see couplet 76
.... ***Pedicia*** (***Tricyphona*** Zetterstedt), in part
4 spp.; western, northern

Body length up to about 5 mm .... ***Dicranota*** (***Polyangaeus*** Doane), in part
1 sp., *subapterogyne* Alexander, female only; western
.... ***Dicranota*** (***Plectromyia*** Osten Sacken), in part
1 sp., ***reducta tehamicola*** Alexander, both sexes; western

166. Antenna with 12 flagellomeres .... LIMONIINI.... ***Limonia*** (***Alexandriaria*** Garrett), in part
1 sp., ***phalangioides*** Alexander, both sexes, wing to about 1 mm; western
.... ***Limonia*** (***Dicranomyia*** Stephens), in part
2 spp.; northwestern, Asiatic

Antenna with 14 flagellomeres, except in *Chionea* with 2–9 flagellomeres 167

167. Legs with tibial spurs. Wing present as a short stub to virtually lacking .... HEXATOMINI....*Dactylolabis* (*Eudactylolabis* Alexander), in part
1 sp., *vestigipennis* Alexander, both sexes; southwestern

.... *Limnophila* (*Prionolabis* Osten Sacken), in part
1 sp., *rudimentis* Alexander, female only; eastern

Legs without tibial spurs. Wing present only as a microscopic vestige in both sexes. Small brown hairy insects, superficially resembling spiders, usually found on snow in winter .... ERIOPTERINI....*Chionea* Dalman
8 spp.; northern

Larva

1. Thoracic and abdominal segments with dorsal and lateral longitudinal rows of conspicuous usually elongate fleshy projections (Fig. 65) .... CYLINDROTOMINAE....2

   Thoracic and abdominal segments without dorsal longitudinal rows of conspicuous projections; lateral projections, if present, occurring on abdomen only, and blunt, shorter than their basal diameter 5

2. Dorsal projections mostly long, slender, simple on thoracic segments; posterior projections on most abdominal segments either deeply bifurcate or, if simple, approximately 10 times as long as basal diameter. Larva found in aquatic or semiaquatic mosses .... ***Phalacrocera***

   Dorsal projections shorter, with length one to three times basal diameter; those of posterior annulus of most abdominal segments longest on that segment, not deeply divided 3

3. Dorsal projections simple, without serrations on anterior surface. Posterior spiracles much farther apart than diameter of a spiracle. Larva feeding on leaves of certain flowering plants .... ***Cylindrotoma***

   Dorsal projections serrate on anterior convex surface. Posterior spiracles set close together, separated by about width of a spiracle 4

4. Posterior pair of dorsal projections on abdominal segments 1–7 with three or four serrations. Body color brownish. Larva found in semiaquatic mosses .... ***Triogma***

   Posterior pair of dorsal projections on abdominal segments 1–7 with two or only one serration (Fig. 65). Body color greenish with dark brown maculation. Larva found in terrestrial mosses .... ***Liogma***

5. Spiracular disc bordered by six (rarely eight) usually subconical lobes usually arranged with two dorsally, two dorsolaterally, and two below spiracles; these lobes sometimes short and blunt or sclerotized and hook-like (Figs. 66, 68, 70–73) .... TIPULINAE....6

   Spiracular disc bordered by five (rarely seven) or fewer lobes; lobes variable in shape, often arranged with one dorsomedially, two laterally, and two below spiracles or spiracles absent (Figs. 74, 75, 78–81) .... LIMONIINAE....15

6. Anal papillae pinnately branched. Dorsal lobes of spiracular disc short, bluntly rounded; lower lobes more than twice as long as their basal diameter. Larva aquatic or semiaquatic .... ***Leptotarsus* (*Longurio*)**

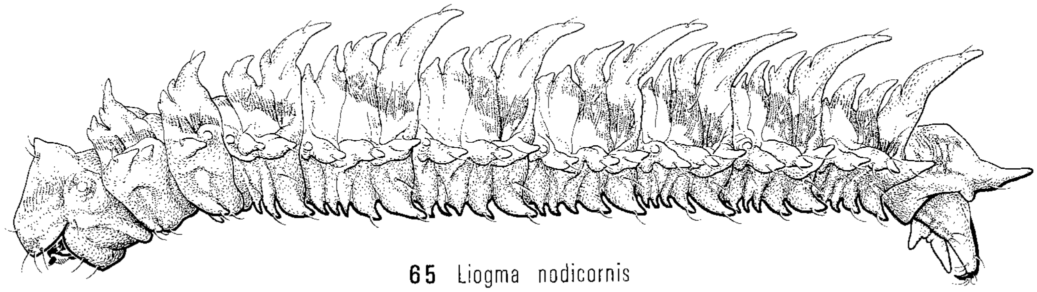
   Anal papillae not pinnately branched. Lobes of spiracular disc variable 7

7. Dorsal lobes of spiracular disc closely appressed to one another (subgenus *Dolichopeza*) or abdominal segment 8 bearing a subconical lobe at each side below and before dorsolateral lobe of spiracular disc (subgenus *Oropeza*, Fig. 68). Larva found in terrestrial mosses and liverworts .... ***Dolichopeza***

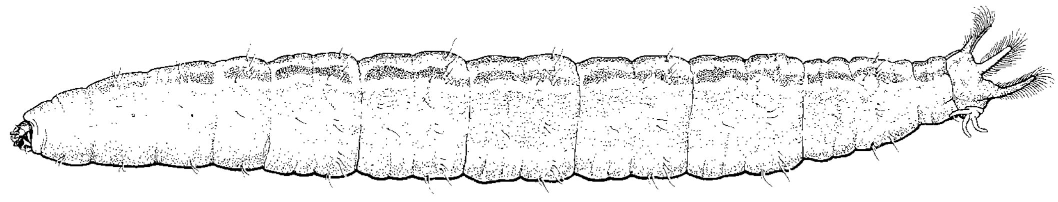
   Dorsal lobes of spiracular disc not appressed; abdominal segment 8 without lateral subconical lobes 8

8. All lobes of spiracular disc elongate; lateral and ventral lobes three or four times as long as their basal width, with numerous long hairs bordering each lobe; outer hairs two or three times as long as width of lobe at point of attachment (Fig. 66) 9

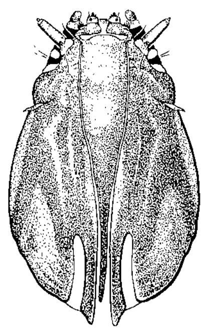
   Some lobes of spiracular disc not elongate; longest ones rarely more than twice their basal width, except when in form of densely sclerotized hooks; bordering hairs usually sparse, but if numerous not long 10

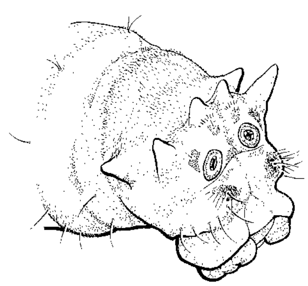


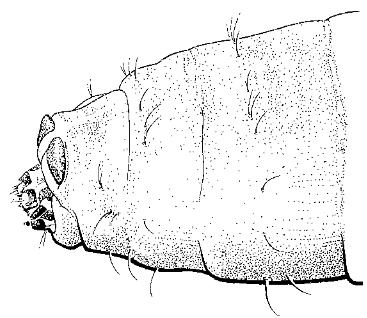
65 Liogma nodicornis



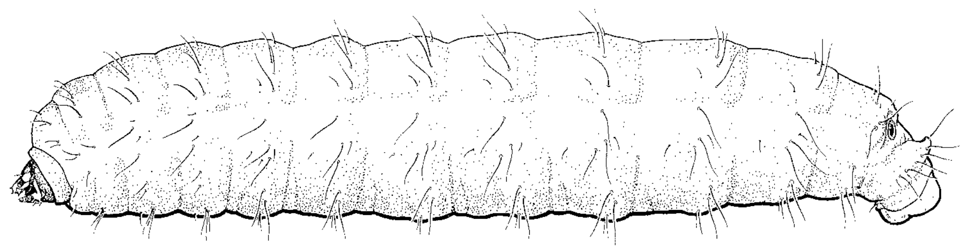
66 Prionocera sp.



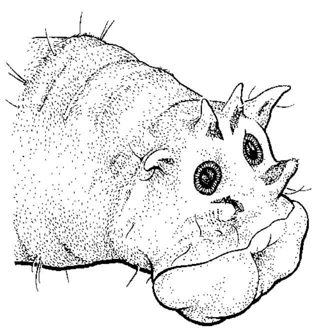


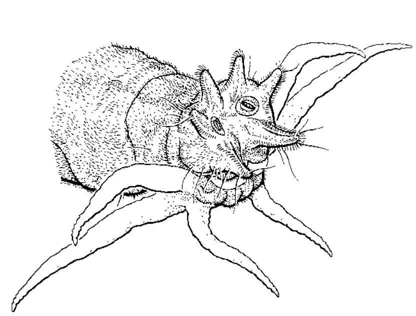


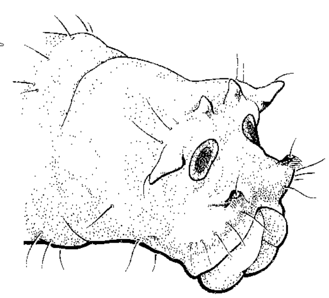
67 Prionocera dimidiata 68 Dolichopeza (Oropeza) sp. 69 Nephrotoma sp.



70 Ctenophora dorsalis





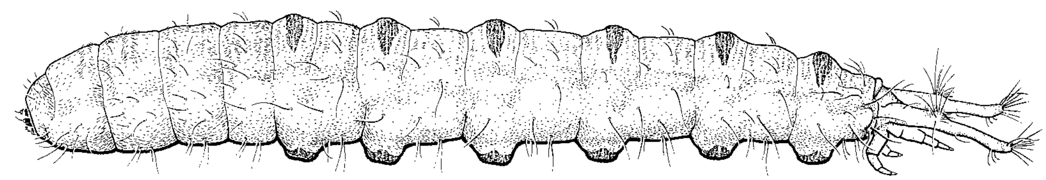


71 Tipula trivittata 72 Tipula (Yamatotipula) strepens 73 Ctenophora angustipennis

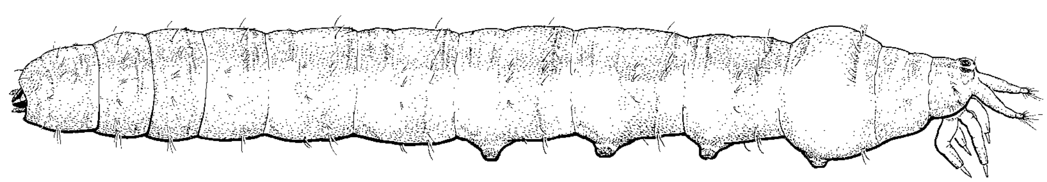
Figs. 7.65–73. Larvae: (65) *Liogma nodicornis* (Osten Sacken), lateral view; (66) *Prionocera* sp., lateral view; (67) *Prionocera dimidiata* (Loew), dorsal view of head capsule; (68) *Dolichopeza* (*Oropeza*) sp., oblique posterior view of terminal segments; (69) *Nephrotoma* sp., dorsolateral view of head capsule and thoracic segments; (70) *Ctenophora dorsalis* Walker, lateral view; (71) *Tipula trivittata* Say, oblique posterior view of terminal segments; (72) *Tipula* (*Yamatotipula*) *strepens* Loew, oblique posterior view of terminal segments; (73) *Ctenophora angustipennis* Loew, oblique posterior view of terminal segments (*continued*).

9. Two pairs of elongate retractile anal papillae present. Lobes of spiracular disc darkened along margins, pale medially. Larva found in open-ended tube of floating vegetation.... ***Megistocera***

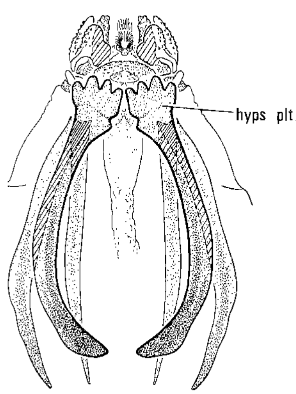
Three pairs of elongate anal papillae (Fig. 66) present. Lobes of spiracular disc darkened along margins but each with a thin submedian dark line. Larva not found in tubes of vegetation [included here are larvae of species of *Tipula* (*Angarotipula*), formerly assigned on basis of adult structures to *Prionocera*] .... ***Prionocera***



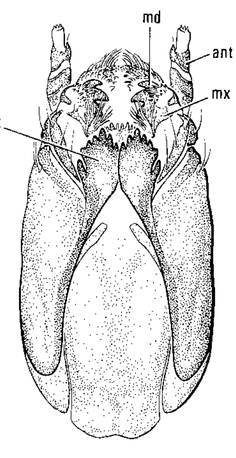
74 Antocha sp.

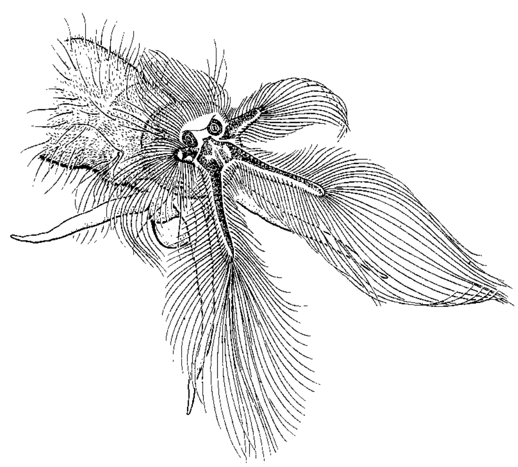


75 Pedicia sp.

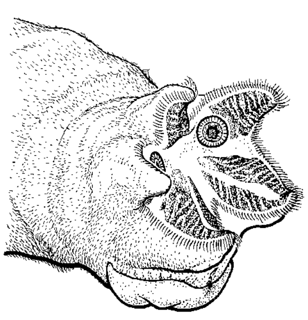


76 Molophilus sp.

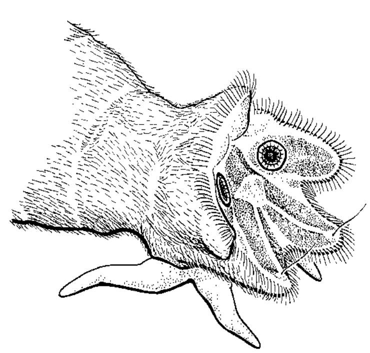




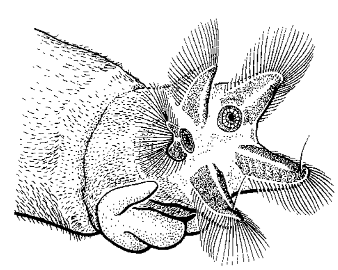
77 Pseudolimnophila inornata **78**



79 Gnophomyia toschiae



80 Gonomyia sp.



81 Ormosia sp.

Figs. 7.74–81. Larvae (*continued*): (74) *Antocha* sp., dorsolateral view; (75) *Pedicia* sp., dorsolateral view; (76) *Molophilus* sp., ventral view of head capsule; (77) ventral view of head capsule and (78) oblique posterior view of terminal segments of *Pseudolimnophila inornata* (Osten Sacken); (79) *Gnophomyia toschiae* Alexander, oblique posterior view of terminal segments; (80) *Gonomyia* sp., oblique posterior view of terminal segments; (81) *Ormosia* sp., oblique posterior view of terminal segments (*continued*).
Abbreviations: ant, antenna; hyps plt, hypostomal plate; md, mandible; mx, maxilla.

10. Pilosity on abdominal segments and posterior ring of metathorax uniformly dense giving larva a woolly appearance; thoracic segments otherwise with only short pubescence (microsetae), nearly bare by contrast. Spiracular disc rather small, only about half as wide as abdominal segment 8; dorsal lobes of disc low, inconspicuous, with their darkened posterior faces continued ventrally as wedge-shaped spots with apices between spiracles; lateral lobes of disc only about as long as diameter of spiracle, with bluntly rounded apices; ventral lobes darkened on discal face, narrowed near mid length, expanded apically. Larva found in dark thin organic mud by small streams, seepage areas, and other similar habitats .. ***Brachypremna***

Pilosity not dense on abdomen, contrastingly absent on entire thorax. Spiracular disc of normal size; ventral lobes of disc not constricted near mid length 11

11. Prothoracic dorsum with two transverse somewhat roughened and elevated welts slightly behind line of attachment to head capsule, readily visible only when head extended (Fig. 69). Lobes of spiracular disc elongate–conical. Larva found in soil, usually near surface, in woodlands or less often in grasslands, pastures, and lawns .... ***Nephrotoma***

Prothoracic dorsum without transverse welts. Lobes of spiracular disc variable 12

12. Dorsal and lateral lobes of spiracular disc not well-developed, low, bluntly rounded; ventral lobes small (Fig. 70); strong setae (macrosetae), longer than diameter of a spiracle, on each lateral lobe; three or four such setae below and beside each ventral lobe. Larva pale, thin-skinned, feeding in dead but still fairly sound wood .... ***Ctenophora (Tanyptera)***

Dorsal and lateral lobes of spiracular disc moderately to strongly developed. Larva usually grayish or brownish, but if pale, not thin-skinned 13

13. Central smooth area of spiracular disc surrounded by fringe of short hairs, with dorsal and dorsolateral lobes outside this fringe. Larva found in decaying hardwood stumps and logs .... ***Ctenophora***, in part

Smooth area of disc continued onto posterior faces of lobes; fringing hairs usually confined to margins of lobes 14

14. Posterior spiracles large, separated by less than diameter of a spiracle; lobes of spiracular disc less than twice as long as basal width, fringed with long hairs; a thin black median line present on discal face of each lobe. Body length more than 50 mm in fourth instar. Larva found in moist soil, in Pacific drainage area .... ***Holorusia***

Posterior spiracles usually separated by more than diameter of a spiracle; lobes of spiracular disc highly variable, from short and rounded to elongate, subconical to densely sclerotized, hook-like; ventral pair rarely divided. Larva found in various terrestrial and aquatic habitats (Figs. 71, 72) .... ***Tipula***

15. Posterior spiracles absent; tracheal system closed; dorsal and lateral lobes of abdominal segment 9 absent or extremely reduced 16

Posterior spiracles present, usually conspicuous, but sometimes concealed when lobes of spiracular disc are infolded; dorsal and lateral lobes of abdominal segment 9 usually present, but absent in some species 17

16. Ventral lobes of abdominal segment 9 elongate, deeply separated, slightly divergent, with a few tufts of hairs (Fig. 74). Anal papillae elongate. Dorsal and ventral creeping welts conspicuous on abdominal segments 2–7. Larva in silken tube found on stones in swift well-oxygenated water .... ***Antocha***

Abdominal segments 8 and 9 covered with dense long pilosity; segment 9 elongate, tapering, shallowly bifurcate at apex. Anal papillae short, not extending beneath segment 9. No conspicuous creeping welts. Larva found in sandy bottoms of cold clear rapid streams of Pacific drainage .... ***Hesperoconopa***

17. Dorsal and lateral lobes of spiracular disc absent or extremely reduced; ventral lobes elongate (Fig. 75). Larva aquatic or semiaquatic (larvae of *Ornithodes* and *Nasiternella*, at present unknown, may key out here) 18

Dorsomedial lobes of spiracular disc or lateral lobes, or both, well-developed if ventral lobes elongate; ventral lobes usually short, less often absent 20

18. Paired prolegs with sclerotized apical crochets present on venter of abdominal segments 3–7. Creeping welts absent .... ***Dicranota***, in part

Prolegs with apical crochets absent. Roughened creeping welts or broad tubercles present on basal rings of abdominal segments 4–7 19

19. Creeping welts on both dorsum and venter, bearing microscopic spicules .... ***Dicranota*** **(*Rhaphidolabina*)**

Creeping welts or broad tubercles on venter only, without spicules but with microscopically roughened surface (Fig. 75) .... ***Pedicia***

20. Spiracular disc surrounded by seven lobes, situated one dorsomedially and one each dorsolaterally, laterally, and ventrally on each side; spiracles small, widely separated, at bases of lateral lobes of spiracular disc. Larva found in organic silt in small streams of Pacific drainage .... ***Gonomyodes***

Spiracular disc with five or fewer peripheral lobes, or without distinct lobes................................21

21. Spiracular disc with four or five peripheral lobes 22

Spiracular disc with only three lobes, or without distinct lobes 58

22. Internal portion of head extensively sclerotized dorsally and laterally, with shallow posterior incisions (Figs. 77, 87) (determined by cutting prothoracic skin at one side, or often visible through skin)..23

Internal portion of head divided by deep posterior incisions into elongate slender rod-like to spatulate sclerites (Figs. 76, 83, 88), or if sclerites plate-like, darkly sclerotized only along margins giving appearance of separate rods 51

23. Hypostomal bridge divided medially by membranous area (hypostomal plates in contact though not fused in *Pseudolimnophila*, Fig. 77). Abdominal segments without creeping welts 24

Hypostomal bridge undivided (Fig. 87), though sometimes deeply incised posteriorly. Creeping welts present on basal rings of abdominal segments (Fig. 82), or abdominal segments with transverse bands or patches of dense pilosity on both basal and apical rings 39

24. Spiracular disc surrounded by five lobes, each in form of a black spatulate plate with finely toothed margins. Larva found in marshy soil .... ***Ormosia*** **(*Scleroprocta*)**

Spiracular disc surrounded by four or five lobes of rounded or subconical form 25

25. Plane of spiracular disc approximately perpendicular to long axis of body; disc surrounded by five lobes 26

Plane of spiracular disc diagonal to long axis of body; disc with four peripheral lobes................37

26. Hypostomal prolongations each expanded into a sclerotized plate with anterior margin toothed (Fig. 76) 27

Hypostomal prolongations, if expanded, not sclerotized or not toothed anteriorly 28

27. Hypostomal plates each with four teeth (Fig. 76). Spiracular disc extensively blackened; black spots on dorsolateral and ventral lobes divided medially by pale line; spot on dorsal lobe nearly always undivided. Larva found in wet humous soil (larva of *Tasiocera*, at present unknown, may key out here) .... ***Molophilus***

Hypostomal plates each with five to eight teeth. Spiracular disc small, without extensive blackened areas. Larva found in organic mud ....***Erioptera***, in part

28. Posterior faces of all five lobes of spiracular disc each bearing solidly blackened spot 29

Spots on some or all lobes of spiracular disc divided medially by pale line or wider pale zone ..30

29. Blackened areas of dorsolateral lobes of spiracular disc continued between spiracles. Larva found in organic mud near water ....***Ormosia***, in part

No blackened areas between spiracles. Larva found in muddy stream banks .... ***Erioptera*** **(*Trimicra*)**

30. Dorsomedial lobe of spiracular disc bearing densely sclerotized horn-like projection with apex bent downward over disc; black wedge-shaped spots present at periphery of disc between ventral lobes, between ventral and lateral lobes, and between lateral and dorsomedial lobes. Larva found in fine sand, silt, and organic debris at margins of clear streams of Pacific and Arctic drainages..***Arctoconopa***

Dorsomedial lobe of spiracular disc without sclerotized horn-like projection; no wedges of black pigmentation between lobes of disc..31

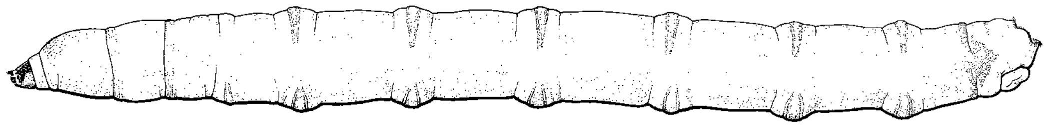
31. Dorsolateral lobes of spiracular disc with solidly blackened spots; spots on ventral lobes divided (Figs. 79, 80) 32

Dorsolateral lobes of spiracular disc and ventral lobes with spots divided (Fig. 81), but if spots of dorsolateral lobes more completely darkened, four to six small dark spots present on central disc 33

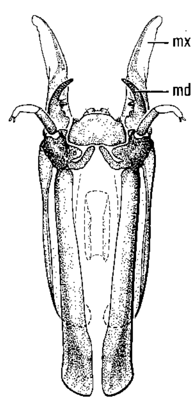
32. Blackened areas of dorsolateral lobes of spiracular disc continuous around spiracles and extending to midline or nearly so. Larva found in moist earth or sand, usually near water .... ***Gonomyia***, in part

Blackened areas of dorsolateral lobes of spiracular disc not continuous around spiracles (Fig. 79), but if dark area present between spiracles, this joined to pigmented areas of ventral lobes. Larva dark yellowish to amber, living beneath bark of dead somewhat decayed hardwood logs or in decaying inner parts of living hardwoods (larva of one *Idiognophomyia* species keys out here, found in decaying *Yucca* in southern California) .... ***Gnophomyia***

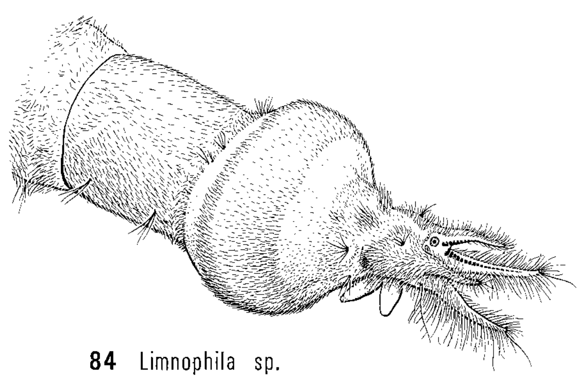
33. Peripheral lobes of spiracular disc short, blunt; blackened areas of dorsolateral lobes continuous around spiracles, fading toward midline .... ***Gonomyia***, in part



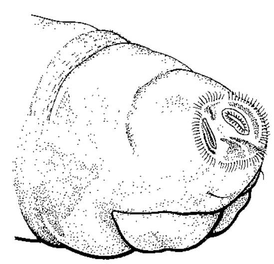
82 Limonia sp.



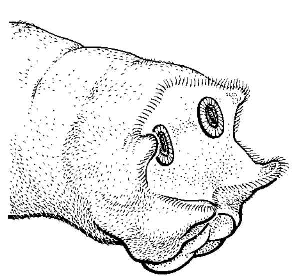
83 Limnophila sp.



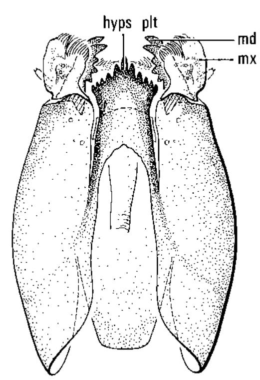
84 Limnophila sp.



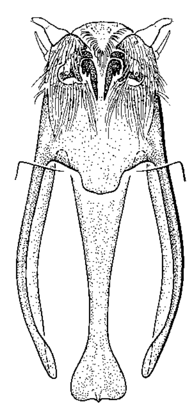
85 Limonia sp.



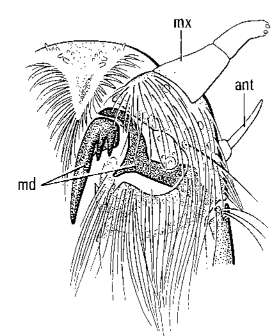
86 Epiphragma fascipennis



87 Limonia sp.



88 Pilaria recondita



89 Pilaria recondita

Figs. 7.82–89. Larvae (*concluded*): (82) *Limonia* sp., lateral view of larva; (83) *Limnophila* sp., dorsal view of head capsule; (84) *Limnophila* sp., oblique posterior view of terminal segment; (85) *Limonia* sp., oblique posterior view of terminal segment; (86) *Epiphragma fascipennis* (Say), oblique posterior view of terminal segment; (87) *Limonia* sp., ventral view of head capsule; (88) ventral view and (89) enlarged view of left mandibular region of head capsule of *Pilaria recondita* (Osten Sacken).

Abbreviations: ant, antenna; hyps plt, hypostomal plate; md, mandible; mx, maxilla.

Peripheral lobes of spiracular disc nearly as long as their width at base, or longer; blackened areas of dorsolateral lobes not continuous around spiracles 34

34. Blackened area of dorsomedial lobe of spiracular disc not divided. Larva found in organic mud .... ***Ormosia***, in part

Blackened area of dorsomedial lobe (and all others) of spiracular disc divided medially by pale line 35

35. Area between spiracles generally unpigmented, not blackened. Larva found in organic mud .... ***Ormosia***, in part

Area between spiracles with some darkly pigmented spots 36

36. Two round spots between spiracles; spiracular disc small compared with body size. Larva found in organic mud .... ***Erioptera***, in part

Four to six small spots (as two or three pairs) between and below spiracles; spiracular disc not small compared with body size. Larva found in moist earth .... ***Erioptera* (*Symplecta*)**

37. Ventral lobes of spiracular disc not darkly pigmented on upper surface, not fringed with long hairs; spiracles pale. Hypostoma reduced to small longitudinal rod below maxilla on each side. Larva found in sandy bottoms of clear cold streams .... ***Cryptolabis***

Ventral lobes of spiracular disc darkly pigmented on upper surface (Fig. 78), fringed with long hairs that are longer than lobes; spiracles dark. Hypostoma in form of a toothed plate at each side 38

38. Hypostomal plates each bearing four anterior teeth. Larva found in organic mud in wet woodlands .... ***Paradelphomyia***

Hypostomal plates each bearing seven or eight anterior teeth (Fig. 77). Larva found in thin organic mud in swampy woods, pond margins, and similar habitats .... ***Pseudolimnophila***

39. Spiracular disc with five peripheral lobes 40

Spiracular disc usually with four peripheral lobes, but if vestigial dorsomedial lobe present, it is unpigmented 45

40. Posterior faces of all five lobes of spiracular disc bearing a solidly blackened spot; central disc generally unpigmented. Scape about as thick as long. Larva found in fungi .... ***Ula***

Posterior faces of all lobes not solidly blackened, unpigmented to only partially darkened. Scape much longer than its diameter 41

41. Creeping welts on abdominal segments only slightly raised, pale, without microscopic hairs or with hairs indistinct except at high magnifications 42

Creeping welts on abdominal segments distinct, conspicuous 43

42. Hypostomal bridge with seven teeth. Ventral lobes of spiracular disc with single linear dark brown spot. Larva found in pieces of damp to saturated much decayed hardwood .... ***Atarba***

Hypostomal bridge with three teeth. Ventral lobes of disc short, broadly rounded, with triangular dark spot enclosing pale setal base. Larva found in damp punky wood .... ***Austrolimnophila***, in part

43. Abdominal segments 2–7 with both dorsal and ventral creeping welts on basal rings (Fig. 82). Lobes of spiracular disc wider than long, broadly rounded, unpigmented or with only limited darkened spots (Fig. 85). Larva found in numerous terrestrial and aquatic habitats .... ***Limonia***, in part

Abdominal segments 2–7 with ventral creeping welts only. Ventral lobes of spiracular disc as long as their width at base, or longer 44

44. Ventral lobes of spiracular disc longer than their width at base, darkened at margins with a broad median pale zone on each. Hypostomal bridge with five teeth. Larva brownish with long appressed pubescence, found in marsh borders in decomposing aquatic vegetation or in marshy areas in woods .... ***Helius***

Ventral lobes of spiracular disc only about as long as basal width, almost uniformly brownish posteriorly (Fig. 86). Hypostomal bridge with three teeth. Larva pale, with short appressed pubescence, found in decayed wood of deciduous trees .... ***Epiphragma***, in part

45. Abdominal segments 2–7 without distinct creeping welts; all segments with transverse bands or patches of dense pilosity. Lateral lobes of spiracular disc broadly pigmented from spiracles outward; broadly pigmented faces of ventral lobes narrowly connected across lower disc. Larva found in thin mosses and algal mats on wet rocky cliffs, rarely in soil........***Dactylolabis***

Abdominal segments 2–7 with distinct creeping welts, without transverse bands of dense pilosity........46

46. Abdominal segments 2–7 with ventral creeping welts only. Hypostomal bridge with three teeth........47

Abdominal segments 2–7 with both dorsal and ventral creeping welts on basal rings. Hypostomal bridge with more than three teeth........48

47. Body smooth-skinned, shiny, nearly transparent, long, slender; length about 18–20 times diameter. Hypostomal bridge with three subequal blunt-tipped teeth, sometimes with a smaller lateral tooth at each side. Larva terrestrial, found in humous forest soil........***Dicranoptycha***

Body opaque whitish, more robust; length about 12 times diameter. Hypostomal bridge with three unequal teeth; outer ones broader and more narrowly tipped than median one. Larva found in decayed wood of deciduous trees........***Epiphragma***, in part

48. Ventral lobes of spiracular disc longer than their width at base, tapering to subacute apex, fringed with long hairs........49

Ventral lobes of disc shorter than width at base, broadly rounded, without long marginal hairs........50

49. Body wide, flattened. Ventral creeping welts without minute spines. Spiracles dorsoventrally elongate. Larva semiaquatic, found in indistinct tunnels beneath algal mats on wet cliffs, beside waterfalls, and in other similar locations........***Elliptera***

Body nearly cylindrical, only slightly flattened. Ventral creeping welts with numerous rows of minute spines. Spiracles transversely elliptical; lobes of spiracular disc narrowly darkened at margins. Larva found in sodden decayed wood, at or just below water level........***Lipsothrix***

50. Nearly entire spiracular disc except spiracles and outer margins of lobes dark reddish brown; spiracles horizontally elongate. Larva found in wet extremely decayed pulpy wood........***Orimarga*** (***Diotrepha***)

Spiracular disc with only isolated spots of dark pigmentation, generally pale; spiracles oval, inclined together dorsally. Larva found in various habitats........***Limonia***, in part

51. Maxilla not prolonged forward, inconspicuous in dorsal aspect........52

Maxilla prolonged forward as a dorsoventrally flattened tapering (less often subconical) blade; maxillae appearing as divergently curved tusks (Fig. 83) with apices visible even when head is withdrawn into thoracic segments........53

52. Plane of spiracular disc roughly perpendicular to long axis of body; disc surrounded by five lobes........ERIOPTERINI....26

Plane of spiracular disc diagonal to long axis of body; disc concave, with four peripheral lobes; lateral lobes bluntly rounded at apex; ventral lobes longer, without dark pigmentation, each with a single long terminal seta. Larva slender, tapering toward head, yellowish, found in moist to wet decayed logs of deciduous trees........***Elephantomyia***

53. Mandible complex, jointed near mid length (Figs. 88, 89); maxilla and labrum-epipharynx densely fringed with long yellowish to golden hairs. Dorsal plates of head fused into spatulate plate widest posteriorly. Spiracular disc small, with its upper lobes often infolded to conceal spiracles; marginal hairs protruding from cavity formed by infolding........54

Mandible not jointed near mid length; maxilla and labrum-epipharynx with mostly short pilosity. Dorsal plates of head not fused, although each may be widest posteriorly........55

54. Pigmentation of ventral lobes of spiracular disc discontinuous, either as transverse striations near base of lobe, more continuous coloration toward apex, or reduced to short darkened median line; all four lobes (lateral pair sometimes reduced) fringed with long golden hairs. Basal tooth or teeth of apical portion of mandible much less than half as long as main outer tooth. Larva found in moist to wet humous soil or decomposing vegetation in swampy woodlands........***Pilaria***

Pigmentation of ventral lobes of disc more evenly distributed, but more intense toward apex of lobe; all four lobes fringed with long hairs. Basal tooth of apical portion of mandible about half as long as main outer tooth. Larva found in organic mud in swampy woodlands .... ***Ulomorpha***

55. Spiracular disc surrounded by five short bluntly rounded lobes; ventral lobes not fringed with long hairs; dorsomedial and lateral lobes sometimes with a densely sclerotized horn-like projection near apex. Larva found in sandy bottoms and margins of clear streams .... ***Rhabdomastix***, in part

Lobes of spiracular disc (usually four) not all short and bluntly rounded; ventral ones usually elongate; ventral lobes fringed with long hairs; upper lobes without sclerotized horn-like projections 56

56. Midventral region of head before line of attachment of thorax entirely membranous, without darkened transverse bar just beneath surface. Larva found in sand or gravel near margins of clear cool brooks and streams. *Note:* in this genus especially, but also in some others in similar habitats, larva sometimes with abdominal segment 7 much swollen (Fig. 84), possibly as an aid in locomotion or anchorage; swelling sometimes persisting in preserved specimens .... ***Hexatoma***

Midventral region of head before line of attachment of thorax membranous, with darkened narrow transverse bar (part of hypopharynx) visible just beneath surface 57

57. Lateral lobes of spiracular disc unpigmented on posterior face. Mandible with long outer tooth and two smaller teeth of similar size and shape near mid length of inner margin; maxillary projections subconical. Larva found in wet organic debris .... ***Polymera***

Lateral lobes of spiracular disc pigmented at least along one margin, usually much more extensively (Fig. 84). Mandible without two small similar teeth near mid length of inner margin (with more or fewer dissimilar teeth); maxillary projections flattened. Larva carnivorous, aquatic, found usually in organic mud in swampy woods and pond margins, less often in mud or sand at bottom of small streams .... ***Limnophila***

58. Spiracular disc broadly emarginate dorsally. Larva found in a hardened flattened elliptical case, in marshy soil near small streams or springs of Pacific drainage (description based on a European species) .... ***Thaumastoptera***

Spiracular disc not broadly emarginate dorsally. Larva not in a hardened case 59

59. Internal portion of head divided by deep posterior incisions into elongate slender or spatulate sclerites (determined by cutting prothoracic skin at one side, or often visible through skin) 60

Internal portion of head extensively sclerotized dorsally and laterally; sclerites plate-like, with shallow posterior incisions (Fig. 87) 61

60. Spiracular disc lightly pigmented, vertically subrectangular, with two claw-like projections at ventral margin; posterior spiracles minute, pale, separated by about three times diameter of a spiracle. Larva yellowish, aquatic, found in bottoms and margins of clear streams .... ***Rhabdomastix***, in part

A single broadly rounded ventral protuberance below posterior spiracles; spiracular disc without pigmented spots; spiracles darkly pigmented, separated by less than twice diameter of a spiracle. Larva pale yellowish white, found beneath bark of moist to wet decayed hardwood trees .... ***Teucholabis***

61. Hypostomal bridge well-developed, toothed anteriorly (Fig. 87). Ventral creeping welts distinct 62

Hypostomal bridge not complete; hypostomal plates sometimes present and toothed anteriorly, but clearly separated medially by membranous region. Ventral creeping welts distinct or not 63

62. Abdominal segments 2–7 with both dorsal and ventral creeping welts (of differing structure in some species) on basal rings. Posterior spiracular disc roughly circular or broadly oval to transversely subrectangular; spiracles often large, oval, inclined together dorsally (Figs. 82, 85). Larva found in various terrestrial and aquatic habitats .... ***Limonia***, in part

Abdominal segments 2–7 with ventral creeping welts only; welts pale, without microscopic setae. Spiracles subcircular. Larva found in damp punky wood .... ***Austrolimnophila***, in part

63. A broad thick transverse lobe present beneath posterior spiracular disc; lobe bearing dense short pale hairs. Larva found in humous forest soil (larva of *Neocladura*, at present unknown, may key out here) .... ***Cladura***

No such pilose transverse lobe beneath posterior spiracular disc. Larva found in organic debris, often associated with mouse burrows .... ***Chionea***

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BLEPHARICERIDAE 8

CHARLES L. HOGUE

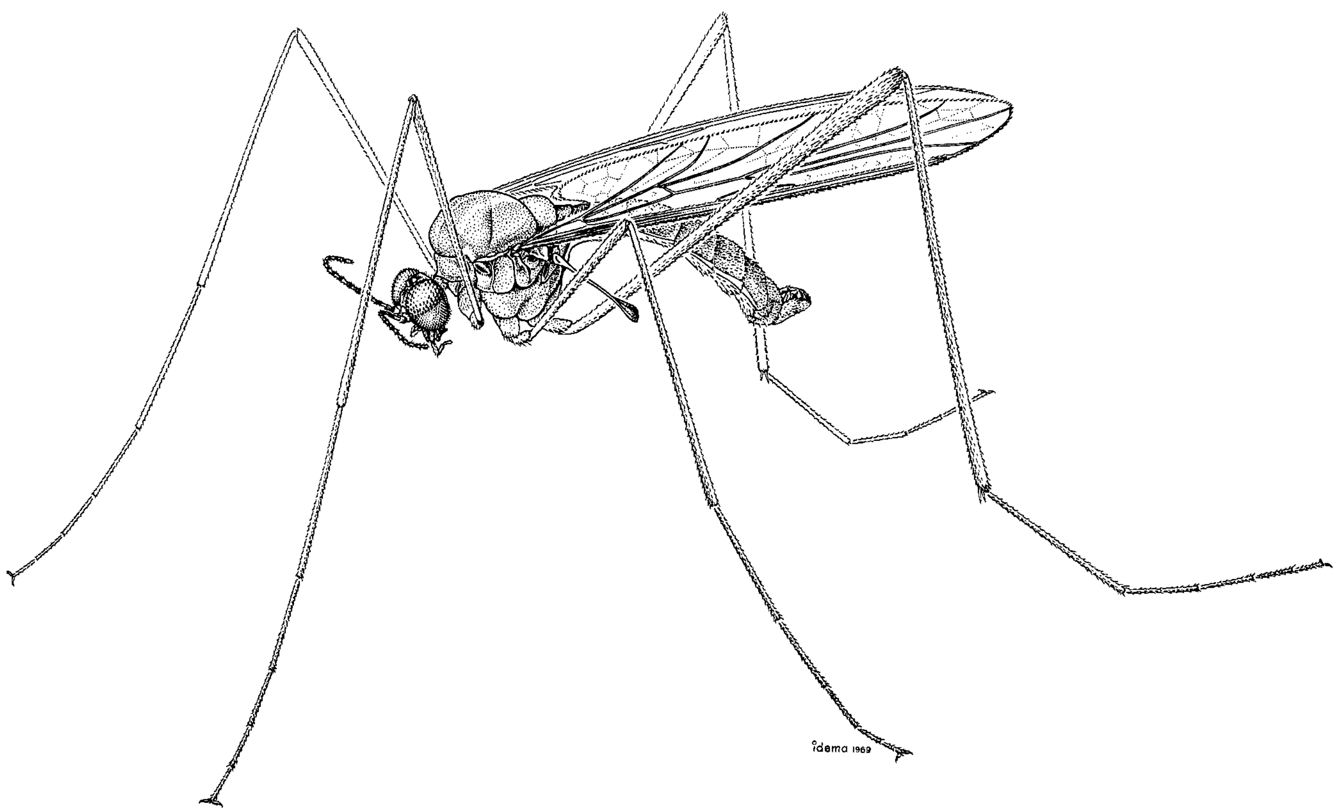


Fig. 8.1. Male of *Agathon comstocki* (Kellogg).

Slender delicate flies, 3.0–13.0 mm long (Fig. 1). Eye in both sexes usually divided transversely into an upper region with larger ommatidia and a lower region with smaller ommatidia. Legs long; hindleg stouter than others. Wing membrane with net-like pattern of folds; M_2 completely detached. Coloration usually uniform, mostly dull testaceous or gray without bright colors or conspicuous markings, occasionally with indistinct bands or areas of darker shades on scutum and abdominal tergites.

Adult. Head: capsule usually gray. Eyes usually holoptic in male, dichoptic in female, large, conspicuous, finely pubescent, each one usually divided into two regions that are contiguous or separated by an unfaceted band (callis oculi); upper region rufous in color, usually composed of larger ommatidia than lower region, rarely reduced to a small indistinct region containing four or five rows of ommatidia subequal to those of lower region; lower region black in life, subequal to upper region in female, larger than upper region in male, sometimes with long black pile, e.g. in *Bibiocephala* Osten Sacken. Three ocelli present, large, prominent, set on a common tubercle. Antennae short, simple, set close together between eyes, and with 11–13 flagellomeres; scape slightly elongate; flagellomeres cylindrical, usually barrel-shaped; penultimate flagellomere sometimes reduced; terminal flagellomere sometimes elongate; microtrichia of antenna generally distributed; macrotrichia of antenna sparse, short, usually more numerous in female.

Mouthparts usually sexually dimorphic. Mandible present in female of all Nearctic species except *Blepharicera ostensackeni* Kellogg and a form of *Dioptopsis aylmeri* (Garrett), and consisting of a heavy flat blade with numerous conspicuous strongly recurved even teeth occupying about two-thirds length of inner margin; mandible absent in male. Marginal teeth on hypopharynx present in female, curving outwardly, fewer in number and smaller than those of mandible; hypopharyngeal teeth absent in male. Clypeus usually longer and heavier in female than in male. Remaining elements essentially similar in both sexes. Labrum in form of a well-sclerotized sagittate lobe with smooth rounded apex. Palpus with five segments in Nearctic species; basal segment small and fused with clypeus; remaining segments variably elongate; third segment with a conspicuous large circular sense organ ventrally near extremity. Labella, palpus, and clypeus clothed with numerous short setae.

Thorax: often gray on scutum, light testaceous or gray on pleurites. Most sclerites without setae; only sparse short setae present on presutural area of scutum, on posterior margin of scutellum, and on postnotum; scutellum with dense patches of setae at least on lateral corners; a dense black pile usually present on scutum, pleuron (except katepisternum), coxae, and basal abdominal segments in *Bibiocephala*.

Wing (Figs. 2–6) broad, with a complete simple fringe of short hairs; anal angle very prominent; calypter sometimes fringed; tegula and alula absent. Venation variable; Sc short, gradually becoming evanescent distally; only three or fewer branches of R reaching wing margin in Nearctic species; R_{2+3} partially or completely fused apically with R_1; M_2 (often called M_3) completely detached basally; other posterior veins often weak. Pattern of macrotrichia on veins variable; a single row usually present ventrally along R_4 and dorsally along R_5, less often distally on M_1 and M_2; C and R_1 with multiple rows of setae. Wing membrane usually hyaline and often iridescent or showing a violet blue opalescence, slightly fuscous-tinged in some *Bibiocephala* and *Dioptopsis* Enderlein, heavily infuscated basally in male *Philorus yosemite* (Osten Sacken); a secondary net-like pattern of fine folds present throughout membrane. Halter long, with slender stalk rapidly expanding into a flattened spatulate knob.

Legs long and slender, yellow, light testaceous or gray proximally, darkening distally; hindleg slightly longer than others; femora stout; mid coxa in some (especially female *Blepharicera* Macquart) projecting medially to form a setose tubercle (coxal spur); median articulation of trochanter and femur on all legs conspicuously blackened; a heavy black groove present on each femur protruding into a sharp trochanteral emargination; fore tibia in Nearctic species lacking spurs; mid and hind tibiae lacking spurs or with one or two spurs; first tarsomere of each leg nearly as long as remaining tarsomeres combined. In Nearctic species last tarsomere simple, cylindrical; claws simple; pulvilli and empodia absent or rudimentary.

Abdomen: somewhat compressed, especially in dried specimens, casting bronze, black, or silvery reflections in varying light. Tergites gray with broad darker shade subcaudally; tergites and sternites simple quadrate sclerites, with sparse short setae.

Male terminalia not rotated, extremely variable but in Nearctic species usually as described below. Segment 8 reduced, especially tergite 8, permitting terminalia to bend dorsally and anteriorly as in Mecoptera. Epandrium, or tergite 9, subquadrate, sometimes emarginate posteromedially. Tergite 10 produced posteriorly as two lobes that may be rounded, elongate, or subquadrate and that may be simple or produced into secondary lobes of various sizes and shapes, some of which may represent surstyli (these primary lobes have wrongly been called lobes of tergite 9 or cerci but can be neither because of ventral sclerotized apodemes or processes that unite ventrally (internally) with sternite 10 that in turn is often represented as a sclerotized plate or rod fused with the membranous hypoproct). Hypoproct usually conical in shape and membranous; anal opening situated dorsal to hypoproct; a rounded membranous lobe representing fused cerci present dorsally to anus, usually bearing two or three fine setae on each side near apex. Variably invaginated pouch (subanal pouch) opening to rear, situated ventral to hypoproct and dorsal to aedeagus; floor of pouch variously prolonged posteriorly into a flattened or slightly hollowed plate (tegmen) formed from an extension of base of paramere; this plate-like portion of paramere sometimes disconnected from rest of base of paramere which, in turn, surrounds and supports base of aedeagus, and frequently gives rise to two subtending attenuate parameral processes that may be tubular or flattened or even absent in some exotic species. Aedeagus composed of three variably elongate slender filaments arising from a bulbous base-like sperm pump (vesica); sperm pump sometimes with a posterior transverse or vertical ejaculatory apodeme. Aedeagal and parameral complexes supported from beneath by a transverse often wing-like gonocoxal apodeme (ventral bridge of tegmen) articulating laterally with gonocoxites and sometimes dorsally with paramere. Hypandrium, or sternite 9, and gonocoxites fused; aedeagal guide variably shaped, variably sclerotized, arising posteromedially between gonocoxites from either ventral or dorsal surface. Gonostylus articulating with dorsomedial apex of gonocoxite, and always bilobate; outer lobe of gonostylus invariably larger than inner lobe, usually simple in outline and heavily setose, but sometimes bilobate or otherwise modified; inner lobe of gonostylus a strongly arching smooth nude sclerotized process of variable outline.

Female terminalia fairly similar among Nearctic species. Tergite 9 conspicuous, often with a fringe or row of fairly strong setae posteriorly. Tergite 10 large, well-developed, with a posteriorly directed lateroventral setose lobe on each side ventral to cerci (these lobes considered by previous authors to be cerci); true cerci basically composed of two dorsal more membranous and weakly demarcated rather colorless lobes situated dorsomedial and posterior to lobes of tergite 10; lobe of tergite 10 and especially basal lobe of cercus bearing a number of peculiar sensory papillae, each papilla in form of a hyaline tubule tipped with a setiform process. Posterior margin of sternite 8 with a V- or U-shaped emargination; hypogynial plate (oviscapt) subquadrate to pentagonal, continuous posteriorly with this emargination, usually finely setose and often bearing several longer setae; a smaller oval to subtriangular plate-like setose lobe of sternite 9 present flanking hypogynial plate, and connecting with or articulating with ventrolateral margin of tergite 9; internal sternite 9 (genital fork) somewhat Y- or T-shaped; stem of this fork variously developed but usually with well-developed sclerotized arms that may be convoluted into various shapes. Sternite 10 present usually as a sclerotized plate-like structure sometimes with lateral extensions of various shapes that may articulate with lower margins of tergite 10; apex of sternite 10 often with two or more setae. Usually three sclerotized spermathecae present, but sometimes only two, variable in shape, subspherical to elongate, with a fairly straight or coiled neck.

Larva. Body form unique, cylindrical with venter flattened, strongly lobulate, with five definite constrictions forming six major divisions (Figs. 7, 8). First division (cephalic division) comprising fused head, thorax, and abdominal segment 1; general shape subspherical with sclerotized anterior portion demarcating head capsule; sclerites of head capsule including a median triangular frontoclypeal apotome and a pair of genae; each gena often deeply cleft posteriorly to form a median and two lateral sclerotized areas; head capsule with large circular opening ventrally enclosing mouthparts; mouthparts with mandible and maxilla well-developed and modified for browsing; antenna short in Nearctic species, with two or three segments. Five median divisions of body similar, each representing one abdominal segment; terminal division of body representing fused abdominal segments 7–10.

Lateral margins of cephalic and median divisions each produced into a rigid down-curving cone-shaped proleg bearing apically a dense patch of fine pubescence; a second conical or tubular dorsal proleg often present above this process and projecting laterally, sometimes arising from a secondary lateral shelf-like portion of the pleuron, and bearing apically a pair of conspicuously large setae (Figs. 9–12); a reduced dorsal proleg also present on posterior division of body. Dorsal integument with variously shaped and distributed fine spicules, setae, sclerotized plates, and projections. Each body division bearing midventrally a conspicuous circular complex sucking disc, with various anatomic elements forming a series of concentric rings; gills present on both sides of body anterior to sucking discs on each of the median body divisions; each gill composed of a tuft of three to seven finger-like filaments; four larger gills flanking anus on venter of anal division also present. A row of three conspicuous large setae, in a random field of much smaller setae, characteristically present on ventrolateral region of cephalic body division; also, a linear series of very large setae present on posterior margin of terminal body division.

Pupa. General facies in life similar to that of a miniature abalone, rounded limpet, or other flattened univalve mollusc; shape semiovoid; outline subfusiform, elliptical or ovate, flattened ventrally, moderately to strongly convex dorsally; dorsum usually black but sometimes with an indistinct pattern of light and dark; venter pale and colorless. Integument rigid dorsally, with flattened or spiculate stipples or granules on abdomen; integument of thorax often beaded or rugose; ventral integument thin and soft.

Arrangement of sclerites and appendage sheaths as shown in Figs. 13 and 14. A pair of anterodorsal respiratory organs (branchiae) present, transverse in position, each composed of four thin plates called lamellae; in Nearctic species lamellae either contiguous or nearly so and horn-like, i.e. smooth, elongate, rigid, and erect or porrect in posture, or divergent and leafy, i.e. broad, thin, and usually undulate (Figs. 15–17). A pair of adhesive pads present ventrolaterally on abdominal segments 3–5. In *Bibiocephala* rudimentary gills present medial to adhesive pads.

Biology and behavior. Alexander (1963) summarized the biology of the family. The following essentially is a rewording of his discussion with additional notes from my own observations.

Members of this family are confined to areas in the immediate vicinity of rapidly flowing streams. Larvae and pupae occur on rocks and boulders in swiftly moving or torrential waters, often in waterfalls. In order for the larvae and pupae to inhabit these areas, the rock faces must be smooth and free from mineral encrustments or precipitates.

Eggs are glued firmly in small groups to rock surfaces by the female soon after she emerges and copulates. With Nearctic species oviposition evidently occurs when the water level of the stream drops after the onset of the dry season. Eclosion is initiated when the eggs become submerged with the coming of the wet season.

There are four larval instars. The larvae are able to adhere to rock surfaces because of their flattened bodies and ventral sucking organs. Locomotion is slow and is accomplished in two ways. Sideways progression, which occurs only when the larva is alarmed, is done by releasing the terminal suckers at one end, rotating the body, reattaching the suckers, then repeating the action at the opposite end. Forward motion is accomplished by undulation. The larva eats diatoms and perhaps algae, browsed from the surface of the substratum.

The prepupal larvae migrate to cracks, depressions, crevices, hollows, or the bare faces of rocks and orient themselves with head either upstream or downstream. Only 5–10 min are required for transformation to the pupal stage. The pupa is white with dark gills at first, but it quickly turns black. It adheres to rock surfaces, singly or in groups, by means of its three pairs of ventrolateral adhesive pads.

The time required for the emergence of the adult from the pupal case is unusually short, only 3–5 min. Emergence occurs when the pupa is submerged or in shallow water, but is probably most common when the pupa is at the edge of receding water. The wings expand to full size during growth within the pupal case. They merely unfold during emergence, and the adult is able to fly immediately. Copulation and insemination typically occur while the teneral female is still holding on to the pupal exuvium. This mating habit for *Philorus jacinto* Hogue was observed twice by the author. The adult rests on vegetation, completely under or beneath the overhanging sides of fallen logs and rocks or in hollow trees near a stream. It prefers a shady spot and sometimes clusters in large numbers in such perches. The resting position on flat surfaces is characteristic. The wings are held flat and at a moderate angle from the body, with body and legs close to the surface; the hindlegs are extended with the tibiofemoral joint angled posteriorly (knock-kneed). Flight is swift and directional. Members of this family rarely hover or dance in swarms.

Females having mandibles suck the blood of other similar-sized or smaller, weak, slow-flying Diptera, such as the Chironomidae, Dixidae, and Tipulidae. The food of the male and nonmandibulate females is unknown; possibly they feed on flower nectar or on nothing at all. The feeding mandibulate female holds onto its prey with its heavy hindlegs, macerates it with thrusts of the labrum, inflicts lacerations with the mandibles and hypopharynx, and siphons out the blood. The adult life-span is short, probably averaging 1–2 wk. The male lives a shorter time than the female. Activity normally occurs during the day. Specimens are occasionally taken at an ultraviolet light at night.

Classification and distribution. The classification of the North American Blephariceridae is unsatisfactory. The genera are provisional, some doubtlessly polyphyletic (*Agathon*) or worthy of new status distinct from Old World genera (*Dioptopsis*). Only recently have the immature stages of many of the known Nearctic species been correlated with their adults (Hogue 1973), but many remain in doubt. The only subfamily found in North America is the Blepharicerinae with two tribes, the Blepharicerini and the Paltostomini. The Blepharicerini includes the genera *Agathon* Röder, *Bibiocephala* Osten Sacken, *Blepharicera* Macquart, *Dioptopsis* Enderlein, and *Philorus* Kellogg. *Paltostoma* Schiner (Paltostomini) enters the southern fringe of the Nearctic zoogeographic region in central Mexico but is typically a Neotropical genus and therefore not included here. The Blepharicerini are characterized by the presence of a well-developed but detached distal section of M_2 and three or fewer branches of R reaching the wing margin (Figs. 2–6).

All five Nearctic genera are found throughout western North America. *Blepharicera* is also found in the Appalachian mountains, northeastern United States, and southeastern Canada. Vast areas suitable for the occurrence of these flies in the mountainous western third of the continent are unexplored, and new species no doubt remain to be described.

The work of C. P. Alexander on this family must be acknowledged here. His comprehensive studies through the years, summarized in his paper of 1958, form the basis for a reliable family diagnosis and better taxonomic placement of the North American forms in the world scheme than was previously available.

There is no fossil record for the family. Alexander (1958) states that fossil genera previously assigned to the Blephariceridae are now believed to belong to other nematocerous groups.

Keys to genera

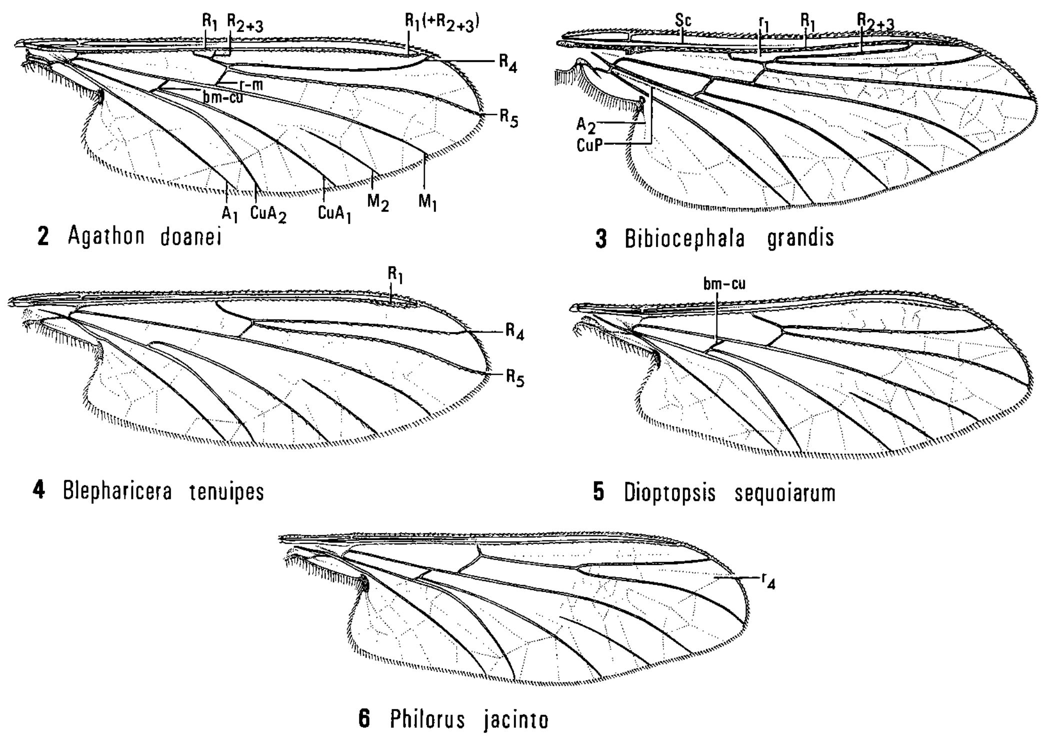
Adult

1. R with four branches; second branch, R_{2+3}, fused basally or apically with R_1, forming distally vein R_{1+2+3} and a closed cell r_1 (Figs. 2, 3) 2
   R with three free branches, without a closed cell r_1 (Fig. 4–6) 3

2. R_4 much longer than terminal fusion of R_{1+2+3} (Fig. 3). Fore femur strongly curved upward. Gonocoxite extremely large, at least three times length of gonostylus. Thoracic pleurites setose; hairs often black pilose .... ***Bibiocephala*** Osten Sacken
   1 sp., *grandis* Osten Sacken; western mountains of Yukon Territory to northern New Mexico
   R_4 subequal in length to fused R_{1+2+3} (Fig. 2). Fore femur straight. Gonocoxite about same length as gonostylus. Thoracic pleurites mainly glabrous .... ***Agathon*** Röder
   3 spp.; western mountains

3. Crossvein bm-cu present (Figs. 5–6) 4
   Crossvein bm-cu absent (Fig. 4) .... ***Blepharicera*** Macquart
   11 spp.; western mountains, Appalachians, northeastern United States, southeastern Canada; Hogue 1978

4. Cell r_4 sessile (Fig. 5). Species small; body length 6.0 mm or less .... ***Dioptopsis*** Enderlein
   5 spp.; western mountains
   Cell r_4 long-petiolate (Fig. 6). Species mostly large; body length 8.0–10.0 mm .. ***Philorus*** Kellogg
   4 spp.; mountains of the Pacific states; Hogue 1966



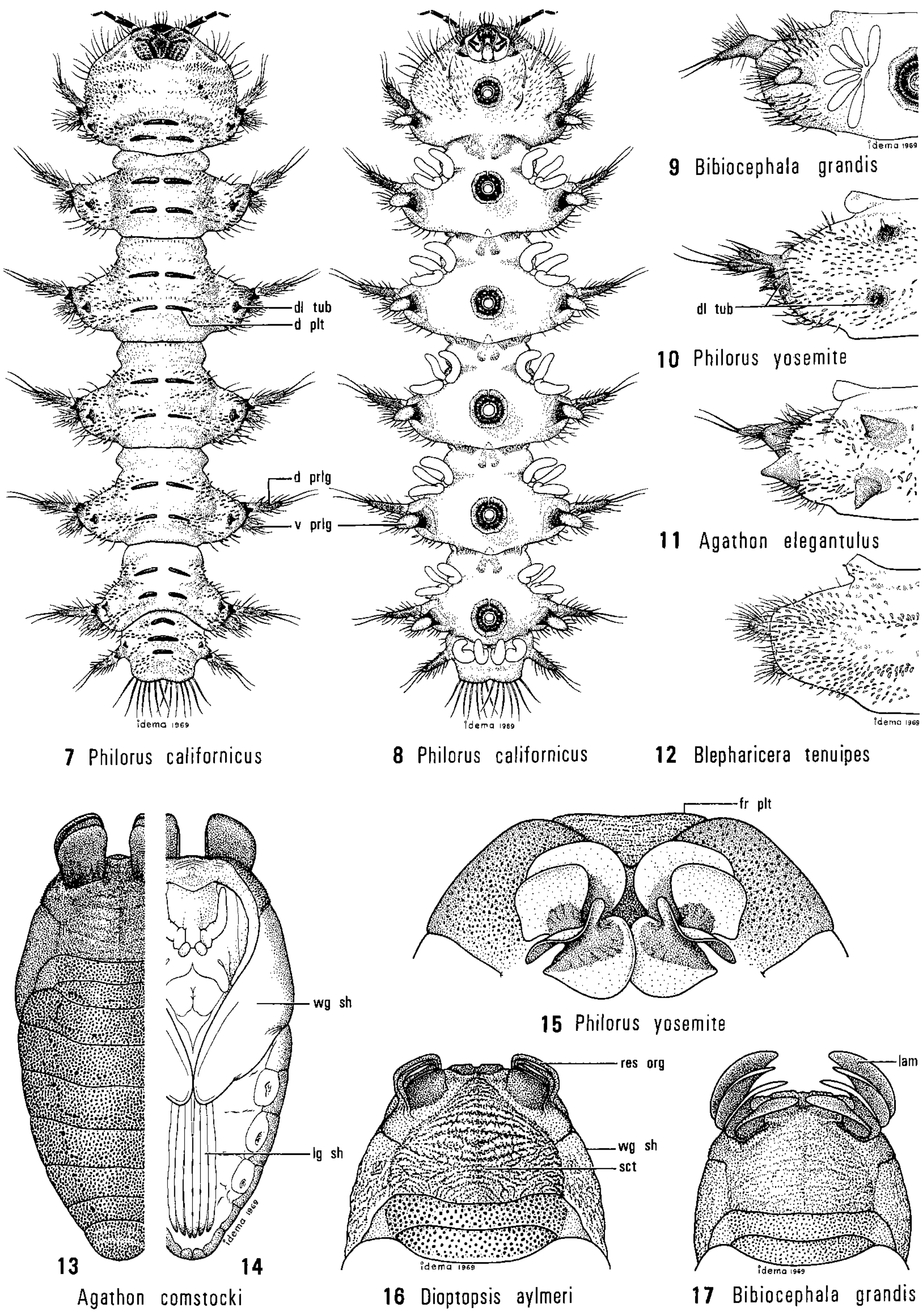
Figs. 8.2–6. Wings: (2) *Agathon doanei* (Kellogg); (3) *Bibiocephala grandis* Osten Sacken; (4) *Blepharicera tenuipes* (Walker); (5) *Dioptopsis sequoiarum* (Alexander); (6) *Philorus jacinto* Hogue.

Larva

1. Dorsal proleg absent, at least from anal division of abdomen (Fig. 12) ....***Blepharicera***
   Dorsal proleg present 2
2. Ventral gill tufts composed of six filaments, arranged in a plane semirosette pattern (Fig. 9) ....***Bibiocephala***
   Ventral gill tufts composed of three to five or seven filaments, spreading and all directed generally anterolaterally (Fig. 8) 3
3. Dorsal sclerotized plates or tubercles usually present on abdominal segments; if absent, at least a small dorsolateral tubercle present above dorsal proleg on abdominal segment 1 4
   Dorsal sclerotized processes absent. If conical processes present, two transverse series of minute plates also present, across thoracic region of anterior body division ....***Dioptopsis***
4. Dorsal proleg double, with a subequal elongate dorsal branch (Fig. 10); or ventral gill tufts with three filaments (Fig. 8) ....***Philorus***
   Dorsal proleg single, with only a small proximodorsal mamillate process or setal swelling (Fig. 11); ventral gill tufts with five to seven filaments ....***Agathon***

Pupa

1. Lamellae of respiratory organ spreading, consisting of thin translucent flexible leafy projections (Fig. 15) ....***Philorus***
   Lamellae of respiratory organ contiguous or nearly so, consisting of heavy darkly opaque rigid erect horn-like projections (Figs. 16, 17) 2
2. Body form ellipsoid, strongly convex dorsally. Size large, approximately 9.0–10.0 mm long. Antennal sheath short, barely exceeding base of wing sheath, and strongly incurved. Vestigial gills present ventrally on abdomen ....***Bibiocephala***
   Body form ovoid, moderately or only slightly convex dorsally. Size smaller, usually not exceeding 7.0 mm long. Antennal sheath longer, extending approximately one-fourth the



Figs. 8.7–17. Immature stages: (7) dorsal view and (8) ventral view of larva of *Philorus californicus* Hogue; first abdominal divisions of larvae of (9) *Bibiocephala grandis* Osten Sacken ventral view, (10) *Philorus yosemite* (Osten Sacken) dorsal view, (11) *Agathon elegantulus* Röder dorsal view, and (12) *Blepharicera tenuipes* (Walker) dorsal view; (13) three-fifths dorsal and (14) three-fifths ventral views of pupa of *Agathon comstocki* (Kellogg); anterodorsal portion of pupae of (15) *Philorus yosemite*, (16) *Dioptopsis aylmeri* (Garrett), and (17) *Bibiocephala grandis*.

Abbreviations: dl tub, dorsolateral tubercle; d plt, dorsal plate; d prlg, dorsal proleg; fr plt, frontal plate; lam, lamella; lg sh, leg sheath; res org, respiratory organ; sct, scutum; v prlg, ventral proleg; wg sh, wing sheath.

length of the wing case; apex paralleling margin of wing case, i.e. not strongly incurved. Ventral gills entirely absent 3

3. Wing sheath and scutum rugose (Fig. 16). Lamellae of respiratory organ short, never more than 1.5 times their widths .... ***Dioptopsis***

   Wing sheath and scutum smooth (Fig. 13) or rugose. If wing sheath and scutum rugose, lamellae of respiratory organ longer than twice their widths 4

4. Frontal plate triangular (Fig. 15) .... ***Agathon***

   Frontal plate semispherical, with dorsal apex broadly rounded .... ***Blepharicera***

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DEUTEROPHLEBIIDAE 9

H. D. KENNEDY

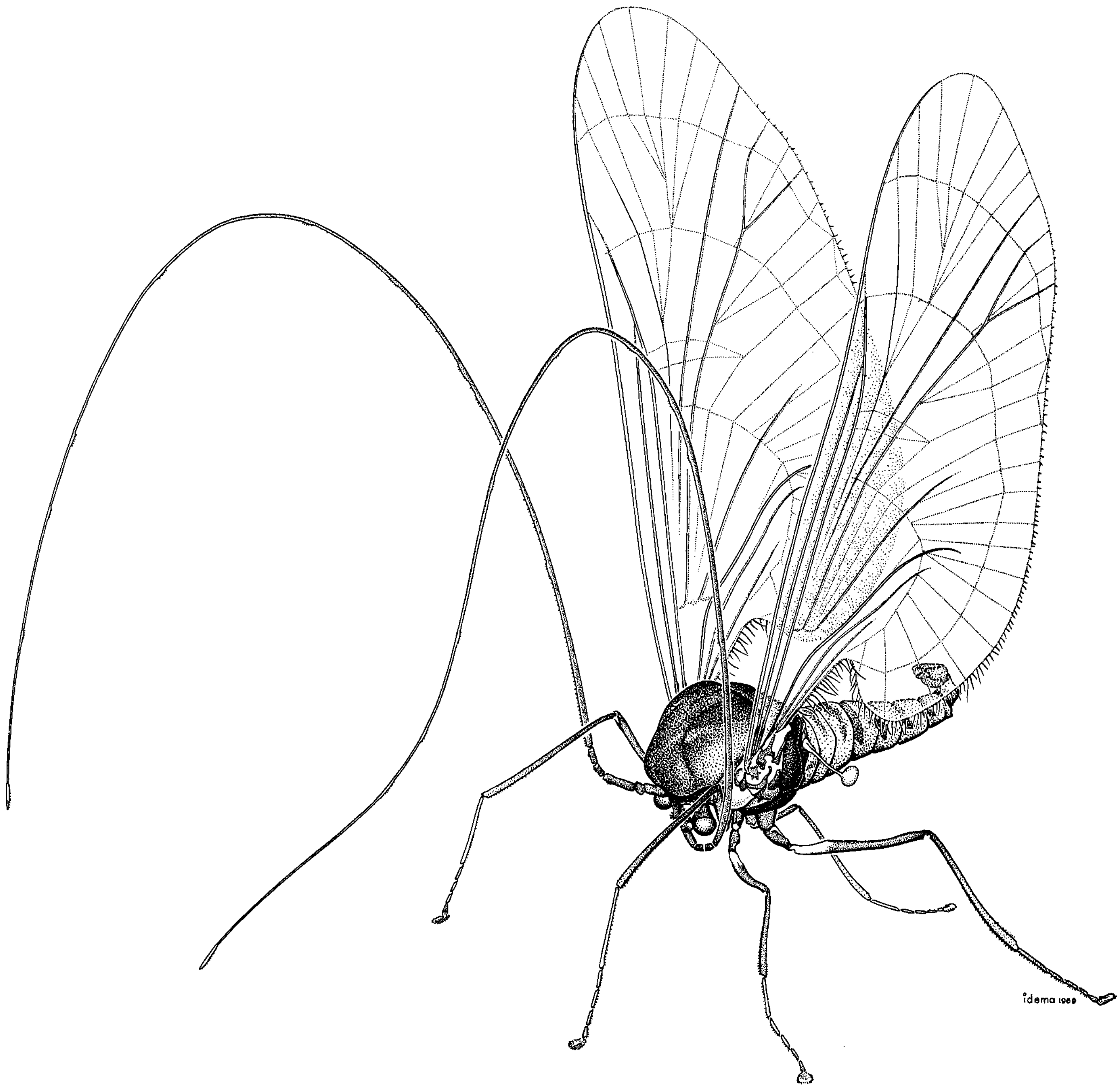


Fig. 9.1. Male of *Deuterophlebia inyoensis* Kennedy.

Delicate midge-like flies, about 3.0 mm long (Fig. 1). Head and thorax dark brown to black; abdomen light brown in male and dark green in female; wing silvery blue. Antenna about four times as long as body in male, but less than 0.50 mm in female, with four flagellomeres. Thorax high and broad; legs all similar, thin, longer in female than in male. Abdomen broad at base, tapering distally.

Adult. Head: small, transverse and somewhat flattened, pubescent. Eye relatively small, situated ventrally to antenna; ommatidia equal in size, without pubescence between them; ocelli absent. Subcranial cavity present, but functional mouthparts absent.

Antenna sexually dimorphic, with four flagellomeres. In male, antenna 10–13 mm long; terminal flagellomere excessively lengthened, bearing several minute sensillae on surface; scape, pedicel, and proximal three flagellomeres short, with combined length a little greater than that of fore femur. In female, antenna only 0.20–0.50 mm long; length of terminal flagellomere subequal to that of preceding two flagellomeres combined.

Thorax: obliquely elongate, broad, strongly arched, projecting anteriorly over head, and glabrous or covered with a dense pile-like pubescence. Antepronotum greatly reduced, present as a weakly sclerotized slender rod-like structure; postpronotum also markedly reduced, evident as a slender rod-like structure medially, and with a tiny postpronotal lobe laterally. Scutum highly arched, extending forward at middle as a canopy above head, with partially distinct suture separating presutural and postsutural regions; scutellum short but rather broad, subrectangular in shape; postnotum large, convex, with prominent laterotergites. Pleural region obliquely elongate; proepisternum greatly reduced; anepisternum with a prominent anepisternal membrane; katepisternum broadly rounded but not strongly convex, extending posteriorly to just beyond hind margin of middle coxa; meron large, subquadrate. Anterior and posterior thoracic spiracles large, oval, and ringed with a sclerotized band.

Wing (Fig. 4) in male very large, averaging about 5.4 mm long and 2.5 mm wide, with anal lobe prominent; in female, wing smaller averaging about 3.4 mm long and 1.8 mm wide, with anal lobe less pronounced. Posterior margin of wing with long fine setae near base but these shorter and more sparse distally; microtrichia more densely arranged on anterior half of wing than on posterior half. Veins represented by only a few variably distinct vestiges; C almost reaching wing tip; Sc terminating beyond middle of wing and often in R_1; R_1 obvious basally but variably so distally; R_{2+3} and R_{4+5} rather faint; M_1, M_2, CuA_1, and CuA_2 variably distinct, usually short; CuP faint or absent; A_1 variably distinct, at times obscure or absent. Secondary venation, due to folding of wing, evident; arrangement fan-like, with three concentric lines and two dark transverse lines in middle of wing. Halter covered with very fine pubescence; stem with a few delicate setae near base.

Legs elongate, longer in female than in male; size and proportions of segments generally similar in all legs; coxae elongate; trochanters obliquely two-segmented; tibiae longer and more slender than femora. Empodia in male very conspicuous, each appearing as a flattened nearly circular disc that is densely provided with long yellow-knobbed setae and shorter normal setae; female empodia linear and smaller, about two-thirds as long as claw, densely setose. Male with one claw of each leg slender and about two-thirds as long as diameter of empodium, and with second claw reduced; female with a pair of stout curved claws of equal size; pulvilli apparently absent.

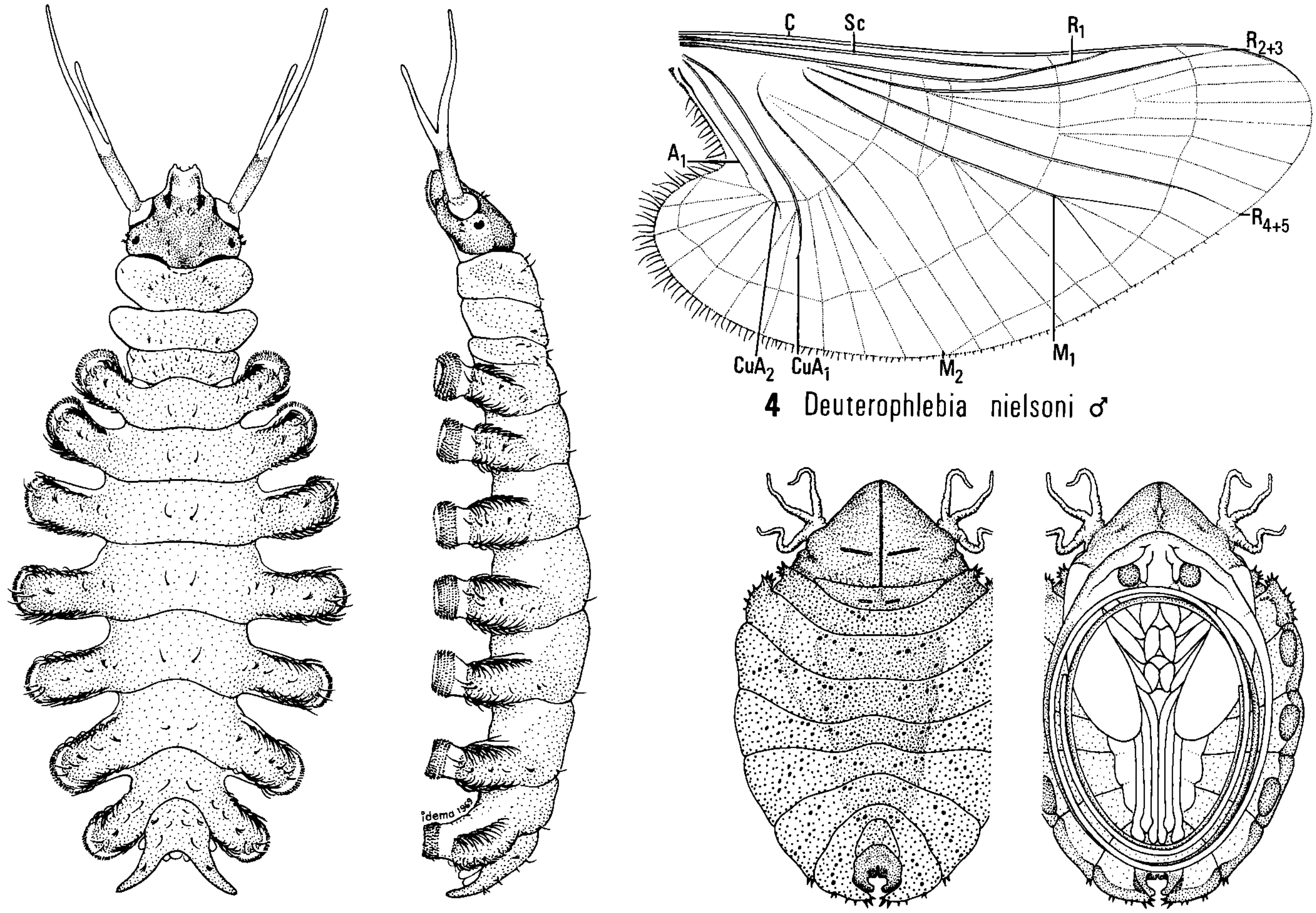
Abdomen: broad at base tapering distally, with eight pregenital segments; spiracles lacking. Terminalia in male simple; tergites 9 and 10 fused into a single plate; gonocoxite pubescent, slightly tapering, with fine setae covering median surface; gonostylus simple, pubescent, about one-fourth as long as gonocoxite, slightly tapering distally, with flexor surface slightly concave and set with scattered curved short spinose setae; aedeagus membranous, tube-like, without pubescence, slightly tapering posteriorly; paramere forming a short, sclerotized tube-like aedeagal sheath arising between bases of gonostyli, with rounded tip reaching to or beyond apices of gonostyli.

In female, abdomen swollen when filled with eggs, returning to size similar to that of male when these are removed. Terminalia small, simple, pale, with fine pubescence; tergite 9 distinct, shorter than broad; tergite 10 laterally bilobate, V-shaped; cercus slender, glabrous, slightly knobbed outwardly. Sternite 8 with short slender hypogynial valves; sternite 9 V-shaped, sclerotized, with apex of each arm expanded plate-like.

Egg. Green, about 0.35 mm long and 0.08 mm wide. Body cavity of mature female pupa completely filled with about 40 to 100 eggs.

Larva. Ranging from 3.0 to 5.5 mm long, eucephalic; fresh specimens having head dark brown, antenna dark brown basally and yellowish white distally, mouthparts blackish brown, dorsum of body mottled orange brown, and ventral surface light greenish; three thoracic and eight abdominal segments; anterior segments smaller than posterior ones; dorsal surface covered with dense fine pubescence consisting of simple and branched hairs and setae (Figs. 2, 3); venter of abdomen bare, with internal nervous system showing through thin cuticle. Head flattened; antenna bifurcate, with two unequal branches; eye spots small, widely separated. Abdomen with seven proleg-bearing segments; each proleg terminating in from one (first instar) to thirteen (fourth instar) transverse rows of small blackened claws that permit larva to adhere to substrate; spiracles or tracheal papillae lacking; five large sausage-shaped anal papillae lying on ventral surface of abdominal segment 8; segment 8 extended caudally into two tapered processes each bearing two clusters of blackened peg-like bristles and additional elongate simple hairs.

Pupa. Dark brown to black, varying between 2 and 4 mm long. Body with 11 broadly oval segments; dorsal surface convex anteriorly, more flattened behind (Fig. 5); ventral surface flattened, with a thin greenish blue cuticle that is appressed to the substrate (Fig. 6).



2 D. nielsoni 3 D. nielsoni 5 D. nielsoni ♂ 6 D. nielsoni ♂

Figs. 9.2–6. *Deuterophlebia nielsoni* Kennedy: (2) dorsal view and (3) lateral view of larva; (4) wing; (5) dorsal view and (6) ventral view of pupa of male.

Prothorax and mesothorax fused. Prothorax with a pair of respiratory processes at anterior margin that are enlarged basally and short-stemmed, with each terminating in three or four thin crooked filaments. Mesonotum with a median longitudinal line and one or more transverse sclerotized bands or dots on either side; large conical tubercle sometimes present dorsal to each respiratory organ, raised and extending beyond lateral margin of mesothorax, with no spines or one or more spines of various sizes and shapes. Metanotum small, not reaching lateral margins, with pair of transverse lines of granulations similar to those of mesonotum.

Lateral margins of anterior two abdominal segments directed slightly anteriorly and projecting as heavily sclerotized prominences; first segment with about eight blackened thorn-like spines and second segment with about 12 such spines. Lateral margins of ventral surface of abdominal segments 3, 4, and 5 with paired oval adhesive pads by which pupa adheres to substrate. Abdominal segments 1–7 with small sclerotized dots forming a semicircular pattern across longitudinal axis of body and with additional small sclerotized dots scattered randomly. Sexes, viewed from beneath, readily differentiated by characters of developing imago; male with excessively lengthened antennal sheaths coiled around periphery, and with leg sheaths extending backward to posterior margin of abdominal segment 7; female with antennal sheaths short and slightly overlapping bases of wing pads, and with leg sheaths extending from segment 7 to segment 8.

Biology and behavior. All known species of Deuterophlebiidae are intimately connected with fresh, rapidly flowing, well-aerated mountain streams. Larvae are found near the water–air interface on the upper surface of smooth, light-colored rocks that have cracks and depressions; they are conspicuously absent on rough or multicolored substrates such as granite. Immature stages prefer the splash line and are seldom found in water deeper than 30 cm. Immature forms are seldom found where water velocity is less than 75 cm/s or where flow volume is small, such as in side channels. The pupae occur in the same habitat as the larvae, but mature larvae choose to pupate in small depressions and hollows on dark-colored rocks. Species occurring at low elevations produce several generations a year. High-altitude forms, however, only produce one generation a year. These latter species presumably overwinter in the egg stage; the first larval instar appears in mid-July and adults emerge in late August. The life cycle of the high-altitude species approximates 27 days, whereas that of species inhabiting lower elevations and warmer waters is only 19 days. The basic life histories of only *D. nielsoni* Kennedy and *D. inyoensis* Kennedy are known (Kennedy 1958, 1960; Alexander 1963). Adults of *D. nielsoni* emerge between 7 and 9 a.m., and those of *D. inyoensis,* between 8 and 10 a.m. During this astonishingly short adult life both copulation and egg laying are accomplished. The adult, while resting after emergence, carries its large wings at an angle of 45° from the body, legs outstretched, and antennae curved in a horizontal plane. The long antennae appear to be cumbersome. Adults probably do not rest after flight has begun. Detailed information on biology and life history for most described species is lacking because it is difficult to locate and collect all the life-forms.

Classification and distribution. The family contains the single genus *Deuterophlebia* Edwards. Only four Nearctic species, all from western North America, have been described, although several recent collections made in western United States and Canada might result in an increase of this number. These insects are called mountain midges, although some have been collected at less than 90 m above sea level. Species have been distinguished by certain characters of the thoracic region of the pupae; however, when additional specimens are collected and studied, the adult male terminalia should provide the most reliable taxonomic characters. At present, the family is known from widely separated geographic regions; all species are north temperate except for one undescribed but questionable species reported from Chile. No fossil records of the family are known.

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NYMPHOMYIIDAE 10

D. KEITH McE. KEVAN AND FELICITY E. A. CUTTEN

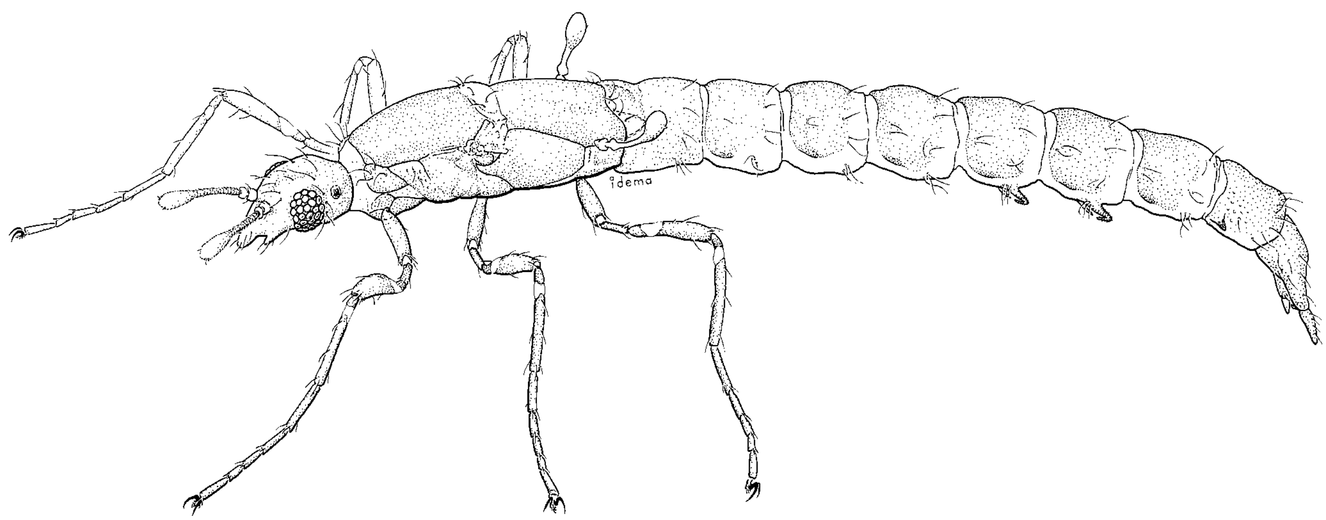


Fig. 10.1. Male of *Palaeodipteron walkeri* Ide.

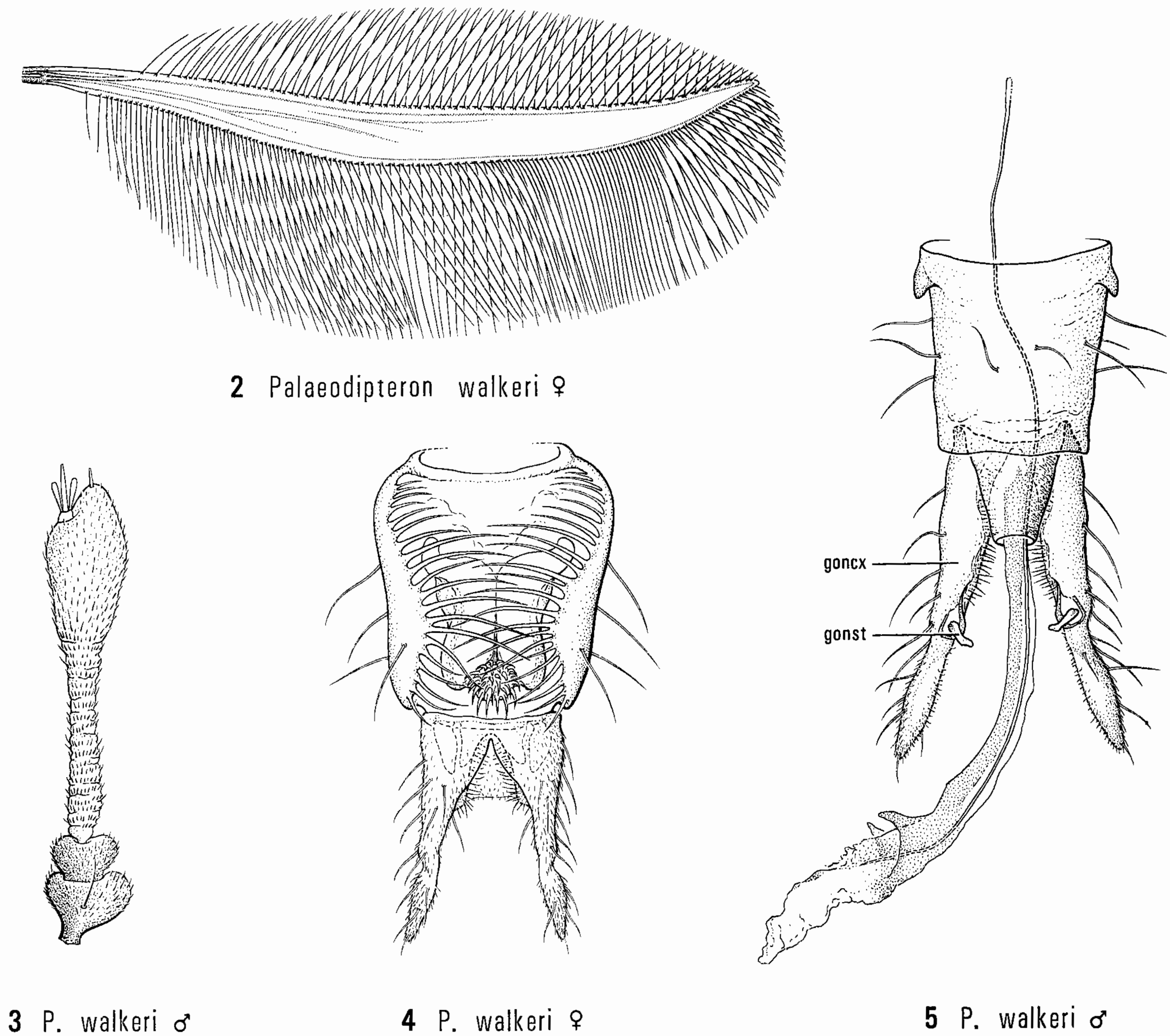
Very small flies, 1.5–2.5 mm long, pale, slender, weakly sclerotized, sparsely setose (Fig. 1). Flagellum clavate, stalk-like and annulated basally, inflated apically (Fig. 3). Compound eye holoptic ventrally but not dorsally. Thorax elongate–subcylindrical, with three large independent sternites. Wing (Fig. 2) long, slender, narrowly triangular or strap-like, without anal lobe, and deciduous along a definite line of weakness near base leaving a short truncated scale-like stub; margin with dense fringe of long delicate setae, longer on posterior margin than on costal margin. Legs slender; fore coxae more widely spaced than mid or hind coxae; femora and tibiae each subdivided by a subbasal membranous area.

Adult. Head: produced anteriorly to form a conical snout. Antenna clavate (Fig. 3); scape subpyriform, larger than pedicel; pedicel globular; flagellum with one large basal flagellomere and two or three minute terminal flagellomeres; basal flagellomere clavate, with its base narrowed stalk-like and annulated; second flagellomere spine-like, often associated with a few minute spatulate sensilla. Compound eyes holoptic ventrally but not dorsally. Mouthparts consisting of a single small median forwardly directed membranous structure (possibly the labium) bearing a pair of very minute papillae (possibly the labella) situated ventrally at base of snout. Side of head, posterior to eye, with a large prominent ocellus-like lens (possibly the remnant of the larval eye).

Thorax: pronotum small, divided medially into two halves by a forward prolongation of scutum; scutum together with scutellum subequal in length to greatly elongate; postnotum produced caudally to form an endoskeletal phragma within base of abdomen. Legs slender; anterior pair articulated laterally; others articulated more or less ventrally; coxae long and expanded, with double basal articulations; trochanters elongate, much smaller and more slender than coxae; femora elongate, expanded apically, subdivided by a membranous subbasal region; tibiae approximately as long as their corresponding femora, more slender and less expanded apically, also subdivided by a membranous subbasal region similar to that of the femora, and lacking apical spurs. Tarsi slender; fifth tarsomere the longest; first tarsomere next in length; claws long, symmetric, strongly curved, each sharply pointed with a basal tooth.

Wing (Fig. 2) with surface lacking macrotrichia but covered with microtrichia. Venation greatly reduced to a few weakly differentiated veins; R_1 the most distinct, ending in basal quarter of costal margin. Halter very long and well-developed, racket-shaped, widely separated from wing base.

Abdomen: elongate, slender, nearly uniform in diameter, with nine apparent segments covered with microscopic pubescence and with a few setae toward posterior



Figs. 10.2–5. *Palaeodipteron walkeri* Ide: (2) wing; (3) antenna; ventral views of (4) female terminalia and (5) male terminalia.
Abbreviations: goncx, gonocoxite; gonst, gonostylus.

margin of each tergite. Abdominal spiracles lacking. Spermathecae not apparent. Anterolateral paratergal extensions present on segments 3–7.

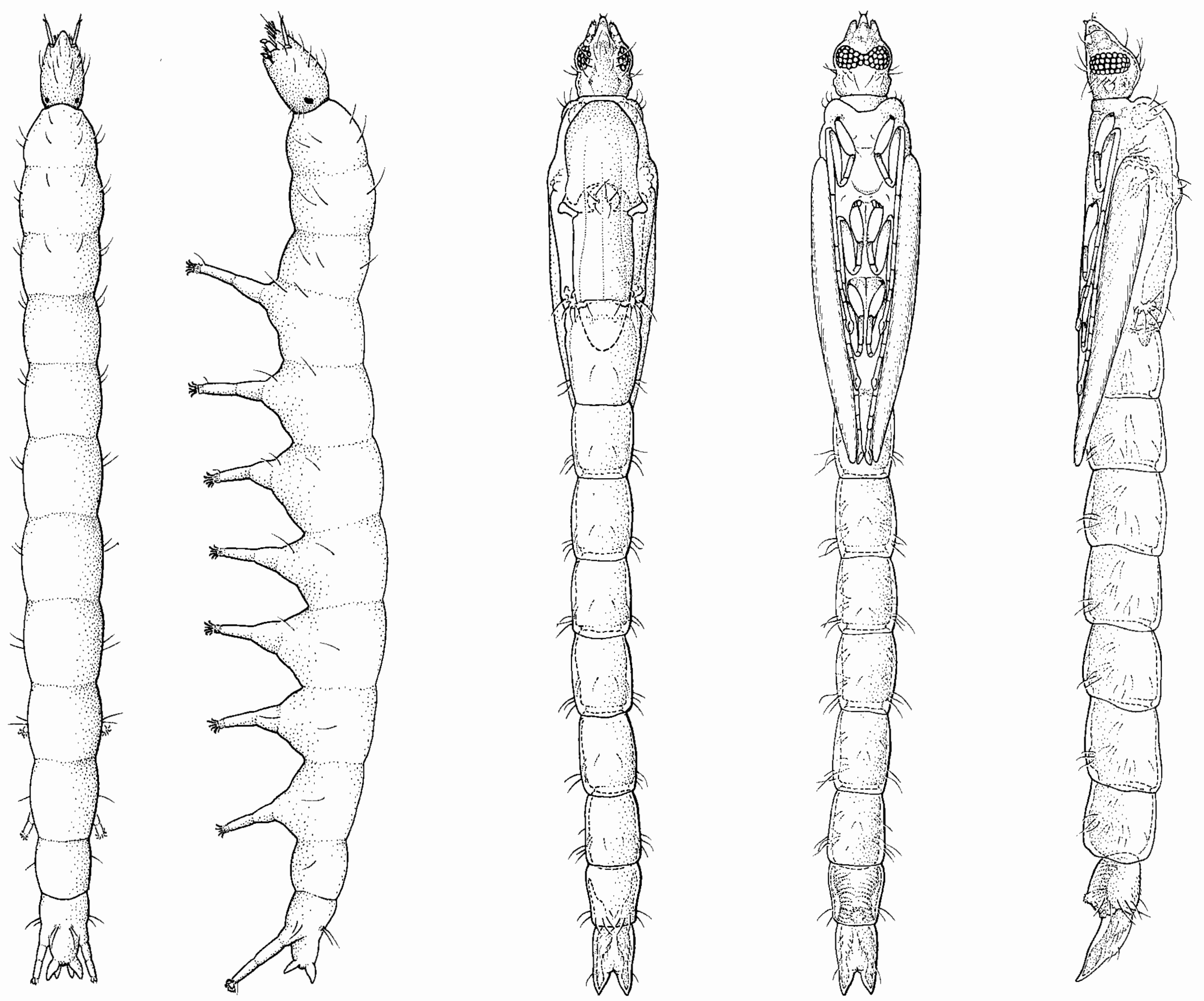
Segments 5 and 6 of male each with a pair of elongate flexible ventrolateral processes. Tergite 8 with a tubercle toward each anterolateral angle, associated with a long bifid backwardly directed paratergal projection. Gonocoxite partially fused at base with cercus; in *Palaeodipteron* Ide (Fig. 5), gonocoxite and cercus either completely fused, or gonostylus arising near middle of gonocoxite at base of a cercus-like apical portion. Aedeagus long, protrusible, normally withdrawn into a cone-shaped median structure (possibly fused parameres); slender aedeagal apodeme extending forward at least as far as abdominal segment 6 (Fig. 5).

Cercus of female one- or two-segmented, sometimes with a curved ventrally directed process arising from basal segment (Fig. 4).

Egg. Known only for *Palaeodipteron*; short, sausage-shaped, semitransparent, with an anterior filament; eggs attached by their filaments in groups to apex of abdomen of female parent. Abdominal segments of developed embryo with pairs of ventrolateral lobes that are precursors of prolegs.

Larva. Small, slender, delicate, whitish, sparsely setose, apneustic, with eight pairs of long slender ventrally projecting abdominal prolegs (Figs. 6, 7).

Head ovate, with capsule complete, not retractile within thorax, brownish, sclerotized when fully grown, with a Y-shaped ecdysial line and a prominent strongly and complexly setose conical labrum; lateral or posterolateral pigmented eyespot present at maturity. Antenna elongate, inserted at base of labrum, with long cylindrical basal segment, short second segment, and slender elongate pointed terminal segment; basal segment also with terminal spur-like stylus giving antenna a biramous appearance. Mouthparts complex; labrum bearing specialized setae of various kinds; ventral surface of labrum consisting of a semicircular finely setose proximal part and an elongate distal part margined by strong setae situated lateral to narrow torma; mandible short and stout, with a large fan-like medially projecting process in *Palaeodipteron walkeri* Ide; maxilla somewhat jaw-like, with two thickened spines (possibly the galea and the lacinia) projecting medially; labium broad, flat, apically toothed, and bearing laterally a pair of broad paralabial plates; spinose plate (possibly the lingua of the hypopharynx) lying dorsal to labium.



6 7 8 9 10

Figs. 10.6–10. Immature stages of *Palaeodipteron walkeri* Ide: (6) dorsal view and (7) lateral view of larva; (8) dorsal view, (9) ventral view, and (10) lateral view of pupa.

Thorax with segments subequal, cylindrical, without appendages or processes.

Abdomen with nine apparent segments. Segments 1–7 each bearing a pair of long ventrally directed two-segmented prolegs; each proleg borne on a process of the body wall and terminating in a crown of specialized spines. Segment 8 without prolegs. Terminal (compound) segment pointed apically, bearing a pair of longer narrower two-segmented prolegs; each proleg terminating in a pair of pectinate plates and a pair of hooks.

Pupa. Slender, exarate, elongate–cylindrical, sparsely setose, apneustic, without prothoracic or other respiratory organs (Figs. 8–10).

Head distinct, bearing a few scattered setae, prognathous, narrower than thorax, and separated from thorax by a constriction; epicranial suture present but usually indistinct. Region of developing compound eye slightly convex; that of clearly visible lateral ocellus-like lens prominently convex. Anterior region snout-like, with a pair of minute median thorn-like articulated projections that are slightly downwardly directed (possibly the mandibles). Antennal sheath forwardly directed, with a large and flattened broadly triangular base occupying a large part of the externolateral region of the head, and terminating in a narrow two-segmented point.

Thorax elongate, flattened ventrally; mesothoracic region very large, wider than abdomen. Leg sheaths long, arranged closely along body wall; third pair extending to posterior region of abdominal segment 3. Wing sheath parallel-sided, bluntly pointed apically, very long and narrow, extending to or beyond posterior margin of abdominal segment 2.

Abdomen with nine distinct segments. Posterior margin of most segments, except for last, with a row of minute denticular setae in addition to general sparse body setae. Terminal segment caudally with a pair of short, widely spaced, acutely pointed ventrally decurved cercus-like processes.

Biology and behavior. All known larvae and pupae occur in rapidly flowing, small, stenothermal streams. Larvae are found among aquatic mosses and on stones, to which they cling with their prolegs. They presumably feed on microscopic plant material, although one species is believed to be ectoparasitic on soft-bodied insect larvae (Rohdendorf and Kalugina 1974). Adults cannot feed because their mouthparts are atrophied. Adults of all species except *Nymphomyia levanidovae* Rohdendorf & Kalugina, of which only pharate specimens have been found, are known in a fully winged condition as well as in a dealated state. The wings are shed along a predetermined line of weakness. Indeed, *Palaeodipteron* adults were known for some years only in a dealated condition. *Nymphomyia alba* Tokunaga is known to fly in subdued light, when it may occur in swarms (Tokunaga 1932). It is not yet definitely known whether *Palaeodipteron walkeri* can fly, although the presence of wings suggests that flight does occur.

Because adults of both *Nymphomyia alba* and *Palaeodipteron walkeri* occur in spring and late summer, these species are believed to have two generations a year (Kevan and Cutten-Ali-Khan 1975). Coupled, dealated adults of *P. walkeri* occur under water and cling to the substrate with specially adapted, enlarged tarsal claws. Eggs are laid in batches of up to 50, which remain attached to the female until after she dies, and develop *in situ*.

Classification and distribution. The family is small with no close relatives, although it is perhaps distantly related to the Deuterophlebiidae (Cutten and Kevan 1970). Three genera are recognized: *Nymphomyia* Tokunaga from Japan and the Soviet Far East, *Felicitomyia* Kevan from the Himalayas (Cutten and Kevan 1970), and *Palaeodipteron* from Quebec as far north as James Bay, New Brunswick, and Maine. Except for *Nymphomyia,* the genera are monotypic and all show a limited and widely disjunct geographic distribution. A fourth, anomalous genus, *Oreadomyia* Kevan & Cutten-Ali-Khan 1975, has now been transferred to the orthocladiine Chironomidae. The literature on the Nymphomyiidae is fully reviewed by Cutten and Kevan (1970), Rohdendorf and Kalugina (1974), and Kevan and Cutten-Ali-Khan (1975). Details of morphology are given by Tokunaga (1932, 1935*a*, 1935*b*, 1936) for adults and pupae of the type species *Nymphomyia alba*, by Ide (1964, 1965) for dealated adults and pupal exuvia of *Palaeodipteron walkeri*, by Cutten and Kevan (1970) for the larvae of *P. walkeri*, and by Rohdendorf and Kalugina (1974) for pharate pupae and larvae of *Nymphomyia levanidovae*. Further details of the life history of *P. walkeri* are given by Kevan and Cutten-Ali-Khan (1975). *Palaeodipteron walkeri* was recently recorded for the first time in the United States by Mingo and Gibbs (1976). In the literature good illustrations of adult and larva are given by Merritt and Schlinger (1978) and by Teskey (1978).

No fossil nymphomyiid is known. Rohdendorf (1964, 1974) discussed relationships with extinct families and placed the Nymphomyiidae in its own infraorder, Nymphomyiomorpha. Rohdendorf and Kalugina (1974) maintain the view of Rohdendorf that the group is quite distinct from other living Diptera and that the nearest relatives are a few Mesozoic forms. Downes (1975) does not agree. Kevan and Cutten-Ali-Khan (1975) briefly reviewed the subsequent conflicting opinions on the systematic position of the family and believe that among recent Diptera, the family appears to form an archaic sister group of the Deuterophlebioidea, whose inclusion in the Psychodomorpha is, at best, dubious.

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AXYMYIIDAE 11

D. M. Wood

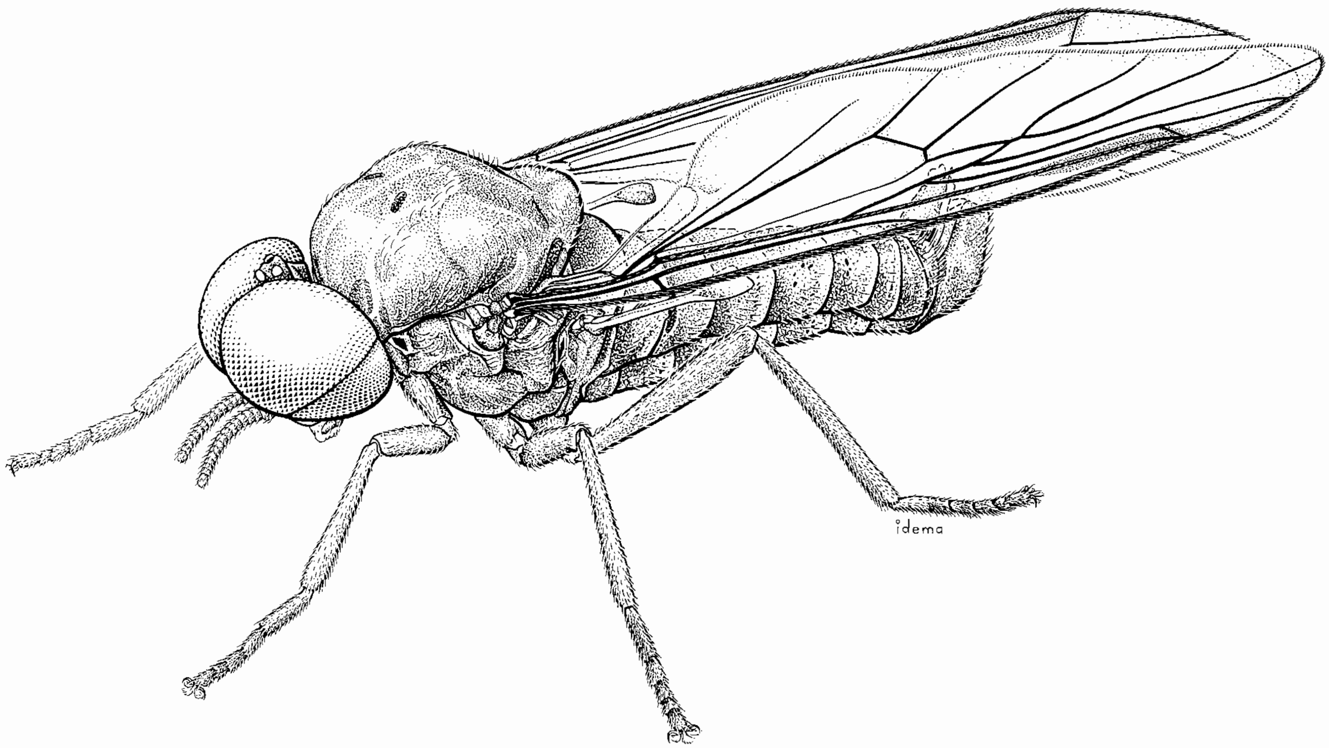
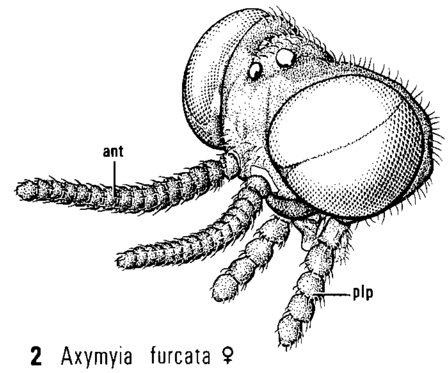


Fig. 11.1. Male of *Axymyia furcata* McAtee.

Medium-sized fairly stout-bodied flies, with large eyes and rather short antennae and legs (Fig. 1); about the size and proportions of *Bibio* Geoffroy, with which the family can readily be confused, but to which it is not closely related.

Adult. Head: large. Compound eyes of male holoptic, contiguous above; those of female broadly separated; each eye divided longitudinally in both sexes into upper and lower portions by a fine line or shallow groove; facets not meeting one another regularly along the groove (Fig. 2); upper portion of male eye larger than lower portion, with larger facets; upper portion of female eye smaller than lower portion, with facets uniform in size in both parts; inner margin of female eye shiny and without facets; ocelli large, all three on a prominent convex tubercle more strongly raised in male than in female. Hind margin of head behind compound eye with a pronounced pale swelling or tubercle (somewhat suggestive of remnant of larval eye in some simuliids). Antenna longer and more slender in male than in female, comprising 16 small moniliform segments; scape and pedicel scarcely differentiated from flagellomeres except by color. Mouthparts vestigial; palpus small, with five moniliform segments; labrum minute, triangular; labella minute. Tentorium short, straight, broadly open along its length, with its relatively large anterior tentorial pit occurring just above point of palpal attachment.

Thorax: cervical sclerite rather massive, triangular; antepronotum greatly reduced, linear medially, and laterally flattened, narrow, and without setae; postpronotal lobes separated medially by scutum, with neither one distinctly delineated from scutum; proepisternum in form of a long parallel-sided half-cylinder; proepimeron reduced to a small sclerite below anterior thoracic spiracle, obliterated or infolded on lower half, not visible externally, with fore coxa thus appearing suspended below proepisternum and anteroventral corner of anepisternum; precoxal bridge absent; basisternum a pair of small triangles, each with a somewhat protruding posteroventral angle overhanging fore coxa. Scutum strongly arched; presutural area of scutum divided transversely into an anterior portion and a posterior portion by a pair of weak sutures, each extending posteromedially from a point above anterior thoracic spiracle to a dark shiny oval spot near middle of scutum (Fig. 1); transverse



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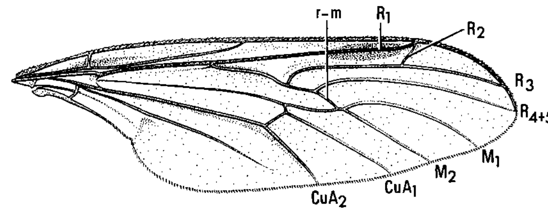

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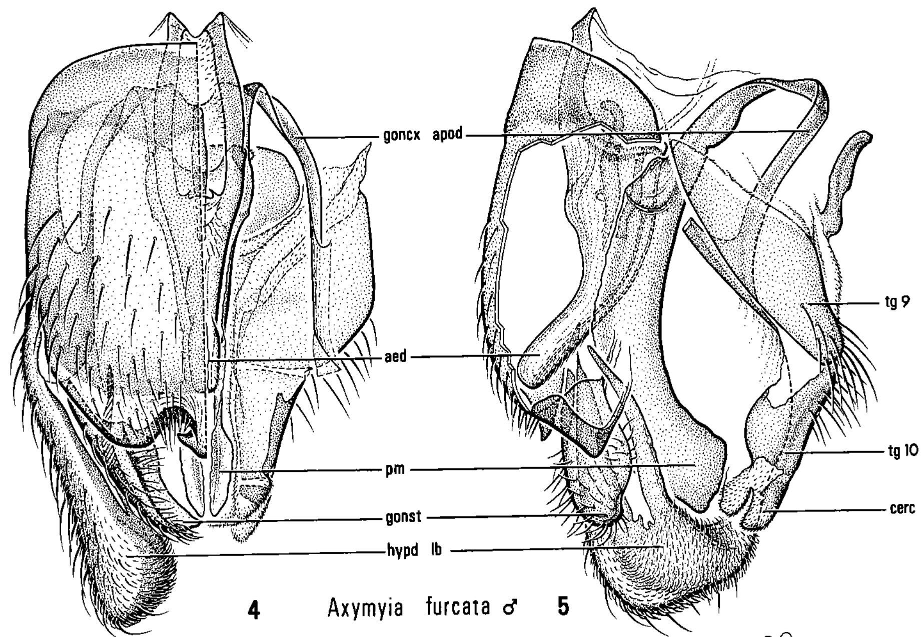
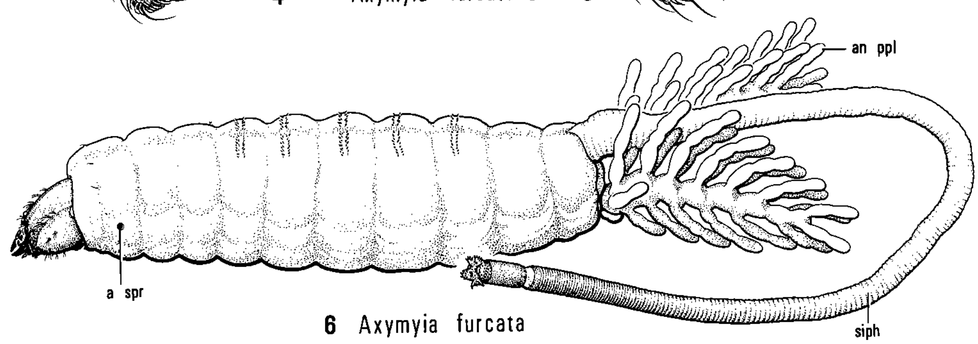
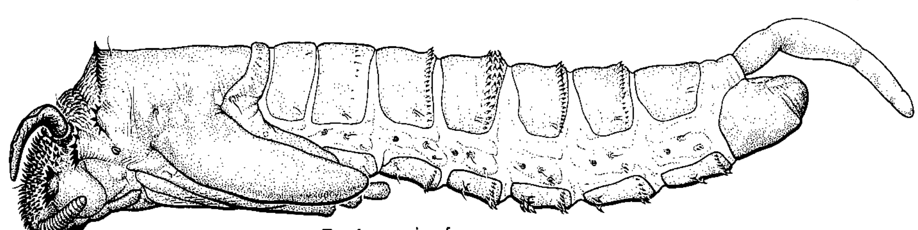


4 Axymyia furcata ♂ 5



6 Axymyia furcata



7 Axymyia furcata

Figs. 11.2–7. *Axymyia furcata* McAtee: (2) dorsolateral view of head of female; (3) wing; (4) ventral view and (5) lateral view of male terminalia with left half of hypandrium removed; (6) dorsolateral view of larva; (7) lateral view of pupa.

Abbreviations: aed, aedeagus; an ppl, anal papilla; ant, antenna; a spr, anterior spiracle; cerc, cercus; goncx apod, gonocoxal apodeme; gonst, gonostylus; hypd 1b, hypandrial lobe; plp, palpus; pm, paramere; siph, siphon; tg, tergite.

suture arising at wing base, and extending medially to disappear behind shiny oval spot; postsutural area of scutum deeply concave medially in front of large rounded scutellum. Anepisternum long and deep, almost completely cleft by linear anepisternal membrane into a large portion anteriorly and a small narrow parallel-sided portion posteriorly; katepisternum long but not especially deep, not overhanging mid coxa. Anepimeron broad, scarcely narrowed by pleurotergite; katepimeron indistinctly differentiated from anepimeron, but distinctly separated from meron; meron very large, subcircular in outline, more than half as long as katepisternum. Metepisternum and metepimeron greatly reduced, each a narrow parallel-sided sclerite. Thoracic vestiture consisting only of small semirecumbent pale hairs; bristles or long erect hairs absent.

Legs fairly short, without spines or long hairs. Fore coxa slightly longer than adjacent katepisternum; mid and hind coxae each half this length, short and more globular, entirely sclerotized medially, without trace of an apicomedial lobe. Empodia spatulate to triangular, with truncate apex, and twice as long as pulvilli.

Wing (Fig. 3) longer than body including extended antennae, with a faint pterostigma in some species. R_2 appearing as a short branch nearly perpendicular to R_{2+3}, ending in C at or just distal to end of R_1; crossvein r-m strongly oblique, appearing as a continuation of Rs; M two-branched. Alula absent. Halter with extremely long stem.

Abdomen: with short sparse recumbent hairs only. Gonocoxites and sternite 9 of male fused into a conspicuous scoop-shaped hypandrium with a prominent lateral lobe that superficially resembles a gonostylus (Figs. 4, 5); true gonostylus minute, hidden below lower edge of lateral lobe; aedeagus tubular; parameres laterally flattened, partially fused to each other medially; segment 10 and cercus not reduced in size, partially concealed in profile by upper border of lateral lobe. Sternite 8 of female enlarged, scoop-shaped, extending posteriorly under genital opening; tergite 8 much smaller than tergite 7; cercus soft, pad-like, two-segmented, with a rather elongate basal segment, and with distal segment bearing numerous rod-like sensilla.

Larva. Amphipneustic; body plump, white; anal papillae greatly elongated, complex; posterior siphon long, rope-like (Fig. 6).

Head capsule partially invaginated into thorax, with a fold of thoracic cuticle covering almost entire posterior half of cranium dorsally and laterally (as in Tanyderidae); invaginated portion of cranium less strongly sclerotized than exposed portion. Frontoclypeal apotome obovate, separated anteriorly from clypeus by a transverse strongly sclerotized bar connecting dorsal mandibular articulations, gradually narrowing posteriorly to a sharp point just short of hind cranial margin. Antenna reduced to a sensory pit located on a small prominence lateral to dorsal mandibular articulations. Labrum a small conical lobe, covered ventrally with anteriorly directed setae; dorsal labral plate delineated from clypeus. Mandibles conical, strongly prognathous, inserted rather close to midline, crowding small narrow labrum, and extending forward more or less parallel to each other; apex strongly sclerotized; one large and one smaller median tooth on biting edge behind apical tooth; inner angle without molar surface or groups of setae; round flattened lobe situated on posterodorsal edge medial to mandibular epicondyle, and fitting into a notch on cranium; apodeme for insertion of mandibular adductor situated on inner angle of mandible, almost touching opposite mandible below labrum. Maxilla greatly reduced, with two-segmented palpus and a slender finger-like setose endite lobe. Labrum a minute finger-like setose papilla, similar to but smaller than maxillary endite lobe. Cranium fully closed ventrally, with a concave semicircular hypostomal bridge; anterior margin devoid of teeth. Setae stout, flattened, branched whisk-like, arranged on head capsule as follows: a longitudinal row of three behind mandibular epicondyle, a curved transverse row of three along anteroventral cranial margin, a curved row of four behind these, one pair on labrum, two pairs on clypeus, and a group of three on outer face of mandible. Pharyngeal filter comprised of two long narrow pairs of opposing plates, each with about 20 longitudinal ribs that each bear a row of branched parallel setae; outline similar to but narrower than outline of frontoclypeal apotome through which it can readily be seen.

Body robust, white or translucent; each segment readily discernible. Anterior spiracle prominent, situated at level of invaginated posterodorsal margin of head. Abdominal segments 1–5 dorsally and ventrally with an inconspicuous transverse row of minute anteriorly projecting spines in front of a similar but sparser row of posteriorly directed spines. Segment 8 in form of an elongate siphon of approximately uniform width throughout, longer than head and body together, arising from an indentation along posterior margin of segment 7; basal one-half to two-thirds of siphon white like the body, movable, and slightly retractable; distal remainder sclerotized, reinforced with closely packed ring-like thickenings; apex of siphon lacking rings, crowned with five tubercles, suggestive of the posterior end of a minute tipulid larva; each tubercle bearing recurved spines of various sizes probably for clearing debris from the tunnel opening; the two dorsolateral tubercles each larger than either the middorsal or two ventral tubercles, and each with a small black posterior spiracle on its inner surface; dorsal tubercle surmounted by a pair of hair tufts. Two anal papillae present (four in exotic species), half as long as body, with three rows of branches in *Axymyia furcata* McAtee (Fig. 6); both branches and main stalk with moniliform thickenings.

Pupa. Antennal sheath free, but wing and leg sheaths closely appressed (Fig. 7). Upper surface of head and prothorax strongly sclerotized, forming a flattened nearly circular disc with strong spines over its surface and around the periphery, especially on dorsum of prothorax, and on a lobe below respiratory organ and above eye. Prothoracic respiratory organs long, slender, curving downward around periphery of disc to suggest the horns of a water buffalo; each respiratory organ with a double row of minute openings arranged in a sinuous row along dorsolateral edge. Remainder of pupa white or translucent. Abdominal segments 2–7 each with a pair of small spiracles. One or two transverse rows of denticles occurring on posterior borders of tergites 3–6 and sternites 3–7; denticles usually small and backwardly projecting but noticeably larger and more numerous on tergite 4 where some are also directed anteriorly; additional row of larger denticles also present on sternites 4–7, placed more anteriorly. Tail-like process on segment 8 in *A. furcata* evidently a remnant of larval siphon, apparently retaining connection with pupal hemolymph, and thus possibly functioning as a pupal gill.

Biology and behavior. The life cycle was first described in detail by Krogstad (1959). Larvae occur together in two sizes, suggesting a 2-yr life cycle. They excavate a flask-shaped cavity in rotting wood of various species of trees. The cavity descends from a minute opening at the surface that accommodates the apex of the siphon more or less vertically down into the saturated wood where it widens gradually to house the larval body. The larva apparently remains head down in the same cavity throughout its life and enlarges the cavity as it grows. It therefore must obtain all its nourishment from the material it excavates and from organisms growing in the cavity. Only logs that are free from bark and moss and continuously in contact with water or damp mud have been found to contain larvae; the wood itself, though water-logged, remains light-colored and is often hard enough to be difficult to pry open with a pocketknife. The larva must use some of the microorganisms or fungi that inhabit the cavity for food because the mandibles, though obviously well suited for creating the cavity, lack any structures for grinding wood into fine particles; the labrum, maxillae, and labium also appear singularly unfitted for feeding on solid matter. Furthermore, the cavity alone hardly seems large enough to provide enough food material. Although Mamaev and Krivosheina (1966) have reported many small larvae living together in one cavity, each larva of *A. furcata* was found alone in its own cavity (D. M. Wood, unpublished). The presence of elaborate anal papillae on the larva and a long, translucent tail-like extension on the pupa suggests that the immature stages can withstand total immersion in water during spring flooding.

When mature in autumn or early spring, the larva reverses its direction, enlarging the tunnel upward until it reaches the surface (Krogstad 1959). Pupation takes place at the mouth of the cavity (Krogstad 1959) or just below the surface (D. M. Wood, unpublished); the circlets of spines on the head and prothorax are apparently used for breaking the paper-thin covering at the mouth of the cavity upon emergence. Adults emerge in April or early May depending on latitude. They are seldom collected, and their behavior is unknown.

Classification and distribution. The family Axymyiidae contains, at present, five described species (Mamaev 1968). One species, *Axymyia furcata* McAtee (McAtee 1921), has been found in Minnesota, Ontario, and Quebec, and in the mountains as far south as North Carolina. A second North American species has recently been discovered in Oregon. The remaining species, all occurring in the Palaearctic region, have the same basic structure but are segregated into two genera: *Protaxymyia* Mamaev & Krivosheina, including *melanoptera* Mamaev & Krivosheina and *japonica* Ishida; and *Mesaxymyia* Mamaev, including *kerteszi* Duda from eastern Europe and *stackelbergi* Mamaev from eastern Siberia. An additional undescribed species from Alaska, which Hennig (1973) mentioned under the Perissommatidae, is known from a single damaged female. The wing lacks an anal vein, a derived character of *Perissomma,* but the thoracic structure and the rest of the wing venation are more consistent with Axymyiidae. This species probably represents a new subfamily.

The systematic position of *Axymyia* has had a long unsettled history. Adult morphology early led to its association with the Anisopodidae or the Bibionidae; but because R_2 and R_3 are separate, more recent authors have preferred to place it in the Pachyneuridae. Even though larvae of both *Pachyneura* and *Axymyia* bore in rotting wood, they are so different that close relationship between the two seems remote, and Mamaev and Krivosheina (1966) have accordingly suggested a separate superfamily status, the Axymyioidea.

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PACHYNEURIDAE 12

D. M. Wood

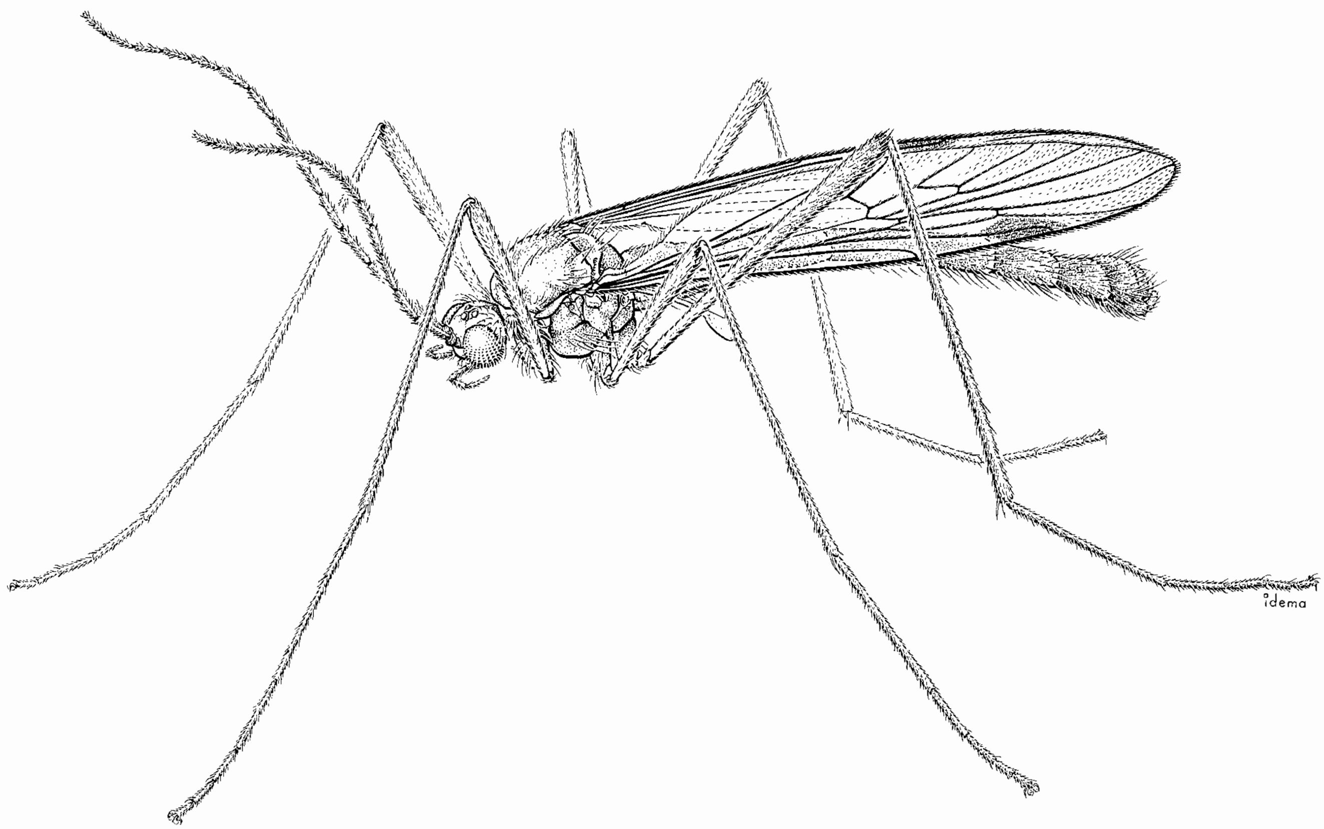


Fig. 12.1. Male of *Cramptonomyia spenceri* Alexander.

Slender medium-sized long-winged long-legged tipulid-like flies (Fig. 1). Only a single Nearctic representative, *Cramptonomyia spenceri* Alexander (Alexander 1931).

Adult. Head: fairly small, globose. Eye subspherical in profile, with size and shape similar in both sexes, slightly emarginate medially to accommodate antennal bases, covered with short hairs; eye facets all of equal size. Three prominent ocelli, each on its own tubercle, separated from one another by a deeply impressed Y-shaped groove. Frons broad (except in male *Pergratospes* Krivosheina & Mamaev), narrowing slightly toward vertex. Occiput broadly rounded behind, with sparse erect bristly hairs; occipital foramen open to mentum. Antenna short, scarcely as long as thorax, except in male of *Cramptonomyia* Alexander where it is as long as abdomen; scape and pedicel hardly more than twice as long as wide; 13–15 flagellomeres, cylindrical (*Pachyneura* Zetterstedt and *Cramptonomyia*) or moniliform (*Haruka* Okada and *Pergratospes*), gradually decreasing in length distally; apical flagellomere pointed, slightly longer than penultimate flagellomere. Palpus five-segmented, almost half length of antenna in female of *Cramptonomyia,* with last palpomere enlarged and rounded apically; sensory vesicle of palpomere 3 absent in both sexes. Prementum short; labella small.

Thorax: cervical sclerite broad, triangular, with short anterior supporting rod; antepronotum linear with group of bristly hairs, almost obliterated middorsally, well-developed laterally, overhung by convex anterior edge of scutum; postpronotal lobe shortened and elevated, strongly convex, slightly curved, about as wide as antepronotum, and separated posteromedially from scutum by a deep crease; proepisternum with a patch of hairs, and connected to prosternum by rather broad precoxal bridge; proepimeron fairly well-developed, long, narrow, triangular, no wider than anterior spiracular opening, and separated from proepisternum by a deep groove-like apodemal invagination above fore coxa. Scutum evenly and shallowly convex, with weak triangular depression behind postpronotum, an even more weakly marked transverse suture, two faint longitudinal dorsocentral impressions, and with a few scattered acrostichal hairs, one pronounced row of bristly dorsocentral hairs, one row of bristly supra-alar hairs, a group of postalar hairs, and a few irregularly placed bristles above wing base; scutellum broadly rounded, fringed apically with bristles and hairs extending horizontally; anepisternum rather small, triangular, distinct from proepimeron; katepisternum broadly rounded below, scarcely overhanging mid coxa anteriorly, with middle of upper half bearing an irregular longitudinal row of short bristly hairs; epimeron long, rectangular; meron mainly membranous posteriorly, sclerotized along anterior margin only. Metanotum present but reduced to a narrow band at base of abdomen; metepisternum quadrate; metepimeron linear.

Legs very long. Coxae all of similar length; fore coxa cylindrical, sclerotized medially; mid and hind coxae membranous medially except for a prominent sclerotized medially projecting lobe near apex. Empodia pulvilliform, about the same size as pulvilli, shorter than claws.

Wing slightly to moderately infuscate or patterned with distinct pterostigma (Fig. 2). Rs bifurcate at level of crossvein r-m; R_{2+3} branched in *Pachyneura*, but unbranched, more or less sinuate, and connected to R_{4+5} in other genera by a short supernumerary radial crossvein; M_1 and M_2 usually with common basal petiole, or less often arising separately at level of crossvein r-m; cell dm usually present, but lacking in *Pachyneura* and sometimes partially or completely lacking on one or both sides in some specimens of *Cramptonomyia*, due to atrophy of crossvein dm-cu. Wing base narrowed, almost petiolate; alula absent; calypter moderately well-developed.

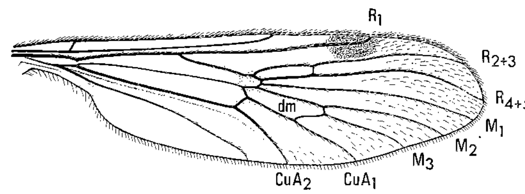
Abdomen: slender, longer than wing. Sternite 9 of male very narrow, separate from anteroventral margin of gonocoxite, and fused laterally to tergite 9 to form ring-like segment (Figs. 3, 4); tergite 9 broad, flat, truncate posteriorly, overhanging remaining segment and cerci, and fringed along posteroventral edge with fine dense downwardly projecting setulae; gonostylus clavate, with inner surface of rounded apex studded with numerous minute black setulae; parameres fused medially, complexly lobed and folded forming hood over tubular aedeagus; male cercus greatly reduced. Female cercus prominent, two-segmented.

Larva. Peripneustic, with rounded dorsoventrally flattened reddish brown head, stout mandibles, and elongate whitish body; strongly suggestive of larva of bibionid *Hesperinus* Walker, but with larger setae, broader flatter head, and more widely placed antennae (Fig. 5; see also Krivosheina and Mamaev 1970).

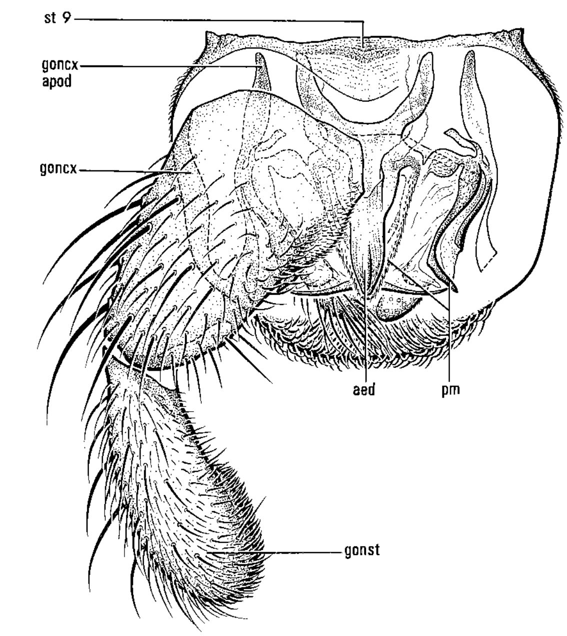
Head extremely broad, wider than long, flattened dorsally, with posterolateral angle especially enlarged to accommodate origin of mandibular adductor. Labrum short and broad, weakly bilobate (much as in Bibionidae); dorsal labral shield broadly rounded anteriorly, with a fairly straight to broadly V-shaped posterior margin delineating it from clypeus; each labral lobe ventrally resembling a broad flat pad, and bearing four to six small sharp peg-like setae distally and a group of finer spines proximally; narrow torma subtending each lobe. Clypeus continuous with and not distinguishable from frontoclypeal apotome; apotome arrowhead-shaped, broadest anteriorly behind clypeus, extending back half to three-quarters length of head, with two pairs of strong setae behind clypeus, a third pair near margin at narrowest part of apotome, and a fourth pair proximal to posterior widening. Antennae widely separated, each located proximal to mandibular epicondyle, each with short stout basal segment and minute conical or ovoid second segment, and with a two-segmented cylindrical peg arising beside it. Lens-like spot small, convex, unsclerotized, just below and to side of antennae, apparently an ocellus. Cranium with setae at each side of frontoclypeal apotome as follows; one at narrowest part of midventral line or gular cleft, one posterior to mandibular hypocondyle, one just below ocellus, one on side of head well behind ocellus, one on upper part of head behind antennae opposite narrowest part of apotome, and in *Pachyneura* only, one at proximal apex of apotome. Mandible massive, broad basally, constricted somewhat at midpoint, widening apically, terminating in three or four large blunt teeth; maxilla with clearly differentiated median lobe and small two-segmented palpus; labium vestigial, reduced to a small unadorned plate. Head capsule open or less strongly sclerotized longitudinally along gular cleft.

Prothorax dorsally with two pairs of lightly sclerotized areas in *Cramptonomyia* and *Pergratospes* around origins of some of the muscles evidently used to turn the head. Anterior thoracic spiracle about equal in size to that on abdominal segment 8, and about three times as large as those on abdominal segments 1–7; posterior thoracic spiracle lacking in *Cramptonomyia* and *Pergratospes*, but present in *Pachyneura* (as in the Bibionidae), intermediate in size between anterior thoracic and first abdominal spiracles. One transverse row of regularly placed hairs more or less encircling the prothorax and a second row across dorsum; each subsequent segment with a single encircling row (19–24 hairs per segment). All three thoracic segments each with transverse ventral swelling that may be a creeping welt, with a pair of strong setae on each posterolateral corner.

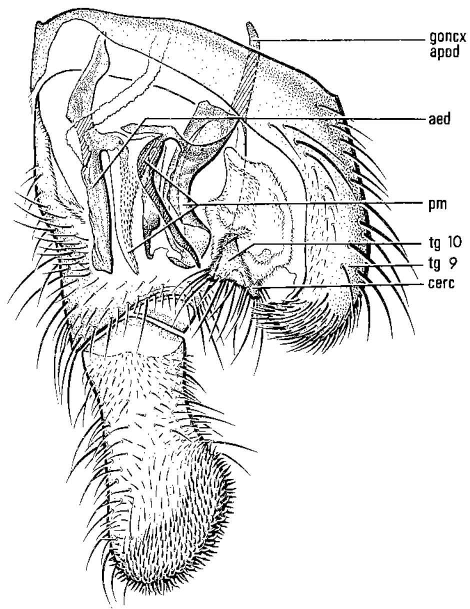
Pupa. Exarate, slender, elongate. Antennal sheath of *Cramptonomyia* well-separated from head and body except at apex. Posterior margins of abdominal tergites 3–8 each with a transverse dorsal row of four pairs of fairly large colorless spine-like projections; each spine furnished, in *Cramptonomyia*, with a darkly sclerotized somewhat hooked apex and a basal seta that is exceptionally elongate on the secondmost lateral spine; abdominal pleurites 3–8 armed with two similar spine-



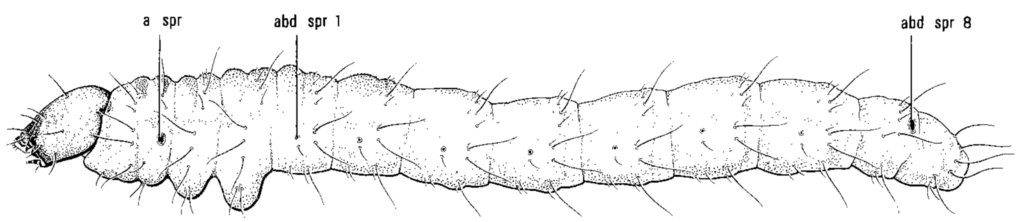
2 Cramptonomyia spenceri ♂



3 Cramptonomyia spenceri ♂



4 Cramptonomyia spenceri ♂



5 Cramptonomyia spenceri

Figs. 12.2–5. *Cramptonomyia spenceri* Alexander: (2) wing; (3) ventral and (4) lateral views of male terminalia, with left gonopod removed; (5) lateral view of larva.

Abbreviations: abd spr, abdominal spiracle; aed, aedeagus; a spr, anterior spiracle; cerc, cercus; goncx, gonocoxite; goncx apod, gonocoxal apodeme; gonst, gonostylus; pm, paramere; st, sternite; tg, tergite.

like projections, each with an exceptionally long basal seta; terminal abdominal segment with an exceptionally strong pair of apical hooks that have a prominent spine-studded tubercle dorsally at the base of each.

Biology and behavior. The immature stages of *Haruka* are unknown, but larvae of other genera of the Pachyneuridae have been found boring in rotten wood. The life history of *Cramptonomyia spenceri* was discussed by Vockeroth (1974). He stated that this species is associated with alder (*Alnus rubra*) and that adults occur in late winter (February to April) in wet coastal forests of southern British Columbia, Washington, and Oregon. He also noted that females lay their eggs on decayed alder wood and that newly hatched larvae tunnel superficially under the bark or just below the surface of the bare wood; larval development probably takes more than 1 yr. Empty pupal skins have been found protruding from well-rotted alder logs. Males, which were more often collected than females, were taken by sweeping low vegetation. They apparently do not form a mating swarm.

Classification and distribution. The Pachyneuridae includes only four species: *Pachyneura fasciata* Zetterstedt from Europe and Asia, *Haruka elegans* Okada from Japan, *Pergratospes holoptica* Krivosheina & Mamaev from eastern Siberia, and *Cramptonomyia spenceri* Alexander from western North America. The last three genera share several characters that differ from *Pachyneura*, which has led to their segregation as a separate family, the Cramptonomyiidae (see Krivosheina and Mamaev 1970). They all have an unbranched R_{2+3} and a supernumerary crossvein connecting R_{2+3} with R_{4+5} (or depending on the interpretation, a recurrent branch of R_{2+3}, perhaps R_2); all three have cell dm, although it is often incomplete in *Cramptonomyia*; and the larvae all lack a posterior thoracic spiracle. These similarities suggest that the three genera are monophyletic. *Pachyneura*, which also exhibits the branched R_{2+3} but not the loss of posterior thoracic spiracles in the larva, is evidently their closest relative and may be their primitive sister group. The three genera are considered here to form the subfamily Cramptonomyiinae of the Pachyneuridae. On the basis of larval and genitalic structures they are evidently closely affiliated with the Bibionidae (including *Hesperinus*), not with the Anisopodidae.

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BIBIONIDAE 13

D. E. HARDY

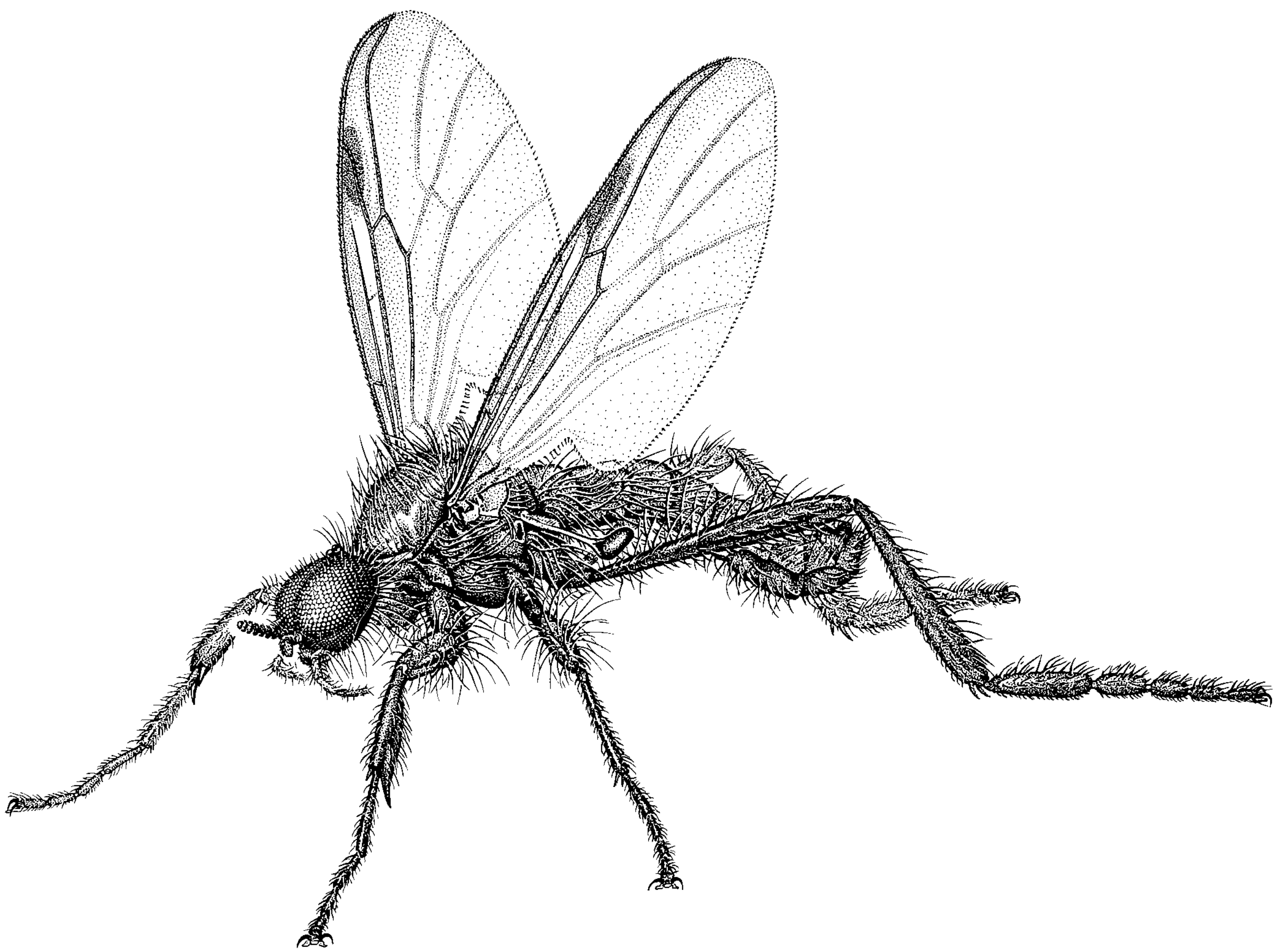


Fig. 13.1. Male of *Bibio longipes* Loew.

Small to moderately large, mainly dark-colored rather setose flies (Fig. 1). Wing varying from about 4.7 to 7.0 mm long, with long basal radial and basal medial cells, and with fork of Rs, when present, arising at or beyond crossvein bm-cu.

Adult. Head: distinctively shaped, narrower and more elongate in female (Fig. 3) than in male (Fig. 1). Eyes of male holoptic; upper two-thirds of each eye consisting of larger facets, and lower one-third with smaller facets; eyes of female widely separated, usually about the length of that part of head behind eyes; ocelli situated on well-developed prominence. Antenna fairly short (except very long in *Hesperinus* Walker), situated on lower part of head near lateral margin of subcranial cavity; flagellomeres rounded and compact but more elongate in *Hesperinus*, usually numbering from seven to ten. Proboscis usually short, but sometimes elongate; palpus usually with five segments.

Thorax: antepronotum moderately well-developed, with rather prominent lateral setose lobes each sometimes bearing a dorsomedial row of short spines; postpronotal lobes small, sometimes obscure. Scutum conspicuously raised dome-like, narrow anteromedially, widening posteriorly, sometimes with a row of short spines along the anterior margin; scutellum small; subscutellum also somewhat reduced; pleural sclerites well-developed, variously bare or setose. Legs simple in Hesperininae and Pleciinae, with strong apical spurs or with an apical ring of spines and one or more sets of proximal spines on fore tibia in Bibioninae (Figs. 4, 5); claws short and simple; empodia and pulvilli pad-like, setose. Sc extending approximately three-fourths length of wing (Figs. 6–11), often complete or nearly so; R_1 ending shortly beyond Sc; Rs simple (R_{4+5}), or forked (R_{2+3} and R_{4+5}) with position and course of R_{2+3} generically important; crossvein r-m situated at or beyond middle of wing; M two-branched; CuA_1 and CuA_2 extending to margin; CuP poorly developed; A_1 variably developed but usually weak, sometimes extending to margin; A_2 when present short and faint.

Abdomen: usually long and slender, often upturned at apex in male, densely setose in *Bibio* Geoffroy, relatively sparsely pilose in other genera.

Female tergites 1–8 and sternites 1–8 well-developed; tergite 9 usually well-developed but sometimes reduced medially; tergite 10 small. Cercus prominent, basically two-segmented in *Hesperinus* and Pleciinae although basal segment sometimes greatly reduced, but one-segmented in Bibioninae. Sternite 8 with variably developed hypogynial valves. Genital fork, or sternite 9, variably developed but usually conspicuous. Hypoproct usually prominent, membranous or variably sclerotized, sometimes notched posteriorly, and occasionally with an additional pair of short lobes. Three spermathecae present, varying in shape from moderately large elongate sacs to tiny sclerotized spheres.

Male terminalia usually large, heavily sclerotized. Epandrium usually large, often emarginate posteromedially, sometimes projecting over and partially or completely concealing cerci and hypoproct. Cercus well-developed. Hypandrium narrow, often greatly reduced. Gonocoxites enlarged, fused ventrally, with a variable posteromedial emargination, sometime fused with epandrium dorsally to form a capsule-like structure; gonostylus usually a rather short and simple digitiform structure but sometimes bilobate as in *Hesperinus* and *Bibiodes* Coquillett. Aedeagus relatively simple, with variously sclerotized and membranous areas, often with short stout setae apically and with a variously developed aedeagal apodeme. Parameres fused medially, variously sclerotized, often plate-like, and partially to almost entirely surrounding aedeagus.

Egg. Cylindrical, oblong, rounded on each end, larger on one end, faintly shining, microscopically sculptured, covered with minute projections. Sculpturing of chorion sometimes showing specific characteristics.

Larva. Body subcylindrical, slightly flattened dorsoventrally, 6.0–24 mm long, with slight downward curvature in lateral view, distinctly 12-segmented with segment 1 the longest and sometimes appearing partially divided (Figs. 12–14).

Head protruding, slightly longer than wide, shining brown to black, much darker and more heavily sclerotized than body; hind part pale brown and bare, retractile into segment 1 of thorax; front part darker, bearing several strong setae. Antenna small, setose. Eye absent, or consisting of a single ocellus or inconspicuous eyespot. Mandible strong, heavily sclerotized; arrangement and number of teeth on inner surface specifically important; inner surface possessing characteristic clump of long fine hairs near middle. Maxilla short, stout, bearing numerous strong spine-like setae at apex of palpus and endite of stipes. Labium often characteristic in different species; hypopharynx usually about one-half wider than prementum.

Respiratory system holopneustic, with 10 pairs of spiracles located on all body segments except segment 2 (mesothorax), and segment 8 in all but *Hesperinus* (posterior spiracle in *Hesperinus* on segment 8, but on segment 9 in all other genera); spiracles usually darker than body integument, sometimes partially protruded; posterior pair (Figs. 15–17) two to four times longer and more dorsal than other spiracles, with one ecdysial scar in *Penthetria* Meigen, two scars in *Bibio* Geoffroy, and three scars in *Dilophus* Meigen; other spiracles located laterally, with a single scar; spiracular openings numerous, in a line encircling periphery of spiracular plate. Integument covered with characteristic rows of spines and processes, as well as microscopic scale-like spicules; spicules variable in size and shape and important taxonomically, differing mainly in number and position of short sharp-pointed spinules that they bear (Figs. 12–14, 18).

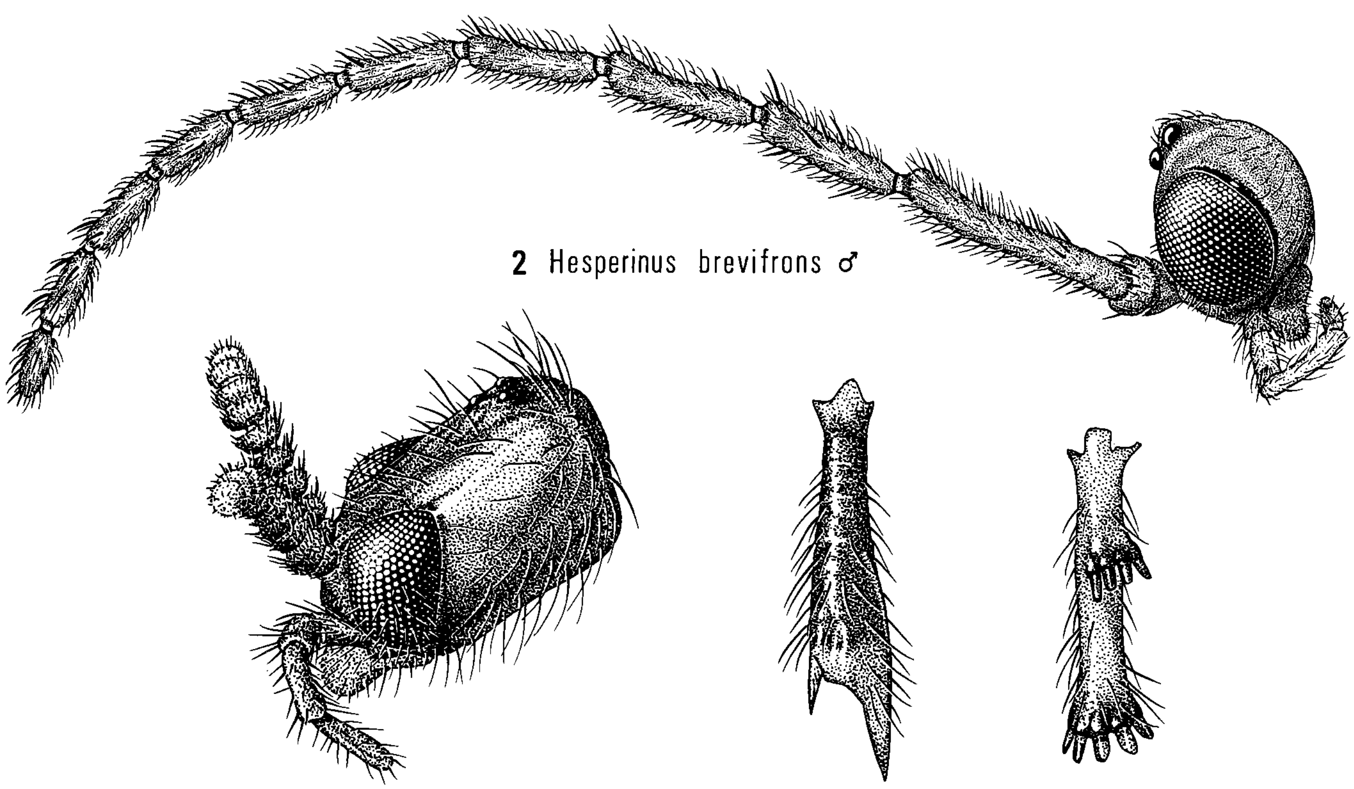
Pupa. Elongate, rather slender, slightly tapering toward posterior end. Cuticle pale, white, smooth, transparent in newly formed pupa with darker parts of head and thorax plainly visible through integument; anterior portion often armed with small projections. Female usually slightly larger than male, with smaller eye and more abruptly narrowing anterior end; eye in male large, slightly protruding, visible through pupal case. Head pressed flat on front part of thorax; short antenna extended laterally under eye. Thorax short; legs and wing pressed closely together on venter. Ecdysial line of pupal case on dorsomedial longitudinal ridge.

Biology and behavior. Larvae of Bibionidae are mainly scavengers living in decaying organic materials, in soils rich in humus, and among roots of grasses and other plants; they are most commonly found in manures and decaying leaves, grassy meadows, forest litter, and pastures. They frequently feed on roots of grasses or roots and underground parts of other plants. The literature records numerous instances of severe damage to cereal crops, vegetables, forage crops, pasture lands and grasses, and seedlings of many other plants. The importance of damage caused by Bibionidae has been substantiated by many researchers, including Strickland (1916), Maier-Bode (1936), Hardy (1945, 1958), Bollow (1954), and Spitzer (1966).

In the Nearctic region, bibionids occur almost exclusively in the spring. Species of *Bibio* are often seen swarming in tremendous numbers. The swarms consist predominantly of males and are obviously mating dances. Adults of *Dilophus* are often captured at flowers. Adults are evidently short lived, lasting only a few days, just long enough for copulation and laying of eggs. The gravid female digs a burrow several centimetres deep in moist earth with fossorial spurs (*Bibio*) or spines (*Dilophus*) on the fore tibiae. Each egg mass ordinarily contains 200–300 eggs. Very little is known of the biologies of Nearctic species. Most of the life cycle is spent in the larval stage and most species probably overwinter as mature larvae. Morris (1917, 1921, 1922), Hennig (1948), Brauns (1954), Brindle (1962), and Krivosheina (1962) have discussed the immature stages.

Classification and distribution. The most recent monograph of the Nearctic species was published in 1945 by Hardy, who described 78 species and three subspecies. This number is only about one-tenth of the 700 known species for the world. Species are most abundant in the tropics, where *Plecia* Wiedemann is predominant.

The earliest positively identified bibionid is *Plecia myersi* Peterson from Canadian amber of Upper Cretaceous age, from Cedar Lake, Manitoba (Peterson 1975). Except for this record, all the fossils definitely known to belong to this family are from the Cenozoic era. The Bibionidae apparently enjoyed their heyday in the middle and late Tertiary period. From fossil evidence they were one of the most abundant insects of the time. Bibionid remains are abundant in most Oligocene and Miocene deposits although they are not common in amber deposits. Rice (1959) indicates that some doubt exists concerning the dating of the Tertiary basins of British Columbia; they may be older than originally believed, probably belonging to the Eocene. Only a single species, *Bibio sereri* Massalongo from Italy, is listed by Handlirsch (1908) from Eocene deposits. James (1937), Carpenter *et al.* (1938), Melander (1949), and Rice (1959) discuss fossil species. Bibionids are among the most characteristic fossils of the Florissant shales and Creede formations of the Colorado and Tertiary basins of British Columbia. It is interesting that 20 out of the 22 species described from the British Columbia deposits are *Plecia*, which now mainly inhabit the tropics.



2 Hesperinus brevifrons ♂

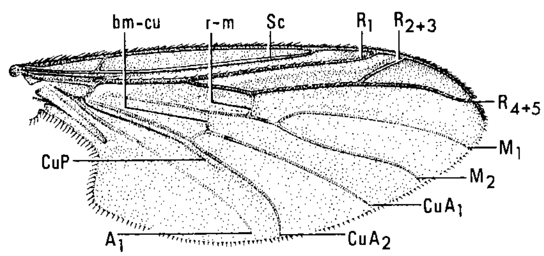
3 Bibio sp. ♂ 4 Bibio sp. ♂ 5 Dilophus stigmaterus ♂

Figs. 13.2–5. Details of head and leg: lateral view of head of (2) *Hesperinus brevifrons* Walker and (3) *Bibio* sp.; anterior view of foreleg of (4) *Bibio* sp. and (5) *Dilophus stigmaterus* Say.

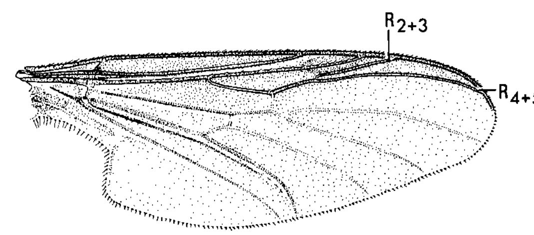
Keys to genera

Adult

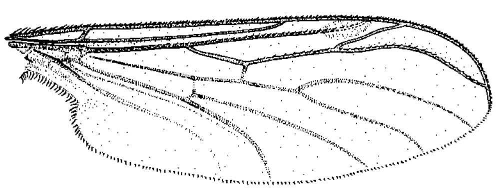
1. Rs furcate (Figs. 6–8). Legs simple 2
   Rs unbranched (Figs. 9–11). Fore tibia with large apical spurs (Fig. 4) or with ring of spines at apex and one or two sets of spines above apex (Fig. 5) .... BIBIONINAE....4
2. Antenna with rather short and compact flagellomeres that are scarcely longer than wide (Fig. 3) .... PLECIINAE....3
   Antenna elongate (Fig. 2), with flagellomeres three to ten times longer than wide; first flagellomere one-half longer than head .... HESPERININAE....***Hesperinus*** Walker
   1 sp., *brevifrons* Walker; boreal, Rocky Mountains
3. R_{2+3} short, oblique or vertical in position (Fig. 6) .... ***Plecia*** Wiedemann
   2 spp.; southern North America and 1 sp., Newfoundland; Hardy 1945
   R_{2+3} rather elongate, extending almost parallel to R_{4+5} (Fig. 7) .... ***Penthetria*** Meigen
   1 sp., *heteroptera* (Say); widespread



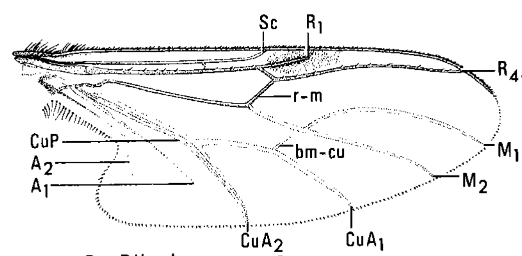
6 Plecia americana ♂



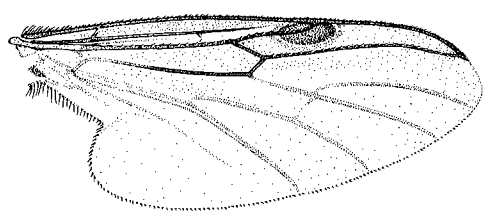
7 Penthetria heteroptera ♂



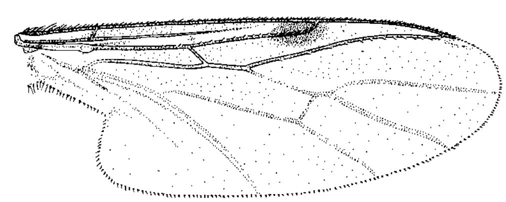
8 Hesperinus brevifrons ♂



9 Dilophus sp. ♂



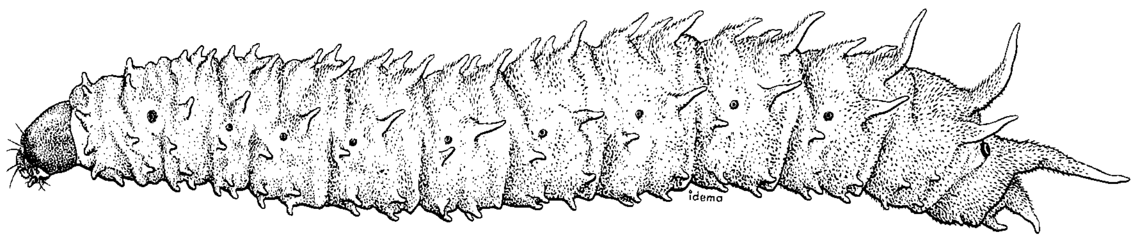
10 Bibio xanthopus ♂



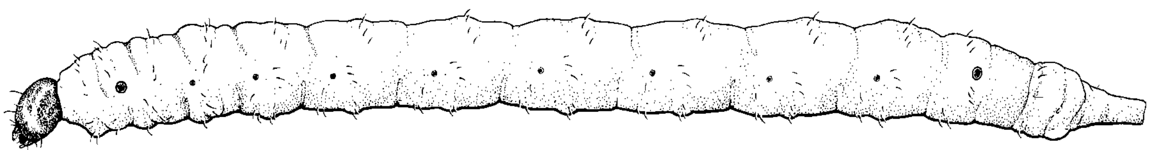
11 Bibiodes aestivus ♂

Figs. 13.6–11. Wings: (6) *Plecia americana* Hardy; (7) *Penthetria heteroptera* (Say); (8) *Hesperinus brevifrons* Walker; (9) *Dilophus* sp.; (10) *Bibio xanthopus* Wiedemann; (11) *Bibiodes aestivus* Melander.

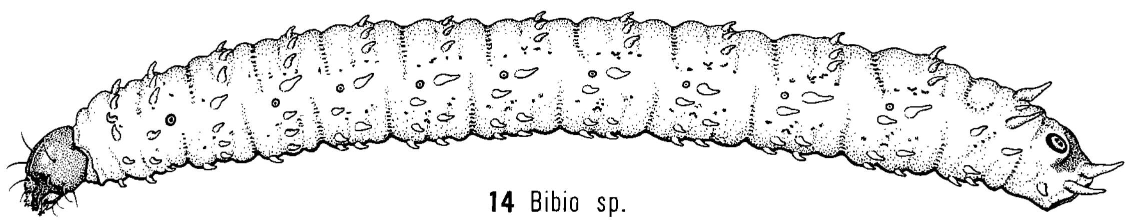
4. Fore tibia produced apically to form two spurs (Fig. 4) 5
   Fore tibia with ring of apical spines and one or two other sets of spines (Fig. 5) .... ***Dilophus*** Meigen
   18 spp., 2 subspp.; widespread; Hardy 1945
5. Stem of R_{4+5} fused with stem of M_{1+2} for a short distance, obliterating crossvein r-m (Fig. 11). Gonostylus of male bilobate .... ***Bibiodes*** Coquillett
   3 spp.; Canada, western U.S.A., Mexico; Hardy 1945
   Stem of R_{4+5} not fused with stem of M_{1+2}; these veins joined by crossvein r-m (Fig. 10). Gonostylus of male simple .... ***Bibio*** Geoffroy
   53 spp., 1 subsp.; widespread; Hardy 1945



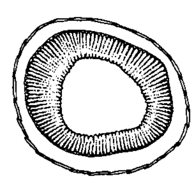
12 Plecia nearctica



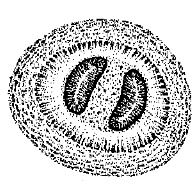
13 Hesperinus rohdendorfi



14 Bibio sp.

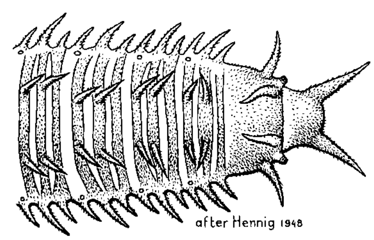


15 Penthetria sp.



16 Bibio sp.

17 Dilophus sp.



18 Penthetria holosericea

Figs. 13.12–18. Larvae: lateral view of (12) *Plecia nearctica* Hardy, (13) *Hesperinus rohdendorfi* Krivosheina & Mamaev (not Nearctic), and (14) *Bibio* sp.; posterior spiracle of (15) *Penthetria* sp., (16) *Bibio* sp., and (17) *Dilophus* sp.; (18) terminal abdominal segments of *Penthetria holosericea* Meigen (not Nearctic).

Larva

1. Body with prominent fleshy processes, especially on last two body segments (Figs. 12, 14, 18); segments lacking black bristles 2
   Body smooth, lacking fleshy protuberances; all segments with short black bristles (Fig. 13) .... HESPERININAE.... ***Hesperinus***
2. Posterior spiracle with single large ecdysial scar (Fig. 15). All body segments conspicuously covered with long protuberances (Figs. 12, 18) .... PLECIINAE....3
   Posterior spiracle with two or three ecdysial scars (Figs. 16, 17). Anterior body segments with short processes; only two posterior segments with prominent protuberances (Fig. 14) .... BIBIONINAE....4
3. Abdominal segments with eight protuberances arranged in three irregular rows over dorsum, with strongest protuberances on posterior portion of body (Fig. 12) .... ***Plecia***
   Each abdominal segment with four long protuberances arranged in two rows (Fig. 18) .... ***Penthetria***
   Krivosheina 1971, personal commun.
4. Two ecdysial scars in posterior spiracle (Fig. 16). Body processes well-developed, arranged in irregular transverse rows on each segment (Fig. 14) .... ***Bibio***
   Three ecdysial scars in posterior spiracle (Fig. 17). Body processes less numerous, small and inconspicuous, except on last two posterior segments .... ***Dilophus***

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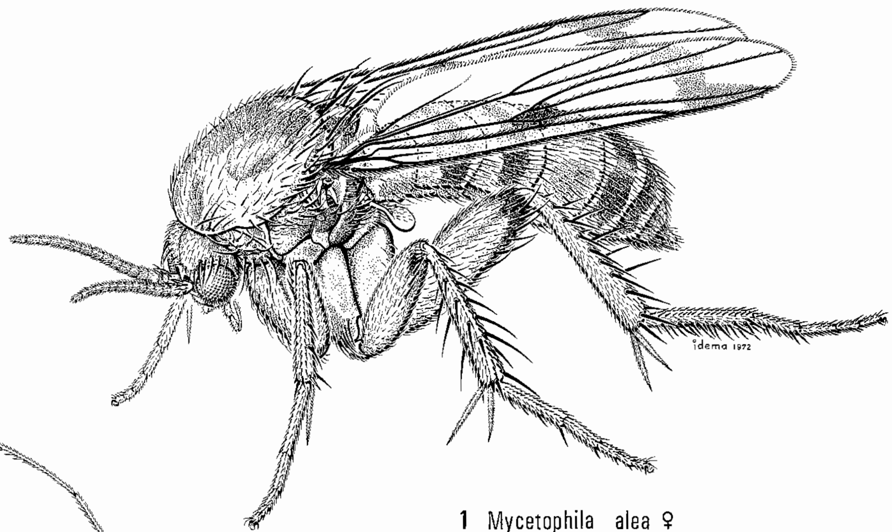
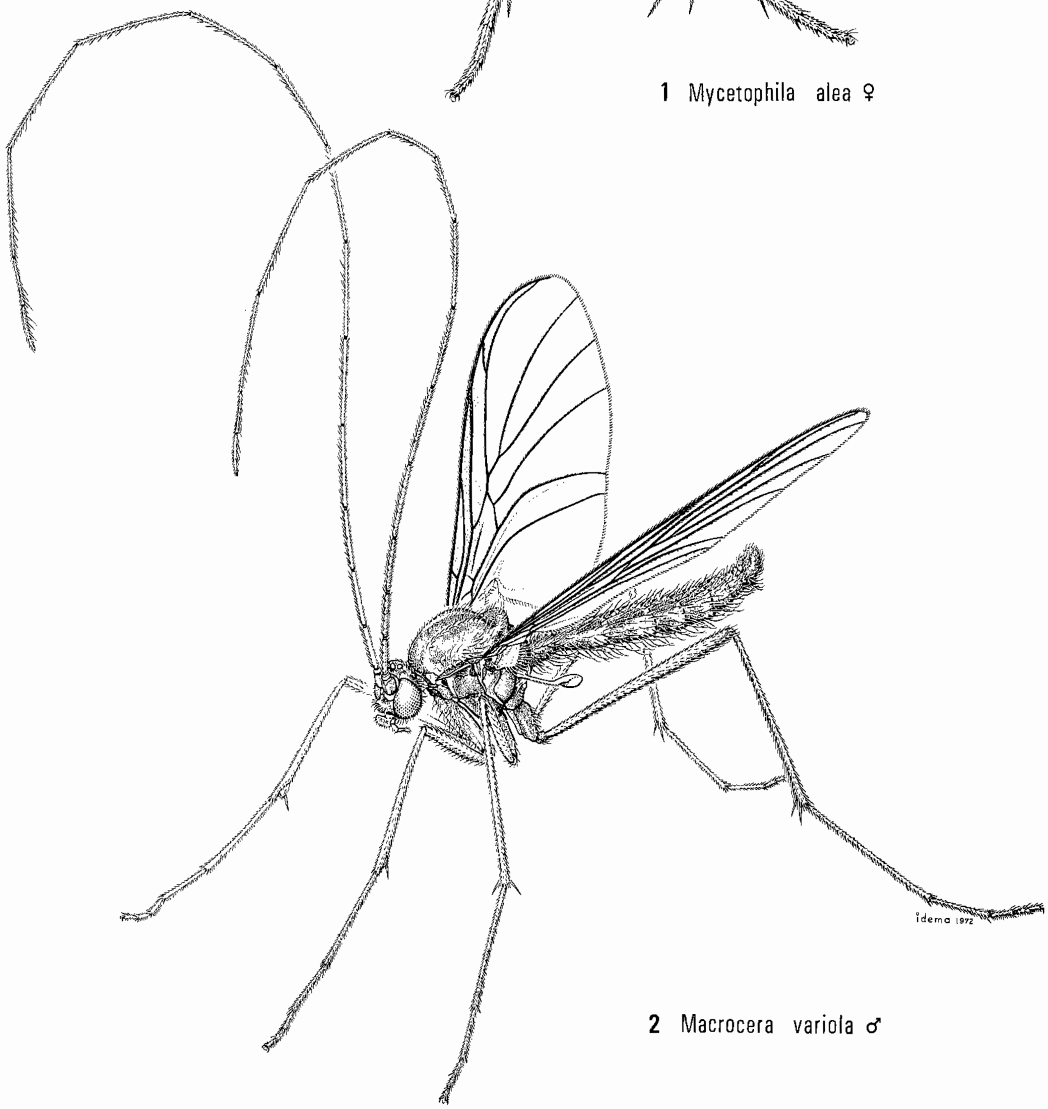
MYCETOPHILIDAE 14

J. R. VOCKEROTH



1 Mycetophila alea ♀



2 Macrocera variola ♂

Figs. 14.1–2. (1) Female of *Mycetophila alea* Laffoon; (2) male of *Macrocera variola* Garrett.

Slender to moderately robust flies, 2.2–13.3 mm long (Figs. 1, 2). Thoracic and tibial bristles often strong. Coxae long; tibiae usually with long strong apical spurs (Figs. 77–83). Color varied; body usually dull yellow, brown, or black, but sometimes brightly marked; wing often conspicuously marked.

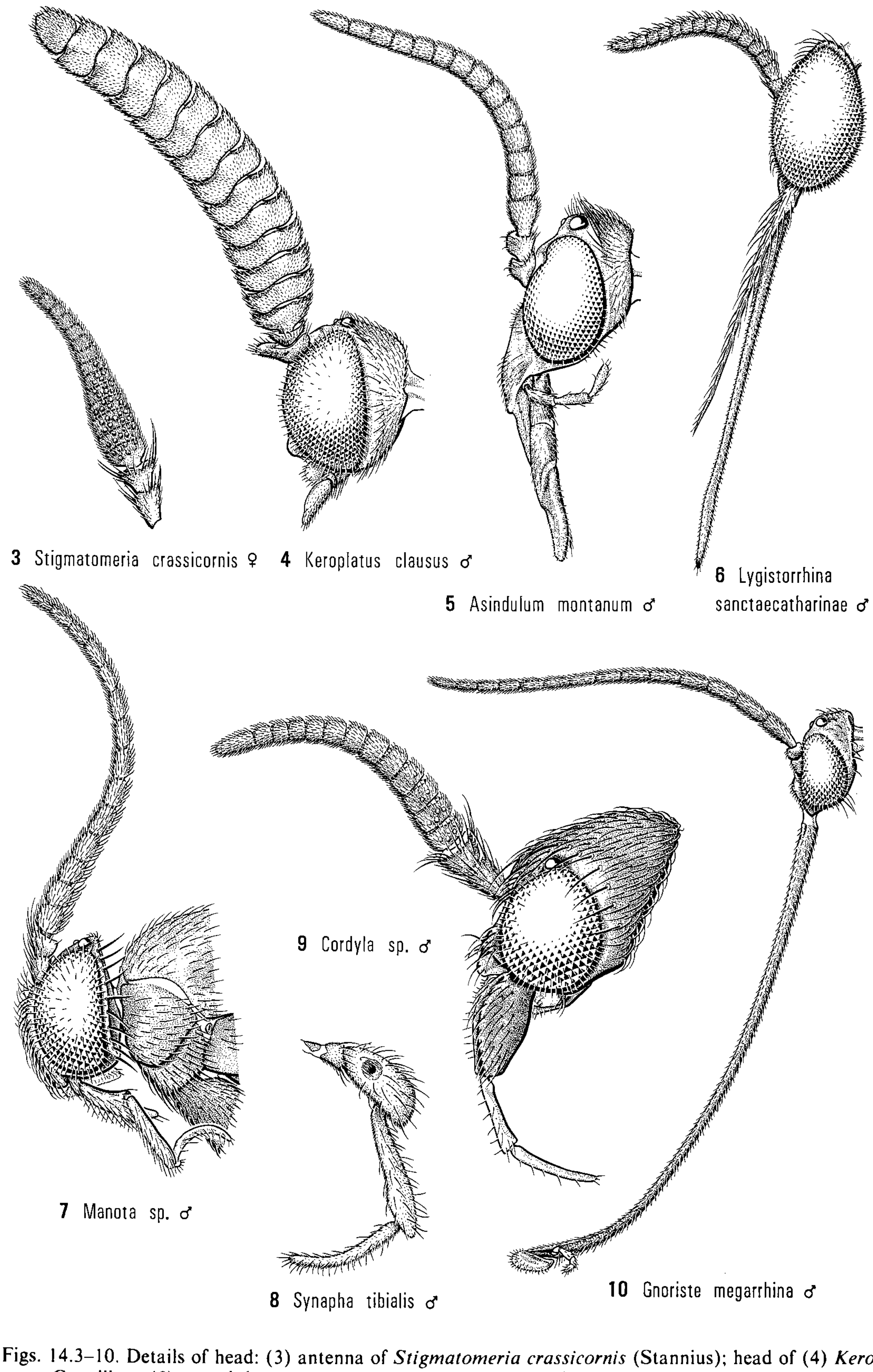
Adult. Head: usually flattened from front to back and inserted well below level of upper margin of strongly arched thorax, but semicircular in profile and inserted on anterior end of thorax in Manotinae and some Sciophilinae. Eyes usually densely haired, rarely with a few short hairs, usually situated on lower part of head and widely separated above, with an incomplete eye bridge in some Ditomyiinae and a complete bridge in some Manotinae. Three ocelli usually present, variable in position, with median ocellus sometimes very small or absent; all ocelli absent only in *Hesperodes* Coquillett and in *Syndocosia* Speiser (Afrotropical). Frons between ocelli and antennal bases usually bare but haired in some Keroplatinae and Sciophilinae. Antenna (Figs. 3–7, 9, 10) usually inserted at middle of head, inserted well above middle only in Manotinae and in some Keroplatinae, varying in length from scarcely longer than head to several times as long as body; flagellum usually cylindrical, sometimes thickened basally and tapering toward apex, usually with 14 flagellomeres, but with an additional very small terminal flagellomere in some Keroplatinae and with fewer than 14 flagellomeres in other Keroplatinae and in *Cordyla* Meigen, which has 9–13; flagellomeres strongly compressed or pectinate or both in some Ditomyiinae and Keroplatinae, usually clothed with short dense hairs, but sometimes with short bristles among the hairs, or with long hairs as in some species of *Bolitophila* Meigen. Mouthparts usually much shorter than half height of head, but about as long as height of head in *Asindulum* Latreille (Fig. 5), *Antlemon* Haliday (Palaearctic), *Aphrastomyia* Coher & Lane, and *Paramorganiella* Tonnoir (Australian), and produced into a slender cylindrical proboscis several times as long as height of head in *Rhynchoplatyura* de Meijere (Oriental), *Gnoriste* Meigen (Fig. 10), and *Lygistorrhina* Skuse (Fig. 6). Labella usually large and fleshy, but greatly reduced in all above-named genera except *Lygistorrhina*, in which they are very long and slender. Palpus apparently prehensile in *Paramorganiella*, usually with five segments although first two are usually very short and not apparent in dry specimens, but sometimes with fewer than five segments—four in many Mycetophilinae (but not in *Mycetophila* Meigen or *Epicypta* Winnertz), three in *Keroplatus* Bosc (Fig. 4) and several related genera, two to four in some Neotropical species of *Dziedzickia* Johannsen, one very short segment in *Metanepsia* Edwards (Palaeotropical), and one very long filamentous segment in *Lygistorrhina* (Fig. 6); segments variable in length and form, usually slender, but sometimes one or more broadened (Fig. 8) or swollen (Fig. 9); specialized sensory structures presumably always present on segment 3, taking following forms—a pit containing modified setae, a surface patch of modified setae, scattered slightly clubbed setae (*Bolitophila*), a dorsal and ventral pit (*Asindulum*, Fig. 5), or a longitudinal groove with a highly modified surface and a deep internal invagination (*Cordyla*, Fig. 9).[1]

Thorax: varying in form from compressed and deep to depressed and low. Thoracic sclerites varying considerably in size, shape, and distinctness; thoracic structure used to determine relationships among genera and subfamilies by Shaw (1948) and Shaw and Shaw (1951), but not satisfactorily and therefore requiring more study. Thoracic vestiture variable, consisting of fine setae, moderately strong bristles with apices bifid or otherwise modified (Tuomikoski, personal commun.), scale-like setae, or very fine appressed or erect setae; nature and distribution often used in taxonomic studies, but other times overlooked (e.g. very fine erect setae on various sclerites of *Bolitophila* spp.); hairs or bristles always present on pronotum, scutum, and scutellum, but only occasionally present on most other thoracic sclerites; one or several strong erect setae immediately medial to base of halter in some Keroplatinae and Sciophilinae.

Wing (Figs. 11–76) considerably reduced in size only in female of one species of *Macrocera* Meigen from Crozet Island and of one species of *Baeopterogyna* Vockeroth (Fig. 34) and in some specimens of both sexes of one species of *Boletina* Staeger (Fig. 52). Veins often with setae (Figs. 75, 76); membrane usually densely clothed with microtrichia and often also with few to many macrotrichia; if microtrichia absent, macrotrichia present on at least most of membrane. Venation most nearly complete in *Ditomyia* Winnertz (Fig. 11), *Paleoplatyura* Meunier (Fig. 19), and *Platyura* Meigen (Fig. 18) although these lacking most of Sc, crossvein sc-r, and crossvein r-m (due to partial fusion of Rs and M_{1+2}), respectively; venation variously reduced in other genera, extremely reduced in *Lygistorrhina* (Fig. 21), *Manota* Williston (Fig. 22), and *Azana* Walker (Fig. 27).

Legs with coxae elongate and stout (Figs. 84, 85); mid coxa of male of some species of *Mycomya* Rondani and all *Echinopodium* Freeman (Neotropical) with an anterior process; arrangement and strength of bristles and hairs of hind coxa variable. Femora usually slender, sometimes swollen, with vestiture variable; mid femur in male of some species of *Leptomorphus* Curtis with a subbasal spur. Tibiae (Figs. 82, 83) usually slender, with vestiture variable, with short setae arranged irregularly (Fig. 83) or in regular rows (Fig. 82), and usually with bristles varying in strength and arrangement; fore tibia often with an anteroapical depressed area bearing very fine dense setae; in *Synapha* Meigen depressed area extending up to five-sevenths length of tibia; mid tibia of

[1] This account of the palpus is based on examination of species, mostly males, of about 45 genera representing all subfamilies; it may require modification. A sexual difference in the palpus has been reported only in the Afrotropical *Euceroplatus incolumis* Matile, which has the palpus of the female much larger than that of the male.



Figs. 14.3–10. Details of head: (3) antenna of *Stigmatomeria crassicornis* (Stannius); head of (4) *Keroplatus clausus* Coquillett, (5) *Asindulum montanum* Röder, (6) *Lygistorrhina sanctaecatharinae* Thompson, and (7) *Manota* sp.; (8) palpus of *Synapha tibialis* (Coquillett); head of (9) *Cordyla* sp. and (10) *Gnoriste megarrhina* Osten Sacken.

male sometimes with a specialized sensory depression; hind tibia sometimes with a posteroapical comb of stiff setae or with a dorsoapical cleft. One apical spur present on fore tibia; two apical spurs on each of mid and hind tibiae, one of which may be very short; tibial spurs extremely short only in *Dolichodactyla* Freeman (Neotropical). Tarsi (Fig. 81) usually slender, sometimes with modified hairs below, or with some segments swollen below in female. Tarsal claws rarely simple, usually with one or more teeth below, and in male of some genera of Keroplatinae thick, blunt, and serrate below; in male of some *Boletina* spp. and several related genera one or more claws greatly distorted; pulvilli absent; empodia, if present, variable in size.

Abdomen: usually broadest at mid length, but in many Keroplatinae broadest near apex. Tergites and sternites 1–6, 1–7, or 1–8 in male and 1–7 in female well-developed except for sternite 1; sternite 1 often reduced in size, V-shaped, sometimes lacking hairs; sternites 2–6 or 2–7 in many Sciophilinae (but not in *Mycomya* or in *Leia* Meigen and several related genera) and probably in all Mycetophilinae with a pair of submedian or sublateral weakly sclerotized lines and sometimes also with a similar median line (fold lines) so the sternites may be partially folded longitudinally. Spiracles present below margins of tergites 1–7, but sometimes apparently lacking in segment 1 and sometimes also in segment 2.

Male often with sclerites of segments 7 and 8 (tergites especially) short and telescoped into segment 6 (Figs. 92, 93); terminalia usually symmetric, but sometimes markedly asymmetric (one western Nearctic species of *Acnemia* Winnertz, and some *Mycetophila* spp.), usually directed caudally, sometimes rotated clockwise through 90° or more with segments 7 and 8 sharing in the rotation; in *Calliceratomyia* Lane (Neotropical) tergite 7 large, sternite 7 very reduced, segment 8 small, and terminalia reflexed anteroventrally and appressed against the venter of segment 7. Segment 9 and associated structures (Figs. 92–96) extremely varied in form but with an apparently constant basic pattern: tergite 9, sternite 9, a pair of lateral gonocoxites each with an articulated gonostylus, a pair of submedian parameres each articulated laterally with gonocoxite and bearing aedeagus between them (structure of parameres and aedeagus often difficult to determine), and an anus-bearing proctiger lying below the posterior end of tergite 9 and consisting of a pair of lateral unsegmented cerci and a ventral sclerite or hypoproct. Tergite 9 and sternite 9 distinct or partly or entirely fused with gonocoxites, and sometimes bearing spines or processes; midventral line sometimes membranous (possibly a divided sternite 9). Gonostylus particularly varied, sometimes slender and tapering, but more often with lobes or processes bearing a variety of hairs, spines, or striate areas. Aedeagus sometimes with long anterior apodemes; in some species of *Orfelia* Costa a well-sclerotized structure (probably a sperm pump) attached to its anterior end and strong anterior apodemes also present. Hypoproct weak, sometimes divided medially or fused with cerci; cercus usually weak but variable in form, very large in Ditomyiinae, with transverse rows of short stout bristles in most *Boletina* spp. (Figs. 92, 93).

Female (Figs. 88–91) with tergite 8 usually shorter than sternite 8, rarely very short and medially divided, or absent; sternite 8 separate from tergite 8, well-developed, rounded or emarginate posteriorly or medially divided, sometimes with a posterior pair of semiarticulated lobes or with posterior margin invaginated. Tergite 9 well-developed or very short, haired or bare, rarely medially divided or absent; sternite 9 usually fused laterally with tergite 9, lying above tergite 8, usually weakly sclerotized and with membranous areas, sometimes with an anterior apodeme extending above sternites 8 and 7, in many Mycetophilinae with a posterior triangular process that may extend beyond apices of cerci. Tergite 10 short or absent; sternite 10 well-developed, membranous medially, and entire, or absent. Cercus articulated with last sclerotized tergite, usually weakly sclerotized and two-segmented with a larger basal and a smaller apical segment; sometimes one-segmented; rarely strongly sclerotized, one-segmented, elongate, slender, curved, and tapering [*Boletina oviducta* (Garrett); *Drepanocercus* Vockeroth, Fig. 88]. Two spermathecae probably always present, usually spherical or nearly so if sclerotized, with a conical posterior projection in some Keroplatinae. Spermatheca strongly sclerotized in at least one species of each of the genera *Bolitophila*, *Diadocidia* Ruthe, and *Lygistorrhina*; strongly to very weakly sclerotized in various genera of Keroplatinae; apparently absent in macerated specimens of Ditomyiinae, some Keroplatinae, Manotinae, Sciophilinae, and Mycetophilinae; but detected in unsclerotized form after maceration and dissection in *Orfelia genualis* (Johannsen), *Saigusaia cincta* (Johannsen), and one species of *Dynatosoma* Winnertz (and distal ends of spermathecal ducts detected in species of several other genera). Spermathecal ducts usually slender, sometimes swollen over part of their length, apparently opening separately on a weakly sclerotized or membranous area of sternite 9 or into a slight invagination of sternite 9.

Larva. Poorly known, especially non-European forms; usually cylindrical and slender (Figs. 97, 103), but extremely slender and oligochaete-like in some Keroplatinae, and flattened and slug-like in *Phronia* Winnertz; forming a dark conical dorsal case from frass and from larval excrement in at least one species of *Epicypta*; occurring in mucous tubes or webs formed from salivary excretion in Diadocidiinae, Keroplatinae, and Sciophilinae (except *Docosia* Winnertz); possessing light-producing tissues in several species of Keroplatinae; bearing spiracles on prothorax and eight abdominal segments in Ditomyiinae and on prothorax and seven abdominal segments in most other groups; propneustic in *Diadocidia* and *Speolepta* Edwards, and apneustic in Keroplatinae, although nonfunctional spiracles apparently also present in these groups.

Head (Figs. 98–102) important taxonomically, strongly sclerotized, free, well-developed, without tentorial arms, with a few dorsal setae only in Ditomyiinae. Antenna usually very short, nonsclerotized and one-segmented (with apical sensory organs in Ditomyiinae), elongate and three-segmented only in *Bolitophila*. Labrum fleshy, supported by a chitinous frame that articulates with two movable arms, each of which carries a fan-shaped organ. Mandible lamelliform, toothed along inner margin, with prostheca at inner basal angle except in *Bolitophila*. Maxilla consisting of an inner blade-like lobe and an outer oval lobe; blade-like lobe serrated along inner margin, and ending in a sclerotized bar that lies dorsal to a basal plate-like cardo; oval lobe with a circular membranous area that carries several papillae; maxilla reduced and palpus large in Ditomyiinae. Hypopharynx consisting of two curved horizontal processes that join in midventral line and two vertical processes that join horizontal processes. Labium reduced to a small sclerotized plate (or sometimes two plates in Ditomyiinae) at base of hypopharynx.

Body with three thoracic and eight or nine abdominal segments. [Madwar (1937) gives 11 as the number of body segments for Ditomyiinae and *Keroplatus* and 12 for other genera; Hennig (1948) gives 11 as the number of body segments. Further study is needed.] Thoracic segments bare except for two ventral groups of three or four minute setae marking position of imaginal leg discs on each segment; abdominal segments bare except for a few setae mostly near the spiracles in Ditomyiinae and in one *Phronia* sp. Nine to eleven ventral creeping welts between segments of thorax and abdomen in *Bolitophila* and Mycetophilinae; each welt with an armature of spicules and hooks.

One comprehensive account of the larval stage is that of Madwar (1937), from which most of the description here is taken. Hennig (1948) gave a more extended summary, also based mainly on Madwar; he included keys to genera of Ditomyiinae and Sciophilinae. Plachter (1979*a*, 1979*b*, 1979*c*) has recently provided extensive studies of web structure, of larval structure, and of pupal structure, respectively.

Pupa. Probably distinguishable from other groups (except Sciaridae) by having leg sheaths side by side rather than overlapping, visible apical tibial spurs, and a sessile undivided anterior thoracic spiracle.

Biology and behavior. Mycetophilidae are most abundant in humid areas, especially moist woodland; during the day adults of many species, especially of Mycetophilinae, congregate in moist dark places such as overhanging stream banks and cavities under tree roots. Many species can be swept from undergrowth in woods. Lewis and Taylor (1965) showed that three species in England were most active at dusk and less active at dawn; this behavior may be true of many species and is perhaps the reason why so many specimens, even of apparently rare genera such as *Symmerus* Walker and *Novakia* Strobl, are often taken in Malaise traps. Some species, especially those with elongate mouthparts, visit flowers; species of a number of genera have been observed to feed on honeydew on leaves (J. A. Downes, personal commun.). A few species are brightly colored and probably mimic Hymenoptera. In cool temperate regions some species overwinter as adults under bark or in hollow plant stems.

Many larvae live in fleshy or woody fungi, on or in dead wood, under bark, or in nests of birds or squirrels; most or all of these are probably mycetophagous. Larvae of some Mycetophilini feed on Myxomycetes. Larvae of one (and perhaps all) *Boletina* sp. feed on Hepaticae. Larvae of some Keroplatinae spin webs and capture and feed on small arthropods (Mansbridge 1933). Larvae of some species live mainly or entirely in caves (Matile 1970). The larva of the Tasmanian *Planarivora insignis* Hickman (Keroplatinae) is endoparasitic in land planarians. Edwards (1925), Buxton (1960), and Hackmann and Meinander (1979) give much information on larval habitats and hosts.

Pupation usually takes place in the ground but some Mycetophilinae pupate in the host fungus (adults may remain quiescent in the pupal cocoon for some time and emerge very rapidly if disturbed) and most Sciophilinae have the pupa hanging in a sparse web of salivary threads. The pupa is free in Ditomyiinae and in *Bolitophila*, enclosed in a dense cocoon in Mycetophilinae and in *Docosia*, and apparently enclosed in a weak cocoon, which may be reduced to a few threads, in other groups.

Classification and distribution. Mycetophilidae occur on all continental areas except Antarctica (from northern Greenland to Tierra del Fuego) and on most oceanic islands. About 3000 species have been described but the number is undoubtedly much greater. The Mycetophilidae plus Sciaridae of the present work, which Hennig (1948, 1973) treats under the Mycetophiloidea, are generally considered a holophyletic group. There is, however, great divergence in the ranking of the subgroups by different authors. Edwards (1925), who laid the basis for subsequent classifications, recognized one family with 10 subfamilies, one of which was the Sciarinae; subsequently Edwards (1941) included the Macrocerinae in the Keroplatinae. Hennig (1973) considered six of the nine subfamilies recognized by Edwards in his later papers as separate families: the Lygistorrhininae he included in the Keroplatidae, following Tuomikoski (1966*c*); the Manotinae, following Tuomikoski (1966*b*), and the Sciophilinae he placed in the Mycetophilidae, although Hennig (1948) had treated the Sciophilidae as a separate family. Madwar (1937), following Keilin (1919), treated the Ditomyiidae as a separate family because of similarities between their larvae and those of the Bibionidae; the rest of the superfamily, including the Sciaridae, he treated as the family Mycetophilidae. Most recent authors treat the Sciaridae as a family, possibly so they can ignore it when treating the Mycetophilidae, and consider the rest of the superfamily as the

Mycetophilidae with eight subfamilies. This arrangement is adopted here because of its general acceptance, although the Mycetophilidae in this sense is probably a paraphyletic group. A thorough phylogenetic analysis is necessary to clarify the problem.

Two of the subfamilies, Sciophilinae and Mycetophilinae, are normally divided into tribes. The sciophiline tribes Mycomyini and Sciophilini are readily defined. The Mycomyini includes, in the Nearctic region, only *Mycomya* and *Neoempheria* Osten Sacken. The Sciophilini includes all those Sciophilinae with abundant macrotrichia on the wing membrane (couplets 30–46); it may be a monophyletic group, but *Paratinia* Mik shows several similarities with *Acomoptera* Vockeroth, a genus that lacks wing macrotrichia. The validity and limits of the two other generally recognized Nearctic tribes, the Gnoristini and Tetragoneurini (=Leiini), are doubtful; I am unable to distinguish them satisfactorily. They include genera in couplets 48–73 (except *Megalopelma* Enderlein) plus *Aphrastomyia*. The two tribes of the Mycetophilinae, Exechiini and Mycetophilini, have been redefined by Tuomikoski (1966*a*). The Exechiini includes all the genera in the key below from *Anatella* Winnertz to *Cordyla*; the Mycetophilini includes the eight genera following *Cordyla*.

Certain genera or generic complexes require further study. *Orfelia* on a world basis is at present divided into about 24 subgenera, some of which have been, and more of which probably should be, treated as distinct genera. *Coelosia* Winnertz shows great diversity, especially in the male terminalia, and may be a complex of genera. *Dziedzickia* is undoubtedly a complex of several genera. One or more of the Nearctic species referred here probably belong to *Palaeodocosia* Meunier, but other distinct genera are probably included as well. An attempt to divide the genus seems premature until the world fauna, and particularly the many Neotropical species, can be reviewed. *Leia* requires further study; even with the recognition of *Greenomyia* Brunetti and of *Garrettella* Vockeroth as separate genera, the remaining species show diversity in ocellar position, wing venation, and structure of male and female terminalia. Study of the world fauna may show that several other distinct genera are grouped under this name. The genera of the Exechiini were revised by Tuomikoski (1966*a*); most of the genera recognized by him are recognizable in the Nearctic region, but further study of the group, and especially of his subgeneric segregates, would be desirable. The nominal genera related to *Mycetophila* (*Epicypta*, *Platurocypta* Enderlein, and their synonyms) are separable from *Mycetophila*, although only with difficulty, in the Holarctic region; however, in tropical regions these groups are well developed and the generic limits are still very confused.

Probably fewer than half the Nearctic species have been recorded from the region; many Holarctic species await recognition and many species are still undescribed. For example, a recent revision of *Phronia* (Gagné 1975) increased the number of species from 14 to 49, of which 33 are known to be Holarctic. Several species are incorrectly assigned to genera and, especially in the Exechiini, the correct assignment of many species of genera recently divided is uncertain. Therefore the information about distribution and number of species given for each genus is subject to correction.

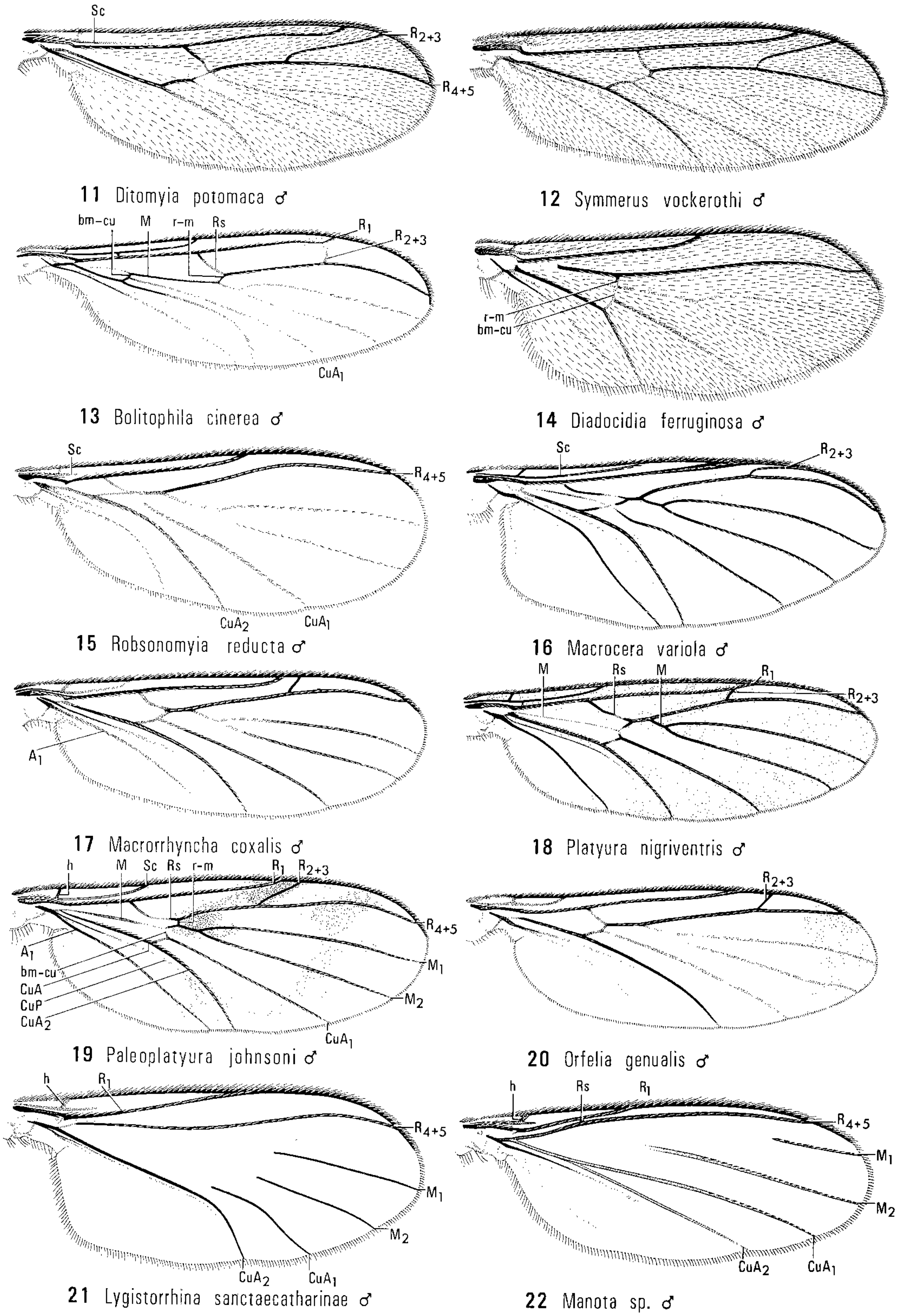
Johannsen (1910*a*, 1910*b*, 1912*a*, 1912*b*) revised the Nearctic fauna; because of the many species not included and the many subsequent changes in generic limits and nomenclature, his work is of limited value. Shaw and Fisher (1952) gave keys to the species of the northeastern United States, but some are unsatisfactory. These two papers are not cited below under individual genera; only references to the few other generic revisions or keys published since Johannsen's revisions are listed.

Rohdendorf (1974) has referred fossils of various periods from Upper Triassic onward to several extinct genera and families of Fungivoroidea (=Sciaroidea), but the oldest fossil definitely referable to the Mycetophilidae is an undescribed species of Sciophilinae from Canadian Upper Cretaceous amber. The early Tertiary Baltic amber is very rich in Mycetophilidae; all subfamilies recognized here, except Ditomyiinae, and a number of recent genera have been reported. About 250 species have been described from Baltic amber. A few species are known from Tertiary sediments.

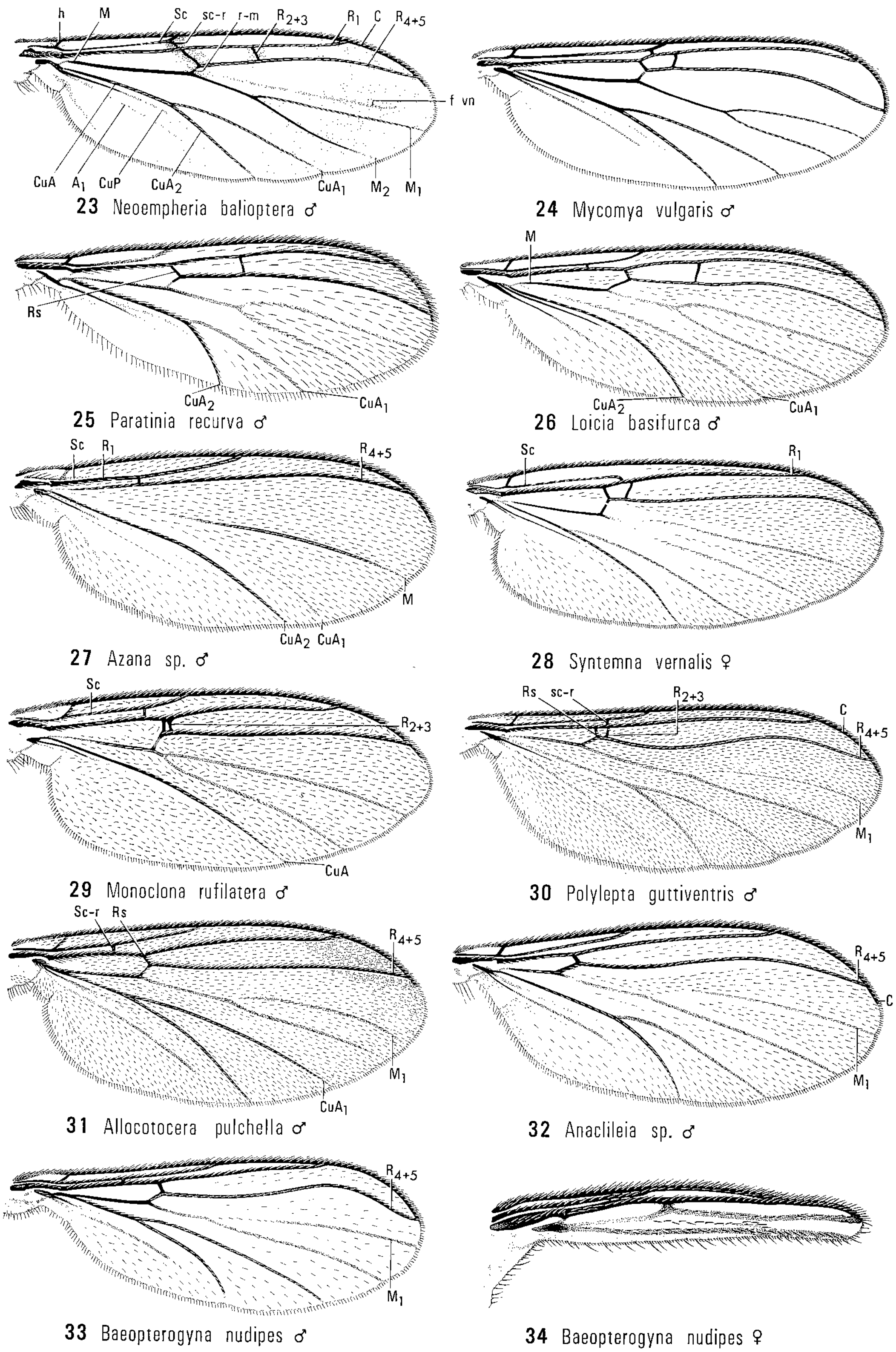
Key to genera

1. Wing short, about half as long as abdomen .... SCIOPHILINAE, in part....2
   Wing of normal size, about as long as abdomen 3
2. Wing very narrow; venation reduced and obscure (Fig. 34). Female only .... ***Baeopterogyna*** Vockeroth, in part
   1 sp., *nudipes* Vockeroth; northwestern
   Wing moderately broad; venation complete or nearly so and distinct (Fig. 52). Male and female .... ***Boletina*** Staeger, in part
   1 undescr. sp., dimorphic in wing length; eastern; see couplet 59
3. M and CuA_1 connected well beyond level of crossvein h by a distinct crossvein bm-cu or by a brief contact or fusion of M and CuA_1 (Figs. 11–20) 4
   M and CuA connected at most basally at or very near level of crossvein h (Figs. 21–74) 22

4. R_{2+3} present and at least half as long as R_{4+5}; Sc distinctly sclerotized for only a short distance, continuing as a weak fold that ends free (Figs. 11, 12); wing membrane with macrotrichia. Postpronotum with one or more long fine setae .... DITOMYIINAE....5

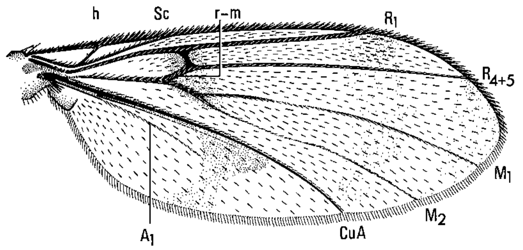


Figs. 14.11–22. Wings: (11) *Ditomyia potomaca* Fisher; (12) *Symmerus vockerothi* Munroe; (13) *Bolitophila cinerea* Meigen; (14) *Diadocidia ferruginosa* (Meigen); (15) *Robsonomyia reducta* Matile & Vockeroth; (16) *Macrocera variola* Garrett; (17) *Macrorrhyncha coxalis* (Loew); (18) *Platyura nigriventris* (Johannsen); (19) *Paleoplatyura johnsoni* Johannsen; (20) *Orfelia genualis* (Johannsen); (21) *Lygistorrhina sanctaecatharinae* Thompson; (22) *Manota* sp. (*continued*).

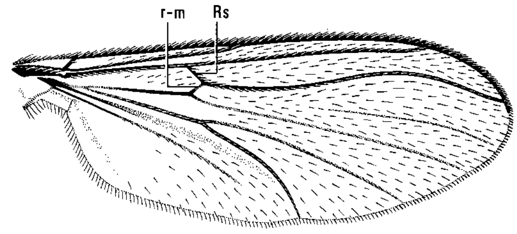


Figs. 14.23–34. Wings (*continued*): (23) *Neoempheria balioptera* (Loew); (24) *Mycomya vulgaris* Garrett; (25) *Paratinia recurva* Johannsen; (26) *Loicia basifurca* Vockeroth; (27) *Azana* sp.; (28) *Syntemna vernalis* (Sherman); (29) *Monoclona rufilatera* (Walker); (30) *Polylepta guttiventris* (Zetterstedt); (31) *Allocotocera pulchella* (Curtis); (32) *Anaclileia* sp.; (33, 34) *Baeopterogyna nudipes* Vockeroth (*continued*).

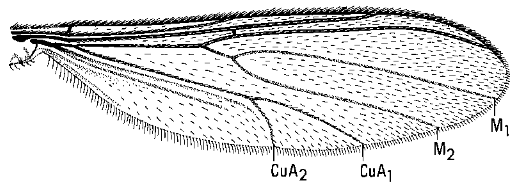
Abbreviation: f vn, false vein.



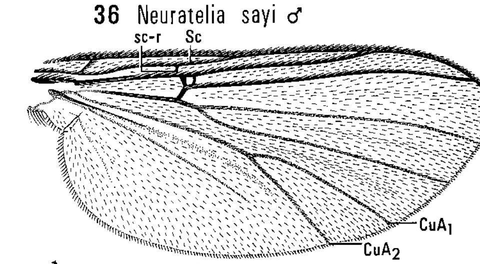
35 Cluzobra sp. ♀



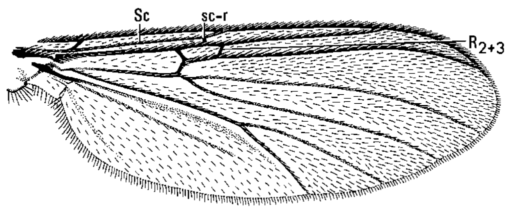
36 Neuratelia sayi ♂



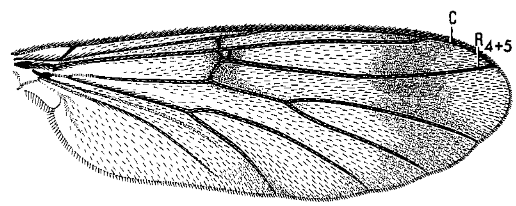
37 Phthinia tanypus ♂



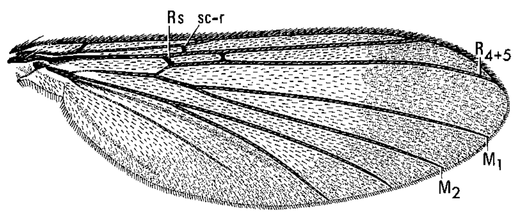
38 Sciophila novata ♂



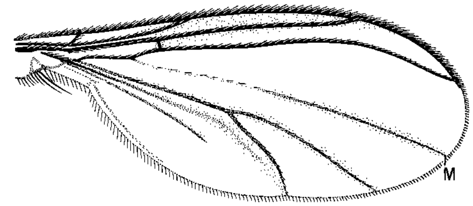
39 Megalopelma glabanum ♂



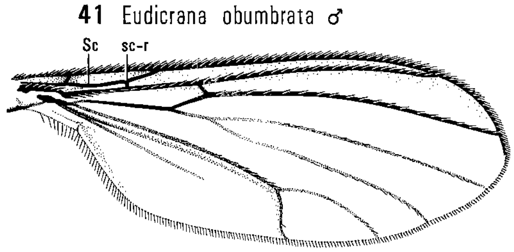
40 Leptomorphus nebulosus ♂



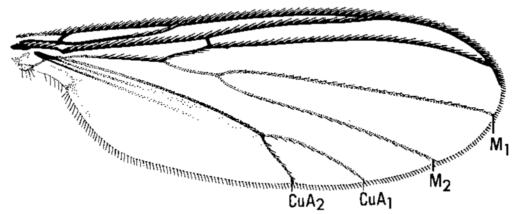
41 Eudicrana obumbrata ♂



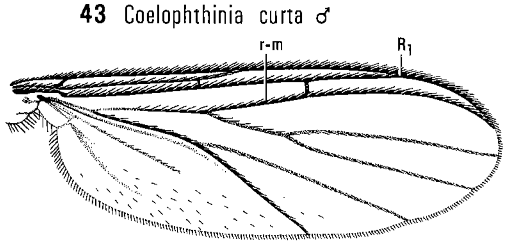
42 Adicroneura biocellata ♀



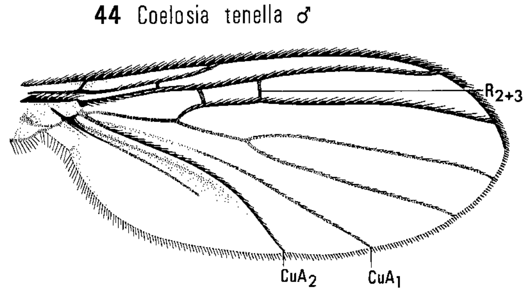
43 Coelophthinia curta ♂



44 Coelosia tenella ♂

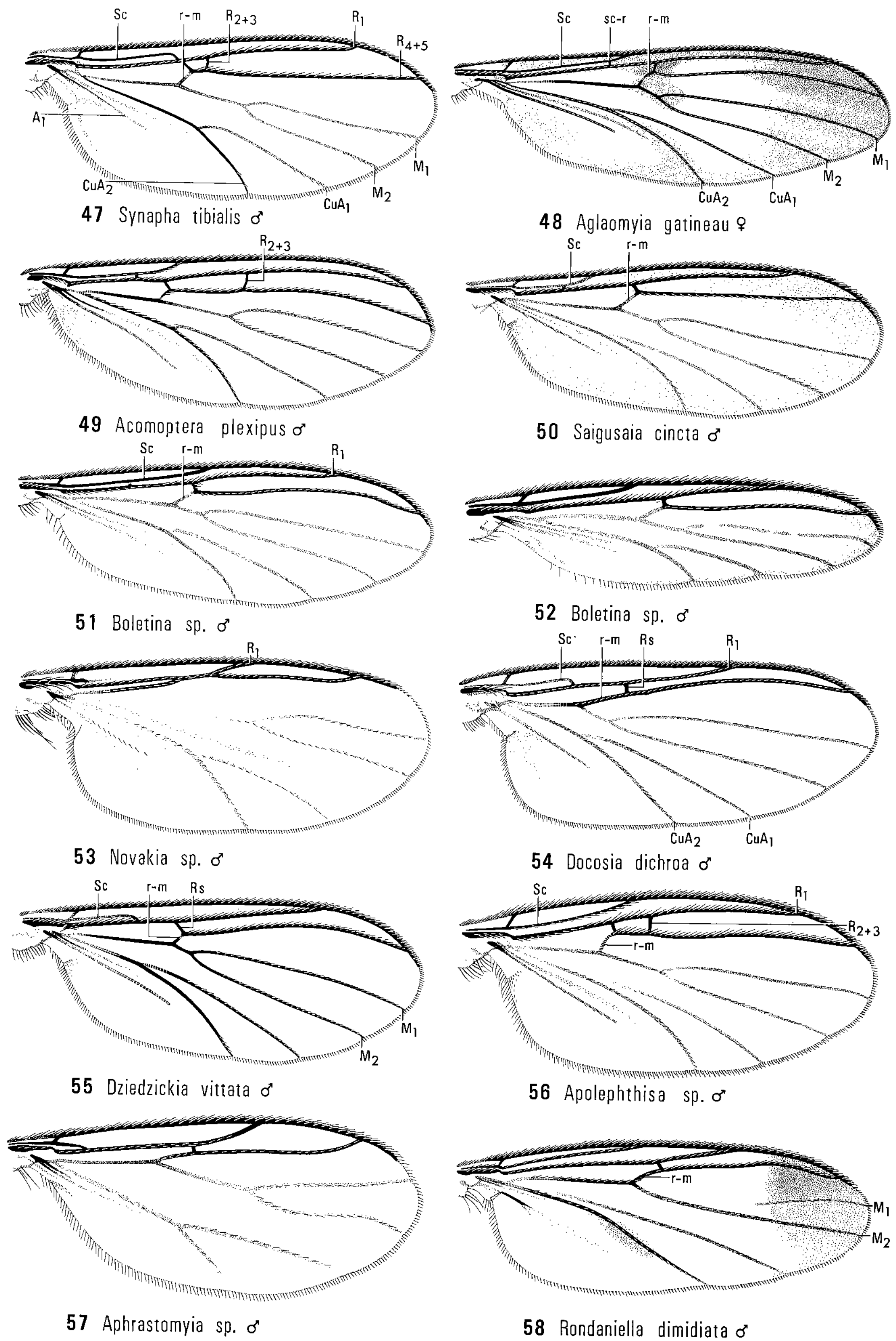


45 Garrettella shermani ♂

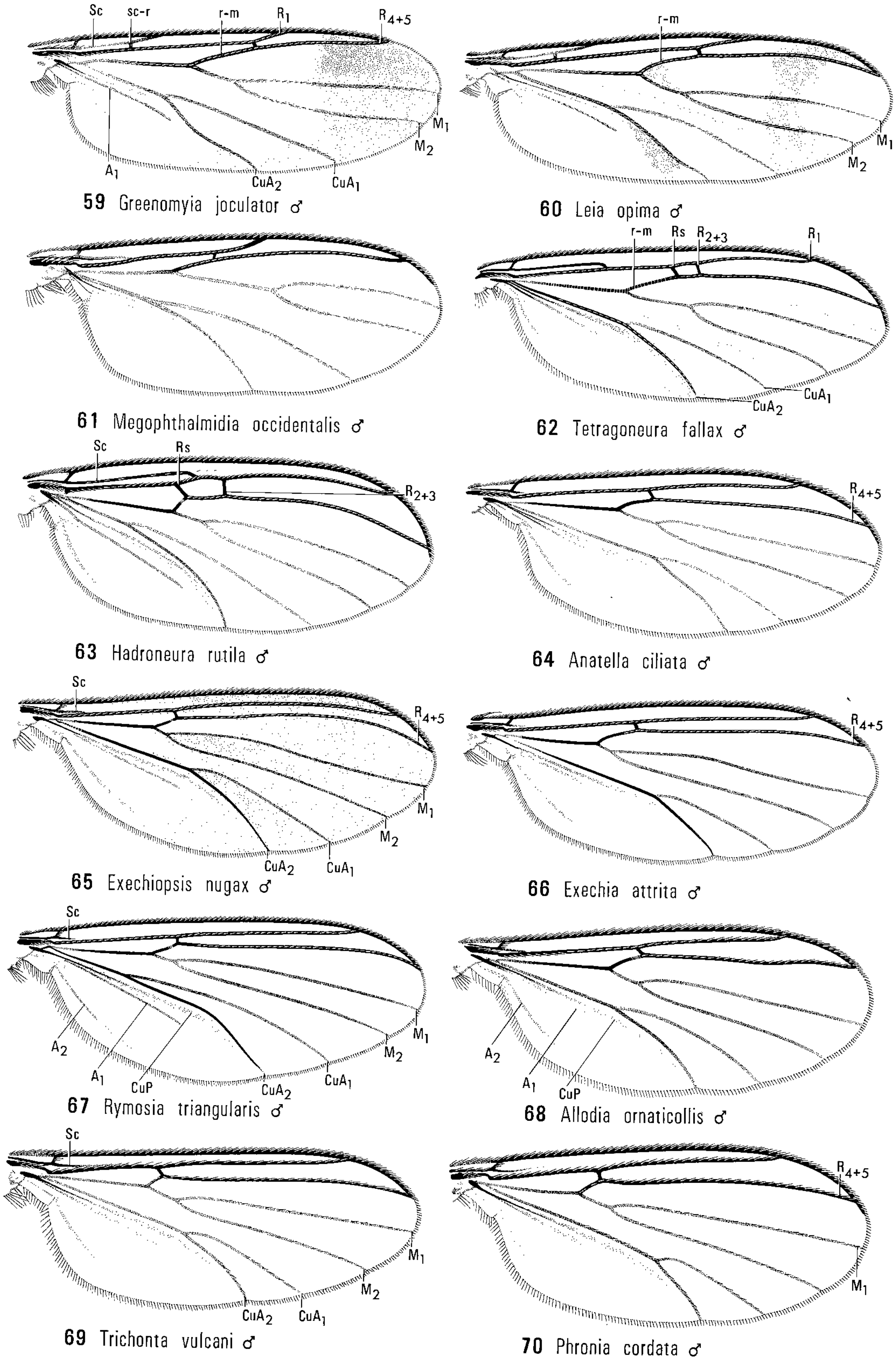


46 Drepanocercus ensifer ♂

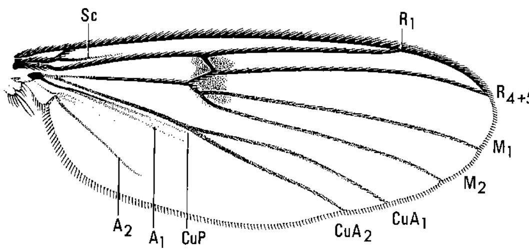
Figs. 14.35–46. Wings (*continued*): (35) *Cluzobra* sp.; (36) *Neuratelia sayi* (Aldrich); (37) ***Phthinia tanypus*** Loew; (38) *Sciophila novata* Johannsen; (39) *Megalopelma glabanum* (Johannsen); (40) ***Leptomorphus nebulosus*** (Walker); (41) *Eudicrana obumbrata* Loew; (42) *Adicroneura biocellata* Vockeroth; (43) ***Coelophthinia curta*** (Johannsen); (44) *Coelosia tenella* (Zetterstedt); (45) *Garrettella shermani* (Garrett); **(46)** *Drepanocercus ensifer* Vockeroth (*continued*).



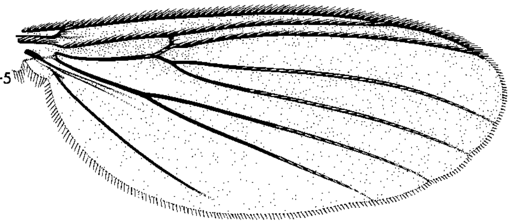
Figs. 14.47–58. Wings (*continued*): (47) *Synapha tibialis* (Coquillett); (48) *Aglaomyia gatineau* Vockeroth; (49) *Acomoptera plexipus* (Garrett); (50) *Saigusaia cincta* (Johannsen); (51, 52) *Boletina* sp.; (53) *Novakia* sp.; (54) *Docosia dichroa* Loew; (55) *Dziedzickia vittata* (Coquillett); (56) *Apolephthisa* sp.; (57) *Aphrastomyia* sp.; (58) *Rondaniella dimidiata* (Meigen) (*continued*).



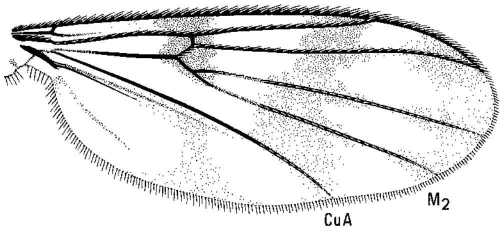
Figs. 14.59–70. Wings (*continued*): (59) *Greenomyia joculator* (Laffoon); (60) *Leia opima* (Loew); (61) *Megophthalmidia occidentalis* Johannsen; (62) *Tetragoneura fallax* Sherman; (63) *Hadroneura rutila* (Sherman); (64) *Anatella ciliata* Winnertz; (65) *Exechiopsis nugax* (Johannsen); (66) *Exechia attrita* Johannsen; (67) *Rymosia triangularis* Shaw; (68) *Allodia ornaticollis* (Meigen); (69) *Trichonta vulcani* (Dziedzicki); (70) *Phronia cordata* Lundström (*continued*).



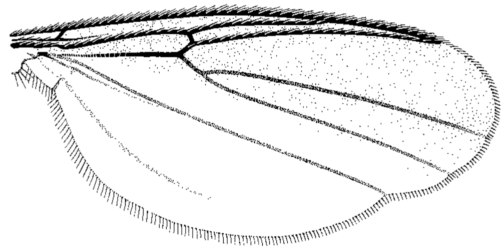
71 Mycetophila unipunctata ♂



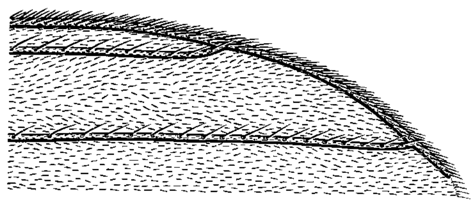
72 Epicypta scatophora ♂



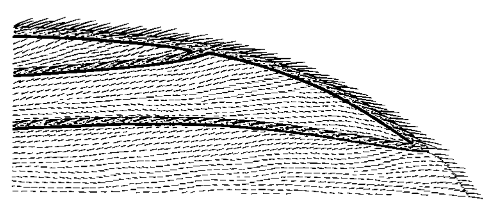
73 Zygomyia ornata ♂



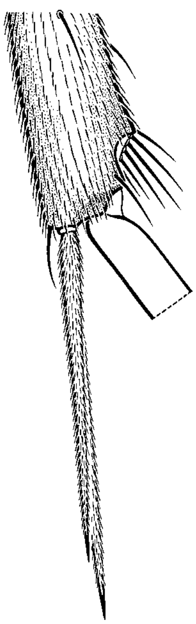
74 Sceptonia johannseni ♂

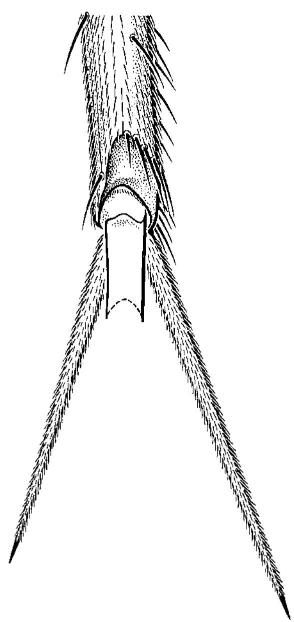


75 Synapha tibialis ♂

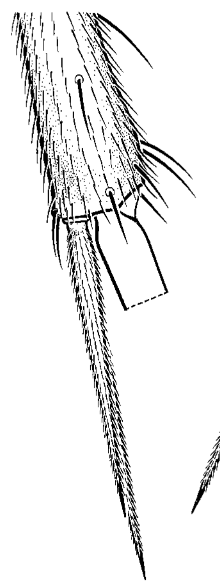


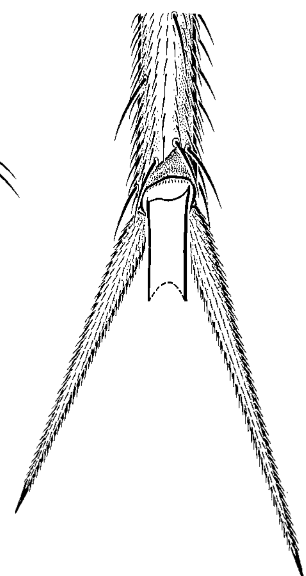
76 Exechia attrita ♂





77 Exechiopsis nugax ♂ **78**





79 Exechia attrita ♂ **80**

Figs. 14.71–80. Wings (*concluded*) and hind tibiae: wing of (71) *Mycetophila unipunctata* Meigen, (72) *Epicypta scatophora* (Perris), (73) *Zygomyia ornata* Loew, and (74) *Sceptonia johannseni* Garrett; anteroapical portion of wing of (75) *Synapha tibialis* (Coquillett) and (76) *Exechia attrita* Johannsen; apex of left hind tibia of (77) *Exechiopsis nugax* (Johannsen) in anterior view, (78) *E. nugax* in dorsal view, (79) *Exechia attrita* in anterior view, and (80) *E. attrita* in dorsal view.

R_{2+3} present and less than half as long as R_{4+5} (Figs. 13, 16–20), or absent (Figs. 14, 15); Sc ending in C or in R or ending free; wing membrane with or without macrotrichia. Postpronotal setae very short or absent 7

5. Eyes almost touching above antennae, separated by scarcely more than width of median ocellus. Point of furcation of Rs well beyond level of point of furcation of M (Fig. 12). Anepisternum haired above .... ***Symmerus*** Walker....6

Eyes separated above antennae by more than width of ocellar triangle. Point of furcation of Rs very near level of point of furcation of M (Fig. 11). Anepisternum bare ..***Ditomyia*** Winnertz
2 spp.; eastern; Fisher 1941

6. Mediotergite with setae on posterior half .... ***Symmerus*** (***Symmerus*** Walker)
1 sp., *lautus* (Loew); eastern

Mediotergite bare.... ***Symmerus*** (***Psilosymmerus*** Munroe)
3 spp.; eastern or western; Munroe 1974

7. Crossvein bm-cu, or point of contact of M and CuA_1, far before level of base of Rs; crossvein r-m distinct (Fig. 13) .... BOLITOPHILINAE....***Bolitophila*** Meigen....8

Crossvein bm-cu beyond level of base of Rs, or Rs and M fused for a short distance; crossvein r-m distinct or obliterated by fusion of R and M (Figs. 14–20) 9

8. R_{2+3} ending in C .... ***Bolitophila*** (***Cliopisa*** Enderlein)
12 spp.; widespread; Shaw 1962

R_{2+3} ending in R_1 (Fig. 13).... ***Bolitophila*** (***Bolitophila*** Meigen)
8 spp.; widespread; Shaw 1962

9. Crossveins r-m and bm-cu both distinct, forming a straight line; R_{2+3} absent (Fig. 14) .... DIADOCIDIINAE....***Diadocidia*** Ruthe....10

Crossvein r-m usually absent because of contact or partial fusion of R and M; if crossvein r-m present, situated beyond level of crossvein bm-cu (Fig. 19); R_{2+3} present or absent .... KEROPLATINAE....11

10. Third flagellomere at least four times as long as broad. Anepisternum haired above. Segments of fore tarsus slender in female .... ***Diadocidia*** (***Adidocidia*** Laštovka & Matile)
2 spp.; widespread; Laštovka and Matile 1972

Third flagellomere at most 3.2 times as long as broad. Anepisternum bare above. Segments 2–4 of fore tarsus swollen below in female (Fig. 81) .... ***Diadocidia*** (***Diadocidia*** Ruthe)
2 spp.; widespread

11. Antenna strongly compressed. Palpus very short, often porrect, with three segments (Fig. 4). Prosternum with at least a few hairs 12

Antenna cylindrical or only moderately compressed. Palpus drooping, with five segments. Prosternum haired or bare....15

12. R_{2+3} ending in R_1 (as in Fig. 18). Laterotergite haired .... ***Keroplatus*** Bosc
4 spp.; widespread; Fisher 1941

R_{2+3} ending in C (as in Fig. 20). Laterotergite bare 13

13. Tibial setae irregularly arranged (as in Fig. 83) 14

Tibial setae in regular longitudinal rows (as in Fig. 82).... ***Euceroplatus*** Edwards
3 spp.; widespread; Fisher 1941

14. Mediotergite with triangular membranous area at base .... ***Heteropterna*** Skuse
1 sp., *cressoni* (Fisher); eastern

Mediotergite uniformly sclerotized .... ***Cerotelion*** Rondani
1 sp., *johannseni* (Fisher); eastern

15. Branches of CuA slightly convergent beyond their base, then divergent (Figs. 15, 16); wing membrane with or without macrotrichia. Anepisternum with at least a few long erect hairs on upper half....16

Branches of CuA regularly divergent from their base (Figs. 17–20); wing membrane without macrotrichia. Anepisternum bare or with short hairs above 18

16. Ocelli absent. Upper part of anepisternum with many fine pale hairs. C ending at apex of R_{4+5}. Empodia absent.... ***Hesperodes*** Coquillett
1 sp., *johnsoni* Coquillett; eastern

Ocelli present. Upper part of anepisternum with few to many coarse dark hairs. C extending at least slightly beyond apex of R_{4+5} (Figs. 15, 16). Empodia present, short to long 17

17. Sc short, ending in R well before level of base of Rs; R_{2+3} absent; wing unmarked, without macrotrichia (Fig. 15). Antenna much shorter than body ..***Robsonomyia*** Matile & Vockeroth
1 sp., *reducta* Matile & Vockeroth; western

Sc long, ending in C at or beyond level of base of Rs; R_{2+3} present or absent; wing sometimes with dark markings and sometimes with macrotrichia (Fig. 16). Antenna usually longer than body (Fig. 2) .... ***Macrocera*** Meigen
24 spp.; widespread

18. Mouthparts at least as long as head (Fig. 5) 19
Mouthparts much shorter than head 20

19. A_1 incomplete, becoming faint well before wing margin (Fig. 17). Anterior thoracic spiracle with short erect black setae on posterior margin ....***Macrorrhyncha*** Winnertz
2 spp.; widespread

A_1 extending distinctly to, or almost to, wing margin. Anterior thoracic spiracle without setae on posterior margin ....***Asindulum*** Latreille
1 sp., *montanum* Röder; widespread

20. Crossvein r-m short but distinct (Fig. 19) ....***Paleoplatyura*** Meunier
3 spp.; eastern or western; Fisher 1941

Crossvein r-m absent because of contact or partial fusion of Rs and M (Figs. 18, 20) 21

21. R_{2+3} ending in R_1; base of M weak but distinct (Fig. 18). Empodia present, large ....***Platyura*** Meigen
7 spp.; widespread; Fisher 1941

R_{2+3} ending in C; base of M absent (Fig. 20). Empodia absent ....***Orfelia*** Costa
34 spp.; widespread

22. Rs and R_1 separated from level of crossvein h; stem of M absent; CuA_1 and branches of M present as detached veins on distal part of wing (Fig. 21). Mouthparts long and slender, several times as long as height of head (Fig. 6) ....LYGISTORRHININAE....***Lygistorrhina*** Skuse
1 sp., *sanctaecatharinae* Thompson; southeastern

Rs arising from R well beyond crossvein h; stem of M present or absent (Figs. 22–74). Mouthparts usually much shorter than head; if mouthparts long and slender, both M and CuA entire and normally forked 23

23. Stem of M absent; branches of M present as detached veins on distal part of wing (Fig. 22). Head inserted at anterior end of thorax, projecting as far dorsally as highest part of scutum, and with a row of strong posteriorly directed bristles behind eye (Fig. 7). Pronotum with many short hairs but without distinct bristles....................MANOTINAE....***Manota*** Williston
1 sp., unnamed; western

Stem of M present, although sometimes weak (Figs. 23–74). Head inserted below anterior end of thorax, not extending as far dorsally as highest part of scutum, and without strong posteriorly directed bristles behind eye. Pronotum with distinct bristles 24

24. Wing membrane either with microtrichia irregularly arranged (Fig. 75) and with macrotrichia present or absent, or with microtrichia absent and macrotrichia abundant; Sc variable, ending in C or in R or ending free; R_{2+3} present or absent (Figs. 23–63). Laterotergite haired or bare. Ocelli variable in position, often far from eye margins ............SCIOPHILINAE....25

Microtrichia always present and, especially near wing margin, arranged in more or less regular longitudinal lines (Fig. 76); macrotrichia usually absent, at most a few present in anal area; Sc ending free or in R; R_{2+3} absent (Figs. 64–74). Laterotergite haired. Lateral ocelli touching eye margins ....MYCETOPHILINAE....74

25. Fine tibial setae arranged in regular longitudinal rows (Fig. 82). Ocelli very close together near middle of frons. Wing membrane without macrotrichia..26

Fine tibial setae irregularly arranged (Fig. 83). Ocelli variable in position; lateral ocelli sometimes near eye margins. Wing membrane with or without macrotrichia 28

26. R_{2+3} absent; R_1 ending at or before level of point of furcation of M, subequal in length to crossvein r-m; crossvein r-m nearly horizontal; Sc very short, ending in R (Fig. 57). Three ocelli present; median one small. Laterotergite with a few hairs .... ***Aphrastomyia*** Coher & Lane
1 sp., unnamed; eastern

R_{2+3} present; R_1 ending far beyond level of point of furcation of M, at least six times as long as crossvein r-m; crossvein r-m nearly transverse; Sc long, ending in C or in R (Figs. 23, 24). Two ocelli present. Laterotergite bare 27

27. C extending slightly beyond apex of R_{4+5}; R_{4+5} reaching wing margin slightly before wing apex; wing membrane with a false vein between R_{4+5} and M_1; wing with conspicuous dark markings (Fig. 23) .... ***Neoempheria*** Osten Sacken
7 spp.; widespread

C ending at apex of R_{4+5}; R_{4+5} reaching wing margin at wing apex; wing membrane without false vein between R_{4+5} and M_1; wing unmarked or with obscure clouding (Fig. 24) .... ***Mycomya*** Rondani
61 spp.; widespread; Fisher 1937

28. Wing membrane with many distinct macrotrichia and usually also with microtrichia (Figs. 25–33, 35–41) (*Megalopelma* may have macrotrichia very reduced; it keys either way) 29

Wing membrane without macrotrichia or with at most a few near posterior margin (Fig. 45), always with dense microtrichia 47

29. Laterotergite bare; mediotergite bare 30

Laterotergite with strong erect hairs; mediotergite usually haired at least posteriorly 31

30. Point of furcation of CuA slightly beyond level of base of Rs (Fig. 25). Tibiae without distinct bristles .... ***Paratinia*** Mik
1 sp., *recurva* Johannsen; eastern

Point of furcation of CuA very near wing base; CuA_1 arising from base of M (Fig. 26). Tibiae with short but distinct bristles .... ***Loicia*** Vockeroth
1 sp., *basifurca* Vockeroth; British Columbia

31. M and CuA not clearly branched but a detached branch of one of them (probably of CuA) present near wing margin; Sc short, ending free (Fig. 27) .... ***Azana*** Walker
1 sp., unnamed; widespread

M or CuA, or both, clearly branched; Sc long, ending in C or in R_1 (Figs. 28–33, 35–41) 32

32. Sc ending in C (Figs. 29–41). Mediotergite haired; hairs usually long and erect but sometimes very short 33

Sc ending in R_1 (Fig. 28). Mediotergite bare .... ***Syntemna*** Winnertz
3 spp.; widespread

33. CuA unbranched (Figs. 29, 35) 34

CuA branched, with anterior branch sometimes obsolete basally (Figs. 30–33, 36–41) 36

34. Macrotrichia of wing membrane reflexed, directed toward wing base; R_{2+3} present or absent (Fig. 29). Posteroventral part of metepisternum with fine hairs .... ***Monoclona*** Mik
5 spp.; widespread; Fisher 1946

Macrotrichia decumbent, directed toward wing apex; R_{2+3} absent. Metepisternum bare 35

35. Two ocelli present. Sc ending before or opposite base of Rs (Fig. 35). Anepisternum haired above .... ***Cluzobra*** Edwards
1 sp., unnamed; Louisiana

Three ocelli present. Sc ending well beyond level of base of Rs. Anepisternum bare .... ***Acnemia*** Winnertz
3 spp.; widespread

36. Base of M_1 obsolete or very weak (Figs. 30–33, 36) 37

Base of M_1 entire (Figs. 37–41) 41

37. Crossvein sc-r beyond base of Rs; R_{2+3} present (Fig. 30) .... ***Polylepta*** Winnertz, in part
3 spp.; widespread

Crossvein sc-r, if present, before base of Rs; R_{2+3} absent (Figs. 31–33, 36) 38

38. R_{4+5} moderately to strongly sinuate; M_1 basally obsolete or weak for a moderate distance (Figs. 32, 33, 36) 39
R_{4+5} nearly straight; M_1 weak at base for only a very short distance (Fig. 31) .... ***Allocotocera*** Mik, in part
1 sp., *pulchella* (Curtis); eastern

39. C produced at least one-third of the distance between apex of R_{4+5} and apex of M_1; R_{4+5} moderately sinuate (Fig. 32) .... ***Anaclileia*** Winnertz
3 spp., unnamed; widespread
C produced at most one-fifth of the distance between R_{4+5} and M_1; R_{4+5} strongly sinuate (Figs. 33, 36) 40

40. Upper part of anepisternum, and metepisternum, with fine hairs. Male only .... ***Baeopterogyna*** Vockeroth, in part
see couplet 2
Anepisternum and metepisternum bare .... ***Neuratelia*** Rondani
14 spp.; widespread

41. Point of furcation of CuA beyond point of furcation of M; CuA_1 sometimes obsolete basally (Figs. 37–39) 42
Point of furcation of CuA before point of furcation of M; CuA_1 entire (Figs. 30, 31, 40, 41) 44

42. Legs extremely long and slender; first tarsomere of foreleg more than twice as long as fore tibia. CuA_2 widely divergent from CuA_1 (Fig. 37) .... ***Phthinia*** Winnertz
3 spp.; widespread
Legs normal; first tarsomere of foreleg not longer than fore tibia. CuA_2 only slightly divergent from CuA_1 (Figs. 38, 39) 43

43. Crossvein sc-r at least four times its own length from apex of Sc (Fig. 38); halter unicolorous or nearly so, yellow to pale brown. Anepisternum haired above .... ***Sciophila*** Meigen
23 spp.; widespread
Crossvein sc-r at most twice its own length from apex of Sc (Fig. 39); halter yellow with end of knob blackened. Anepisternum bare .... ***Megalopelma*** Enderlein, in part
2 spp.; widespread

44. C not produced beyond apex of R_{4+5} (Fig. 40) .... ***Leptomorphus*** Curtis
7 spp.; widespread
C produced well beyond apex of R_{4+5} (Figs. 30, 31, 41) 45

45. Crossvein sc-r well before base of Rs (Fig. 31). Anepisternum with many long hairs .... ***Allocotocera*** Mik, in part
see couplet 38
Crossvein sc-r beyond base of Rs (Figs. 30, 41). Anepisternum bare or with a few short hairs near upper margin 46

46. R_{4+5} sinuate; stem of median fork almost as long as M_1 (Fig. 30). Three ocelli present; lateral ocelli far from eye margins .... ***Polylepta*** Winnertz, in part
see couplet 37
R_{4+5} nearly straight; stem of median fork about one-sixth as long as M_1 (Fig. 41). Two ocelli present, touching eye margins .... ***Eudicrana*** Loew
1 sp., *obumbrata* Loew; eastern and central

47. Mediotergite with long erect hairs near posterior end 48
Mediotergite bare 50

48. M branched (Figs. 39, 43). Three ocelli present 49
M unbranched (Fig. 42). Two ocelli present, near middle of frons .... ***Adicroneura*** Vockeroth
1 sp., *biocellata* Vockeroth; Oregon

49. Laterotergite bare. Crossvein sc-r near middle of Sc; R_{2+3} absent (Fig. 43); wing membrane without macrotrichia .... ***Coelophthinia*** Edwards
1 sp., *curta* (Johannsen); widespread
Laterotergite haired. Crossvein sc-r very near end of Sc; R_{2+3} present (Fig. 39); wing membrane with very short erect or slightly reflexed macrotrichia .... ***Megalopelma*** Enderlein, in part
see couplet 43

50. Laterotergite bare 51
Laterotergite haired; hairs usually long and abundant but sometimes short and few in number and confined to posterior declivity of laterotergite 65

51. Sc ending in C (Figs. 44–46, 48–52) 52
Sc ending free or in R (Figs. 47, 53–55) 60

52. Point of furcation of CuA distinctly beyond level of point of furcation of M; crossvein sc-r absent (Fig. 44) .... ***Coelosia*** Winnertz
6 spp.; widespread
Point of furcation of CuA before, below, or very slightly beyond point of furcation of M; crossvein sc-r present or absent (Figs. 45–52) 53

53. R_1 not longer than crossvein r-m (Fig. 45) .... ***Garrettella*** Vockeroth
1 sp., *shermani* (Garrett); western
R_1 at least three times as long as crossvein r-m (Figs. 46–52) 54

54. Mouthparts forming a long slender proboscis that is several times as long as height of head (Fig. 10) .... ***Gnoriste*** Meigen
4 spp.; widespread
Mouthparts shorter than height of head 55

55. Point of furcation of CuA very near wing base; R_{2+3} present (Fig. 46). Female cercus long, strongly sclerotized, scimitar-like (Fig. 88) .... ***Drepanocercus*** Vockeroth
1 sp., *ensifer* Vockeroth; eastern
Point of furcation of CuA well beyond wing base; R_{2+3} present or absent (Figs. 47–52). Female cercus usually short, weakly sclerotized 56

56. Crossvein sc-r present, well beyond middle of Sc (Fig. 48) 57
Crossvein sc-r near middle of Sc, or absent (Figs. 49–51) 58

57. Point of furcation of CuA beyond base of crossvein r-m; stem of median fork three times as long as crossvein r-m; wing unmarked (as in Fig. 47) .... ***Synapha*** Meigen, in part
3 spp.; widespread
Point of furcation of CuA before base of crossvein r-m; stem of median fork less than twice as long as crossvein r-m; wing with dark cloud on crossvein r-m and at apex (Fig. 48) .... ***Aglaomyia*** Vockeroth
1 sp., *gatineau* Vockeroth; Quebec

58. R_{2+3} present (Fig. 49) .... ***Acomoptera*** Vockeroth
1 sp., *plexipus* (Garrett); western
R_{2+3} absent (Figs. 50, 51) 59

59. Sc ending before level of base of crossvein r-m (Fig. 50). Metepisternum with very short hairs that are dark in female but pale and inconspicuous in male .... ***Saigusaia*** Vockeroth
1 sp., *cincta* (Johannsen); eastern
Sc ending beyond level of base of crossvein r-m (Fig. 51). Metepisternum bare .... ***Boletina*** Staeger, in part
36 spp.; widespread

60. Crossvein r-m nearly horizontal; R_1 less than three times as long as crossvein r-m (Figs. 53, 54, 62) 61
Crossvein r-m oblique; R_1 more than 3.5 times as long as crossvein r-m (Figs. 47, 55) 63

61. Basal section of Rs indistinguishable because of crowding of radial veins toward C (Fig. 53) .... ***Novakia*** Strobl
1 sp., unnamed; widespread
Basal section of Rs distinct (Figs. 54, 62) 62

62. Hind coxa with many posterolateral hairs near base, then bare almost to apex (Fig. 84). R_{2+3} absent; point of furcation of CuA well beyond wing base; both branches of CuA entire (Fig. 54). Lateral ocelli very near eye margins .... ***Docosia*** Winnertz, in part
15 spp.; widespread
Hind coxa with a row of rather long setose posterolateral hairs on at least apical three-quarters (Fig. 85). R_{2+3} present (Fig. 62) or absent; point of furcation of CuA very near or well

beyond wing base; anterior branch of CuA sometimes very weak basally or detached. Lateral ocelli variable in position (including *Ectrepesthoneura* Enderlein) ...... ***Tetragoneura*** Winnertz
11 spp.; widespread

63. Stem of median fork at least three times as long as crossvein r-m; R_{2+3} present (Fig. 47) 64
Stem of median fork less than twice as long as crossvein r-m; R_{2+3} present or absent (Fig. 55) .... ***Dziedzickia*** Johannsen, in part
8 spp.; widespread

64. Spurs of mid tibia subequal in length to apical tibial diameter; mid and hind tibiae with bristles few in number and much shorter than tibial diameter. Antepenultimate palpal segment slender .... ***Speolepta*** Edwards
1 sp., unnamed; eastern

Spurs of mid tibia about twice as long as apical tibial diameter; mid and hind tibiae with many bristles, some of which are longer than tibial diameter. Antepenultimate palpal segment broad and flat, projecting well beyond base of fourth segment (Fig. 8) .... ***Synapha*** Meigen, in part
see couplet 57

65. Sc ending in C (Figs. 51, 56, 58–60) 66
Sc ending free or in R (Figs. 54, 55, 61, 63) 70

66. R_1 at least four times as long as crossvein r-m (Figs. 51, 56) 67
R_1 at most three times as long as crossvein r-m (Figs. 58–60) 68

67. R_{2+3} present; crossvein sc-r absent; Sc densely setose above (Fig. 56) ... ***Apolephthisa*** Grzegorzek
1 sp., unnamed; widespread

R_{2+3} absent; crossvein sc-r usually present; Sc usually bare above, rarely with a few setae (Fig. 51) .... ***Boletina*** Staeger, in part
see couplet 59

68. M_1 detached at base, not longer than stem of median fork; crossvein r-m oblique (Fig. 58) .... ***Rondaniella*** Johannsen
1 sp., *dimidiata* (Meigen); widespread

M_1 not detached at base, much longer than stem of median fork; crossvein r-m nearly horizontal (Figs. 59, 60) 69

69. R_{4+5} ending well before level of apex of M_2 (Fig. 59). Prosternum with strong lateral bristles. Lateral ocelli separated from eye margins by about three times their own diameter .... ***Greenomyia*** Brunetti
2 spp.; western

R_{4+5} ending opposite or beyond level of apex of M_2 (Fig. 60). Prosternum bare. Lateral ocelli variable in position, usually separated from eye margins by less than their own diameter .... ***Leia*** Meigen
19 spp.; widespread

70. R_1 at most twice as long as crossvein r-m; crossvein r-m nearly horizontal (Figs. 54, 61) 71
R_1 at least four times as long as crossvein r-m; crossvein r-m oblique (Figs. 55, 63) 72

71. Point of furcation of M well before level of apex of R_1 (Fig. 54). Hind coxa with many posterolateral hairs near base (Fig. 84). Lateral ocelli very near eye margins .... ***Docosia*** Winnertz, in part
see couplet 62

Point of furcation of M below or beyond level of apex of R_1 (Fig. 61). Hind coxa bare on basal two-thirds. Lateral ocelli separated from eye margins by more than their own diameter .... ***Megophthalmidia*** Dziedzicki
1 sp., *occidentalis* Johannsen; western

72. Sc ending in R; point of furcation of CuA well before base of crossvein r-m; R_{2+3} present (Fig. 63) or absent (Fig. 55). Hairs of laterotergite long and strong 73

Sc ending free; point of furcation of CuA below or slightly beyond base of crossvein r-m; R_{2+3} absent. Hairs of laterotergite short and weak .... ***Acadia*** Vockeroth
1 sp., *polypori* Vockeroth; New Brunswick

73. R_{2+3} absent or, if present, less than its own length from outer end of crossvein r-m; Sc ending before or beyond base of Rs (Fig. 55) .... ***Dziedzickia*** Johannsen, in part
see couplet 63

R_{2+3} present, at least twice its own length from outer end of crossvein r-m; Sc ending beyond base of Rs (Fig. 63) .... ***Hadroneura*** Lundström
4 spp.; widespread

74. Anepisternum bare or with short fine hairs (Fig. 86) 75
Anepisternum with strong bristles at least near upper margin (Fig. 87) 85

75. C ending well beyond apex of R_{4+5} (Fig. 64) .... ***Anatella*** Winnertz
5 spp.; widespread; Fisher 1938
C ending at apex of R_{4+5} (Figs. 65–68) 76

76. Point of furcation of CuA beyond level of point of furcation of M (Figs. 65, 66) 77
Point of furcation of CuA before or opposite level of point of furcation of M (Figs. 67, 68) 78

77. R_{4+5} curved caudally at apex; Sc ending in R (Fig. 65). Dorsal surface of hind tibia oblique apically; dorsal surface of apex with a large triangular shining depression (Figs. 77, 78) .... ***Exechiopsis*** Tuomikoski
several spp.; widespread

R_{4+5} nearly straight; Sc ending free or in R (Fig. 66). Dorsal surface of hind tibia nearly transverse apically; dorsal surface of apex with a small triangular depression (Figs. 79, 80).... .... ***Exechia*** Winnertz
many spp.; widespread

78. Branches of M, and usually also of CuA, setulose above especially near apex 79
Branches of M and of CuA without setulae above 82

79. Sc ending free (as in Fig. 66) 80
Sc ending in R (as in Fig. 65) 81

80. Mid and hind coxae each with a vertical blackish mark near apex; hind tibia with posterior bristles on no more than apical third. Flagellum of female antenna strongly swollen basally (Fig. 3) .... ***Stigmatomeria*** Tuomikoski
1 sp., *crassicornis* (Stannius); widespread

Mid and hind coxae without dark mark near apex; hind tibia with posterior bristles on most of its length. Flagellum slender in both sexes .... ***Pseudobrachypeza*** Tuomikoski
1 sp., *bulbosa* (Johannsen); widespread

81. Most flagellomeres shorter than wide and anepisternum haired on upper half .... ***Brachypeza*** Winnertz
3 spp.; widespread

Either flagellomeres longer than wide or anepisternum bare .... ***Allodiopsis*** Tuomikoski
several spp.; widespread

82. Sc ending free; A_1 strong, extending beyond point of furcation of CuA (Fig. 67). Mediotergite usually with short appressed or suberect hairs at upper end of posterior declivity..................... .... ***Rymosia*** Winnertz
several spp.; widespread

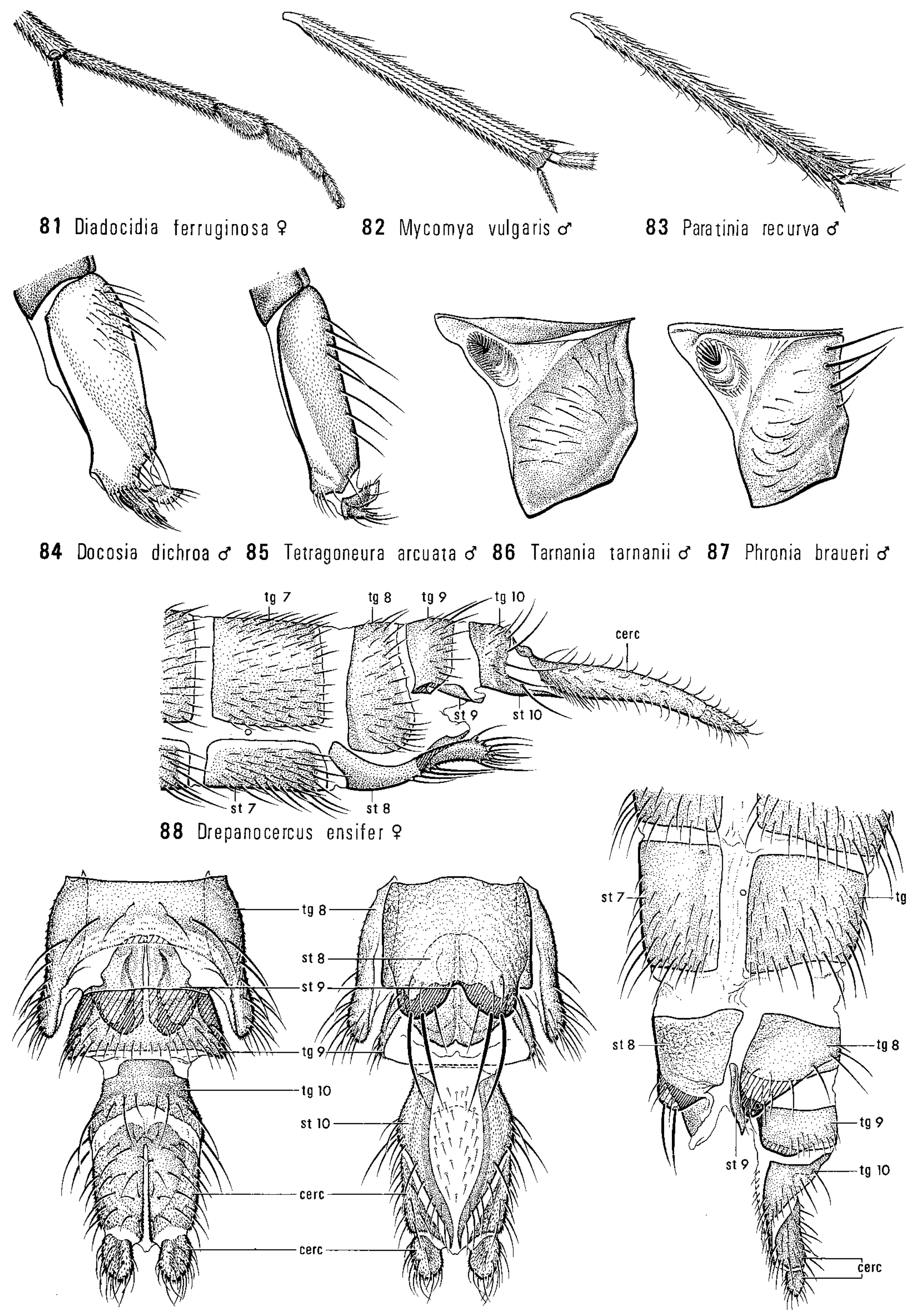
Sc ending in R_1; A_1 variable in length and strength. Mediotergite bare 83

83. Anepisternum with short hairs (Fig. 86). Basal portion of M and crossvein r-m setulose above; A_1 strong, extending beyond point of furcation of CuA (as in Fig. 67) ..***Tarnania*** Tuomikoski
1 sp., *tarnanii* (Dziedzicki); widespread

Anepisternum bare. Basal portion of M and crossvein r-m without setulae; A_1 weak, not extending to point of furcation of CuA (Fig. 68) 84

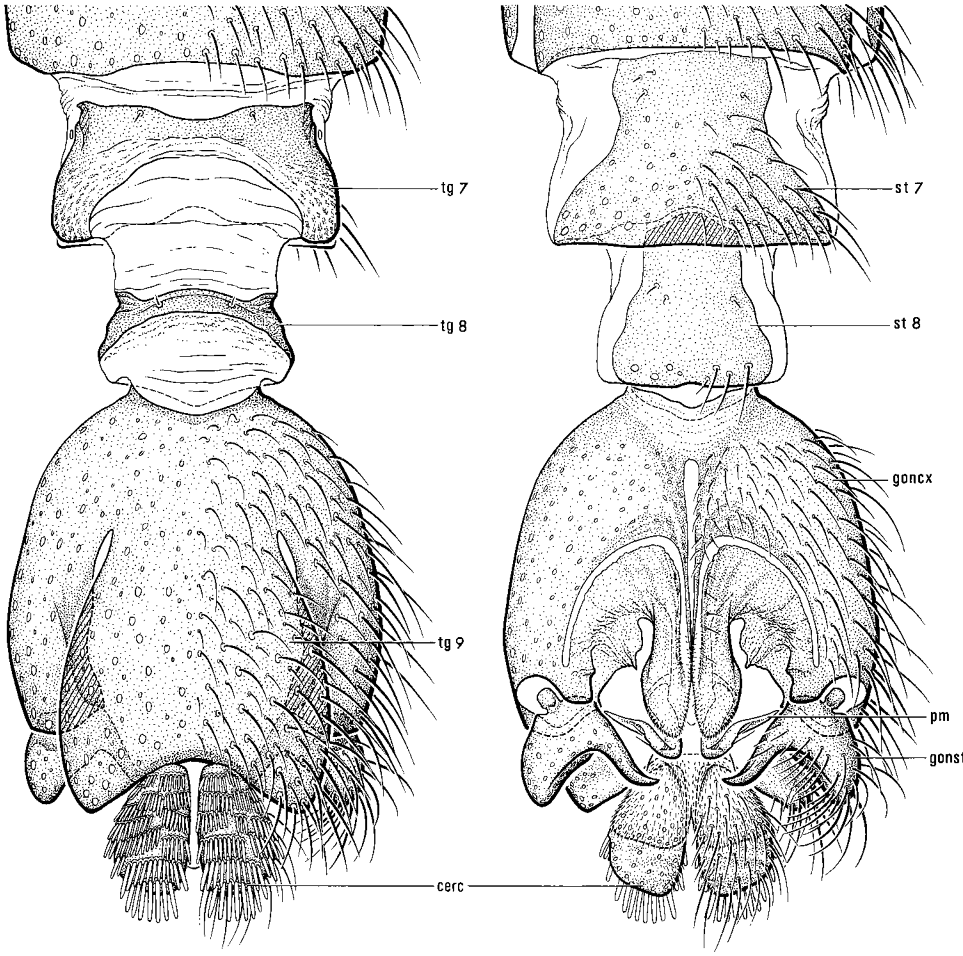
84. Hind tibia with one or more short fine posterior bristles on apical third. Scutum with subappressed bristles on most of disc... ***Brevicornu*** Marshall
several spp.; widespread

Hind tibia without posterior bristles. Scutum either with discal bristles arranged in two sublateral stripes and sometimes also a median stripe, or without discal bristles .... ***Allodia*** Winnertz
several spp.; widespread

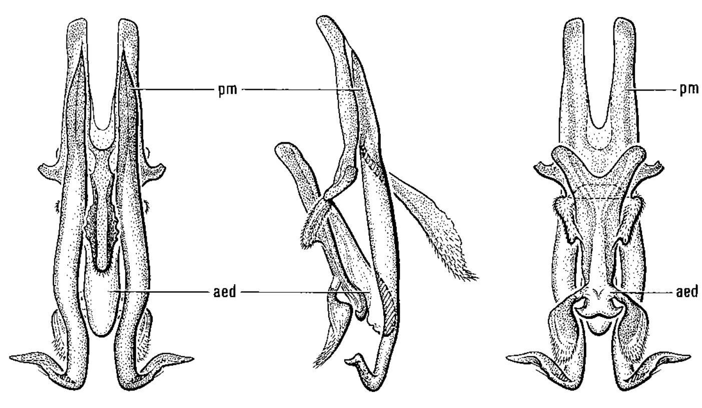


Figs. 14.81–91. Legs, anepisterna, and female terminalia: anterior view of (81) tarsus of foreleg of *Diadocidia ferruginosa* (Meigen); anterior view of tibia of foreleg of (82) *Mycomya vulgaris* Garrett and (83) *Paratinia recurva* Johannsen; lateral view of left hind coxa of (84) *Docosia dichroa* Loew and (85) *Tetragoneura arcuata* Sherman; left anepisternum of (86) *Tarnania tarnanii* (Dziedzicki) and (87) *Phronia braueri* Dziedzicki; terminalia of female of (88) *Drepanocercus ensifer* Vockeroth in lateral view, (89) *Boletina* sp. in dorsal view, (90) *Boletina* sp. in ventral view, and (91) *Boletina* sp. in lateral view.

Abbreviations: cerc, cercus; st, sternite; tg, tergite.



92 Boletina sp. **93** Boletina sp.



94 Boletina sp. ♂ **95** Boletina sp. ♂ **96** Boletina sp. ♂

Figs. 14.92–96. Male terminalia of *Boletina* sp.: (92) terminalia in dorsal view and (93) in ventral view; (94) aedeagus and parameres in dorsal view, (95) in left lateral view, and (96) in ventral view.

Abbreviations: aed, aedeagus; cerc, cercus; goncx, gonocoxite; gonst, gonostylus; pm, paramere; st, sternite; tg, tergite.

85. Antepenultimate palpal segment swollen, much thicker than penultimate segment (Fig. 9). Antenna short and stout; flagellum with 9–13 segments (Fig. 9). Katepimeron with a sharply delimited black mark near anterior margin .... ***Cordyla*** Meigen
10 spp.; widespread

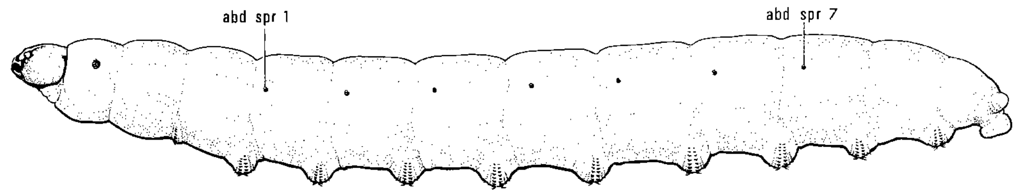
Antepenultimate palpal segment slender, not thicker than penultimate segment. Antenna slender; flagellum with 14 segments. Katepimeron without black mark anteriorly 86

86. Anepimeron bare. Tibial bristles short or long 87

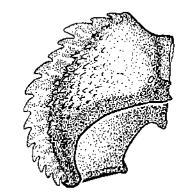
Anepimeron with hairs and bristles. Tibial bristles long, up to three times as long as tibial diameter...90

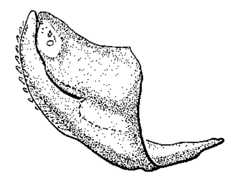
87. Longest tibial bristles about three times as long as tibial diameter. Sc ending in R .... ***Dynatosoma*** Winnertz
8 spp.; widespread

Tibial bristles subequal in length to tibial diameter. Sc ending free or in R 88

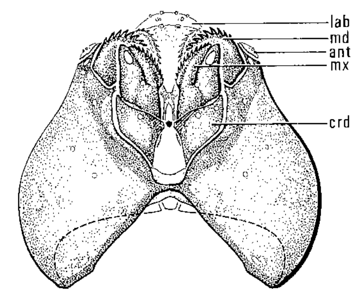


97 Mycetophila sp.

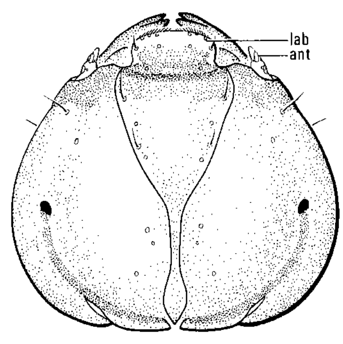




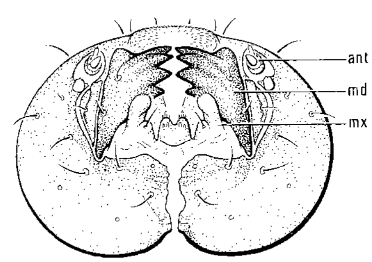
98 Mycetophila fisherae **99**



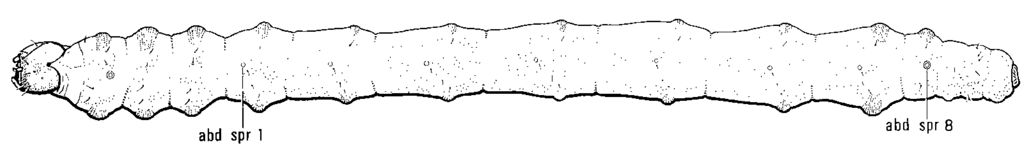
100 Mycetophila fisherae



101 Symmerus coqulus



102 Symmerus coqulus



103 Symmerus coqulus

Figs. 14.97–103. Larvae: (97) *Mycetophila* sp.; (98) *Mycetophila fisherae* (Laffoon), mandible; (99) *M. fisherae*, maxilla; (100) *M. fisherae*, head capsule, ventral view; (101) *Symmerus coqulus* Garrett, head capsule, dorsal view; (102) *S. coqulus*, head capsule, anterior view; (103) *S. coqulus*, general view.

Abbreviations: abd spr, abdominal spiracle; ant, antenna; crd, cardo; lab, labium; md, mandible; mx, maxilla.

88. Point of furcation of CuA before, opposite, or very slightly beyond point of furcation of M; Sc usually ending in R (Fig. 69) .... ***Trichonta*** Winnertz
46 spp.; widespread; Gagné, in press

Point of furcation of CuA well beyond point of furcation of M; Sc ending free (Fig. 70) 89

89. C extending more than halfway between apex of R_{4+5} and apex of M_1 .... ***Macrobrachius*** Dziedzicki
1 sp., *productus* (Johannsen); eastern

C extending at most very slightly beyond apex of R_{4+5} (Fig. 70) .... ***Phronia*** Winnertz
49 spp.; widespread; Gagné 1975

90. CuA forked (Figs. 71, 72) 91

CuA simple (Figs. 73, 74) 92

91. CuA_1 slightly divergent from M_2 but parallel with or convergent toward CuA_2 (Fig. 71) .... ***Mycetophila*** Meigen
97 spp.; widespread; Laffoon 1957 (as *Fungivora* Meigen)

CuA_1 parallel with M_2 but slightly divergent from CuA_2 (Fig. 72) (including *Platurocypta* Enderlein) .... ***Epicypta*** Winnertz
2 spp.; widespread

92. CuA slightly divergent from M_2 (Fig. 73). Mid tibia with one or more short to long ventral bristles .... ***Zygomyia*** Winnertz
9 spp.; widespread

CuA parallel with M_2 (Fig. 74). Mid tibia without ventral bristles .... ***Sceptonia*** Winnertz
2 spp.; widespread

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SCIARIDAE 15

WALLACE A. STEFFAN

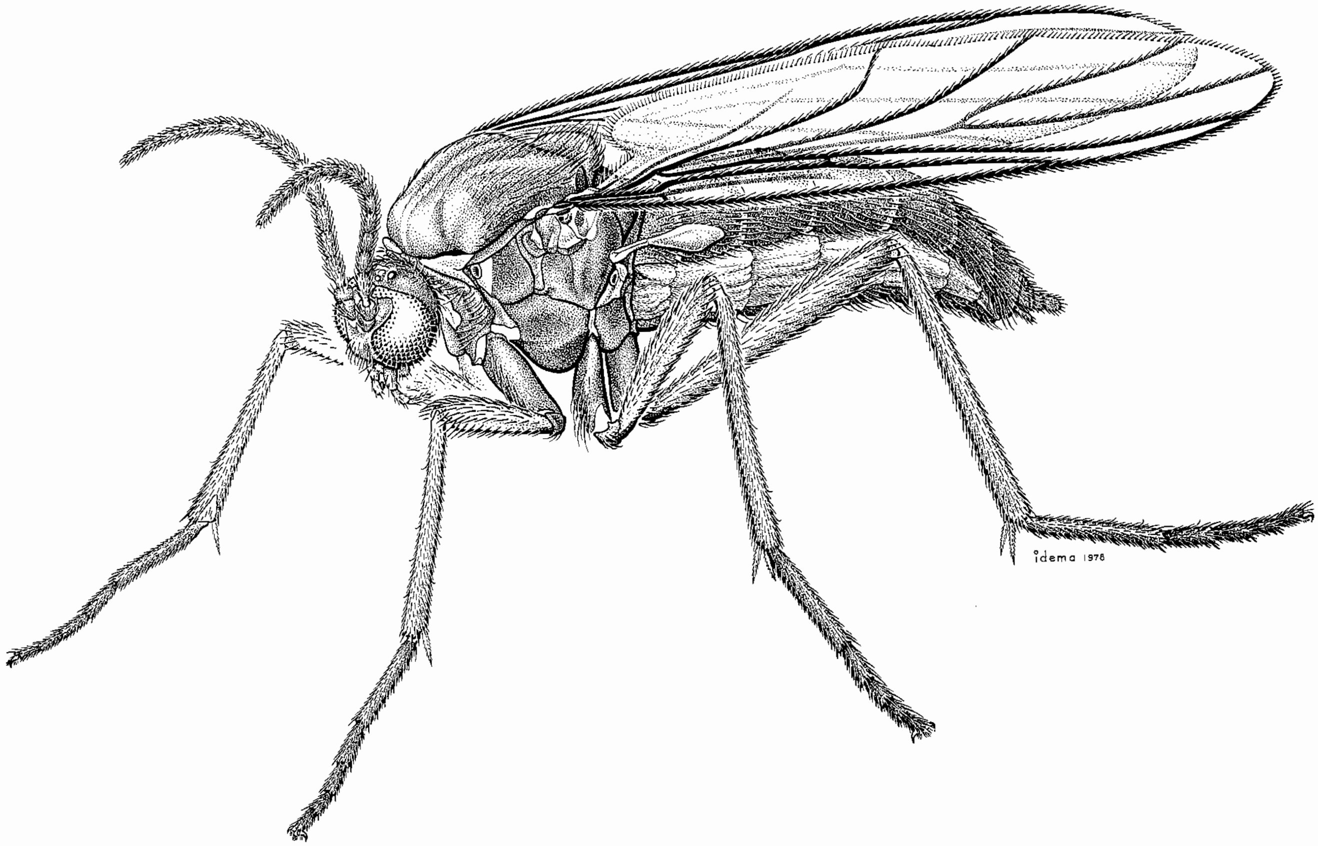


Fig. 15.1. Female of *Sciara* sp.

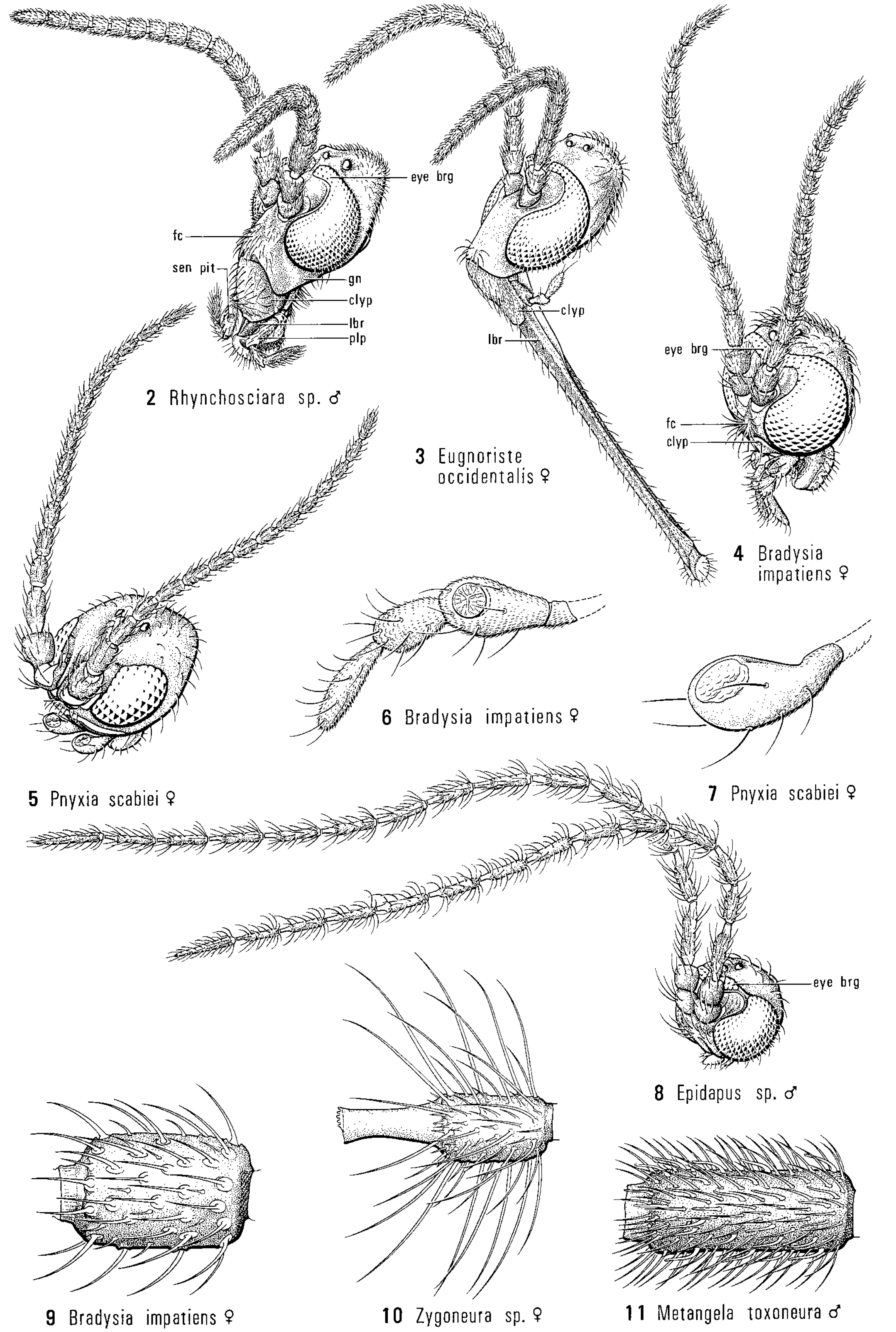
Small flies, 1.0–11 mm long, usually blackish, brownish, or yellowish (Fig. 1). Compound eyes usually forming dorsal bridge above antennal bases (Figs. 2–4, 8). C ending between apices of R_5 and M_1 (Figs. 14–19). Tibiae with one or two apical spurs (Figs. 24–29). Abdomen cylindrical and usually strongly tapering in female.

Adult. Head: usually ovoid, higher than long. Antenna long; scape and pedicel globular; 14 flagellomeres, cylindrical, sessile or stalked, without specialized sensoria (Figs. 9–11), with setae irregularly arranged except in the Palaearctic genus *Pharatretula* Mamaev. Proboscis usually short, but slightly elongate in *Rhynchosciara* Rübsaamen (Fig. 2) and slightly to greatly elongate in *Eugnoriste* Coquillett (Fig. 3). Palpus (Fig. 6) with one to three distinct segments, usually (and perhaps always) with a greatly reduced basal segment; first distinct segment often with a sensory pit or with a group of sensory setae. Compound eyes, except in some subapterous or apterous forms (Fig. 5), united or nearly united above antennal bases by a characteristic eye bridge of variable width (Figs. 2–4, 8); three ocelli present.

Thorax: antepronotum haired; postpronotal lobe sometimes with a few hairs near its inner end; scutum with acrostichal and dorsocentral bristles of variable length; mediotergite and laterotergite sometimes with hairs; proepisternum haired; other pleural sclerites, and prosternum, bare (Figs. 12, 13). Pleural pit distinct, situated on dorsal median edge of katepisternum; katepisternum well-developed, usually triangular in shape (Figs. 12, 13).

Wing (Figs. 14–19) hyaline or fumose, sometimes reduced or absent. C short, ending between apices of R_5 and M_1; Sc weak, ending free; CuP, A_1, and A_2 poorly developed; crossvein r-m in line with R_5; M and CuA forked; crossvein m-cu absent. R and its branches setose above; most other veins sometimes setose above; some veins sometimes setose below. Halter absent in wingless females.

Fore tibia (Figs. 24–29) with one apical spur and usually with a row or patch of modified setae anteroapically; mid and hind tibiae each with one or two apical spurs. Tarsal claws (Figs. 30, 31) simple or toothed. Empodia broad; pulvilli narrow to broad, all much shorter than claws.



Figs. 15.2–11. Details of head: head of (2) *Rhynchosciara* sp., (3) *Eugnoriste occidentalis* (Coquillett), (4) *Bradysia impatiens* (Johannsen), and (5) *Pnyxia scabiei* (Hopkins); palpus of (6) *Bradysia impatiens* and (7) *Pnyxia scabiei*; (8) head of *Epidapus* sp.; fourth flagellomere of (9) *Bradysia impatiens*, (10) *Zygoneura* sp., and (11) *Metangela toxoneura* (Osten Sacken).

Abbreviations: clyp, clypeus; eye brg, eye bridge; fc, face; gn, gena; lbr, labrum; plp, palpus; sen pit, sensory pit.

Abdomen: cylindrical, in female usually strongly tapered posteriorly, bluntly rounded in *Rhynchosciara*.

Male terminalia (Figs. 20–23) exposed, often broader than rest of abdomen, usually not rotated, but apparently sometimes rotated up to 180° during copulation. Tergite 8 and sternite 8 much shorter than preceding sclerites. Tergite 9 large but not extending beyond posterior margin of gonocoxite; sternite 9 possibly represented by a narrow flange at the base of the ventrally fused gonocoxites; gonocoxite with well-developed dorsal apodeme; gonostylus elongate, slender or swollen, sometimes with inner surface excavated or with a tubercle or distinct process, frequently with a strong preapical or apical spine or spines or with setae; aedeagus (tegmen of authors) strongly sclerotized, subtriangular, usually depressed (especially posteriorly) but sometimes with complex flanges extending ventrolaterally; ejaculatory apodeme (genital rod of authors) weak but distinct, usually bifurcate apically; paramere represented only by its internal apodeme which articulates with, or is apparently attached to, the apodeme of the gonocoxite. Sternite 10 reduced to a pair of weak sometimes setose lobes which lie below the bases of the cerci; cercus well-developed, articulated with apex of tergite 9.

Female (Fig. 32) with tergites 7–10 sclerotized but usually weakly so medially or on disc; rarely sclerotization of several preceding tergites also weak medially. Body of sternite 8 weak medially; posterior portion of sternite 8 nearly detached, projecting caudally below segment 9 as two tapering hypogynial valves joined over most of their length by a membrane (this portion of sternite 8 is markedly different in *Rhynchosciara*). Sclerotized portion of sternite 9 Y-shaped, forming a genital fork. Sternite 10 divided; each half closely associated with lateral margin of tergite 10, tapering to a slender apex and usually with an apical seta or up to seven lateral setae; cercus well-developed, two-segmented; spermathecae unsclerotized except in some species of *Pharatretula*.

Larva. Characterized by a shiny black head and a 12-segmented generally featureless white translucent body (Fig. 35). First instar metapneustic; second and third instars propneustic; fourth instar hemipneustic; anterior spiracle with two openings; abdominal spiracles each with one opening. Terminal abdominal segment lobate, acting as a proleg.

Head capsule (Fig. 33) chitinized, black, providing most taxonomic characters, dorsally consisting of a triangular frontoclypeal apotome, a mainly membranous labrum, and two genae. Several sensory pits and papillae present on each side of lateral ecdysial lines and along anterior margin of frontoclypeal apotome. Labrum consisting of a fleshy lobe supported proximally by a well-developed labral sclerite extending ventrally around labrum and forming two distinct ventral branches; dorsal membranous surface with several papillae; ventral surface with several comb-like brushes. Genae extending laterally and meeting ventrally at two points to enclose a distinct pyriform membranous area. Antenna small, arrow-shaped, lying above base of mandible, with several minute papillae usually present in membrane at antennal base. Eye indicated by lightly pigmented area below antennal base. Mandible rectangular with anteromedial teeth and well-defined prostheca on median angle; maxilla bearing several teeth that usually become progressively stronger and most distinct medially; base of maxilla with lateral and proximal rods; maxillary palpus weakly sclerotized and fused to maxilla; cardo triangular; hypopharynx a V-shaped rod between bases of maxillae.

Pupa. Obtect (Fig.34). Head with vertexal plate and dorsal surfaces of antennal sheaths present dorsally; vertexal plate situated between narrow pronotum and two vertexal tubercles; tubercles each bearing a strong bristle; antennal sheath extending obliquely to and along anterior margin of wing sheath. Frontoclypeal apotome situated between base of antennal sheath and proboscial sheath, with posterior margin extending tongue-like over anterior edge of broadly rectangular proboscial sheath. Palpal sheath extending laterally below compound eyes.

Thorax not highly arched; narrow pronotum extending from anterior spiracular tubercles; mesonotum generally featureless; metanotum lying between halter sheaths. Wing sheath extending posteroventrally to posterior margin of abdominal segment 2. Legs closely appressed and folded. Anterior spiracle on blunt tubercle, with 3–13 spiracular openings arranged in a semicircle or in a line.

Abdomen with nine segments, sometimes covered with very short wart-like spines that are denser on tergites and on terminalia than elsewhere. Abdominal spiracles present on segments 2–7; each spiracle slightly stalked, with a single opening. Terminal segment of male bearing a sheath enclosing each gonostylus and a sheath enclosing each cercus; tergite 9 sometimes with two posterolateral prolongations covered with short spines.

Biology and behavior. Sciarid larvae generally feed on decaying plant material, animal excrement, or fungus. Some species feed in rotting wood or under the bark of fallen trees. Several species of Sciaridae have been reported as economic pests in greenhouses and commercial mushroom houses. Other species have been found in animal burrows, bird's nests, and caves. *Bradysia macfarlanei* (Jones) was reported feeding on dead insects in the tubes of the pitcher plant, *Sarracenia sledgei*.

Peculiar mass movements by some sciarid larvae have been well-documented, but the purpose of this behavior has not been investigated adequately.

Some species of Sciaridae have an unusual mode of sex determination undoubtedly related to the anomalous type of spermatogenesis and selective elimination of chromosomes from both the somatic cells and germ line during the early cleavage divisions of the embryo. The sex of the progeny seems to depend on the genetic composition of the mother (Metz 1938, McCarthy 1945, Crouse 1960). Also, the sex ratio of the progeny from a single female differs in some species, i.e. they are either all males or all females. Other species display a more typical sex ratio (Steffan 1966).

Some of these unusual features, plus others such as the loss of the *y* chromosome, are shared with the Cecidomyiidae and differ markedly from those found in the Mycetophilidae. White (1950) suggested that the Sciaridae and the Cecidomyiidae had a common origin from a mycetophilid-like ancestor, probably in the Mesozoic. However, few Mycetophilidae and none of the most primitive Cecidomyiidae (Lestremiinae) have been investigated cytologically, so these conclusions, which are not well supported by morphological evidence, are tentative.

Moehnia erema Pritchard is apparently parthenogenic, as are several species of Cecidomyiidae.

Classification and distribution. The Sciaridae have been treated by most authors as a subfamily of the Mycetophilidae or as a distinct family. The great similarity of the head capsule and mouthparts of larval Sciaridae and of most Mycetophilidae, and the loss of the eighth abdominal spiracle of the larva in Sciaridae and in most Mycetophilidae, indicate that the Sciaridae are probably a sister group of some part of the Mycetophilidae rather than of the Cecidomyiidae.

Only three genera are doubtfully referred to the family. *Ohakunea* Edwards (Chile, New Zealand, Australia), *Colonomyia* Colless (Australia), and *Heterotricha* Loew (south temperate) differ markedly from other Sciaridae in wing venation, in structure of male terminalia, and in the presence of an incomplete eye bridge.

Trichosia Winnertz, to which the Nearctic *T. hebes* Loew has been referred, is not clearly separable from *Sciara* Meigen in the Nearctic region, so only *Sciara* is recognized here.

Rhynchosciara Rübsaamen is Neotropical, but it may extend into the Nearctic region so it has been included in the key. Some Nearctic species at present referred to *Bradysia* Winnertz probably belong to *Chaetosciara* Frey. Gagné (1970) transferred *Moehnia* Pritchard, described as a genus of Cecidomyiidae, to the Sciaridae. This genus is very close to *Epidapus* Haliday and may even be congeneric. The presence of wings in the female of *M. erema* (the male is unknown) versus the absence of wings in the female of *Epidapus* may be of little taxonomic significance. Recent studies of polymorphism in *Plastosciara perniciosa* Edwards indicate that the presence or absence of wings may not be a valid generic, or even specific, character (Steffan 1973, 1975).

Sciaridae occur on all continental areas (except Antarctica) and on many oceanic islands. Several species have undoubtedly been widely distributed by man.

Extensive revisionary studies of both genera and species are needed. A revision of world genera is essential before any systematic stability can be attained. About 150 species are known in the Nearctic region; this number probably represents less than 50% of the actual fauna. Some Nearctic species are undoubtedly synonymous with Palaearctic species. The most important works for study of the Nearctic fauna are Johannsen (1912), Pettey (1918), Frey (1948), Tuomikoski (1960), and Steffan (1966).

Scudder has described one fossil species of *Sciara* Meigen from the Oligocene (Green River, Wyoming) and Melander (1949) provides a key to four *Sciara* spp. from the Miocene in Florissant shales of Colorado. Over 50 species of Sciaridae have been described from Baltic amber, mostly by Meunier (1904).

Key to genera

1. Wing present and major longitudinal veins (at least R_1) distinct (Figs. 14–19) 2
   Wing absent or major longitudinal veins indistinct 21

2. Fork of M asymmetric; M_1 strongly arcuate near base (Fig. 14) 3
   Fork of M symmetric; M_1 weakly arcuate near base (Figs. 15–19) 4

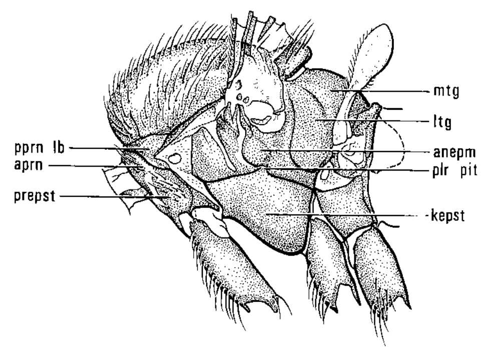
3. Fore tibia with distinct subtriangular preapical patch of more than 10 stout setae (Fig. 24). Flagellomeres of male with short stems that are less than one-third length of flagellomere (Fig. 11) ..... ***Metangela*** Rübsaamen
   1 sp., *toxoneura* (Osten Sacken); eastern

   Fore tibia with indistinct preapical row of less than 10 setae (Fig. 25). Flagellomeres of male with elongate stems that are about one-half length of flagellomere (Fig. 10) ..... ***Zygoneura*** Meigen
   2 spp.; widespread

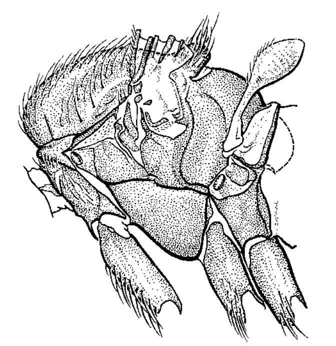
4. Head snout-like or proboscis greatly elongate; gena extending below ventral margin of compound eye; clypeus enlarged (Figs. 2, 3) 5
   Head normal and proboscis less than one-half length of head; gena ending dorsal to ventral margin of compound eye; clypeus small (Figs. 4, 5) 6

5. First segment of palpus with sensory pit; labrum normal, less than half as long as clypeus (Fig. 2). Female abdomen bluntly rounded apically. Large species; wing usually more than 5 mm long, with dark membrane .... ***Rhynchosciara*** Rübsaamen
Neotropical

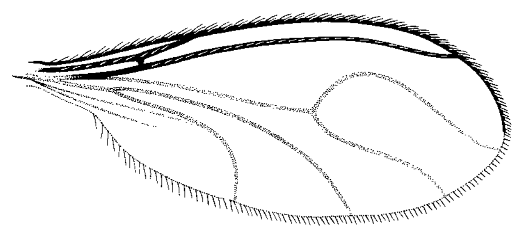
First segment of palpus without sensory pit; labrum elongate, from one to three times as long as clypeus (Fig. 3). Female abdomen strongly tapered apically. Small species; wing usually less than 4 mm long, with clear membrane .... ***Eugnoriste*** Coquillett
3 spp.; widespread



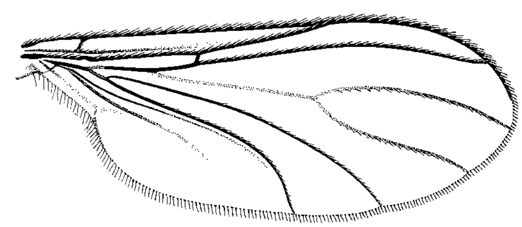
12 Plastosciara sp. ♀



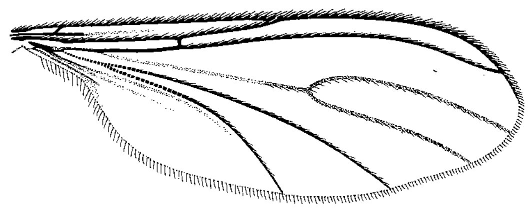
13 Lycoriella mali ♀



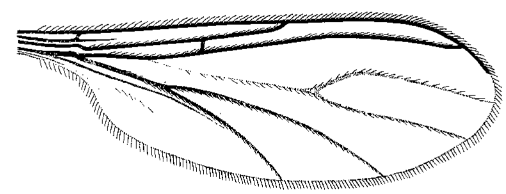
14 Zygoneura sp. ♂



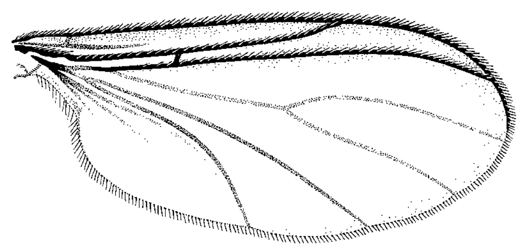
15 Sciara sp. ♂



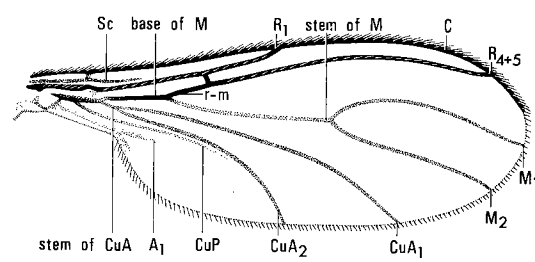
16 Phytosciara flavipes ♀



17 Pseudosciara forceps ♀



18 Schwenkfeldina imitans ♂



19 Lycoriella sp. ♂

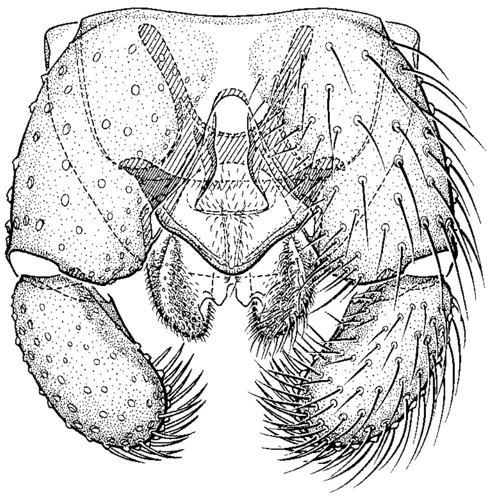
Figs. 15.12–19. Thoraces and wings: left lateral view of thorax of (12) *Plastosciara* sp. and (13) *Lycoriella mali* (Fitch); wing of (14) *Zygoneura* sp., (15) *Sciara* sp., (16) *Phytosciara flavipes* (Meigen), (17) *Pseudosciara forceps* (Pettey), (18) *Schwenkfeldina imitans* (Johannsen), and (19) *Lycoriella* sp.

Abbreviations: anepm, anepimeron; aprn, antepronotum; kepst, katepisternum; ltg, laterotergite; mtg, mediotergite; plr pit, pleural pit; pprn lb, postpronotal lobe; prepst, proepisternum.

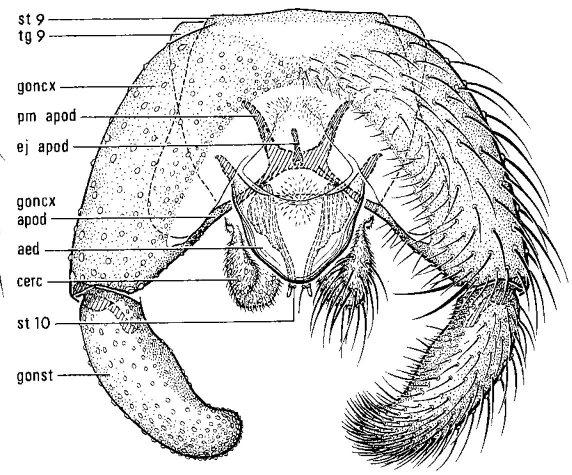
6. Branches of M and usually those of CuA with many setae above (Figs. 15–17) 7
   Branches of M and of CuA bare (Figs. 18, 19) 10

7. Branches of CuA with many setae above. Fore tibia anteroapically with modified setae in a single row (as in Fig. 28) or in a subtriangular patch (Figs. 26, 27). Tarsal claws with or without ventral teeth (Figs. 30, 31) 8
   CuA_1 with at most four setae above; CuA_2 bare. Fore tibia anteroapically with modified setae in two or three irregular rows. Tarsal claws with strong ventral teeth (as in Fig. 31) ....***Odontosciara*** Rübsaamen
   1 sp., *nigra* (Wiedemann); southern

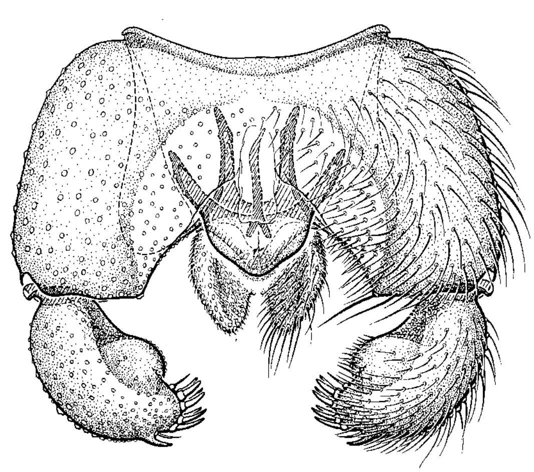
8. Base of M and stem of CuA both longer than crossvein r-m (Fig. 17); stem of CuA with setae above, at least near apex. Fore tibia anteroapically with a subtriangular patch of modified setae (Fig. 26)...***Pseudosciara*** Schiner
   1 sp., *forceps* (Pettey); Florida
   Base of M or stem of CuA (or both) shorter than crossvein r-m (Figs. 15, 16); stem of CuA bare. Fore tibia anteroapically with either a single row (Fig. 28) or a subtriangular patch of modified setae (Fig. 27)..9



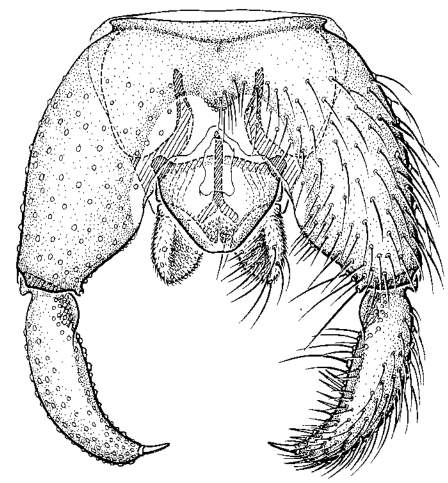
20 Sciara sp. ♂



21 Phytosciara flavipes ♂



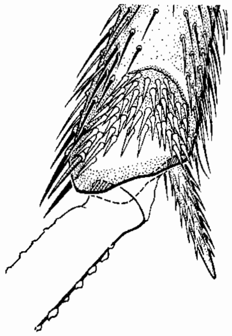
22 Corynoptera sp. ♂



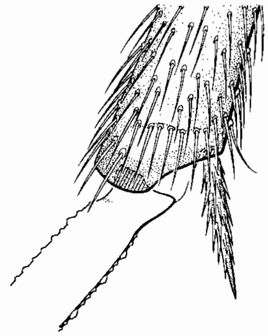
23 Lycoriella sp. ♂

Figs. 15.20–23. Male terminalia, ventral view: (20) *Sciara* sp.; (21) *Phytosciara flavipes* (Meigen); (22) *Corynoptera* sp.; (23) *Lycoriella* sp.

Abbreviations: aed, aedeagus; cerc, cercus; ej apod, ejaculatory apodeme; goncx, gonocoxite; goncx apod, gonocoxal apodeme; gonst, gonostylus; pm apod, parameral apodeme; st, sternite; tg, tergite.

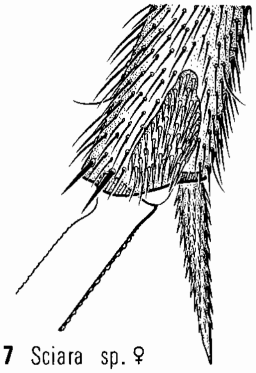


24 Metangela toxoneura ♂

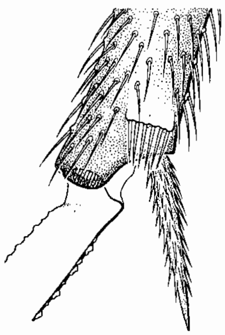


25 Zygoneura sp. ♂

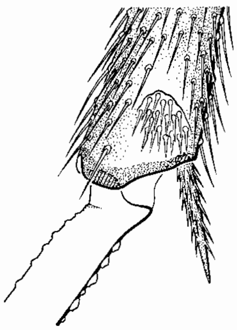
26 Pseudosciara hirtella ♀



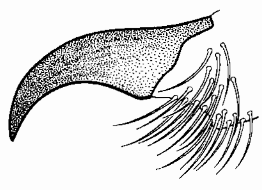
27 Sciara sp. ♀



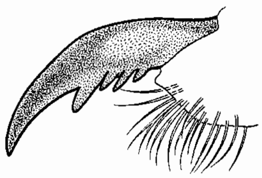
28 Bradysia impatiens ♀



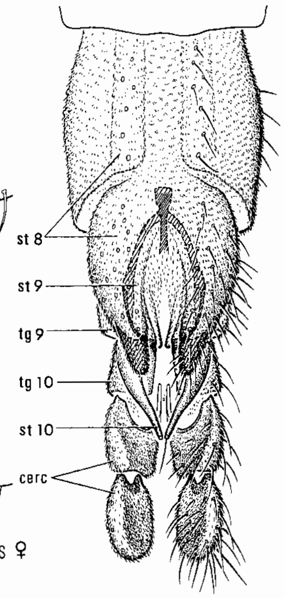
29 Lycoriella sp. ♀



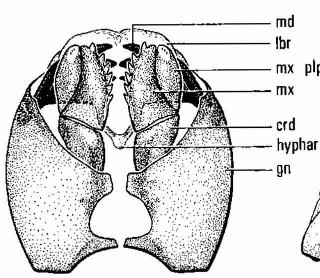
30 Sciara sp. ♀



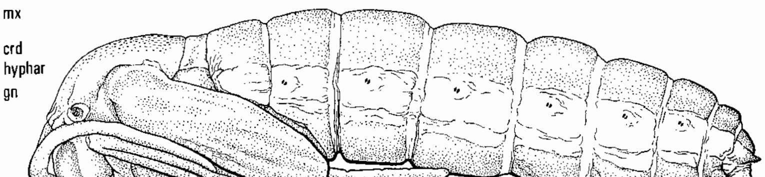
31 Phytosciara flavipes ♀



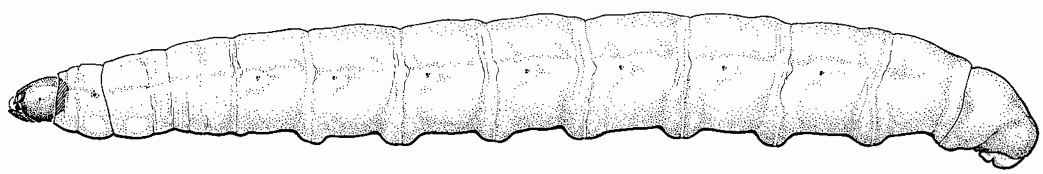
32 Bradysia impatiens ♀



33 Corynoptera sp.



34 Corynoptera sp.



35 Corynoptera sp.

Figs. 15.24–35. Legs, terminalia, and immature stages: anterior view of apex of right fore tibia of (24) *Metangela toxoneura* (Osten Sacken), (25) *Zygoneura* sp., (26) *Pseudosciara hirtella* Schiner (not Nearctic), (27) *Sciara* sp., (28) *Bradysia impatiens* (Johannsen), and (29) *Lycoriella* sp.; fore tarsal claw of (30) *Sciara* sp. and (31) *Phytosciara flavipes* (Meigen); (32) ventral view of female terminalia of *Bradysia impatiens*; (33) ventral view of larval head of *Corynoptera* sp.; (34) lateral view of pupa of *Corynoptera* sp.; (35) lateral view of larva of *Corynoptera* sp.

Abbreviations: cerc, cercus; crd, cardo; gn, gena; hyphar, hypopharynx; lbr, labrum; md, mandible; mx, maxilla; mx plp, maxillary palpus; st, sternite; tg, tergite.

9. Stem of CuA distinctly shorter than base of M; C extending more than halfway between end of R_{4+5} and end of M_1 (Fig. 15); wing membrane sometimes with macrotrichia. Fore tibia anteroapically with a subtriangular patch of modified setae (Fig. 27). Tarsal claws without teeth (Fig. 30). Gonostylus sometimes slender, usually swollen, and with strong preapical spines or setae on inner surface (Fig. 20) or with a distinct preapical process on inner surface .... ***Sciara*** Meigen

   25 spp.; widespread; Pettey 1918

   Stem of CuA subequal to base of M; C ending halfway between end of R_{4+5} and end of M_1 (Fig. 16); wing membrane without macrotrichia. Fore tibia anteroapically with a single regular row of modified setae (as in Fig. 28). Tarsal claws with strong ventral teeth (Fig. 31). Gonostylus slender, with a few slightly enlarged preapical setae on inner surface (Fig. 21). .... ***Phytosciara*** Frey (***Dolichosciara*** Tuomikoski)

   1 sp., *flavipes* (Meigen); widespread

10. R_1 long, joining C beyond base of medial fork (Fig. 18) 11

    R_1 shorter, joining C before or opposite base of medial fork (Fig. 19) 12

11. Palpus with three distinct segments; basal segment minute (as in Fig. 6) .... ***Schwenkfeldina*** Frey

    3 spp.; widespread; Steffan 1974

    Palpus with one distinct segment .... ***Scythropochroa*** Enderlein

    1 sp., unnamed; Arkansas

12. Palpus with one distinct segment, rarely with minute second segment. Eye bridge present or absent 13

    Palpus with two or three distinct segments. Eye bridge always complete 15

13. Eye bridge complete (Fig. 8). Palpus directed ventrally; sensory pit on segment 1 absent or indistinct. Gonostylus usually with strong terminal spine (as in Fig. 23) 14

    Eye bridge absent; compound eyes distinctly separated dorsally (as in Fig. 5). Palpus directed anteriorly; sensory pit on segment 1 distinct and apical (as in Fig. 7). Gonostylus without strong terminal spine. Male only (female wingless—see couplet 21) .... ***Pnyxia*** Johannsen, in part

    1 sp., *scabiei* (Hopkins); widespread

14. Male antenna very long and slender (Fig. 8). CuA_1 much longer than stem of CuA in male. Male only (female wingless—see couplet 21) .... ***Epidapus*** Haliday, in part

    2 spp.; eastern

    Female antenna not elongate. CuA_1 much shorter than stem of CuA. Male unknown .... ***Moehnia*** Pritchard

    1 sp., *erema* Pritchard; California

15. Mid tibia with one distinct apical spur and sometimes with a second very short spur; hind tibia with one apical spur .... ***Scatopsciara*** Edwards

    5 spp.; widespread; Pettey 1918 (as *Neosciara* Pettey, in part)

    Mid and hind tibiae each with two distinct subequal spurs 16

16. Fore tibia anteroapically with modified setae in a single row (Fig. 28) 17

    Fore tibia anteroapically without modified setae in a single row; setae either in a subtriangular patch (Fig. 29) or scattered and indistinct 18

17. Tarsal claws with strong ventral teeth (as in Fig. 31). Subapical spines of gonostylus in a discrete group so apex of gonostylus appears shallowly cleft .... ***Phytosciara*** Frey (***Prosciara*** Frey)

    1 sp., unnamed; Ontario

    Tarsal claws simple (as in Fig. 30) or with fine ventral teeth. Apex of gonostylus not appearing cleft .... ***Bradysia*** Winnertz

    65 spp.; widespread; Pettey 1918 (as *Neosciara*, in part)

18. Postpronotal lobe usually with a few setae near inner end; if bare, posteroventral projection of anepimeron broad, subquadrate (Fig. 12). Palpus short, usually with only two distinct segments .... ***Plastosciara*** Berg

    1 sp., *johnstoni* (Shaw); Massachusetts (plus unnamed western spp.)

Postpronotal lobe bare. Posteroventral projection of anepimeron narrow (Fig. 13). Palpus usually elongate, with three distinct segments; basal segment minute (as in Fig. 6) 19

19. C long, ending about three-quarters to nine-tenths the distance between the ends of R_{4+5} and M_1 .... ***Chaetosciara*** Frey

1 sp., *joffrei* (Pettey); Pennsylvania

C shorter, extending less than three-quarters the distance between R_{4+5} and M_1 (Fig. 19) 20

20. Spurs of hind tibia distinctly longer than width of tibial apex. C usually extending more than halfway between R_{4+5} and M_1. Median surface of gonostylus frequently deeply concave subapically, without long whip-like setae (Fig. 22) .... ***Corynoptera*** Winnertz

6 spp.; widespread; Pettey 1918 (as *Neosciara,* in part)

Spurs of hind tibia shorter or only slightly longer than width of tibial apex. C usually ending before midpoint between R_{4+5} and M_1 (Fig. 19). Median surface of gonostylus only slightly concave to flat, frequently with long whip-like seta, and frequently with stout terminal spine apically (Fig. 23) .... ***Lycoriella*** Frey

14 spp.; widespread; Pettey 1918 (as *Neosciara,* in part)

21. Eye bridge present (as in Fig. 8). Palpus one-segmented, without distinct sensory pit. Female only .... ***Epidapus*** Haliday, in part

see couplet 14

Eye bridge absent (Fig. 5). Palpus one-segmented, with distinct sensory pit (Fig. 7). Female only .... ***Pnyxia*** Johannsen, in part

see couplet 13

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CECIDOMYIIDAE 16

RAYMOND J. GAGNÉ

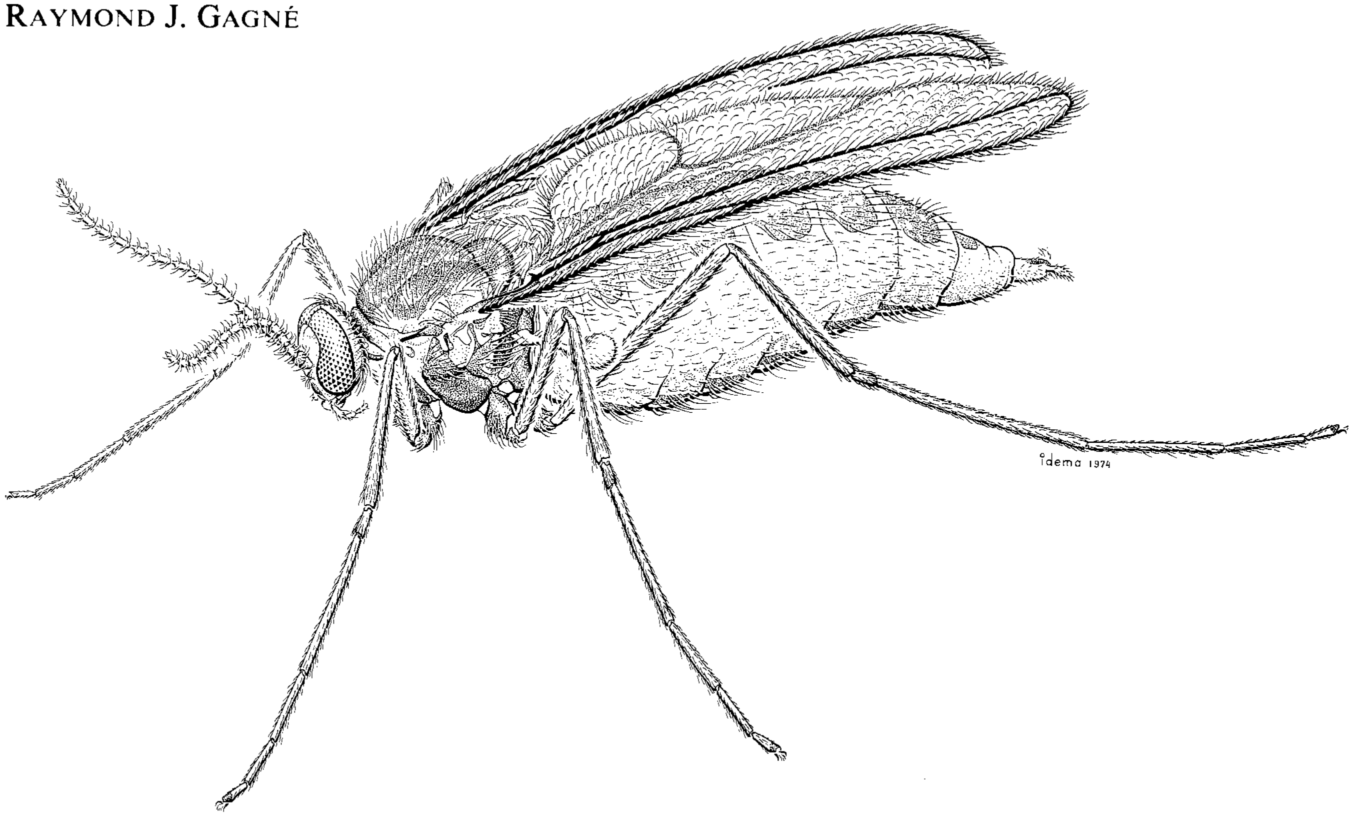


Fig. 16.1. Female of *Cecidomyia resinicola* (Osten Sacken).

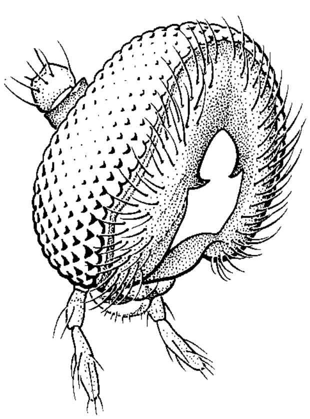
Tiny fragile flies, 1.0–5.0 mm long, rarely to 8.0 mm (Fig. 1). Antenna usually long. Wing veins generally weak, reduced in number; C usually continuous around wing, usually with a break just beyond insertion of R_5 (Figs. 6, 12–35). Tibial spurs absent.

Adult. Head: eyes holoptic or nearly so in both sexes (Figs. 2–4), lacking dorsolateral facets and forming three separate eyes in some predacious forms (Fig. 4); ocelli present in most Lestremiinae, absent in all others. Antenna (Figs. 36–64) usually with 14 or 12 flagellomeres, but occasionally with the number augmented or reduced in some groups; flagellomeres of most Porricondylinae (Figs. 56–58) and Cecidomyiinae (Figs. 59–64) with circumfila which are continuous thread-like sensoria that encircle the nodes. External mouthparts (Figs. 2–4) consisting of a labrum, one- to four-segmented palpi, and a generally fleshy labella; labrum and labella occasionally enlarged or styliform.

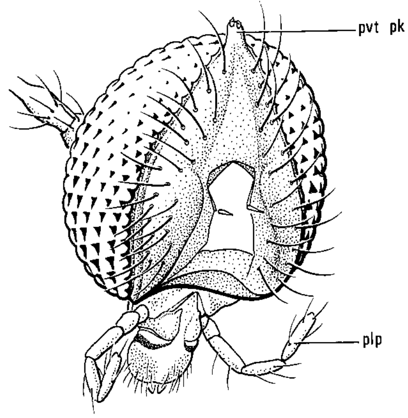
Thorax: about as long as high. Mesonotum convex, usually with two median and two lateral rows of setae. Wing (Figs. 6, 12–35) with microtrichia, often as scales, and occasionally with macrotrichia; C usually continuous around wing, usually with a break just beyond insertion of R_5; R_5 unforked; M, except in Lestremiinae, weak or absent. Legs usually long; coxae conspicuous; tibial spurs absent (Figs. 80, 81); in Porricondylinae and Cecidomyiinae tarsomere 1 much shorter than tarsomere 2, or absent (Figs. 67–69, 81); claws (Figs. 70–79) toothed or untoothed; empodia usually well-developed; pulvilli usually very short (Figs. 70–79).

Abdomen: elongate–cylindrical in male (Figs. 115–118), elongate–ovoid in female (Figs. 119–132).

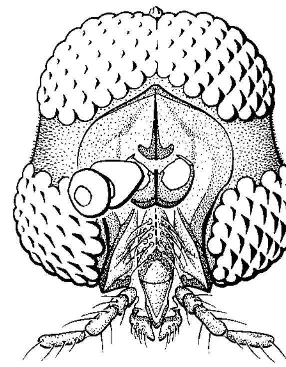
Male terminalia (Figs. 82–110, 113–118) usually with a simple dorsal plate, the epandrium (tergite 9), which frequently bears on its posterior margin median (cercal) (Fig. 102) and lateral lobes. Tergite 10 absent or indistinguishably fused with epandrium. Hypandrium, or sternite 9, greatly reduced and fused with gonocoxites; gonocoxites broadly joined mediobasally (Figs. 82–96) except in Cecidomyiinae (Figs. 97–110), sometimes with mediobasal lobes (Figs. 104, 113, 114); gonostylus always present and distinct, usually with a tooth near apex; gonocoxal apodemes usually strong, frequently with apices fused in a bridge-like fashion (Figs. 87, 96, 98); parameres fused mediodorsally forming an aedeagal sheath, sometimes with each paramere bilobate (Figs. 90, 94); aedeagus relatively small, frequently rod-like, and more or less enclosed within fused parameres. Sternite 10 membranous or fused with hypoproct; hypoproct simple and transverse, to elongate and deeply divided.



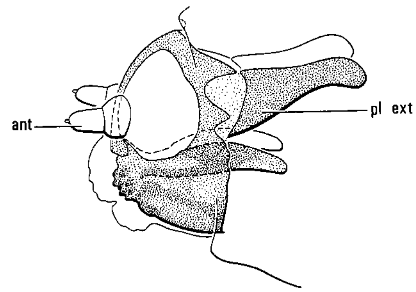
2 Cecidomyia piniinopis ♀



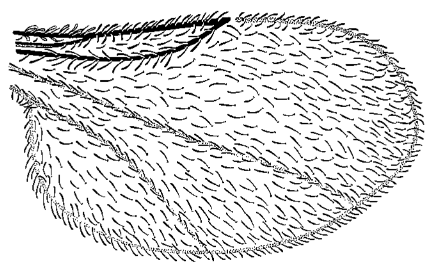
3 Clinodiplosis lappa ♂



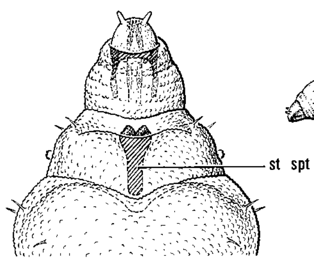
4 Trisopsis sp. ♂



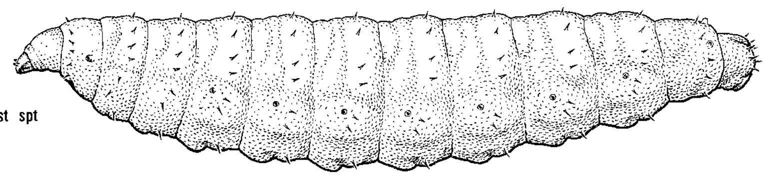
5 Cecidomyia sp. ♂



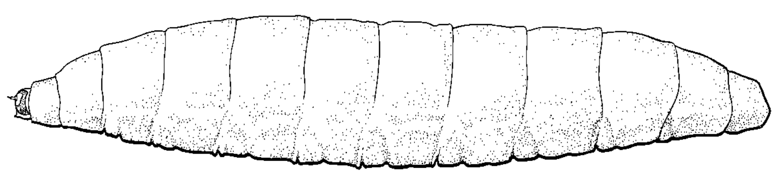
6 Camptoneuromyia adhesa ♂



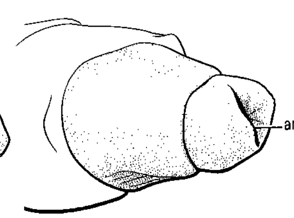
7 Dasineura sp.



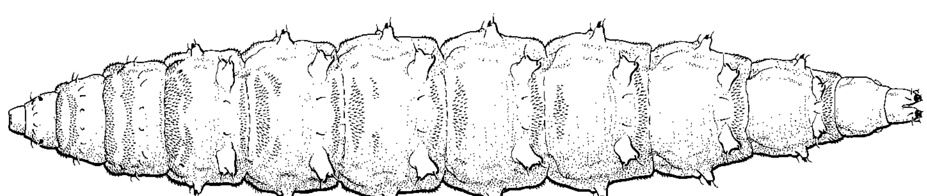
8 Dasineura sp.



9 Lestremiinae



10 Lestremiinae



11 Cecidomyia candidipes

Caudal end of female abdomen often protrusible, sometimes very long, in some groups variously modified for piercing plant tissue (Figs. 123–128, 131); cerci separate, one- or two-segmented though sometimes appearing to be three-segmented, or fused into a single lamella. One or two sclerotized spermathecae present in female of many primitive species, but absent or unsclerotized in some Lestremiini and all Cecidomyiinae.

Egg. Usually elongate–ovoid, but attenuate–elongate at one end in at least some species of *Contarinia* Rondani. Usually tiny with more than 100 eggs per female present at completion of pupation, but large and few in number in paedogenetic forms.

Larva. Head capsule (Figs. 5, 7) tiny, cone-shaped, with two posterolateral extensions; mouthparts reduced, modified for a liquid diet, with minute styliform mandibles; antenna two-segmented, relatively prominent. Tracheal system peripneustic. Integumental setae or papillae with systematic arrangement (Figs. 8, 9, 11), constant in number within groups. Prothorax usually with sclerotized and typically clove-shaped sternal spatula (Fig. 7). Anus terminal in Lestremiinae (Fig. 10) and paedogenetic Porricondylinae, ventral in others.

Pupa. Exarate, in a few species enclosed within the last instar larval skin. Anterior spiracle and anterior angle of antennal bases usually prominent.

Biology and behavior. Larvae of the Lestremiinae are terrestrial and mycophagous and are found in decaying vegetation and wood, in plant wounds, and in mushrooms. Adults may fly in very cool weather, often at windows. Species of *Anarete* Haliday, one of the largest genera, may appear in dense swarms.

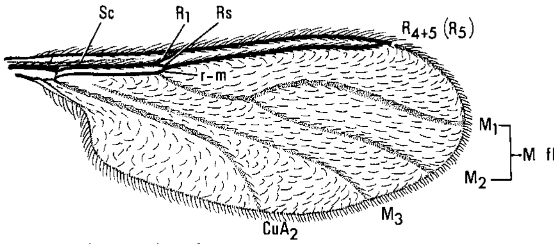
Porricondyline larvae are mycophagous in decaying vegetation and wood and may secondarily infect living tissue of higher plants. Larvae of some species of *Asynapta* Loew and *Camptomyia* Kieffer occur in great numbers in cones of conifers. Adults of this subfamily, as well as some Cecidomyiinae, are frequently found on spider webs, from which they come and go readily.

The Cecidomyiinae contain numerous gall-making forms, which give the family its common name, gall midges; but they also contain many species that are phytophagous in flower heads or stems without making galls, others that are mycophagous, and still others that are predacious or parasitoid. The supertribe Lasiopteridi comprises the Ledomyini, the Oligotrophini, and the Lasiopterini. The larvae of Ledomyini are primitively mycophagous. Those of the Oligotrophini live freely in flower heads or cause simple galls such as leaf rolls or enlarged stems; they can also cause complex galls. The larvae of Lasiopterini are found mainly in simple galls on twigs, petioles, midribs, and leaves; a few are found in seeds of Compositae. Members of the supertribe Asphondyliidi all cause complex galls, mainly on flowers and buds, but also on leaves. The Cecidomyiidi comprise the largest supertribe and have a very wide range of habits: there are free-living, phytophagous, and mycophagous species; simple and complex gall makers; general and selective predators of mites, aphids, coccoids, and other arthropods; and internal parasitoids of aphids and psyllids. Many gall-forming cecidomyiids are treated by Felt (1940) and the gall midges of economic importance are treated in detail in the fine series of volumes by Barnes (1946–1956) and Nijveldt (1969).

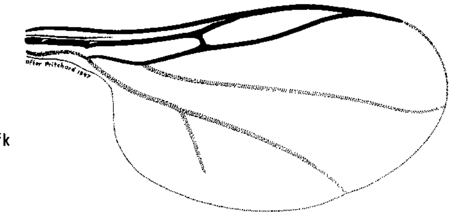
Classification and distribution. There are about 3000 described species of Cecidomyiidae in the world, of which about 1100 are in North America; however, many remain undescribed, so the actual number of species is much greater. Many species are known from very few collections; therefore their actual distributions are frequently unknown. The family is divided into three subfamilies: Lestremiinae, Porricondylinae, and Cecidomyiinae. The Lestremiinae have the least number of species. Many of these have extensive geographical ranges, and the genera are mostly species-poor. The Lestremiinae are the most primitive of the subfamilies, characterized by the presence of ocelli, a strong M vein, elongate first tarsal segments, and the absence of ring-shaped sensoria on the antennae. Species of *Anarete* Haliday superficially resemble Ceratopogonidae with their short antennae and anteriorly concentrated wing veins. The Porricondylinae (Panelius 1965) comprise more species than the Lestremiinae, but their genera are also rather species-poor. Tarsomere 1 in this subfamily and in the Cecidomyiinae is much shorter than tarsomere 2, except in those few species with fewer than five tarsomeres; most species have ring-shaped antennal sensoria. Except in the porricondyline tribe Heteropezini, the larvae of these two subfamilies have a ventral anus rather than a terminal one. Adults of the Porricondylinae are differentiated from those of the Cecidomyiinae by a prominent abdominal segment 9 and usually a strong Rs vein; mature porricondyline larvae have four dorsal papillae

Figs. 16.2–11. Heads, wing, and larvae: head of (2) *Cecidomyia piniinopis* Osten Sacken and (3) *Clinodiplosis lappa* (Stebbins) in posterolateral view; (4) head of *Trisopsis* sp., anterior view; (5) head of larva of *Cecidomyia* sp., lateral view; (6) wing of *Camptoneuromyia adhesa* (Felt); (7) head, prothorax, and mesothorax of larva of *Dasineura* sp., ventral view; entire larva of (8) *Dasineura* sp. and (9) Lestremiinae in lateral view; (10) terminal segments of Lestremiinae, posterolateral view; (11) entire larva of *Cecidomyia candidipes* Foote, dorsal view.

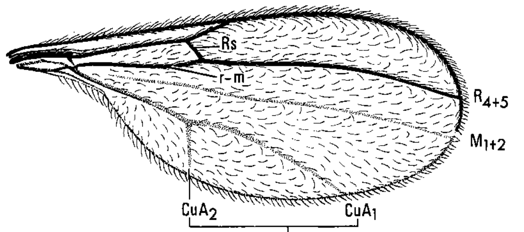
Abbreviations: an, anus; ant, antenna; pl ext, posterolateral extension; plp, palpus; pvt pk, postvertical peak; st spt, sternal spatula.



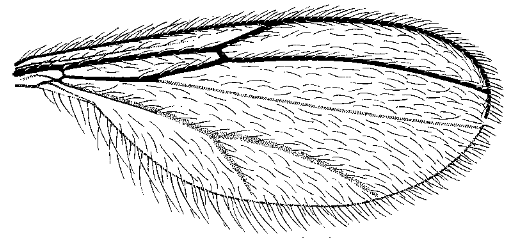
12 Lestremia cinerea ♂



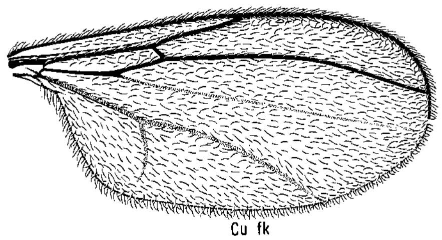
13 Acoenonia perissa ♀



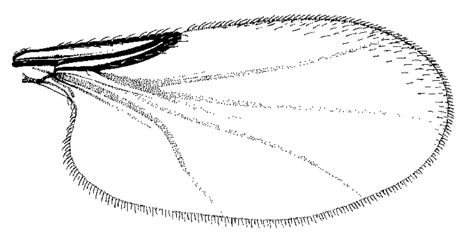
14 Micromya mana ♂



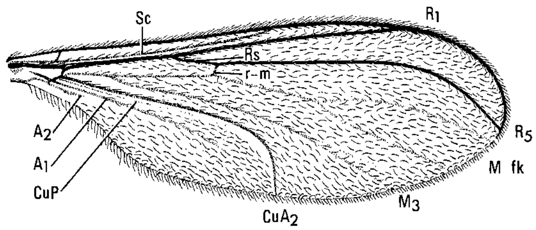
15 Cordylomyia denningi ♂



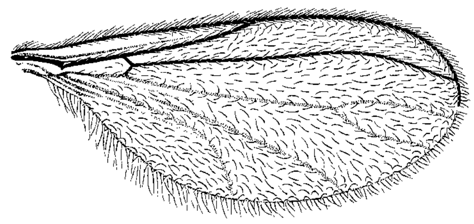
16 Corinthomyia brevicornis ♂



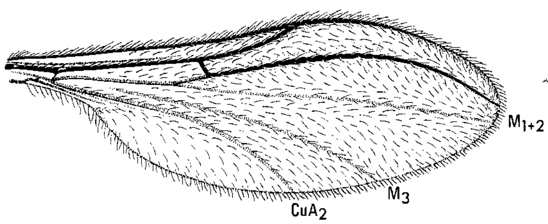
17 Forbesomyia sp. ♀



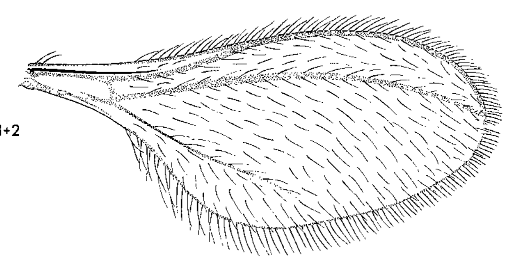
18 Catotricha subobsoleta ♂



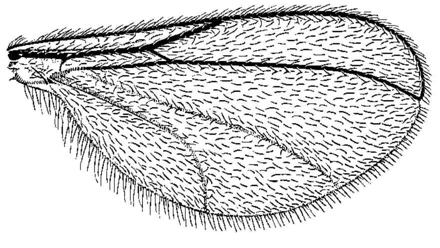
19 Catocha slossonae ♂



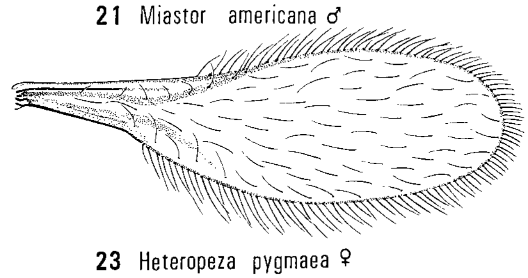
20 Strobliella intermedia ♂



21 Miastor americana ♂



22 Winnertzia fungicola ♂



23 Heteropeza pygmaea ♀

Figs. 16.12–23. Wings: (12) *Lestremia cinerea* Macquart; (13) *Acoenonia perissa* Pritchard; (14) *Micromya mana* Pritchard; (15) *Cordylomyia denningi* Pritchard; (16) *Corinthomyia brevicornis* (Felt); (17) *Forbesomyia* sp.; (18) *Catotricha subobsoleta* (Alexander); (19) *Catocha slossonae* Felt; (20) *Strobliella intermedia* Kieffer; (21) *Miastor americana* Felt; (22) *Winnertzia fungicola* Felt; (23) *Heteropeza pygmaea* Winnertz (*continued*).
Abbreviations: Cu fk, cubital fork; M fk, medial fork; Rs, basal section of radial sector.

on abdominal segment 8 and usually four posterior ventral papillae instead of two in each case in the Cecidomyiinae. Nearly all Cecidomyiinae belong to the supertribes Lasiopteridi, Asphondyliidi, and Cecidomyiidi; the Lasiopteridi, which previously contained only the Lasiopterini, was recently enlarged to include the former Oligotrophidi (Gagné 1976).

A key to larvae is not presented. Because the larvae of many genera are still unknown, one cannot greatly improve upon the well-illustrated keys by Möhn (1955) and Mamaev and Krivosheina (1965). The larvae of the major groups of Cecidomyiidae are separated as follows. The Lestremiinae and the porricondyline tribe Heteropezini have a terminal rounded anus, and the remaining cecidomyiids have a slit-like ventral anus (except in some of the predacious larvae on which it is dorsal). The Porricondylinae typically have four dorsal papillae on abdominal segment 8 and four posteroventral papillae on abdominal segments 1–7 (although these are sometimes imperceptible), but the Cecidomyiinae have only two papillae at each of those locations. Beyond subfamily level, the chief diagnostic characters are the presence or absence of setae on the papillae and the structural modifications of the papillae, especially on the terminal segment. The structural features of the sternal spatula, occasional prolegs, and terminal extensions are also generically diagnostic.

Fossil remains of Cecidomyiidae are fairly numerous. Meunier (1904) summarized the work done on fossil cecidomyiids up to 1903 and described 31 species of Lestremiinae and Porricondylinae from Baltic amber (Eocene); all can be placed in modern genera. Gagné (1973*b*) described a collection of nine species from Mexican amber (upper Oligocene to lower Miocene) that included, besides lestremiines and porricondylines, gall-making and predacious forms of Cecidomyiinae that are difficult to separate from congeners living today. On the other hand, some fossils from Canadian amber (Upper Cretaceous) are Lestremiinae and Porricondylinae that do not fit into modern genera (Gagné 1977). Hennig (1973) has reported a find of lestremiine fossils from Lebanon (Lower Cretaceous).

Key to genera[1]

1. Ocelli usually present. Five tarsomeres, with tarsomere 1 longer than 2. M_{1+2} present (Figs. 12–20) except in apterous forms .... LESTREMIINAE....3

   Ocelli absent. Tarsomere 1 much shorter than 2 (Figs. 1, 81), or fewer than five tarsomeres present. M_{1+2} absent (except in some Porricondylinae) (Figs. 21–35) 2

2. Basal section of Rs as strong as other wing veins (Figs. 22–30). Male gonocoxites united ventrally (Figs. 89–96). Female cercus two-segmented (Fig. 121) (except in *Dirhiza*, Fig. 122) .... PORRICONDYLINAE....48

   Basal section of Rs usually absent or weaker than other veins (Figs. 31–35). Male gonocoxites free ventrally (Figs. 98–100). Female cercus one-segmented (Figs. 129–132), often fused (Fig. 123) .... CECIDOMYIINAE....78

3. Apterous or brachypterous 4

   Macropterous 6

4. Head much reduced, with single-faceted eyes, no ocelli, and one-segmented palpus (Figs. 133–138) .... BAEONOTINI....***Baeonotus*** Byers

   1 sp., *microps* Byers

   Head with multifaceted eyes, with ocelli, and with four-segmented palpus 5

5. Head with three ocelli. Legs with scales. Spermathecae sclerotized .... MICROMYINI, in part....21

   Head with two ocelli. Legs without scales. Spermathecae unsclerotized .... LESTREMIINI, in part....38

6. CuA forked; M_3 absent or faint (Figs. 13–16) 7

   CuA simple; M_3 distinct (Figs. 12, 17–20) 8

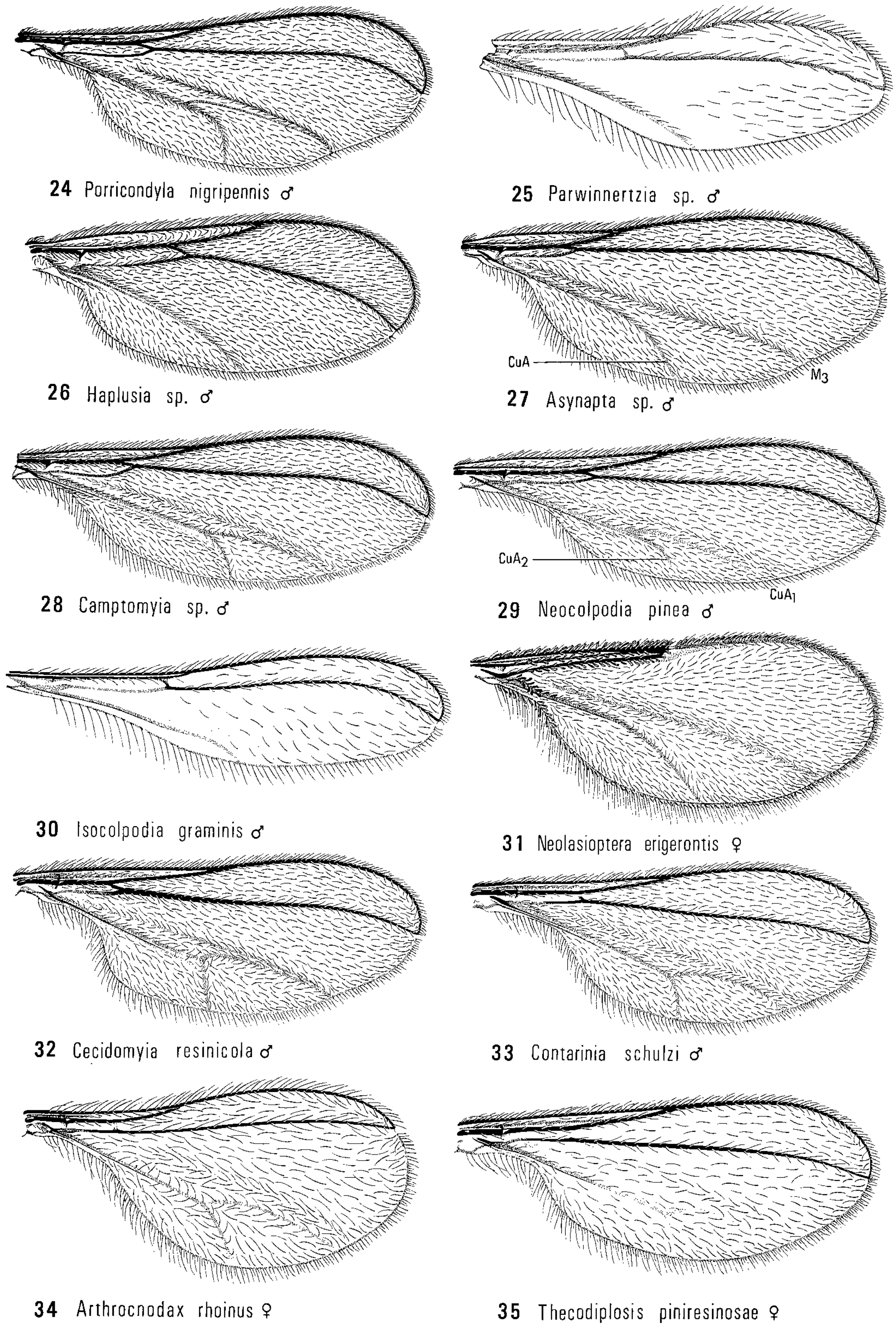
7. R_5 abbreviated,[2] much shorter than wing (Fig. 13). Tibiae with distoventral spines .... ACOENONIINI....***Acoenonia*** Pritchard

   1 sp., *perissa* Pritchard

   R_5 as long as wing, or nearly so (Figs. 14–16). Tibiae without distoventral spines .... MICROMYINI, in part....12

[1] Distributional data are usually omitted for the genera throughout this family because the distributions are so frequently incompletely known.

[2] Probably vein R_{4+5}, but as is customary in this family, it is labeled simply as R_5.



Figs. 16.24–35. Wings (*concluded*): (24) *Porricondyla nigripennis* (Meigen); (25) *Parwinnertzia* sp.; (26) *Haplusia* sp.; (27) *Asynapta* sp.; (28) *Camptomyia* sp.; (29) *Neocolpodia pinea* (Fallén); (30) *Isocolpodia graminis* (Felt); (31) *Neolasioptera erigerontis* (Felt); (32) *Cecidomyia resinicola* (Osten Sacken); (33) *Contarinia schulzi* Gagné; (34) *Arthrocnodax rhoinus* Felt; (35) *Thecodiplosis piniresinosae* Kearby & Benjamin.

8. R_5 less than half length of wing (Fig. 17). Antenna with six flagellomeres, each wider than long. Tibiae with short distoventral spines .... FORBESOMYIINI.... ***Forbesomyia*** Malloch
1 sp., *atra* Malloch

R_5 more than two-thirds length of wing (Figs. 12, 18–20). Antenna usually with more than six flagellomeres, each longer than wide. Tibiae without distoventral spines 9

9. Basal section of Rs distinctly longer than crossvein r-m; M_3 arising from M (Fig. 18) .... CATOTRICHINI.... ***Catotricha*** Edwards
2 spp.; Pritchard 1948

Basal section of Rs shorter than or as long as crossvein r-m; M_3 free (Figs. 12, 19, 20) 10

10. Medial fork shorter than stem (Fig. 19), or absent. Three ocelli 11

Medial fork longer than stem (Fig. 12). Two ocelli .... LESTREMIINI, in part.... 31

11. M_{1+2} simple, evanescent distally; CuP united with CuA (Fig. 20) .... STROBLIELLINI.... ***Strobliella*** Kieffer
1 sp., *intermedia* Kieffer

M_{1+2} forked; CuP free from CuA (Fig. 19) .... CATOCHINI.... 44

12. C ending abruptly at tip of R_5 or reaching slightly beyond. Basal enlargement of flagellomeres subglobular .... ***Peromyia*** Kieffer
5 spp.; Pritchard 1947

C extending well beyond R_5 for more than half the distance between R_5 and M (Figs. 14–16). Basal enlargement of flagellomeres usually subcylindrical 13

13. R_1 almost three times length of Rs (Figs. 15, 16). Empodia broad, as long as claws 14

R_1 less than two times length of Rs (Fig. 14) or more than twice the length of Rs. If R_1 longer than twice the length of Rs, then empodia rudimentary 16

14. Proximal male flagellomeres with small plate-like sensory processes distally (Fig. 39); female flagellomeres each with distal sensory collar (Fig. 40). Female with one sclerotized spermatheca .... ***Campylomyza*** Meigen
7 spp.; Pritchard 1947

Male flagellomeres without distal plate-like sensoria (Figs. 41, 45); female flagellomeres with distal sensory spines only (Fig. 42). Female with two sclerotized spermathecae 15

15. Cubital fork forming an acute angle (Fig. 15). Male flagellomeres each with one complete crenulate whorl of very long bristles (Fig. 41). Both spermathecae similar in size and pigmentation .... ***Cordylomyia*** Felt
6 spp.; Pritchard 1947

Cubital fork forming almost a right angle (Fig. 16). Male flagellomeres each with four complete crenulate whorls of rather short bristles (Fig. 45). Spermathecae unequal in size and pigmentation .... ***Corinthomyia*** Felt
1 sp., *brevicornis* (Felt)

16. Male 17

Female 24

17. Antennal pedicel much larger than scape; flagellum with seven or eight slender flagellomeres without distinct necks (Fig. 36) .... ***Micromya*** Rondani, in part
2 spp.; Pritchard 1947

Antennal pedicel not larger than scape; flagellum with 8–13 flagellomeres with distinct necks.. 18

18. Aedeagal sheath (fused parameres) with one or more opposing pairs of spines; gonocoxal apodeme very long (Fig. 82) .... ***Aprionus*** Kieffer, in part
4 spp.; Pritchard 1947

Aedeagal sheath (fused parameres) without paired spines; gonocoxal apodeme short (Figs. 83–85, 88) 19

19. Aedeagal rod long and unmodified distally (Figs. 83–85); gonostylus with apical spine (Fig. 83) 20

Aedeagal rod short and indistinct (Fig. 88), or modified into distal pair of divergent processes; gonostylus with or without apical spine 23

20. Eye bridge not more than four or five facets long .... ***Monardia*** Kieffer.... 21

Eye bridge six facets long .... ***Trichopteromyia*** Williston, in part
1 sp., *modesta* Williston

21. Empodia rudimentary .... ***Monardia*** (***Monardia*** Kieffer), in part
4 spp.; Pritchard 1947

Empodia broad, as long as claws 22

22. Gonostylus with strong apical tooth (Fig. 85). Antenna with 12 flagellomeres .... ***Monardia*** (***Xylopriona*** Kieffer), in part
4 spp.; Pritchard 1947

Gonostylus with small apical tooth (Fig. 84). Antenna with 11–13 flagellomeres .... ***Monardia*** (***Polyardis*** Pritchard), in part
6 spp.; Pritchard 1947

23. Antenna with 8–10 short-necked flagellomeres. Gonostylus with apical tooth .... ***Mycophila*** Felt, in part
4 spp.; Pritchard 1947

Antenna with 12 long-necked flagellomeres. Gonostylus without apical tooth (Fig. 88) .... ***Bryomyia*** Kieffer, in part
4 spp.; Pritchard 1947

24. Abdomen with one sclerotized spermatheca 25

Abdomen with two sclerotized spermathecae 28

25. Antennal flagellomeres each with one or two distal sensoria (Fig. 46) 26

Antennal flagellomeres each with four or more distal sensoria (Fig. 44) or with sensory setae only 27

26. Cubital fork forming almost a right angle (Fig. 14). Antennal flagellomeres each with a distal sensory collar interrupted in one or two places .... ***Micromya*** Rondani, in part
see couplet 17

Cubital fork forming an acute angle (Fig. 15). Flagellomeres each with a pair of broad sensoria (Fig. 46) .... ***Mycophila*** Felt, in part
see couplet 23

27. Empodia broad, as long as claws .... ***Monardia*** (***Polyardis*** Pritchard), in part
see couplet 22

Empodia rudimentary to half as long as claws and narrow .... ***Aprionus*** Kieffer, in part
see couplet 18

28. Antennal flagellomeres each with two slender or digitate sensoria .... ***Bryomyia*** Kieffer, in part
see couplet 23

Antennal flagellomeres each with three or four sensoria or with sensory bristles only 29

29. Empodia broad, as long as claws .... ***Monardia*** (***Xylopriona*** Kieffer), in part
see couplet 22

Empodia rudimentary 30

30. Eye bridge six facets long. Spermathecae retort-shaped .... ***Trichopteromyia*** Williston, in part
see couplet 20

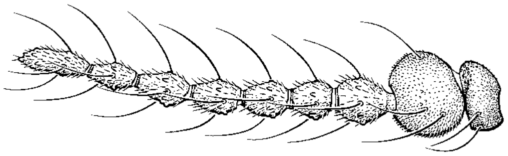
Eye bridge four or five facets long. Spermathecae globular or pyriform .... ***Monardia*** (***Monardia*** Kieffer), in part
see couplet 21

31. Male 32

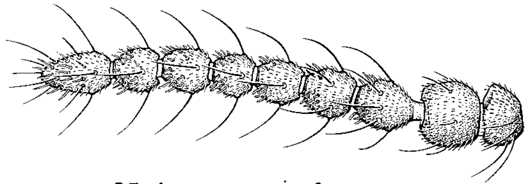
Female 38

Figs. 16.36–50. Antennae: entire antenna of (36) *Micromya mana* Pritchard and (37) *Anarete anepsia* Pritchard; (38) scape, pedicel, and flagellomeres 1–3 of *Lestremia cinerea* Macquart; third flagellomere of (39, 40) *Campylomyza* sp., (41, 42) *Cordylomyia denningi* Pritchard, (43) *Conarete crebra* Pritchard, (44) *Polyardis kasloensis* (Felt), (45) *Corinthomyia brevicornis* (Felt), (46) *Mycophila speyeri* (Barnes), (47) *Wasmanniella clauda* Pritchard, (48, 49) *Anaretella defecta* (Winnertz), and (50) *Lestremia cinerea* Macquart (*continued*).

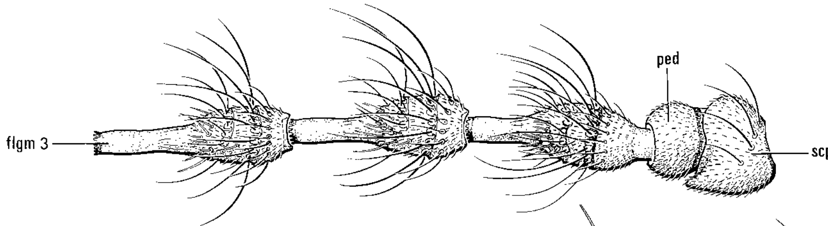
Abbreviations: flgm, flagellomere; ped, pedicel; scp, scape.



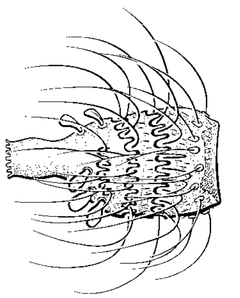
36 Micromya mana ♂



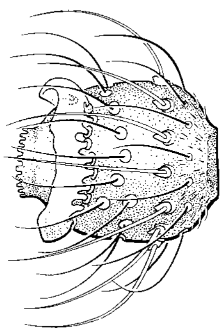
37 Anarete anepsia ♂



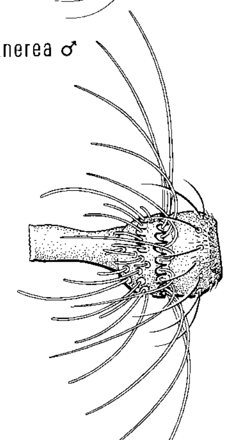
38 Lestremia cinerea ♂



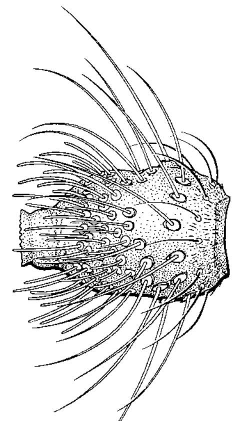
39 Campylomyza sp. ♂



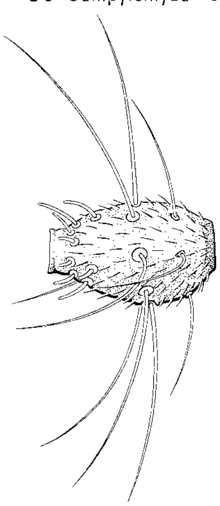
40 Campylomyza sp. ♀



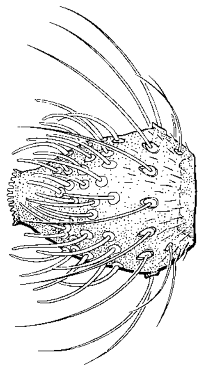
41 Cordylomyia denningi ♂



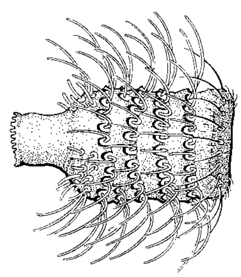
42 Cordylomyia denningi ♀



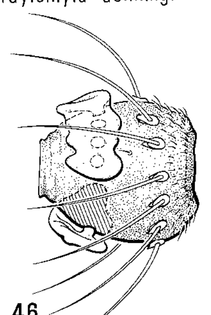
43 Conarete crebra ♂



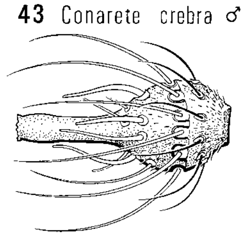
44 Polyardis kasloensis ♀



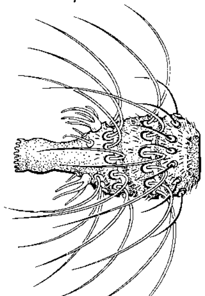
45 Corinthomyia brevicornis ♂



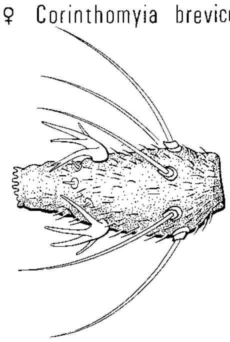
46 Mycophila speyeri ♀



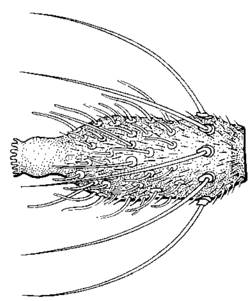
47 Wasmanniella clauda ♂



48 Anaretella defecta ♂



49 Anaretella defecta ♀



50 Lestremia cinerea ♀

32. Antenna with six to eight flagellomeres having short or indistinct necks (Figs. 37, 43) 33
Antenna with 14 long-necked flagellomeres (Fig. 38) 34

33. Flagellomeres without distinct necks (Fig. 37). Roots of parameres nearly parallel (Fig. 86) .... ***Anarete*** Haliday, in part
11 spp.; Kim 1967
Flagellomeres with short necks (Fig. 43). Roots of parameres strongly bent laterally (Fig. 87) .... ***Conarete*** Pritchard, in part
4 spp.; Pritchard 1951

34. Flagellomeres with one crenulate whorl of setae (Fig. 47) 35
Flagellomeres with two crenulate whorls of setae (Fig. 48) 37

35. Eyes separated on vertex. Flagellomeres with blade-like sensoria (Fig. 47) .... ***Wasmanniella*** Kieffer, in part
1 sp., *clauda* Pritchard
Eyes joined on vertex. Flagellomeres with setiform sensoria (Fig. 48) 36

36. R_5 extending beyond apex of M_3. Gonostylus short, stout, bilobate distally; aedeagal rod with two divergent recurved distal projections .... ***Gongromastix*** Enderlein
2 spp.; Pritchard 1951
R_5 extending just proximal to apex of CuA. Gonostylus slender, unlobed; aedeagal rod simple distally .... ***Allarete*** Pritchard, in part
2 spp.; Pritchard 1951

37. Flagellomeres with digitate sensoria (Fig. 48). Proximal end of M_3 distal to crossvein r-m. Paramere broad throughout .... ***Anaretella*** Enderlein, in part
3 spp.; Pritchard 1951
Flagellomeres with setiform sensoria (Fig. 38). Proximal end of M_3 proximal to crossvein r-m (Fig. 12). Paramere narrow distally .... ***Lestremia*** Macquart, in part
3 spp.; Pritchard 1951

38. Apterous. Eyes separated on vertex .... ***Wasmanniella*** Kieffer, in part
see couplet 35
Macropterous. Eyes joined on vertex 39

39. Flagellar sensoria digitate (Fig. 48) .... ***Anaretella*** Enderlein, in part
see couplet 37
Flagellar sensoria setiform (Fig. 38) 40

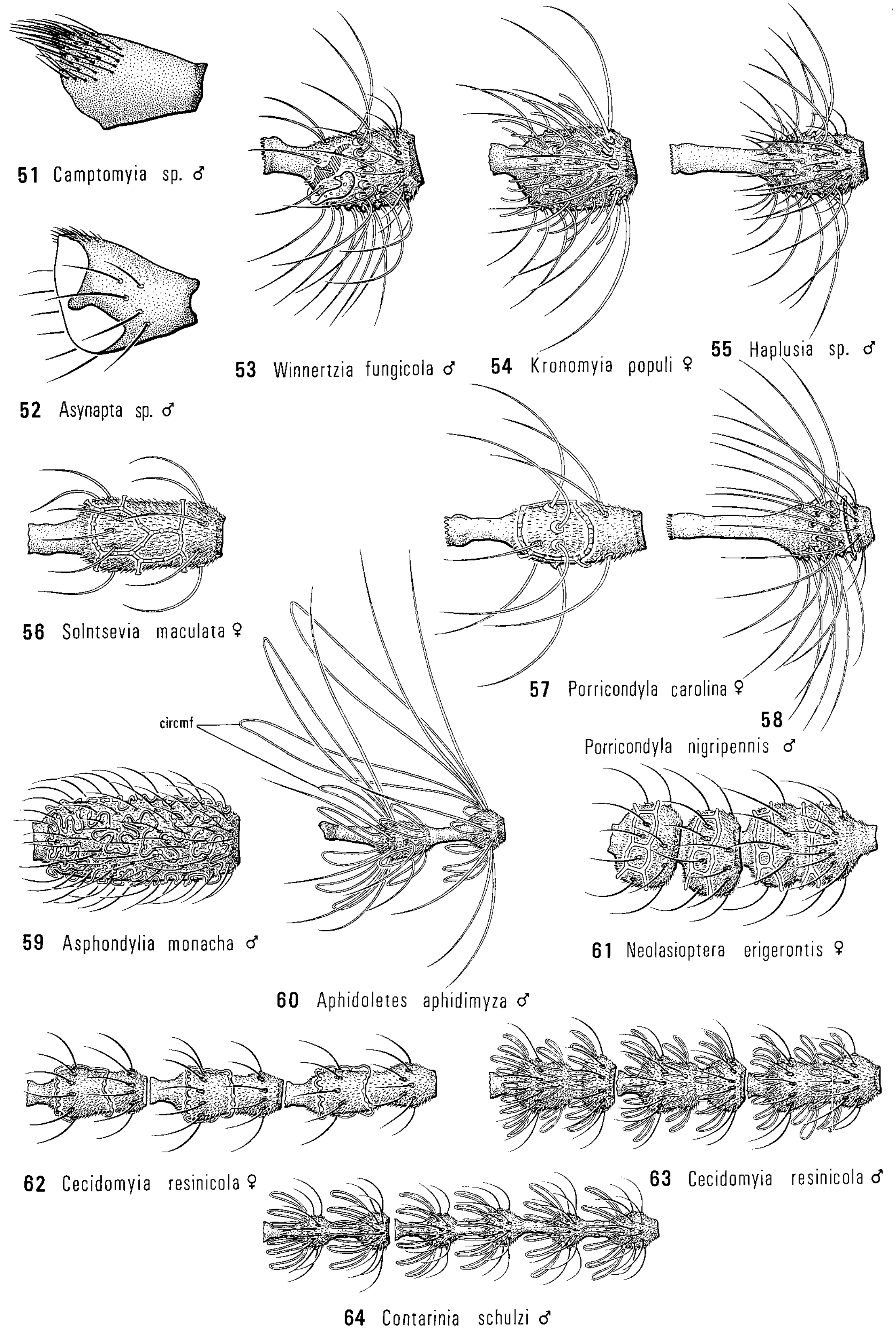
40. Fore tarsus with a sole of dense short bristles (Fig. 65) .... ***Conarete*** Pritchard, in part
see couplet 33
Fore tarsus without a sole of dense short bristles (Fig. 66) 41

41. Medial fork gradually and evenly divergent from base. Usually only eight flagellomeres present (rarely nine and then without a terminal nipple) .... ***Anarete*** Haliday, in part
see couplet 33
Medial fork not evenly divergent; M_1 sinuous. Nine flagellomeres present; ninth with a terminal nipple 42

42. Flagellomeres slender, cylindrical, with well-differentiated distal stems (Fig. 38) .... ***Lestremia*** Macquart, in part
see couplet 37
Flagellomeres obovate, with distal stems not well-differentiated 43

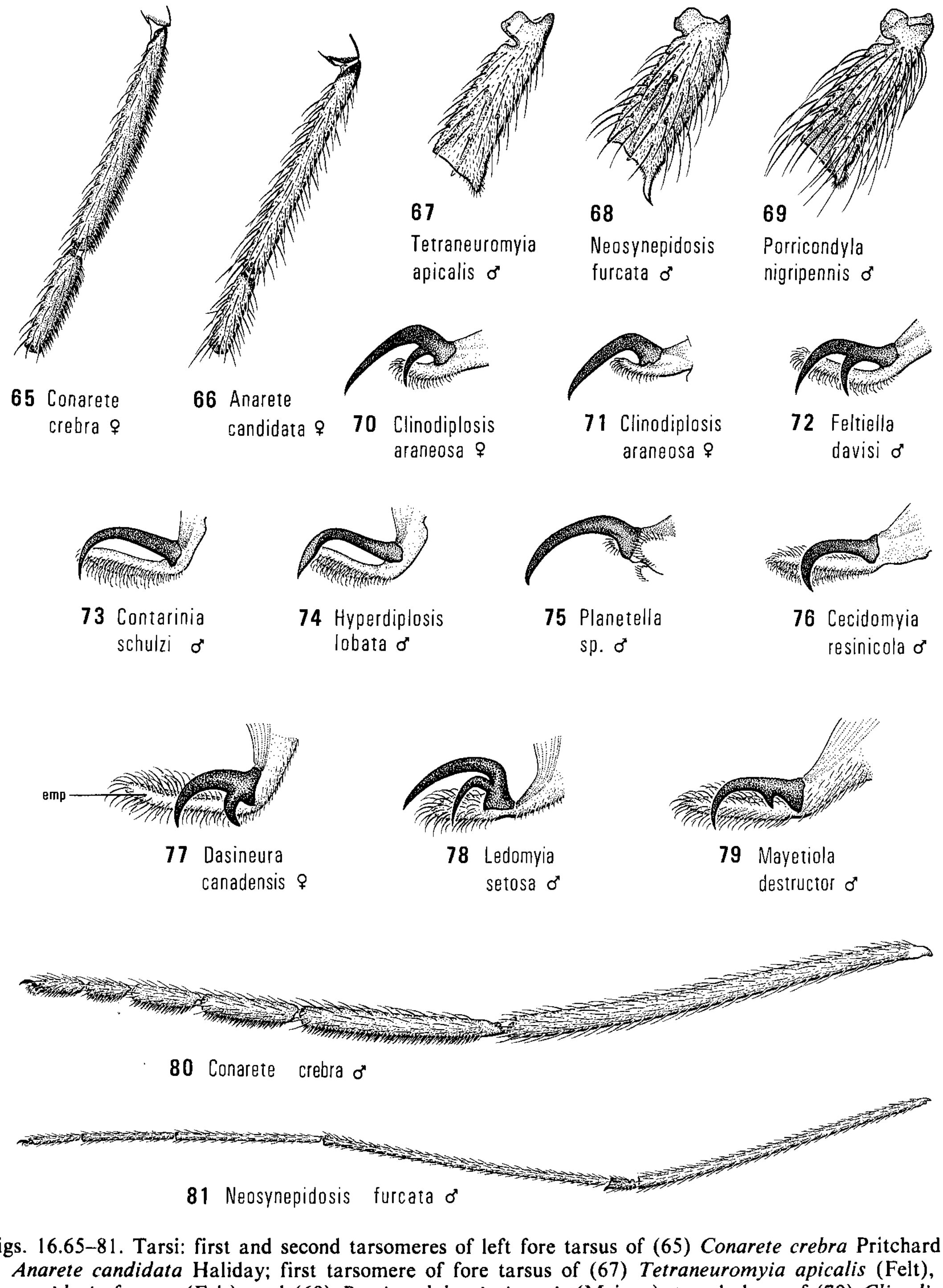
43. Basal segment of cercus twice the length of terminal one. Medial fork with widely spaced setae .... ***Pararete*** Pritchard
1 sp., *elongata* (Felt); female only, California
Both segments of cercus subequal in length. Medial fork with closely set setae .... ***Allarete*** Pritchard, in part
see couplet 36

44. R_5 joining C well before wing apex. Flagellomeres without forked sensoria 45
R_5 joining C near or beyond wing apex (Fig. 19). Flagellomeres with forked sensoria 47



Figs. 16.51–64. Antennae (*concluded*): scape of (51) *Camptomyia* sp. and (52) *Asynapta* sp.; third flagellomere of (53) *Winnertzia fungicola* Felt, (54) *Kronomyia populi* Felt, (55) *Haplusia* sp., (56) *Solntsevia maculata* (Felt), (57) *Porricondyla carolina* Felt, (58) *Porricondyla nigripennis* (Meigen), (59) *Asphondylia monacha* Osten Sacken, and (60) *Aphidoletes aphidimyza* (Rondani); flagellomeres 1–3 of (61) *Neolasioptera erigerontis* (Felt), (62, 63) *Cecidomyia resinicola* (Osten Sacken), and (64) *Contarinia schulzi* Gagné.
Abbreviation: circmf, circumfila.

45. Flagellomeres with only setiform sensoria .... ***Anocha*** **Pritchard**
2 spp.; Pritchard 1960*b*
Flagellomeres each with a pair of bud-like sensoria 46



Figs. 16.65–81. Tarsi: first and second tarsomeres of left fore tarsus of (65) *Conarete crebra* Pritchard and (66) *Anarete candidata* Haliday; first tarsomere of fore tarsus of (67) *Tetraneuromyia apicalis* (Felt), (68) *Neosynepidosis furcata* (Felt), and (69) *Porricondyla nigripennis* (Meigen); tarsal claws of (70) *Clinodiplosis araneosa* Felt (fore, left), (71) *C. araneosa* (hind, right), (72) *Feltiella davisi* Felt (fore, left), (73) *Contarinia schulzi* Gagné (fore, left), (74) *Hyperdiplosis lobata* (Felt) (fore, left), (75) *Planetella* sp. (fore, left), (76) *Cecidomyia resinicola* (Osten Sacken) (fore, left), (77) *Dasineura canadensis* Felt (fore, left), (78) *Ledomyia setosa* Felt (fore, left), and (79) *Mayetiola destructor* (Say) (fore, left); entire left fore tibia and tarsus of (80) *Conarete crebra* and (81) *Neosynepidosis furcata*.
Abbreviation: emp, empodium.

46. Medial fork with branches evenly divergent; C extending almost as far distally as M_1 .... ***Neocatocha*** Felt
1 sp., *marilandica* Felt

Medial fork with branches unevenly divergent; M_1 sigmoid; C ending distal to R_5 .... ***Tritozyga*** Loew
1 sp., *sackeni* Felt

47. Wing membrane bare or with few macrotrichia .... ***Eucatocha*** Edwards
2 spp.; Pritchard 1960*b*

Wing membrane with dense macrotrichia (Fig. 19) .... ***Catocha*** Haliday
1 sp., *slossonae* Felt

48. Flagellomeres usually numbering more than 10 (some exceptions in female). Tarsi with five tarsomeres. CuA simple or forked, usually traceable to wing margin (Figs. 22, 24–30) 49

Flagellomeres numbering 10 or less. Tarsi with two to five tarsomeres. Venation greatly reduced; CuA simple, not traceable to wing margin (Figs. 21, 23)......HETEROPEZINI....54

49. Flagellomeres without ring-shaped sensoria called circumfila; sensoria U-shaped (Fig. 53), blade-like (Fig. 54), or absent (Fig. 55). CuA simple (Figs. 22, 25, 26) 50

Flagellomeres with circumfila (Figs. 56–58). CuA simple or forked 51

50. Antenna with 11–12 flagellomeres bearing U-shaped (Fig. 53) or blade-like (Fig. 54) sensoria. M_3 present (Fig. 22) except in *Parwinnertzia* (Fig. 25) ..................WINNERTZIINI....57

Antenna with 14 flagellomeres bearing no extrasetal sensoria (Fig. 55). M_3 absent (Fig. 26) .... DIALLACTINI....***Haplusia*** Karsch
2 spp. (as *Johnsonomyia*); Parnell 1971

51. Antenna with 14 or fewer flagellomeres, with number constant within a species. Caudal setae of abdominal tergites in a continuous transverse row (Fig. 112) 52

Antenna usually with more than 14 flagellomeres, with number usually variable within a species. Caudal setae of abdominal tergites in two lateral groups (Fig. 111) ....ASYNAPTINI....59

52. Female cercus one-segmented, higher than long, enlarged, bearing numerous short papillae (Fig. 122). Only female known ....DIRHIZINI.... ***Dirhiza*** Loew
1 sp., *papillata* (Felt)

Female cercus two-segmented (Fig. 121). All males 53

53. CuA_1 absent; M_3 present. Gonostylus with tooth absent or not terminal (Figs. 90–92). Female cercus appearing to be three-segmented..................DICERURINI....64

CuA_1 present (Figs. 24, 29, 30) or absent; if absent, M_3 also absent. Gonostylus of male with terminal tooth (Figs. 89, 93–96). Female cercus two-segmented ..PORRICONDYLINI....66

54. Tarsi with five tarsomeres; claws toothed .... ***Henria*** Wyatt
2 spp.; Pritchard 1960*a*

Tarsi with two to four tarsomeres; claws simple 55

55. Tarsi with four tarsomeres. Basal section of Rs present (Fig. 21) ....***Miastor*** Meinert
1 sp., *metroloas* Meinert

Tarsi with two or three tarsomeres. Basal section of Rs absent (Fig. 23)..................56

56. Tarsi with three tarsomeres..................***Heteropezina*** Pritchard
1 sp., *cathistes* Pritchard; Florida

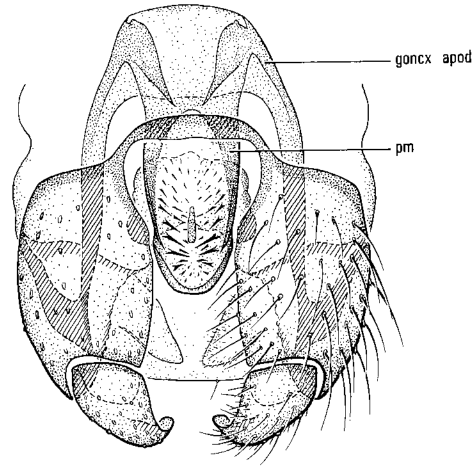
Tarsi with two tarsomeres..................***Heteropeza*** Winnertz
2 spp.; Pritchard 1960*a*

57. Flagellomeres with blade-like blunt-tipped sensoria (Fig. 54). Female without sclerotized spermathecae. Only female known..................***Kronomyia*** Felt
1 sp., *populi* Felt

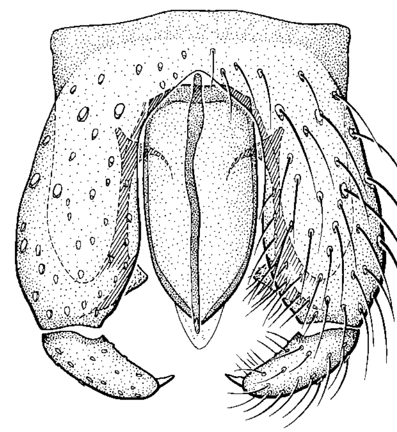
Flagellomeres with U-shaped sensoria (Fig. 53). Female with at least one sclerotized spermatheca 58

58. M_3 distinct; wing broad (Fig. 22). Palpus four-segmented ....***Winnertzia*** Rondani
9 spp.; Parnell 1971

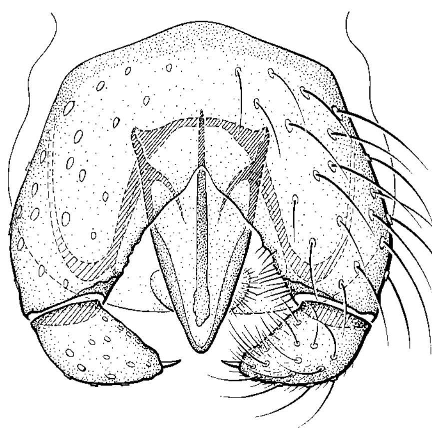
M_3 absent; wing narrow (Fig. 25). Palpus two-segmented..................***Parwinnertzia*** Felt
1 sp., *notmani* Felt



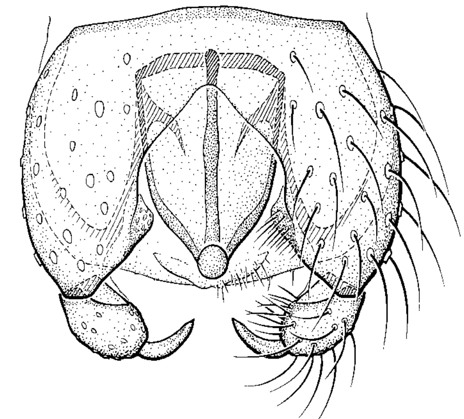
82 Aprionus asemus ♂



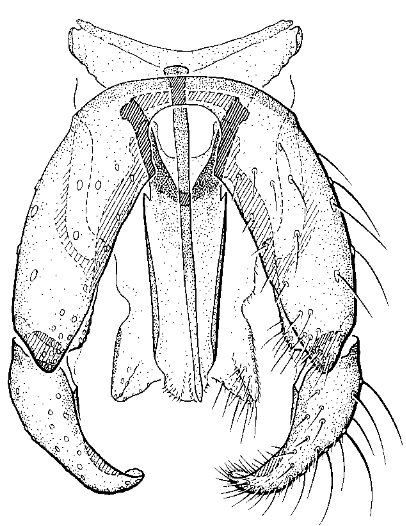
83 Trichopteromyia modesta ♂



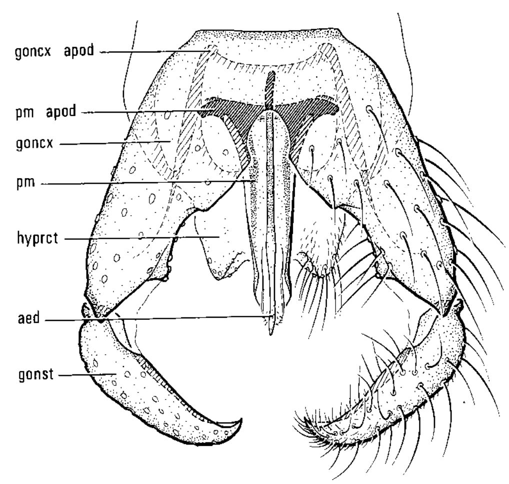
84 Polyardis adela ♂



85 Xylopriona toxicodendri ♂



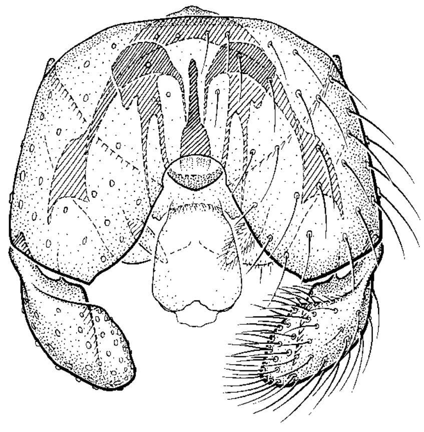
86 Anarete anepsia ♂



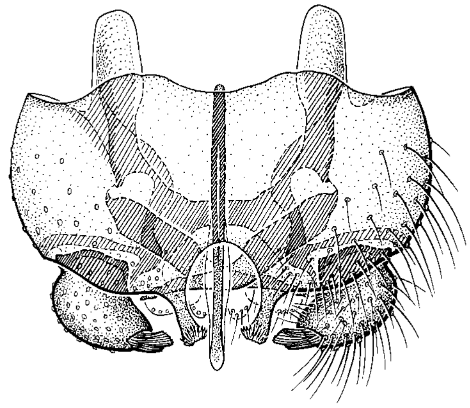
87 Conarete crebra ♂

Figs. 16.82–87. Male terminalia, ventral view: (82) *Aprionus asemus* Pritchard; (83) *Trichopteromyia modesta* Williston; (84) *Polyardis adela* Pritchard; (85) *Xylopriona toxicodendri* (Felt); (86) *Anarete anepsia* Pritchard; (87) *Conarete crebra* Pritchard (*continued*).

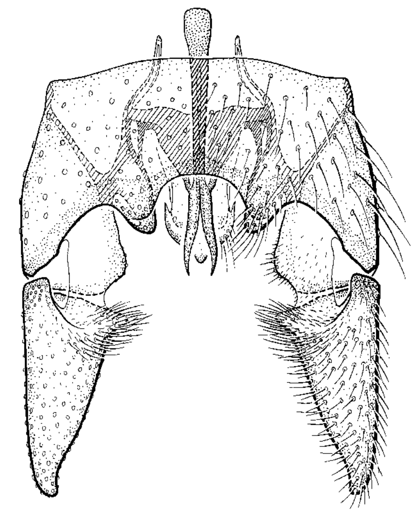
Abbreviations: aed, aedeagus; goncx, gonocoxite; goncx apod, gonocoxal apodeme; gonst, gonostylus; hyprct, hypoproct; pm, paramere; pm apod, parameral apodeme.



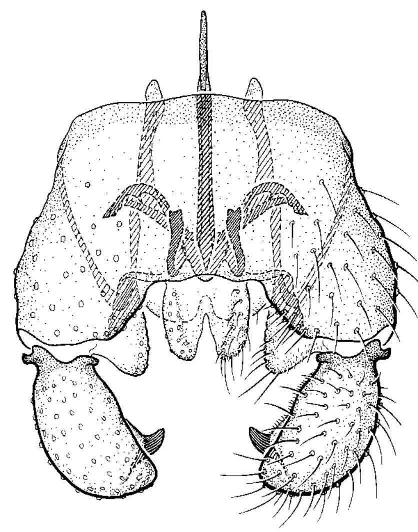
88 Bryomyia apsectra ♂



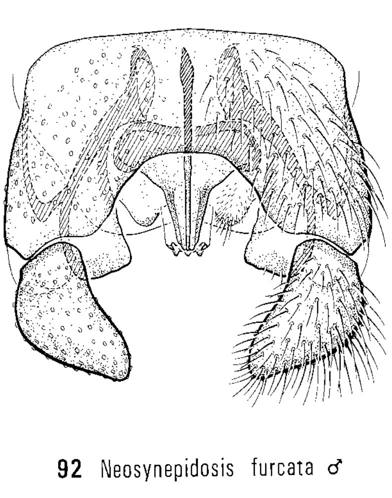
89 Porricondyla nigripennis ♂



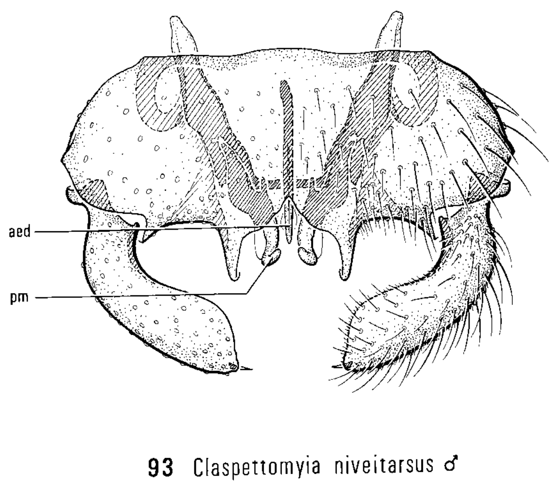
90 Dicerura oregonensis ♂



91 Tetraneuromyia apicalis ♂



92 Neosynepidosis furcata ♂



93 Claspettomyia niveitarsus ♂

Figs. 16.88–93. Male terminalia (*continued*), ventral view: (88) *Bryomyia apsectra* Edwards; (89) *Porricondyla nigripennis* (Meigen); (90) *Dicerura oregonensis* (Felt); (91) *Tetraneuromyia apicalis* (Felt); (92) *Neosynepidosis furcata* (Felt); (93) *Claspettomyia niveitarsus* (Zetterstedt) (*continued*).
Abbreviations: aed, aedeagus; pm, paramere.

59. CuA simple, indistinct distally; M_3 absent. Palpus one-segmented .... ***Colomyia*** Kieffer
1 sp., *hordei* Barnes; Holarctic

CuA simple or forked, distinct to apex; M_3 present (Figs. 27, 28). Palpus four-segmented 60

60. Antennal scape with numerous mediodistal setae (Fig. 51) 61

Antennal scape with only a few median setae (Fig. 52) 63

61. CuA forked (Fig. 28) .... ***Camptomyia*** Kieffer
8 spp.; Parnell 1971

CuA simple (Fig. 27) 62

62. M_3 evident. Claws bent at right angle; tooth parallel. Gonostylus of male terminalia rounded distally; tooth absent .... ***Feltomyina*** Alexander
undescr. spp.; Maryland, Virginia

M_3 absent. Claws curved; tooth not parallel, strongly curved. Gonostylus pointed distally; tooth present .... ***Pseudocamptomyia*** Parnell
1 sp., *photophila* (Felt)

63. CuA simple; M_3 present (Fig. 27) .... ***Asynapta*** Loew
12 spp.; Parnell 1971

CuA forked; M_3 absent .... ***Parasynapta*** Panelius
1 sp., *canadensis* (Felt)

64. Circumfila of male flagellomeres simple, ring-like, without distal extensions; those of female composed of two connected rings. Gonostylus of male terminalia without subapical tooth, but with very setose ventrobasal lobe (Fig. 90) .... ***Dicerura*** Kieffer
1 sp., *oregonensis* (Felt)

Circumfila of male flagellomeres with distal extensions; those of female ramifying. Gonostylus of male terminalia with or without subapical tooth, but without ventrobasal lobe (Figs. 91, 92) 65

65. Tarsomere 1 of foreleg with blunt setulose apicoventral projection (Fig. 67). Gonostylus with subapical tooth (Fig. 91) .... ***Tetraneuromyia*** Mamaev
3 spp.; Parnell 1971

Tarsomere 1 of foreleg with pointed asetulose apicoventral projection (Fig. 68). Gonostylus without subapical tooth (Fig. 92) .... ***Neosynepidosis*** Parnell
1 sp., *furcata* (Felt)

66. Palpus one- or two-segmented. Female flagellomeres with ramifying circumfila (Fig. 56). Only female known .... ***Solntsevia*** Mamaev
1 sp., *maculata* (Felt)

Palpus four-segmented. Female flagellomeres with two simple interconnected circumfila (Fig. 57) 67

67. Empodia rudimentary or absent 68

Empodia more than half as long as claws 70

68. M_3 present; CuA forked .... ***Parepidosis*** Kieffer
2 spp.; Parnell 1971

M_3 absent; CuA simple 69

69. Wing wide; CuA not evident except at extreme apex .... ***Holoneurus*** Kieffer
3 spp.; Parnell 1971

Wing narrow; CuA evident only on basal half of wing .... ***Coccopsis*** de Meijere
1 sp., *marginata* de Meijere; Holarctic

70. Female 71

Male 72

71. Antenna with 13 flagellomeres; last flagellomere with long terminal nipple. Vertex of head produced anteriorly .... ***Didactylomyia*** Felt, in part
1 sp., *longimana* (Felt); Holarctic

Antenna with 10–12 flagellomeres; last flagellomere without terminal nipple. Vertex of head not conspicuously produced anteriorly .... ***Porricondyla*** Rondani, in part
21 spp.; Parnell 1971

72. Male antenna with 13 flagellomeres. Gonostylus widened apically (Fig. 93) .... ***Claspettomyia*** Grover
3 spp.; Parnell 1971

Male antenna with 14 flagellomeres. Gonostylus ovoid, quadrate, or narrowly tapered apically (Figs. 89, 94–96) 73

73. Tarsomere 1 of foreleg with pointed distoventral projection (Fig. 68) 74

Tarsomere 1 of foreleg with blunt projection (Fig. 69) 75

74. Sc evident; cell r_1 normal; CuA forked, not close to wing edge (Fig. 29). Gonostylus rounded apically; tooth slightly subapical .... ***Neocolpodia*** Mamaev
1 sp., *pinea* (Felt)

Sc not evident; cell r_1 almost obliterated; CuA simple, very close to wing edge (Fig. 30). Gonostylus tapered to a pointed and toothed apex .... ***Isocolpodia*** Parnell
3 spp.; Parnell 1971

75. Parameres in shape of furcate ventral lobes forming a pair of strongly sclerotized bifurcate processes (Fig. 94) .... ***Monepidosis*** Mamaev
1 sp., *carolina* (Felt)

Parameres not furcate, without stronger sclerotized ventral processes 76

76. Gonostylus quadrate in lateral view; tooth broad, as wide as gonostylus (Fig. 95) .... ***Schistoneurus*** Mamaev
1 sp., *pectinata* (Felt)

Gonostylus ovoid or long and cylindrical; tooth narrower than gonostylus (Figs. 89, 96) 77

77. Gonostylus long, cylindrical (Fig. 96) .... ***Basicondyla*** Parnell
1 sp., *fultonensis* (Felt)

Gonostylus ovoid to flask-shaped (Fig. 89) .... ***Porricondyla*** Rondani, in part
see couplet 71

78. R_5 usually as long or almost as long as wing (Figs. 33–35); if shorter, then R_5 curved and not closely adjacent to R_1 and C (Fig. 6). Antennal flagellomeres usually sexually dimorphic, with apical necks. Tarsal claws toothed or simple 79

R_5 half to two-thirds length of wing, straight, closely adjacent to R_1 and C (Fig. 31). Antennal flagellomeres short, barrel-shaped, not or barely sexually dimorphic (Fig. 61). Tarsal claws toothed .... LASIOPTERIDI, in part; LASIOPTERINI 86

79. Antennal flagellomeres usually with long necks, at least in male; circumfila usually not anastomosing (Figs. 60, 63, 64). Tarsal claws simple or toothed. Gonostylus of male terminalia caudal. Female abdominal sternite 7 not appreciably longer than sternite 6 80

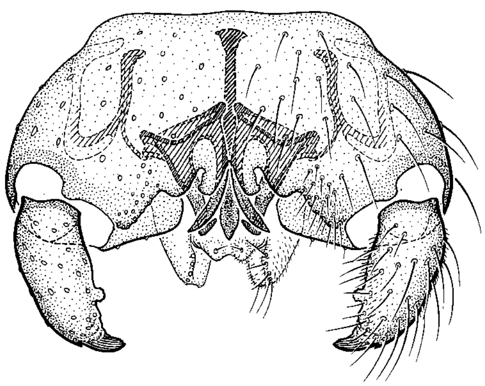
Antennal flagellomeres with short necks, elongate–cylindrical, usually with anastomosing closely appressed circumfila (Fig. 59). Tarsal claws simple. Gonostylus of male terminalia short, wide, situated either dorsally or dorsocaudally on gonocoxite (Fig. 97). Female abdominal sternite 7 about 1.5 times length of sternite 6 (Fig. 128) .... ASPHONDYLIIDI 96

80. Antenna with 7–30 flagellomeres, which are usually irregular in number within a species; nodes of flagellomeres usually elongate–ovoid, with male flagellomeres differing from those of female by the longer necks. Postvertical peak absent. Gonocoxite usually with elongate mediobasal lobes that at least partially clasp or sheath aedeagus (Figs. 113, 114). Female cerci usually fused medially (Fig. 123) 81

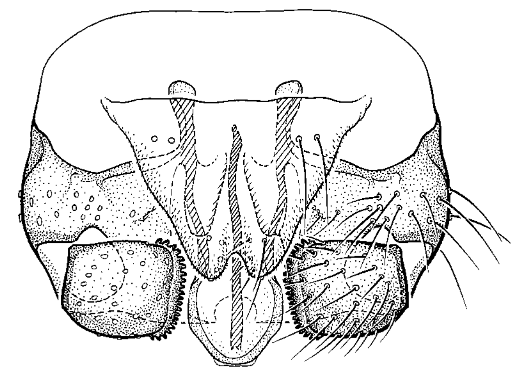
Antenna with 12 flagellomeres (except 13–23 in *Planetella*); male flagellomeres binodal (unless shaped as in female) with two or three separate many-looped circumfila (Figs. 60, 63, 64); nodes of female flagellomeres cylindrical (Fig. 62). Postvertical peak present (Fig. 3) or absent. Gonocoxite without elongate sheathing mediobasal lobes. Female cerci separate (except in *Taxodiomyia*), although sometimes closely appressed .... CECIDOMYIIDI, in part 100

81. Antenna with 10 or 13 flagellomeres, which are regular in number within species and genus. Gonocoxite without elongate sheathing mediobasal lobes, though small lobes sometimes present. Female cerci not fused 82

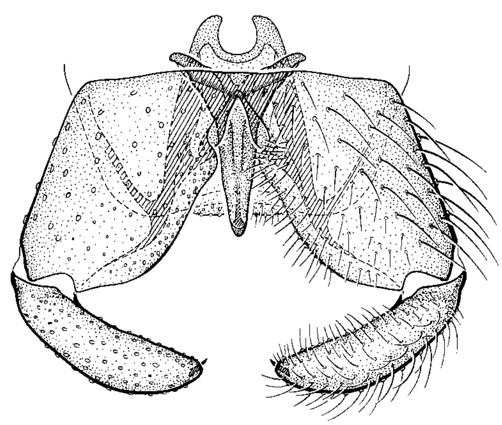
Antenna with 7–42 flagellomeres, which are usually irregular in number within species and genus. Gonocoxite with elongate mediobasal lobes sheathing aedeagus (Figs. 113, 114). Female cerci usually fused medially into a single terminal lamella (Fig. 123) ....LASIOPTERIDI, in part....179



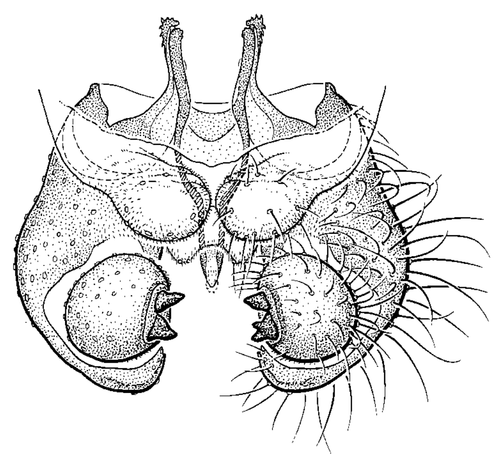
94 Monepidosis carolina ♂



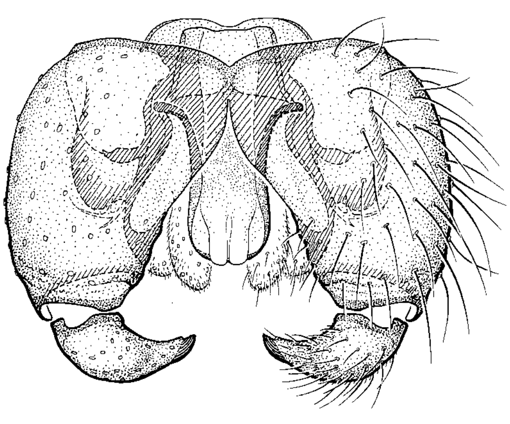
95 Schistoneurus pectinatus ♂



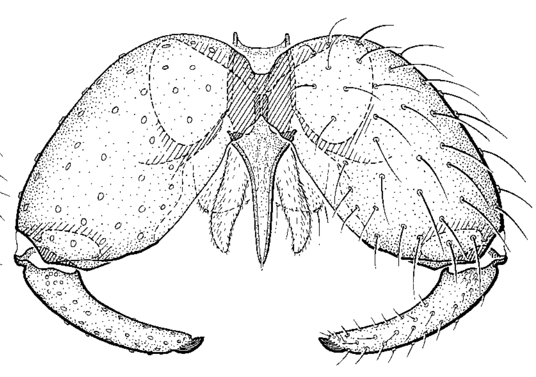
96 Basicondyla fultonensis ♂



97 Asphondylia monacha ♂



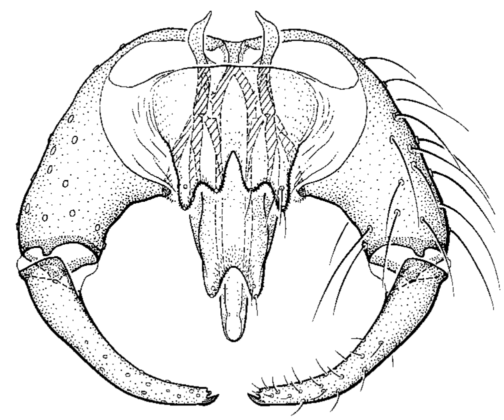
98 Cecidomyia resinicola ♂



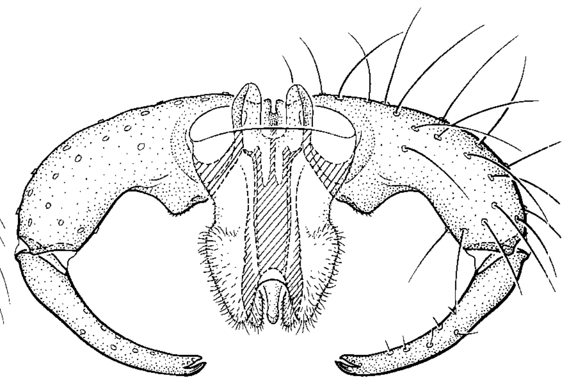
99 Contarinia schulzi ♂

Figs. 16.94–99. Male terminalia (*continued*): (94) *Monepidosis carolina* (Felt), ventral view; (95) *Schistoneurus pectinatus* (Felt), dorsal view; (96) *Basicondyla fultonensis* (Felt), ventral view; (97) *Asphondylia monacha* Osten Sacken, dorsal view; (98) *Cecidomyia resinicola* (Osten Sacken), ventral view; (99) *Contarinia schulzi* Gagné, ventral view (*continued*).

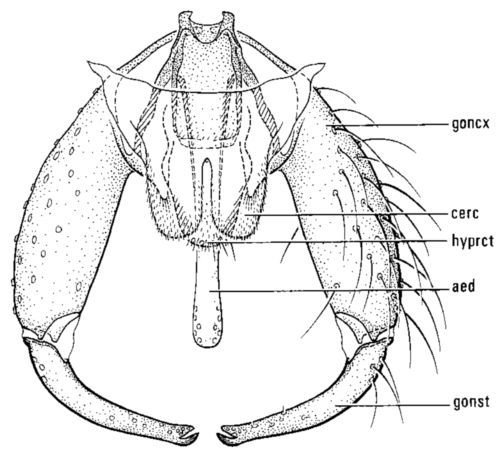
82. Antenna with 13 flagellomeres; the last flagellomere with a terminal nipple. Wing with Rs as strong as other veins; R_5 long and curved, joining C posterior to wing apex. Male with conspicuous setose mediobasal lobe on gonocoxite. Female cercus one- or two-segmented .... STOMATOSEMATIDI....83



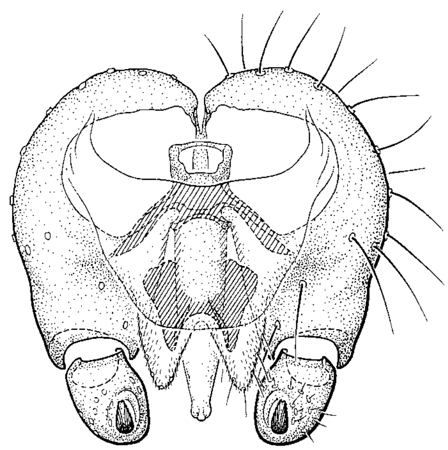
100 Clinodiplosis lappa ♂



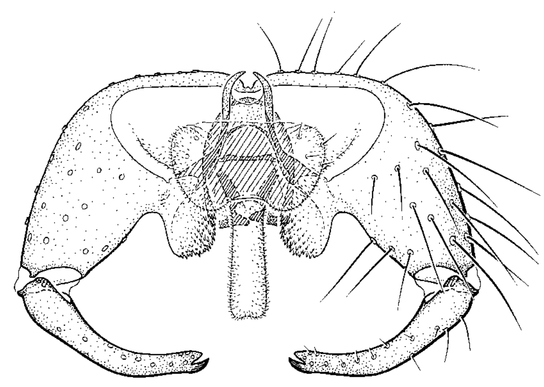
101 Mycodiplosis inimica ♂



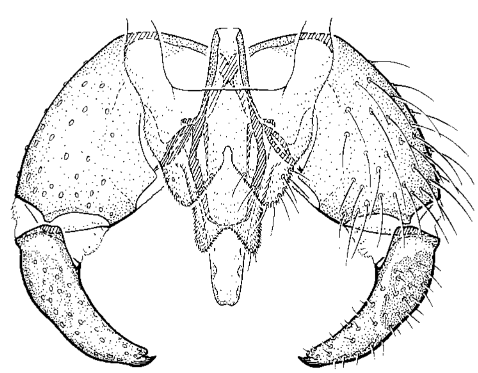
102 Lestodiplosis grassator ♂



103 Prodiplosis morrisi ♂

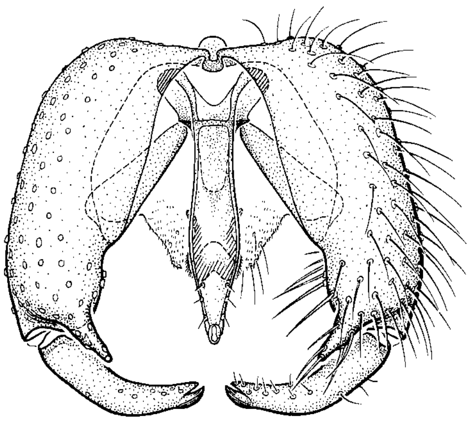


104 Coquillettomyia dentata ♂

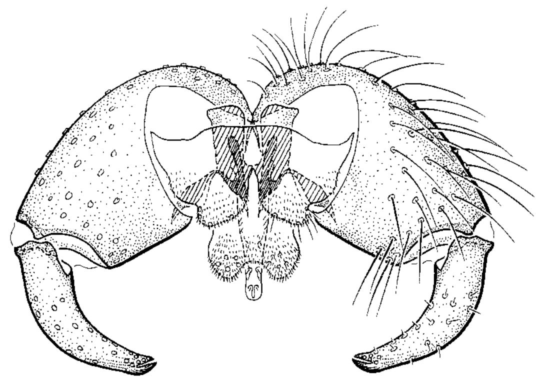


105 Harmandia reflexa ♂

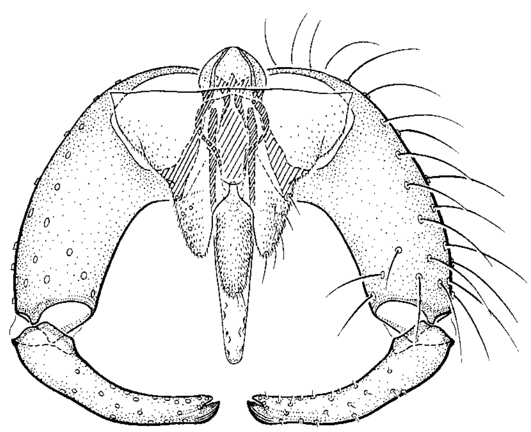
Figs. 16.100–105. Male terminalia (*continued*), dorsal view: (100) *Clinodiplosis lappa* (Stebbins); (101) *Mycodiplosis inimica* (Fitch); (102) *Lestodiplosis grassator* (Fyles); (103) *Prodiplosis morrisi* Gagné; (104) *Coquillettomyia dentata* Felt; (105) *Harmandia reflexa* (Felt) (*continued*).
Abbreviations: aed, aedeagus; cerc, cercus; goncx, gonocoxite; gonst, gonostylus; hyprct, hypoproct.



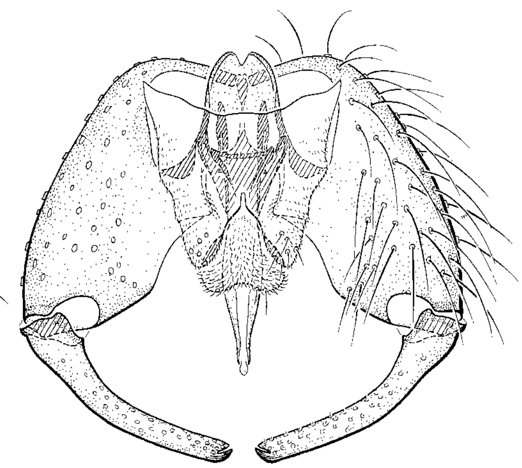
106 Lobodiplosis triangularis ♂



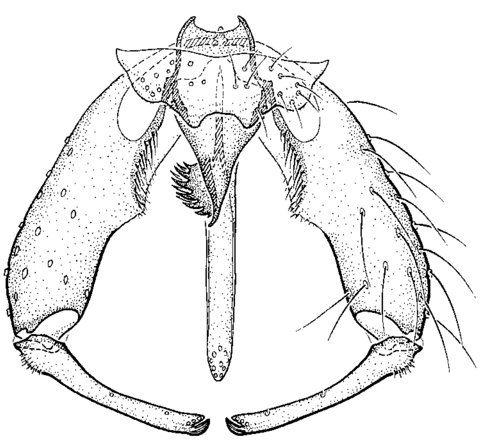
107 Resseliella alternata ♂



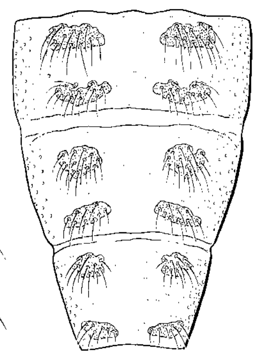
108 Aphodiplosis triangularis ♂



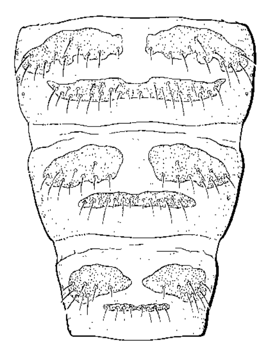
109 Aphidoletes aphidimyza ♂



110 Odontodiplosis americana ♂



111 Camptomyia aestiva ♀



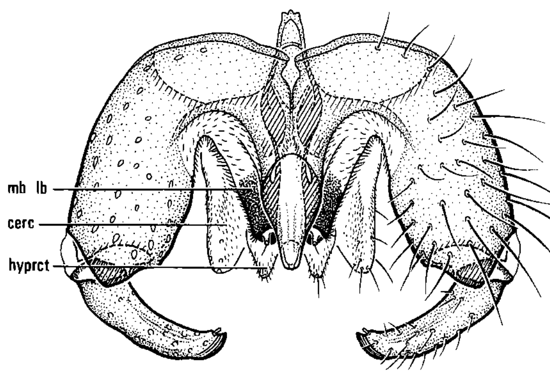
112 Porricondyla nigripennis ♂

Figs. 16.106–112. Male terminalia (*continued*) and abdomens: male terminalia of (106) ***Lobodiplosis triangularis*** Felt in ventral view, (107) ***Resseliella alternata*** (Felt) in dorsal view, (108) ***Aphodiplosis triangularis*** (Felt) in dorsal view, (109) ***Aphidoletes aphidimyza*** (Rondani) in dorsal view, and (110) ***Odontodiplosis americana*** Felt in dorsal view; (111) abdominal segments 3–5 of female of ***Camptomyia aestiva*** Felt, dorsal view; (112) abdominal segments 5–7 of male of ***Porricondyla nigripennis*** (Meigen), dorsal view (***continued***).

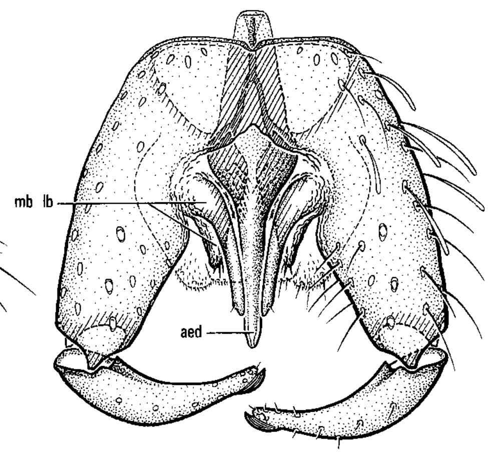
Antenna with 10 flagellomeres. Wing with Rs evanescent; R_5 short, reaching C at or before wing apex. Gonocoxite without or with a minute mediobasal lobe. Female cercus one-segmented 84

83. Very light in color except for often-present dark lateral stripe. Male cercal lobe and aedeagus very tiny compared with gonopod. Female cercus two-segmented .... ***Didactylomyia*** Felt, in part

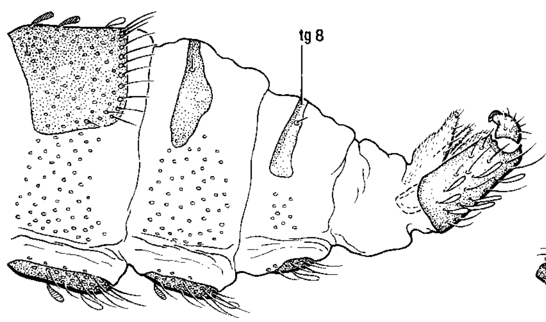
see couplet 71



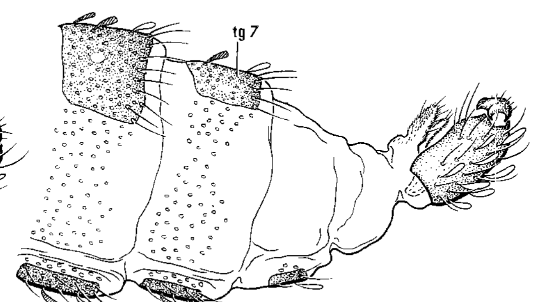
113 Dasineura canadensis ♂



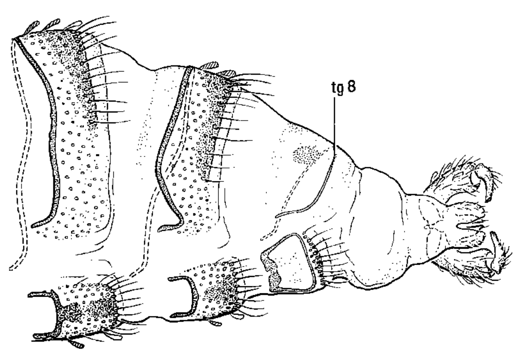
114 Ledomyia setosa ♂



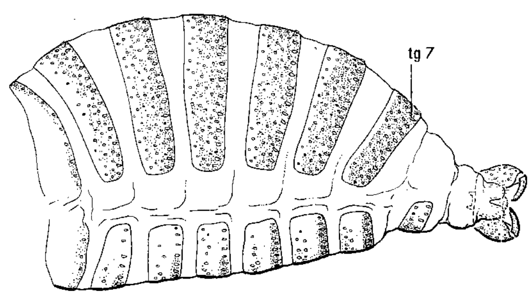
115 Lasioptera solidaginis ♂



116 Neolasioptera erigerontis ♂



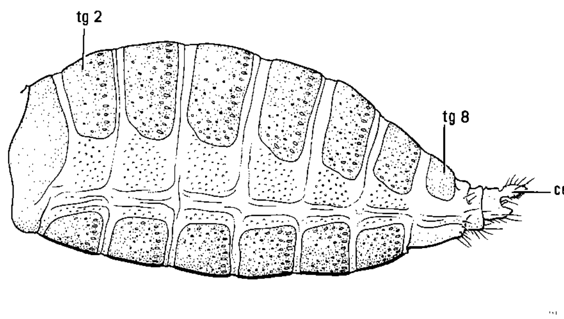
117 Calamomyia flavipes ♂



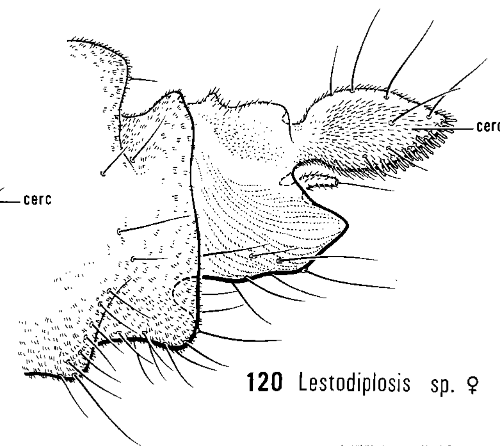
118 Olesicoccus coccidivora ♂

Figs. 16.113–118. Male terminalia and abdomens (*concluded*): ventral view of terminalia of (113) *Dasineura canadensis* Felt and (114) *Ledomyia setosa* Felt; abdomen, left lateral view, showing terminalia of (115) *Lasioptera solidaginis* Osten Sacken, (116) *Neolasioptera erigerontis* (Felt), (117) *Calamomyia flavipes* (Felt), and (118) *Olesicoccus coccidivora* (Felt).

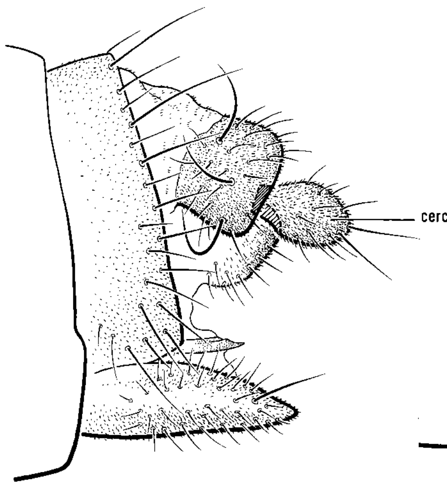
Abbreviations: aed, aedeagus; cerc, cercus; hyprct, hypoproct; mb lb, mediobasal lobe; tg, tergite.



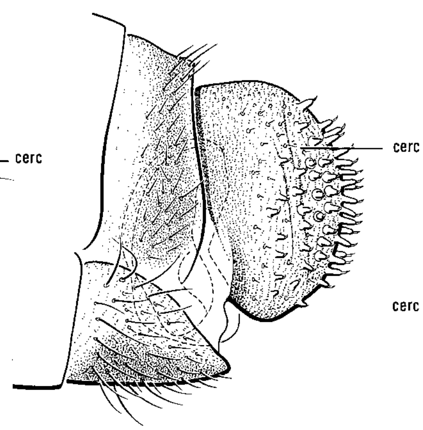
119 Lestodiplosis sp. ♀



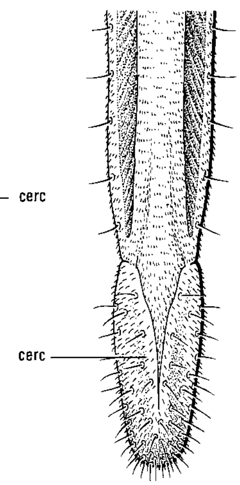
120 Lestodiplosis sp. ♀



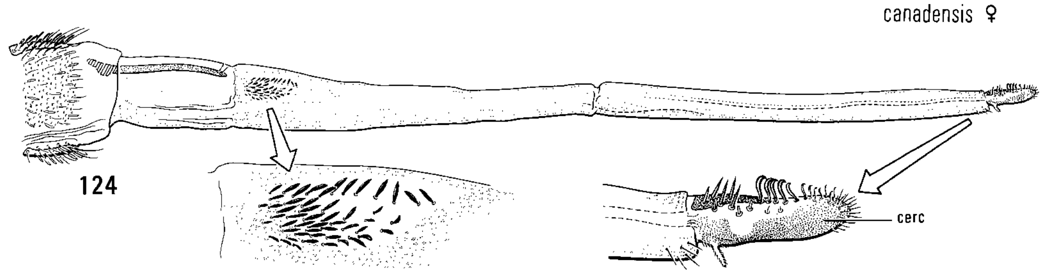
121 Porricondyla carolina ♀



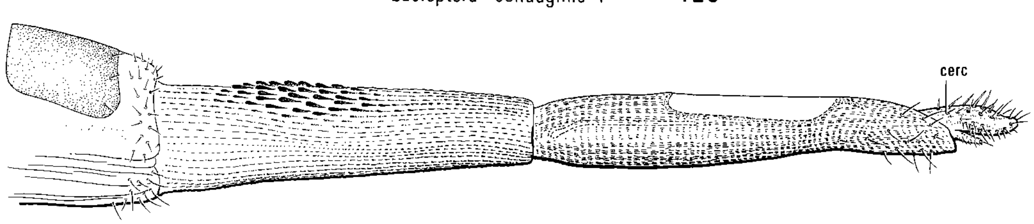
122 Dirhiza papillata ♀



123 Dasineura canadensis ♀



125 Lasioptera solidaginis ♀ 126



127 Neolasioptera erigerontis ♀

Figs. 16.119–127. Female abdomens: (119) left lateral view of abdomen of *Lestodiplosis* sp.; (120) enlargement of terminalia of *Lestodiplosis* sp.; female terminalia of (121) *Porricondyla carolina* Felt and (122) *Dirhiza papillata* (Felt) in left lateral view, (123) *Dasineura canadensis* Felt in dorsal view, (124–126) *Lasioptera solidaginis* Osten Sacken in left lateral view, and (127) *Neolasioptera erigerontis* (Felt) in left lateral view (*continued*).

Abbreviations: cerc, cercus; tg, tergite.

Fuscous. Male cercal lobe and aedeagus normal in length in relation to gonopod. Female cercus one-segmented .... ***Stomatosema*** Kieffer
3 spp.; Gagné 1975*a*

84. Wing with R_5 almost as long as wing. Scutum with dorsocentral rows of setae; body scales sparse, if present 85

Wing with R_5 close to C, about 0.7 length of wing. Scutum without dorsocentral rows of setae; body densely covered with scales 198

85. Tarsal claws toothed. Male hypoproct with sclerotized apicoventral projection; gonocoxite with minute setose mediobasal lobe. Female hypoproct bilobate .... ***Rhizomyia*** Kieffer
8 spp.; Felt 1915

Tarsal claw of foreleg toothed; tarsal claws of midleg and hindleg simple. Male hypoproct and gonocoxite without lobes. Female hypoproct simple. Predator of coccoids .... CECIDOMYIIDI, in part.... ***Coccidomyia*** Felt
1 sp., *pennsylvanica* Felt

86. In male, tergite 8 usually without setae or scales, membranous posteriorly, with sclerotized portion shorter dorsally than laterally (Fig. 115). In female, basal half of ovipositor without longitudinal striae, but on each side with a laterobasal group of numerous strong longitudinally flattened setae; cercus with hooked setae (Figs. 124–126) .... LASIOPTERINA.... 87

In male, tergite 8, if present, setose along caudal margin and sclerotized at least caudally. In female, basal half of ovipositor with longitudinal striae that are proximodorsally interrupted and enlarged to form ovoid sclerotized bumps; cercus without hooked setae (Fig. 127) .... ALYCAULINA.... 89

87. Labella elongate, styliform. Pronotum long; scutum flattened. Reared from achenes of *Achillea millefolium* .... ***Ozirhincus*** Rondani
1 sp., *millefolii* (Wachtl)

Labella short, bulbous. Pronotum short; scutum convex 88

88. In male, setae present laterally on tergite 8; gonostylus narrowest at apical tooth. In female, cercus bilaterally compressed, completely sclerotized. Reared from stems of *Elymus virginicus* .... ***Hybolasioptera*** Rübsaamen
1 sp., *elymi* Gagné

In male, setae usually absent laterally from tergite 8 (Fig. 115); gonostylus longer, narrowing before apical tooth. In female, cercus cylindrical, with only a saddle-shaped dorsal area sclerotized (Figs. 124–126) .... ***Lasioptera*** Meigen
34 spp.; Gagné 1969*b*

89. Male abdominal tergites 1–5 without setae along caudal margins. Ovipositor aciculate, sclerotized. Reared from stems of *Sarcobatus vermiculatus* .... ***Protaplonyx*** Felt
1 sp., *sarcobati* (Felt); western U.S.A.

Male tergites 1–5 with setae along caudal margins. Ovipositor not aciculate, unsclerotized 90

90. Male abdominal tergites 6 and 7 with anterior margins strongly sclerotized, extending ventrolaterally, almost to the sternites; anterior margins of male sternites likewise heavily sclerotized (Fig. 117). Female cercus elongate–cylindrical, sparsely covered with long uniform setae. Reared from stems of Gramineae .... ***Calamomyia*** Gagné
18 spp.; Gagné 1969*b*

Male abdominal tergites 6 and 7 and sternites 6–8 uniformly sclerotized and quadrate (Fig. 116). Female cercus, if elongate–cylindrical, with setae either short or of varying length 91

91. Female sternite 8 strongly sclerotized, about three-quarters length of tergite 8; female cercus bilaterally compressed. Reared from seeds of *Aristida longiseta* .... ***Edestosperma*** Gagné
1 sp., *aristidae* Gagné

Female sternite 8, if present, weakly sclerotized, less than a quarter the length of tergite 8; female cercus ovoid 92

92. Setulae on distal half of ovipositor with one or two points. Reared from stems of Gramineae.... 93

Setulae on distal half of ovipositor with four or five points. Reared from plants other than Gramineae 95

93. Wing margin and abdomen entirely covered with black scales. Female cercus elongate–cylindrical, covered with short setae. Reared from stems of species of *Muhlenbergia* .... ***Astictoneura*** Gagné
1 sp., *muhlenbergiae* (Marten)

Wing margin spotted at junction of C and R_5; abdomen with alternating bands of light and dark areas of scales. Setae of female cercus long or short 94

94. Palpus three-segmented. Mediobasal lobe of gonocoxite short, blunt-tipped. Reared from *Paspalum distichum* .... ***Edestochilus*** Gagné
1 sp., *allioides* (Pritchard); California

Palpus four-segmented. Mediobasal lobe of gonocoxite elongate, tapered .... ***Chilophaga*** Gagné
4 spp.; Gagné and Stegmaier 1971

95. Palpus one-, two-, or three-segmented; if three-segmented, then second segment spherical, greater in diameter than cylindrical third. Reared from leaf, petiole, and stem galls of Astereae (Compositae) .... ***Asteromyia*** Felt
8 spp.; Gagné 1969*b*

Palpus usually four-segmented; if three-segmented, then all segments cylindrical. Reared from stem, petiole, and midrib galls of many plants and from achenes of Compositae .... ***Neolasioptera*** Felt
57 spp.; Gagné 1969*b*

96. Tooth of gonostylus not serrated; leading edge of tooth straight or bifid (Fig. 97). Ovipositor elongate, with the distal half aciculate, glabrous, sclerotized (Fig. 128). Female flagellomeres 10–12 successively and progressively shorter 97

Tooth of gonostylus serrated. Ovipositor short, tapering gradually to apex, with distal half membranous or only partially sclerotized. Female flagellomeres 10–12 not conspicuously shorter than preceding flagellomeres 98

97. Palpus four-segmented. Tooth of gonostylus entire. Ovipositor without large basal lobes; cercus setose .... ***Schizomyia*** Kieffer
12 spp.; Felt 1916

Palpus three-segmented. Tooth of gonostylus bifid (Fig. 97). Ovipositor with large basal lobes; cercus glabrous, asetose (Fig. 128) .... ***Asphondylia*** Loew
54 spp.; Felt 1916

98. Palpus four-segmented; segments 3 and 4 elongate. Distal half of ovipositor sclerotized ventrolaterally, longer than sternite 7. Reared from pill-shaped galls on leaves of *Quercus* .... ***Polystepha*** Kieffer
16 spp.; Felt 1916

Palpus with either one or three short segments. Distal half of ovipositor unsclerotized and shorter than sternite 7. Florida (Neotropical) 99

99. Palpus one-segmented. Empodia about as long as claws. Reared from leaf galls on *Eugenia* .... ***Stephomyia*** Tavares
1 sp., *eugeniae* Tavares; Florida

Palpus three-segmented. Empodia rudimentary. Reared from leaf galls on *Pisonia* .... ***Bruggmannia*** Tavares
1 sp., *pisonifolia* (Felt); Florida

100. Tarsal claws toothed, at least on foreleg (Figs. 70, 72) 101

Tarsal claws simple (Figs. 71, 73–76) 122

101. Tarsal claws bent at or beyond mid length, as long as empodia (Fig. 72) 102

Tarsal claws bent near basal third, longer than empodia (Fig. 70) 106

102. One or two loops of at least circumfilum 1 on each male flagellomere two or three times longer than adjacent loops (Fig. 60). Female with nonprotrusible ovipositor and without modified setae on cercus. Predator of aphidoids .... ***Aphidoletes*** Kieffer
3 spp.; Gagné 1973*a*

Loops of each circumfilum approximately same length. Female with either long protrusible ovipositor or with modified setae on cercus 103

103. Male hypoproct deeply bilobate; gonocoxite without mediobasal lobe; gonostylus tapering gradually from wide base to narrow apex (Fig. 105). Ovipositor long, protrusible. Leaf gall

former on *Populus* .... ***Harmandia*** Kieffer
4 spp.; Gagné 1973*a*

Male hypoproct entire; gonocoxite usually with mediobasal lobe; gonostylus elongate, approximately same width throughout (Fig. 102). Ovipositor short 104

104. Tarsal claws strongly dilated beyond bend. Female cercus elongate, cylindrical .... ***Tanaodiplosis*** Gagné
1 sp., *androgynes* (Felt)

Tarsal claws not appreciably dilated beyond bend. Female cercus ovoid, bilaterally flattened (Fig. 120) 105

105. Postvertical peak absent (Fig. 2). Male flagellomeres with short necks and internodes. Gonostylus longitudinally striated. Female cercus with dense short setae ventromedially. Predator of coccoids and other arthropods .... ***Dicrodiplosis*** Kieffer
3 spp.; Gagné 1973*a*

Postvertical peak present (Fig. 3). Male flagellomeres with long internodes and necks. Gonostylus not striated. Female cercus without dense short setae, but with two or three setae longer and stronger than remainder. Predator of mites .... ***Feltiella*** Rübsaamen
14 spp.; Gagné 1973*a*

106. Abdominal tergites and sternites 2–6 transversely divided between the caudal and lateral groups of setae (Fig. 130) 107

Abdominal tergites and sternites entire (Fig. 119) 108

107. Gonocoxite with setose apicoventral lobe; gonostylus long–attenuate (Fig. 106) .... ***Lobodiplosis*** Felt
6 spp.; Gagné 1973*a*

Gonocoxite with naked median lobe of complex structure; gonostylus wide, variously shaped .... ***Karschomyia*** Felt, in part
10 spp.; Gagné 1973*c*

108. Abdominal tergites and sternites very short and broad, strap-like (Fig. 118). R_5 straight, joining C near wing apex. Predator of coccoids 109

Abdominal tergites long and sternites squarish (Figs. 129, 132). R_5 usually curved to join C posterior to wing apex. Predatory or phytophagous 110

109. Palpus three-segmented. Male hypoproct deeply emarginate .... ***Kalodiplosis*** Felt
1 sp., *floridana* Felt; Florida

Palpus four-segmented. Male hypoproct not emarginate .... ***Diadiplosis*** Felt
3 spp.; Florida, California; Gagné 1973*a*

110. Male terminalia compact (Fig. 107); gonostylus short, tapering gradually from base to narrow apex, setulose throughout; hypoproct approximately as long as aedeagus, either entire or triangularly emarginate. Ovipositor elongate, protrusible (Fig. 132) .... ***Resseliella*** Seitner
15 spp.; Gagné 1973*a*

Male terminalia otherwise. Ovipositor not greatly protrusible 111

111. Female unknown. Male flagellomeres bifilar; nodes subequal in size. Gonocoxite with sclerotized mediobasal spur .... ***Plectrodiplosis*** Gagné
1 sp., *fascipennis* Gagné

Male flagellomeres trifilar; distal nodes longer than basal nodes (Fig. 63). Gonocoxite without sclerotized spur 112

112. One or two loops of circumfilum 1 on each male flagellomere much longer than adjacent loops (Fig. 60); circumfilum 2 reduced to a closely appressed band .... ***Bremia*** Rondani
8 spp.; Gagné 1973*a*

Loops of male circumfila regular 113

113. All tarsal claws toothed 114

Only tarsal claw of foreleg toothed 117

114. Claws pectinate. Male flagellomeres as in female. Reared from leaf galls on *Coccoloba* .... ***Ctenodactylomyia*** Felt
1 sp., *watsoni* Felt; Florida

Claws with single teeth. Male flagellomeres not as in female 115

115. Gonocoxite simple; male hypoproct deeply bilobate. Female unknown .... ***Pitydiplosis*** Gagné, in part
1 sp., *packardi* (Felt)

Gonocoxite with large mediobasal lobe; male hypoproct entire 116

116. Female antennal circumfila irregular, with short and long loops. Female with dense cercal setae clavate, abruptly pointed at apex. Male unknown .... ***Homobremia*** Kieffer
1 sp., *insolens* (Felt)

Female antennal circumfila regular, with short loops. Female with dense but finely tapered cercal setae .... ***Youngomyia*** Felt
1 sp., *podophylli* (Felt)

117. Aedeagus blackened, often divided from base 118

Aedeagus not blackened, entire 119

118. Male hypoproct bilobate, setose; gonocoxite simple .... ***Ancylodiplosis*** Gagné
1 sp., *bryanti* (Felt)

Male hypoproct entire, asetose; gonocoxite with mediobasal lobe (Fig. 104) .... ***Coquillettomyia*** Felt
3 spp.; Gagné 1973*a*

119. Postvertical peak absent. Gonocoxite without mediobasal lobe .... ***Pitydiplosis*** Gagné, in part
see couplet 115

Postvertical peak present (Fig. 3). Gonocoxite with an angular mediobasal lobe 120

120. Male terminalia with large secondary parameral lobe and long acute mediobasal lobe on gonocoxite .... ***Glenodiplosis*** Gagné
1 sp., *callipus* Gagné

Male terminalia without secondary parameral lobe and with obtusely angled mediobasal lobe on gonocoxite 121

121. Male cercal lobes triangular (Fig. 101). Ovipositor short; female cercus short–ovoid. Larva feeding on rust spores .... ***Mycodiplosis*** Rübsaamen, in part
7 spp.; Gagné 1973*a*

Male cercal lobes quadrate or secondarily bilobate (Fig. 100). Ovipositor usually elongate; female cercus elongate–ovoid. Larva feeding on saprophagous fungi .... ***Clinodiplosis*** Kieffer, in part
48 spp.; Gagné 1973*a*

122. Tarsal claws bent at basal third or bowed evenly from base to apex, longer than empodia (Figs. 71, 75) 123

Tarsal claws bent beyond mid length, approximately same length as or shorter than empodia (Figs. 73, 74, 76) 133

123. Tarsal claws bowed (Fig. 75), not strongly bent at basal third. Antennal flagellomeres 1 and 2 usually not fused (Fig. 63) 124

Tarsal claws strongly bent at basal third (Fig. 71). Flagellomeres 1 and 2 fused (Fig. 64) 127

124. Antenna with 13 or more flagellomeres. Thorax usually produced anterior to head .... ***Planetella*** Westwood, in part
22 spp.; Gagné 1973*a*

Antenna with 12 flagellomeres. Thorax not produced anterior to head 125

125. Abdominal tergites 2–6 divided laterally between caudal and lateral setae (Fig. 130). Male cercal lobe quadrate apically .... ***Parallelodiplosis*** Rübsaamen, in part
15 spp.; Gagné 1973*a*

Abdominal tergites 2–6 entire (Fig. 129). Male cercal lobe rounded apically 126

126. Very setose; thorax with more than 80 setae in each dorsocentral row. Ovipositor short; female cerci separate. Found in seeds of *Taxodium distichum* .... ***Sequoiomyia*** Möhn
1 sp., *taxodii* (Felt)

Not as setose; thorax with less than 40 setae in each dorsocentral row. Ovipositor long, protrusible; female cerci fused together. Gall maker on *Taxodium distichum* .... ***Taxodiomyia*** Gagné
2 spp.; Gagné 1973*a*

127. Abdominal tergites 2–6 transversely divided between caudal and lateral groups of setae (Fig. 130) 128

Abdominal tergites 2–6 entire (Figs. 119, 129) 129

128. Abdominal sternites 2–6 transversely divided (Fig. 130). Gonostylus variously modified, not tapering evenly from base to apex .... ***Karschomyia*** Felt, in part

see couplet 107

Abdominal sternites entire. Gonostylus elongate, tapering from base to apex (Fig. 100) .... ***Parallelodiplosis*** Rübsaamen, in part

see couplet 125

129. R_5 shorter than wing (Fig. 34). Male hypoproct entire, wider than aedeagus. Predator of coccoids .... ***Silvestrina*** Kieffer

1 sp., *cincta* (Felt)

R_5 as long as wing (Fig. 32). Male hypoproct bilobate or narrower than aedeagus 130

130. Male hypoproct attenuate to pointed at apex, no wider than aedeagus; male cercal lobes triangular (Fig. 108). Female antennal flagellomeres with barely distinct necks. Reared from cow dung .... ***Aphodiplosis*** Gagné

1 sp., *triangularis* (Felt)

Male hypoproct not appreciably narrowed apically; male cercal lobe quadrate or rounded (Figs. 100, 101). Female flagellomeres with long necks 131

131. Male cercal lobe quadrate or secondarily bilobate (Fig. 100). Ovipositor elongate; female cercus elongate–ovoid .... ***Clinodiplosis*** Kieffer, in part

see couplet 121

Male cercal lobe rounded apically (Fig. 101). Ovipositor barely protrusible; female cercus large, ovoid 132

132. Abdominal tergites and sternites sclerotized only on caudal fourth, naked except for caudal rows of setae .... ***Cartodiplosis*** Gagné

1 sp., *nyssaecola* (Beutenmüller)

Abdominal tergites and sternites completely sclerotized, with setae and scales widely distributed .... ***Mycodiplosis*** Rübsaamen, in part

see couplet 121

133. Male with gonocoxite stout, simple; gonostylus usually robust, tapering evenly and gradually from wider base to apex, setulose throughout; cercal lobe, hypoproct, and aedeagus approximately same length; aedeagus usually tapering gradually from base to narrow apex (Figs. 98, 99). Ovipositor protrusible, usually longer than half remainder of abdomen, more or less dorsoventrally flattened, sometimes modified for piercing, sometimes with cerci in close juxtaposition (Fig. 131) 134

Male with gonocoxite and gonostylus variously shaped; gonostylus usually elongate–attenuate, setulose only basally; cercal lobe, hypoproct, and aedeagus differing in relative lengths; aedeagus variously shaped, usually very long (Fig. 102). Ovipositor very short or not protrusible; cerci large, separated (Figs. 119, 120) 148

134. Abdominal tergites 2–6 with caudal setae only (Fig. 131) 135

Abdominal tergites 2–6 with both caudal and lateral setae (Fig. 129) 136

135. C unbroken at juncture with R_5 (Fig. 35). Empodia longer than claws. Leaf gall maker on *Carya* .... ***Caryomyia*** Felt, in part

13 spp.; Gagné 1973*a*

C broken at juncture with R_5 (Fig. 33). Empodia approximately as long as claws. Found in seeds of Gramineae .... ***Contarinia*** Rondani, in part

6 spp.; Gagné 1973*a*

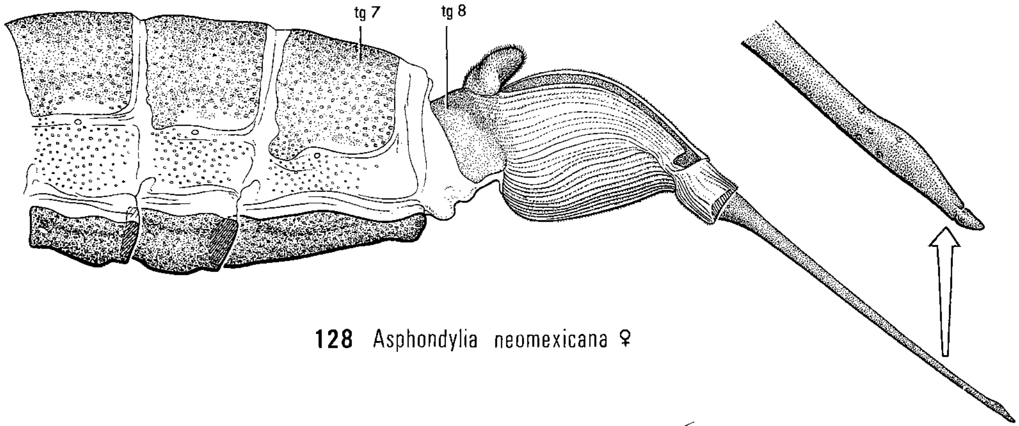
136. Palpus one- or two-segmented 137

Palpus three- or four-segmented 141

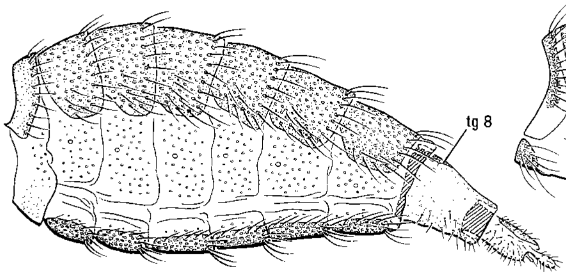
137. Lobes of male hypoproct narrow, pointed apically. Ovipositor cultrate. Leaf gall maker on *Buxus* .... ***Monarthropalpus*** Rübsaamen

1 sp., *buxi* (Laboulbène)

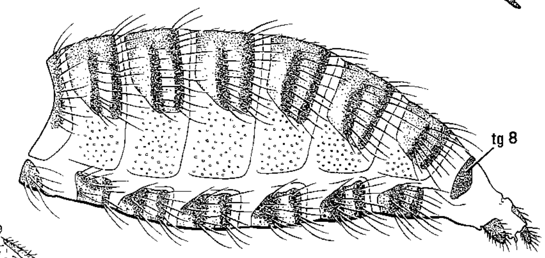
Lobes of male hypoproct broad, rounded apically. Ovipositor not cultrate 138



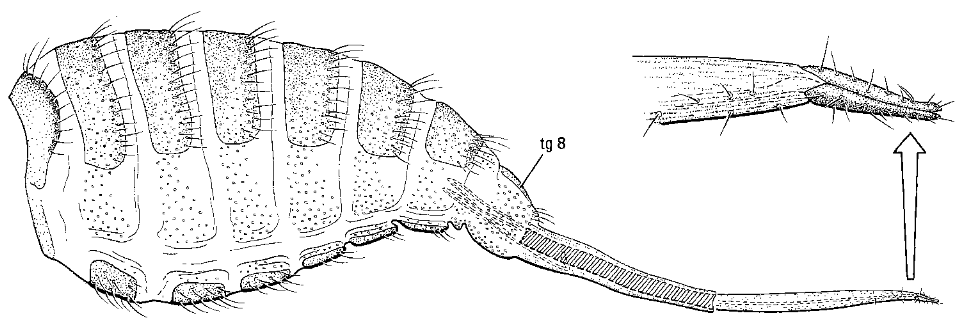
128 Asphondylia neomexicana ♀



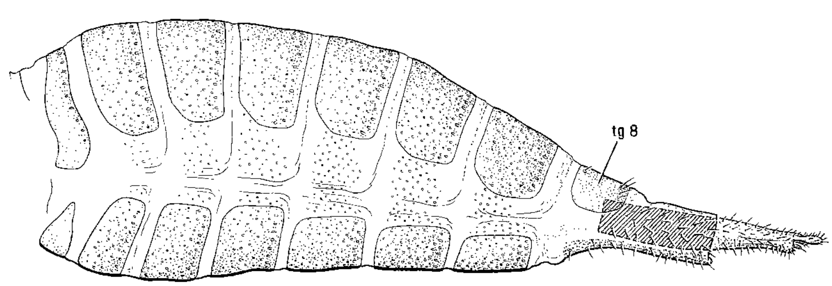
129 Cecidomyia resinicola ♀



130 Lobodiplosis sp. ♀

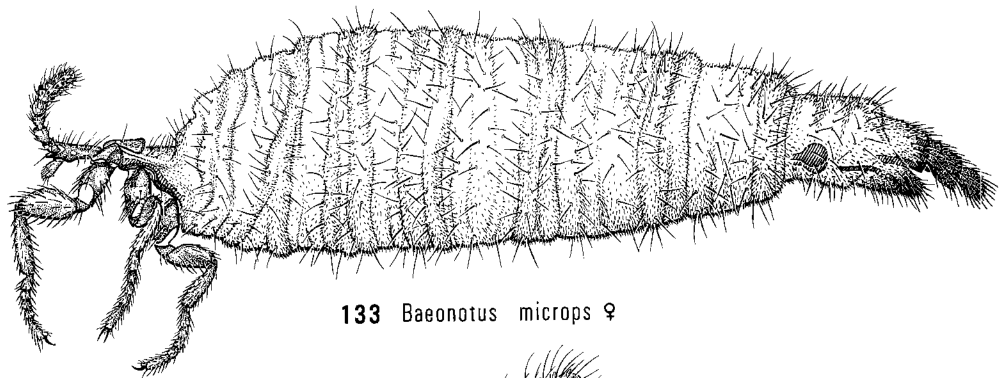


131 Contarinia wattsi ♀

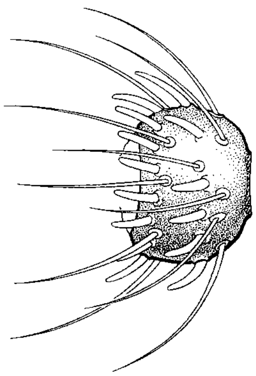


132 Resseliella pinifoliae ♀

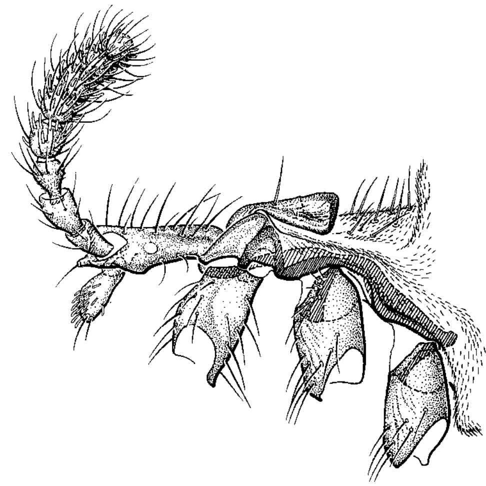
Figs. 16.128–132. Female abdomens (*concluded*), left lateral view: (128) *Asphondylia neomexicana* (Cockerell); (129) *Cecidomyia resinicola* (Osten Sacken); (130) *Lobodiplosis* sp.; (131) *Contarinia wattsi* Gagné; (132) *Resseliella pinifoliae* (Felt).
Abbreviation: tg, tergite.



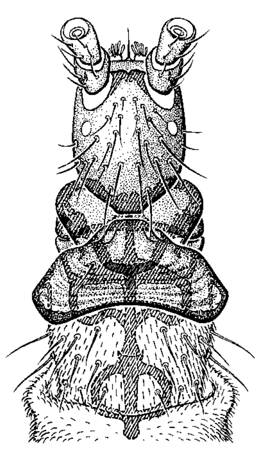
133 Baeonotus microps ♀



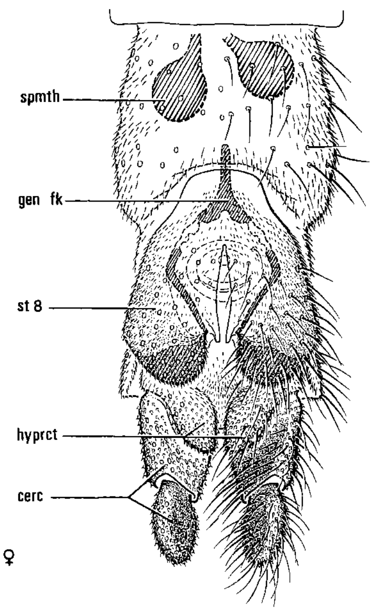
134 Baeonotus microps ♀



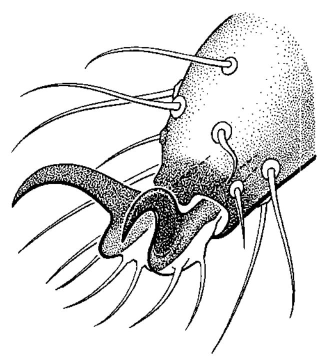
135 Baeonotus microps ♀



136 Baeonotus microps ♀



137 Baeonotus microps ♀



138 Baeonotus microps ♀

Figs. 16.133–138. *Baeonotus microps* Byers: (133) left lateral view of entire female; (134) fourth flagellomere of left antenna; (135) left lateral view of head and thorax; (136) dorsal view of head and thorax, with flagellum removed; (137) ventral view of female terminalia; (138) claws of middle left tarsus.

Abbreviations: cerc, cercus; gen fk, genital fork; hyprct, hypoproct; spmth, spermatheca; st, sternite.

138. Female with cercus triangular, longer than wide, pointed apically. Leaf gall maker on *Pinus edulis*. Male keyed elsewhere .... ***Pinyonia*** Gagné, in part
1 sp., *edulicola* Gagné

Female with cercus rounded apically. All males 139

139. Male antennal circumfila interconnected; female circumfila ramifying. Male abdominal tergite 7 with complete row of caudal setae. Female cercus longer than wide. Leaf gall maker on *Helianthus* .... ***Olpodiplosis*** Gagné
1 sp., *helianthi* (Brodie)

Antennal circumfila regular. Male abdominal tergite 7 with interrupted row of caudal setae. Female cercus stubby, about as wide as long 140

140. Empodia longer than claws. Gonostylus widest near mid length. Distal half of ovipositor with dense long hairs. Gall maker on *Sarcobatus vermiculatus* .... ***Halodiplosis*** Kieffer
1 sp., *sarcobati* (Felt); western U.S.A.

Empodia as long as claws. Gonostylus widest basally. Distal half of ovipositor with only a few scattered short setae. Gall maker on *Ambrosia* .... ***Contarinia*** Rondani, in part
1 sp., *partheniicola* (Cockerell); western U.S.A.

141. Antennal flagellomeres 1 and 2 not fused (Fig. 63). Empodia always longer than claws (Fig. 76) .... ***Cecidomyia*** Meigen, in part
8 spp.; Gagné 1978

Antennal flagellomeres 1 and 2 fused. Empodia longer to shorter than claws 142

142. Palpus three-segmented 143

Palpus four-segmented 146

143. Male antennal flagellomere tricircumfilar (Fig. 63); female circumfila ramifying. Leaf gall former on *Helianthus* .... ***Pilodiplosis*** Gagné, in part
1 sp., *helianthibulla* (Walsh)

Male flagellomeres bicircumfilar (Fig. 64); female circumfila regular (Fig. 62) 144

144. C unbroken at juncture with R_5. Claws shorter than empodia. Leaf gall maker on *Pinus* .... ***Thecodiplosis*** Kieffer
4 spp.; Gagné 1973*a*

C broken at juncture with R_5 (Fig. 33). Claws approximately as long as empodia 145

145. Gonostylus widest near middle. Female cercus widest at base, triangular. Leaf gall maker on *Hypericum perforatum* .... ***Zeuxidiplosis*** Kieffer
1 sp., *giardi* (Kieffer)

Gonostylus widest near base. Female cercus more or less equal in diameter throughout .... ***Contarinia*** Rondani, in part
54 spp.; Gagné 1973*a*

146. Male antennal flagellomeres tricircumfilar. Aedeagus very wide, broadly rounded apically; gonostylus short, wide, with apical tooth as wide as gonostylus. Associated with conifers .... ***Paradiplosis*** Felt
2 spp.; Osgood and Gagné 1978

Male antennal flagellomeres usually bicircumfilar. Aedeagus tapering gradually from base to narrow apex; gonostylus usually attenuate, with narrow tooth 147

147. Wing very wide basally. Female cercus wider than long .... ***Lobopteromyia*** Felt
1 sp., *filicis* (Felt)

Wing not widened basally. Female cercus much longer than wide. Male keyed elsewhere .... ***Prodiplosis*** Felt, in part
6 spp.; Gagné 1973*a*
.... ***Contarinia*** Rondani, in part
see couplet 145

148. Predacious. R_5 usually joining C anterior to or at wing apex. Male hypoproct entire or concave apically, approximately same length as cercal lobe; gonocoxite sometimes with acute mediobasal lobe (Fig. 102), occasionally with one or more apical projections. Ovipositor not protrusible; female cercus large, usually with modified ventral setae (Figs. 119, 120) 149

Mostly phytophagous; some mycophagous. R_5 usually joining C posterior to wing apex (Fig. 32). Male hypoproct bilobate, variously shaped, usually longer than cercal lobe; gonocoxite without apical projections, with mediobasal lobe obtuse if present (Figs. 98, 105, 107). Ovipositor usually somewhat protrusible; female cercus variously shaped (Fig. 129) 160

149. Head with three eyes (due to the absence of dorsolateral ommatidia) (Fig. 4) 150

Eyes normal, not separated dorsolaterally (Figs. 2, 3) 153

150. Abdominal tergites 2–6 with only caudal setae, membranous except for caudal margin. Tooth of gonostylus pectinate .... ***Tropidiplosis*** Gagné
1 sp., *pectinata* Gagné

Abdominal tergites 2–6 with caudal and lateral setae and scales, sclerotized throughout. Tooth of gonostylus entire 151

151. Triangular bilaterally compressed projection with coxcomb margin present between hypoproct and aedeagus (Fig. 110) .... ***Odontodiplosis*** Felt
3 spp.; Gagné 1973*a*

No projection present between hypoproct and aedeagus 152

152. Palpus three-segmented .... ***Adiplosis*** Felt
1 sp., *toxicodendri* (Felt)

Palpus four-segmented .... ***Trisopsis*** Kieffer
4 spp.; Gagné 1973*a*

153. Male flagellomeres bicircumfilar 154

Male flagellomeres tricircumfilar 157

154. R_5 short, not reaching wing apex. Gonocoxite with elongate finger-like unisetose apicoventral extension. Predator of scale insects .... ***Dentifibula*** Felt
1 sp., *viburni* (Felt)

R_5 curved, joining C posterior to wing apex. Gonocoxite without finger-like projection 155

155. Abdominal tergites unsclerotized. Male terminalia very large; gonostylus pointed apically .... ***Thaumadiplosis*** Gagné
1 sp., *magnicauda* Gagné

Abdominal tergites sclerotized. Male terminalia normal sized 156

156. Gonocoxite bare on basal third; tooth of gonostylus pectinate .... ***Pectinodiplosis*** Felt
1 sp., *erratica* (Felt)

Gonocoxite setose throughout; tooth of gonostylus simple (Fig. 102). Internal parasitoid of aphids .... ***Endaphis*** Kieffer
1 undescr. sp.; British Columbia

157. Circumfilum 2 of male flagellomeres band-like, unlooped .... ***Thripsobremia*** Barnes
1 sp., *quercifolia* (Felt)

Circumfilum 2 of male flagellomeres with long loops 158

158. Gonocoxite with long narrow apicoventral projection bearing one apical seta; gonostylus longer than gonocoxite .... ***Epidiplosis*** Felt
1 sp., *sayi* Felt

Gonocoxite without apicoventral projection; gonostylus shorter than gonocoxite 159

159. R_5 very short, weakly sigmoid. Male hypoproct wide, slightly concave apically, approximately as long as aedeagus. Predacious on mites .... ***Arthrocnodax*** Rübsaamen
3 spp.; Gagné 1973*a*

R_5 longer, straight, usually reaching C slightly anterior to wing apex (Fig. 19). Male hypoproct rounded apically, usually much shorter than aedeagus (Fig. 102). Predacious on mites and other arthropods .... ***Lestodiplosis*** Kieffer
47 spp.; Gagné 1973*a*

160. Phytophagous, mostly gall makers. Postvertical peak absent. Gonostylus usually setulose throughout 161

Mainly saprophagous. Postvertical peak present (Fig. 3). Gonostylus setulose only basally 171

161. Tarsal claws shorter than empodia (Fig. 76) 162

Tarsal claws approximately as long as empodia (Fig. 73) 166

162. Palpus one- or two-segmented. Aedeagus much longer than hypoproct. Leaf gall maker on *Pinus edulis* .... ***Pinyonia*** Gagné, in part
see couplet 138

Palpus three- or four-segmented. Aedeagus approximately as long as hypoproct or shorter 163

163. C unbroken at juncture with R_5 (Fig. 35). Tergites 2–6 without lateral setae (Fig. 131) 164

C broken at juncture with R_5 (Fig. 32). Tergites 2–6 with lateral setae (Fig. 129) 165

164. Eye facets rounded. Gonocoxite with median lobe; aedeagus small, narrow, much shorter than hypoproct. Bud gall maker on *Betula* .... ***Apagodiplosis*** Gagné

1 sp., *papyriferae* (Gagné)

Eye facets hexagonoid. Gonocoxite unlobed; aedeagus stout, at least as long as hypoproct .... ***Caryomyia*** Felt, in part

see couplet 135

165. Antennal flagellomeres 1 and 2 fused (Fig. 64). Aedeagus considerably longer than hypoproct. Leaf gall maker on *Prunus* .... ***Putoniella*** Kieffer, in part

1 sp., *marsupialis* (Loew)

Antennal flagellomeres 1 and 2 not fused (Fig. 63). Aedeagus stout, approximately as long as hypoproct (Fig. 98) .... ***Cecidomyia*** Meigen, in part

see couplet 141

166. Palpus one- to three-segmented 167

Palpus four-segmented 169

167. C unbroken at juncture with R_5. Abdominal tergites naked except for caudal and lateral setae .... ***Blaesodiplosis*** Gagné

3 spp.; Gagné 1973*a*

C broken at juncture with R_5. Abdominal tergites with scales 168

168. Basal section of Rs not evident (Fig. 35). Ovipositor protrusible. Leaf gall maker on *Helianthus* .... ***Pilodiplosis*** Gagné, in part

see couplet 143

Basal section of Rs evident (Fig. 32). Ovipositor not protrusible. Leaf gall maker on *Prunus* .... ***Putoniella*** Kieffer, in part

see couplet 165

169. Antenna with 13 flagellomeres; last flagellomere tiny but distinctly separated from penultimate one. Gall maker on *Carex* .... ***Planetella*** Westwood, in part

see couplet 124

Antenna with 12 flagellomeres; last flagellomere not tiny 170

170. Basal section of Rs not evident (Fig. 35). Male hypoproct not surrounding aedeagus, concave apically; gonostylus shorter than gonocoxite. Ovipositor short to elongate, protrusible. Leaf gall maker on *Quercus* .... ***Macrodiplosis*** Kieffer

10 spp.; Gagné 1973*a*

Basal section of Rs strong (Fig. 32). Male hypoproct modified into two orbicular lobes that surround aedeagus; gonostylus longer than gonocoxite. Ovipositor not protrusible. Leaf roller on *Robinia pseudoacacia* .... ***Obolodiplosis*** Felt

1 sp., *robiniae* (Haldeman)

171. Tarsal claws bent at right angle (Fig. 74), dilated beyond the bend 172

Tarsal claws only strongly curved, not dilated beyond mid length (Fig. 73) 174

172. Male antennal flagellomeres bicircumfilar; nodes of female flagellomeres constricted near mid length. Male with portion of C in front of Sc bulging outward. Reared from seeds of Carex .... ***Ametrodiplosis*** Rübsaamen

1 sp., *dulichii* (Felt)

Male flagellomeres tricircumfilar; nodes of female flagellomeres not constricted near mid length. Male with portion of C in front of Sc normal 173

173. Male hypoproct simple, rounded apically, or deeply lobed with lobes long, pointed apically, and splayed .... ***Hyperdiplosis*** Felt

4 spp.; Gagné 1973*a*

Male hypoproct narrow apically, triangularly emarginate .... ***Giardomyia*** Felt

5 spp.; Gagné 1973*a*

174. Hind tarsus greatly enlarged, approximately four times diameter of mid tarsus .... ***Gongrodiplosis*** Gagné

1 sp., *latipes* (Felt)

Tarsi all of same diameter 175

175. Gonocoxite stout; gonostylus bilaterally flattened; aedeagus blackened .... ***Platydiplosis*** Gagné
1 sp., *nigricauda* Gagné

Gonocoxite elongate; gonostylus cylindrical; aedeagus not blackened 176

176. Abdominal tergites 2–6 divided laterally between caudal and lateral setae .... ***Parallelodiplosis*** Rübsaamen, in part
see couplet 125

Abdominal tergites 2–6 entire 177

177. Male antennal flagellomeres trifilar or as in female, uninodal, or binodal; or occasionally, basal ones binodal and distal ones uninodal. Gonocoxite without mediobasal lobe; gonostylus articulated dorsoventrally (Fig. 103). Female keyed elsewhere .... ***Prodiplosis*** Felt, in part
see couplet 147

Male flagellomeres binodal and bifilar. Gonocoxite with obtuse mediobasal lobe; gonostylus articulated mediolaterally (Fig. 100) 178

178. Abdominal tergites sclerotized only apically, without lateral setae and scales. Gonostylus clavate, largest near apex .... ***Cordylodiplosis*** Gagné
1 sp., *molliterga* Gagné

Abdominal tergites sclerotized throughout, with both lateral setae and scales present. Gonostylus largest near base, tapering to apex. Reared from grain of *Triticum aestivum* .... ***Sitodiplosis*** Kieffer
1 sp., *mosellana* (Géhin)

179. Tarsal claws broadly rounded near basal third (Fig. 78); at least fore claw toothed; mid and hind claws usually untoothed; empodia shorter than claws. Antenna with 8–12 flagellomeres, regular in number within species. Mediobasal lobes of gonocoxite usually differentiated into two parts, a basal setulose part and an apical asetose elongate extension (Fig. 114). Female cerci not fused .... LEDOMYINI.... ***Ledomyia*** Kieffer (*sens. lat.*)
16 spp.

Tarsal claws rounded at or beyond mid length (Fig. 77), all either toothed or simple; empodia as long as or longer than claws. Antenna with 7–42 flagellomeres, usually irregular in number within species. Mediobasal lobes of gonocoxite entire, uniformly setulose (Fig. 113) or glabrous. Female cerci usually fused medially into a single terminal lamella (Fig. 123) .... OLIGOTROPHINI.... 180

180. Palpus four-segmented 181

Palpus one- to three-segmented 188

181. Tarsal claws simple 182

Tarsal claws toothed 183

182. R_5 joining C anterior to wing apex. Abdominal tergites 1–7 without lateral setae and with few to no scales .... ***Janetiella*** Kieffer (*sens. lat.*)
8 Nearctic spp.

R_5 joining C at wing apex. Abdominal tergites 1–7 with lateral setae and covered with scales. Reared from beaked-galls on *Salix* and leaf galls on *Celtis* .... ***Mayetiola*** Kieffer (*sens. lat.*), in part
8 spp.

183. Antennal scape three times as long as broad. Eyes not contiguous on vertex. Width of hind femur two times that of mid femur .... ***Trotteria*** Kieffer
2 spp.; Gagné 1969*b*

Antennal scape about as long as broad. Eyes usually contiguous on vertex; hind femur not appreciably wider than mid femur 184

184. R_5 very short, about three-fifths length of wing. Male flagellomeres without necks .... ***Camptoneuromyia*** Felt
6 spp.; Felt 1918

R_5 longer, usually four-fifths length of wing or more. Male flagellomeres with distinct necks 185

185. Tarsal claws with tiny teeth (Fig. 79). Reared from Gramineae, Cyperaceae, or Juncaceae.... 186

Tarsal claws with large teeth (Fig. 77) 187

186. Lobes of male hypoproct acute; tooth of gonostylus wide and blunt. Distal half of female ovipositor bilaterally flattened, sclerotized .... ***Procystiphora*** Felt
2 spp.; Gagné 1975*b*

Lobes of male hypoproct rounded; tooth of gonostylus narrow and pointed. Ovipositor cylindrical, soft .... ***Mayetiola*** Kieffer (*sens. str.*), in part
2 spp.; Gagné 1975*b*

187. R_5 as long as wing, joining C at wing apex. Usually gall maker on twigs and buds of Salicaceae .... ***Rhabdophaga*** Westwood
38 spp.; Felt 1915*a*

R_5 shorter than wing, joining C anterior to wing apex. Usually free-living in flowers or leaf-rollers of various plants .... ***Dasineura*** Rondani
95 spp.; Felt 1915*a*

188. Mediobasal lobe of gonostylus glabrous, elongate, narrow, nearly uniformly wide throughout length. Ovipositor sword-shaped, cultrate, or otherwise modified for piercing 189

Mediobasal lobes of gonostylus setulose, narrowing gradually from wide base to narrow apex. Ovipositor soft, with cercus rounded apically 191

189. Antenna with 18–20 flagellomeres. Male cercal lobes scarcely divided apically; hypoproct deeply bifid. Ovipositor elongate, bilaterally flattened. Reared from twig galls of *Salix* .... ***Lygocecis*** Gagné
2 spp.; Gagné 1975*b*

Antenna with 10–12 flagellomeres. Male cercal lobes deeply divided; hypoproct weakly concave. Ovipositor short, cultrate or cylindrical, abruptly tapered apically. Reared from leaf galls .190

190. Mediobasal lobe of gonocoxite long, thin, glabrous. Female tergites 7 and 8 barely differentiated from surrounding membranous area; ovipositor short, cultrate. Reared from leaf galls on *Viburnum* .... ***Sackenomyia*** Felt
3 spp.; Gagné 1975*b*

Female tergites 7 and 8 well-defined; ovipositor cylindrical, abruptly tapered apically. Reared from galls on Cichoreae (Compositae) .... ***Cystiphora*** Kieffer, in part
1 sp., *canadensis* Felt

191. Palpus one- or two-segmented 192

Palpus three-segmented 195

192. Antenna with 32–42 flagellomeres. Eye very large, with facets hexagonoid. Gonocoxite with apicoventral lobe .... ***Ficiomyia*** Felt
2 spp.; Florida; Felt 1934

Antenna with 23 or fewer flagellomeres. Eye smaller, with facets rounded. Gonocoxite without apicoventral lobe 193

193. Tarsal claws much shorter than empodia. Aedeagus somewhat recurved dorsally. Ovipositor partially sclerotized or female cercus bifurcate, or both. Reared from bud galls on *Juniperus* and *Cupressus* .... ***Walshomyia*** Felt
5 spp.; Gagné 1969*a*

Tarsal claws and empodia approximately same length. Aedeagus short, straight. Ovipositor soft, with cercus entire. Most species reared from galls on Compositae .... ***Rhopalomyia*** Rübsaamen 194

194. Abdominal tergites with lateral setae. Tarsal claws simple. Reared from galls on various plants, chiefly Compositae .... ***Rhopalomyia*** (***Rhopalomyia*** Rübsaamen)
56 spp.; Felt 1915*b*

Abdominal tergites without lateral setae. Tarsal claws toothed or simple. Reared from galls on *Artemisia* and *Chrysanthemum* .... ***Rhopalomyia*** (***Diarthronomyia*** Felt)
30 spp.; Jones *et al.*, in preparation

195. Claws toothed. Reared from leaf galls on Cichoreae (Compositae) .... ***Cystiphora*** Kieffer, in part
see couplet 190

Claws simple 196

196. Tarsal claws approximately as long as empodia. Reared from leaf galls on *Salix*............ ***Iteomyia*** Kieffer
1 sp., *salicifolia* (Felt)

Tarsal claws much shorter than empodia............ 197

197. Palpus with spiniform setae. Aedeagus dorsally recurved, much longer than parameres. Female cerci separate. Reared from bud galls on *Juniperus*............ ***Oligotrophus*** Latreille
1 sp., *betheli* Felt

Palpus without spiniform setae. Aedeagus not recurved, not appreciably longer than parameres. Female cerci fused into a single lamella............ ***Semudobia*** Kieffer
5 spp.; Roskam 1977

198. Male cercal lobe pointed, asetose; gonocoxite with apicoventral lobe............ ***Epimyia*** Felt
1 sp., *carolina* Felt

Male cercal lobe rounded, setose; gonocoxite without apicoventral lobe...... ***Brachyneura*** Rondani
3 spp.; Felt 1908

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PSYCHODIDAE 17

Lawrence W. Quate and J. R. Vockeroth

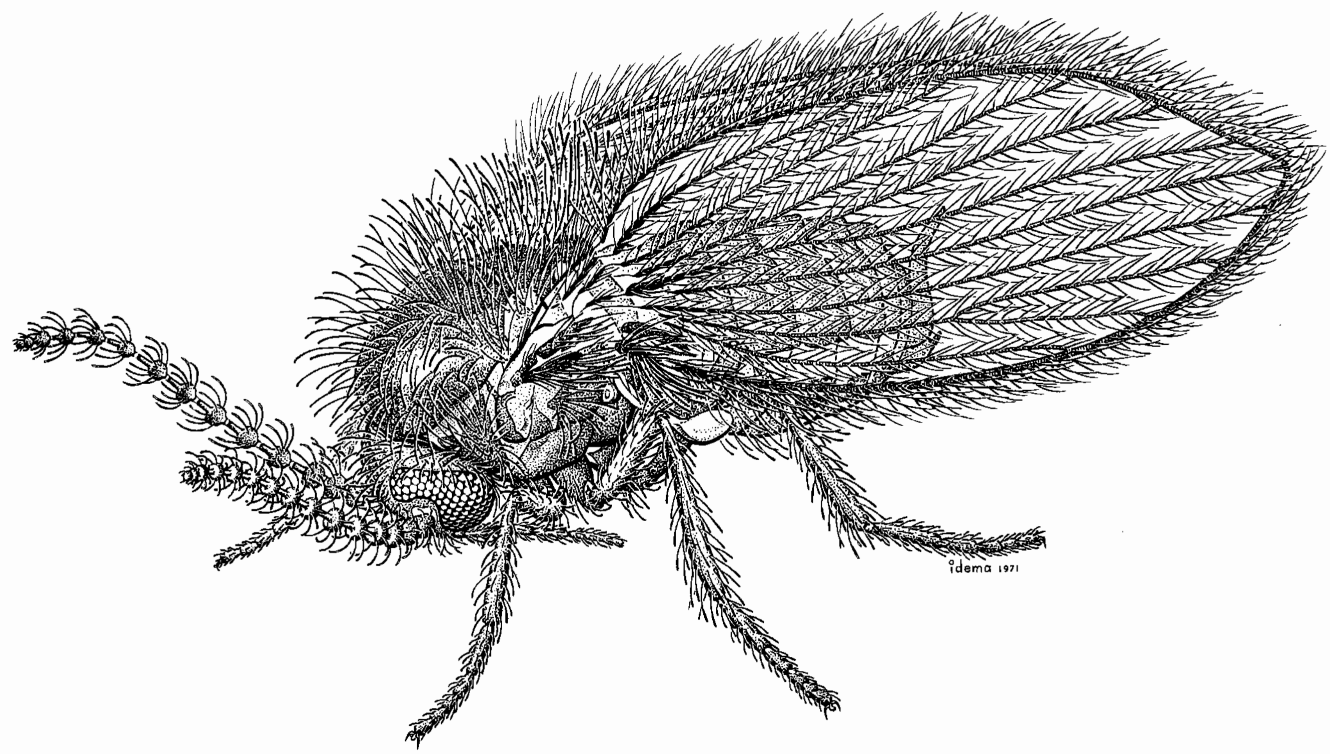


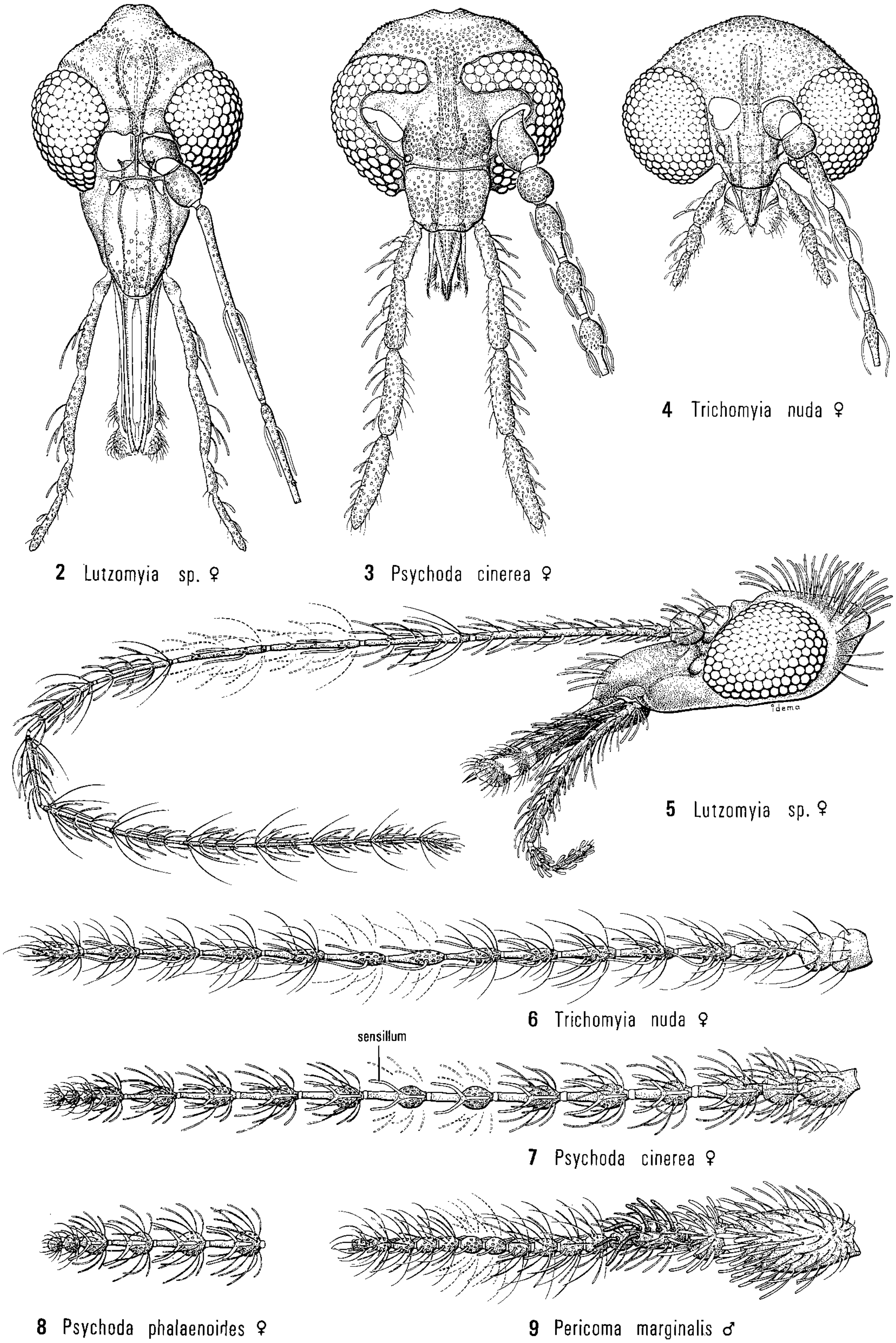
Fig. 17.1. Female of *Psychoda* sp.

Small thickly haired flies (Fig. 1), with characteristic short and erratic flight. Antenna (Figs. 5–9) with 10–14 flagellomeres which are usually pyriform, nodiform, or nearly cylindrical. Wing (Figs. 10–13) usually broad, held roof-like or flat over abdomen at rest; longitudinal veins equally developed; crossveins absent or restricted to basal half of wing; C continuing around wing.

Adult. Head: antenna (Figs. 5–9) longer than head, sometimes longer than body; 10–14 flagellomeres in Nearctic species (up to 111 in one Afrotropical species), usually with dense cupuliform whorls of hairs called verticils, with membranous thin-walled sensilla called ***ascoids*** that may be slender or broad and that may be unbranched or with two to many branches (Fig. 7). Proboscis (Figs. 2–5) usually very short, in bloodsucking species about as long as height of head. Palpus with three to five segments; antepenultimate segment with a sensory pit or a compact group of sensoria. Eye bridge in Psychodinae usually present but often incomplete (Fig. 3), absent in other subfamilies although eyes sometimes closely approximated. Males of some Psychodinae with a sac-like frontal protuberance that is densely covered with hairs or scales, or with a pair of processes (corniculi, scent organs) arising laterally to occipital foramen; each such process consisting of a membranous tubular stalk and an enlarged disciform or globular sclerotized apex (Feuerborn 1922, Hoyt 1950).

Thorax: transverse suture of scutum not V-shaped; metanotum unusually large, projecting into abdomen. Pronotum bare or haired; postnotum bare; pleural sclerites variously haired or bare; in Psychodinae mesopleural sclerites bare except anepisternum and anepimeron.

Male of some Psychodinae with a sac-like organ called a ***patagium*** on cervical membrane above each cervical sclerite; patagium nearly bare or with few to many hairs or scales which may be in compact tufts. Anepisternum of male of some Psychodinae with a glandular area on the surface, or with a protruding organ (tegula of Feuerborn 1922) of varied size and form that may be partly glandular or divided into glandular and nonglandular portions and that may be nearly bare or sparsely or densely covered with hairs and scales. Males of a few species with both prothoracic and mesothoracic organs (see Feuerborn 1922 for illustrations and discussion).



Figs. 17.2–9. Details of heads: head of (2) *Lutzomyia* sp., (3) *Psychoda cinerea* Banks, (4) *Trichomyia nuda* (Dyar), and (5) *Lutzomyia* sp.; antenna of (6) *Trichomyia nuda* and (7) *Psychoda cinerea*; (8) last six flagellomeres of *Psychoda phalaenoides* (Linnaeus); (9) antenna of *Pericoma marginalis* (Banks).

Wing (Figs. 10–13) with anal area reduced, and with longitudinal veins equally sclerotized and often obsolete basally; C broken just beyond base, in Psychodinae with one or two additional breaks; Sc ending free, ending in R_1, or ending in C with crossvein sc-r present; R usually five-branched, four-branched in Trichomyiinae; M three-branched; CuA two-branched; CuA_2 sometimes very short; A_1 sometimes obsolete or nearly so; A_2 absent; crossveins absent or rudimentary except in Trichomyiinae, Bruchomyiinae, and Sycoracinae. Veins densely haired or scaled; membrane with hair-like or scale-like macrotrichia in a few Psychodinae.

Abdomen: sternite 1 sometimes unsclerotized; sternite 2 entire, divided into several areas, or unsclerotized. Tergites 3–7 or tergites 6 and 7 in male of *Nemopalpus* Macquart sometimes with lateral projections bearing dense brushes of anteromedially directed hairs.

Male terminalia (Fig. 18) permanently inverted in all genera except the non-Nearctic *Sycorax* Haliday and *Parasycorax* Duckhouse; inversion beginning with segment 7 in Phlebotominae, with segment 8 in *Nemopalpus*, and with segment 9 in *Trichomyia* Haliday and apparently in Psychodinae. Tergite 9 and sternite 9 in Phlebotominae reduced to a minute ring, or indistinguishable; in other subfamilies tergite 9 large and sternite 9 usually reduced to a very short transverse strip at the base of the gonocoxites but sometimes moderately large; gonocoxites large, sometimes joined medially, each bearing a well-developed gonostylus; gonocoxite and gonostylus widely varying in form and vestiture, and of great taxonomic significance; aedeagus in Phlebotominae consisting of two heavily sclerotized lateral struts between which protrude two slender filaments; in other subfamilies aedeagus entire or deeply divided, sometimes asymmetric; parameres well-developed, varied in form, sometimes projecting well beyond base of aedeagus, sometimes fused medially to form a sheath lying below aedeagus or entirely encircling it (the terms 'above' and 'below' are used here in a descriptive sense referring to the inverted position of structures in the mature male). Epiproct in Phlebotominae elongate, bilobate apically (the lobes probably representing cerci), with a pair of long subcylindrical sclerotized lobes (probably surstyli but called cerci or appendages of tergite 9 by some authors) arising at posterolateral margins of tergite 9; in other subfamilies well-sclerotized surstyli (often called cerci or cercopods) articulated with apex of tergite 9; surstyli varied in form, in Psychodinae with one to more than 20 stiff flattened erect setae called ***tenacula*** (retinacula) on upper side of apical portion; in these subfamilies hypoproct (probably sternite 10) consisting of a variously sclerotized plate lying above apex of tergite 9 and projecting between bases of surstyli and usually a minute median plate lying below apex of upper plate.

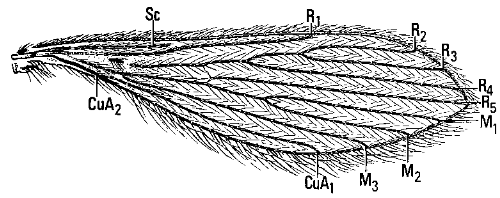
Female with tergite 8 very short to long, fused anterolaterally with anterior corner of sternite 8 (subgenital plate). Sternite 8 long, usually bilobate posteriorly; these lobes sometimes separated from the anterior part of the sternite by a transverse suture; posterior margin of the sternite sometimes infolded to form a sclerotized plate on ventral side of genital chamber. Tergite 9 large to small and weak, in some *Nemopalpus* and in *Trichomyia* apparently fused with tergite 8; lateral margin of tergite 9 usually briefly joined to margin of sternite 9. Sternite 9 lying above sternite 8, in Phlebotominae Y-shaped, in other subfamilies very complex and varied in structure [Genitalnachen of Vaillant (1971–1976), spermathecae plus spermathecal supports of Duckhouse (1966), internal sclerotized plates of Duckhouse (1972)]. Tergite 10 very small and divided, or absent. Sternite 10 very small or absent, when present very slender or V-shaped and lying below bases of cerci; cercus large, usually at least as long as tergites 8 and 9 together, one-segmented, compressed, in Psychodinae slender and tapering to a subacute apex, in other subfamilies broader and bluntly rounded apically. Phlebotominae with two small weakly sclerotized spermathecae of varied form; *Nemopalpus* with one very large spermatheca with a longitudinal membrane-covered slit with fimbriate margins; *Trichomyia* with two unsclerotized sac-like spermathecae with the distal portion of each duct usually strongly sclerotized and annulated; spermathecae not observed in Psychodinae.

Egg. Elongate, rounded at ends, cream to black in color, surface with reticulate or striate sculpturing.

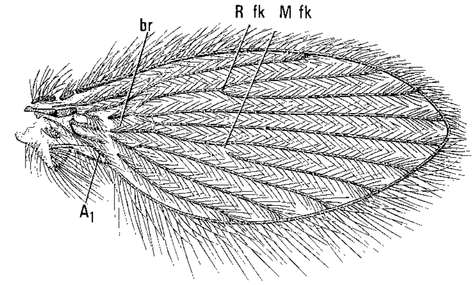
Larva. Head strongly sclerotized, nonretractile in Nearctic species. Mouthparts well-developed; mandible one-segmented and pharynx without filter apparatus in Bruchomyiinae, Phlebotominae, and Trichomyiinae; mandible two-segmented and pharynx with filter apparatus in Psychodinae. Antenna in Nearctic species very short, with at most three segments. Respiratory system amphipneustic; anterior spiracles each on a small tubercle; posterior spiracles on sides of abdominal segment 8 in Bruchomyiinae, Phlebotominae, and Trichomyiinae, and at apex of a respiratory siphon on segment 8 and usually surrounded by four setose lobes in Psychodinae.

General habitus differing widely among subfamilies. In Phlebotominae (Fig. 16) body elongate, cylindrical; each thoracic segment divided into two annuli; each of the first seven abdominal segments divided into three annuli. Some setae of head simple; at least posterior head setae and those of thorax and of abdominal segments 1–7 stout and covered with scales (brush-like setae); setae of segment 8 simple; each half of segment 8 with a tubercle bearing two very long undivided setae; integument smooth. A prominent creeping welt present on each of abdominal segments 1–7; the last welt divided medially. Antenna three-segmented, projecting from head capsule; third segment flattened.

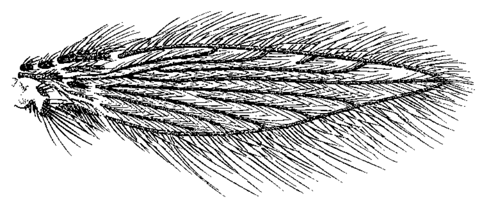
In Bruchomyiinae (only *Bruchomyia* Alexander known) habitus similar to that of *Phlebotomus* Rondani.



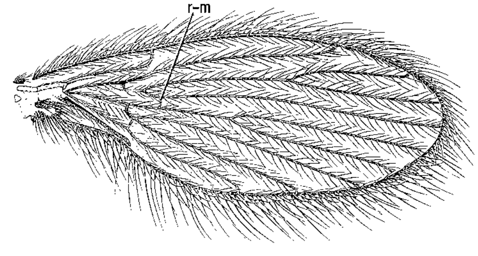
10 Lutzomyia sp. ♀



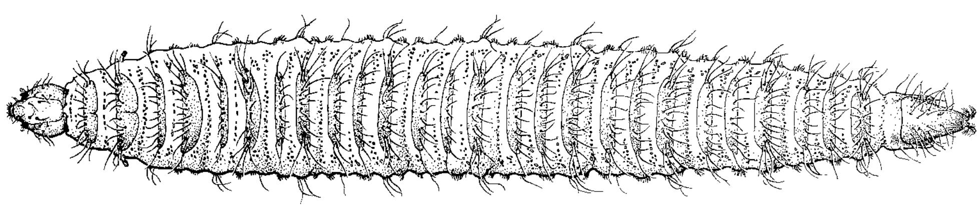
11 Pericoma marginalis ♂



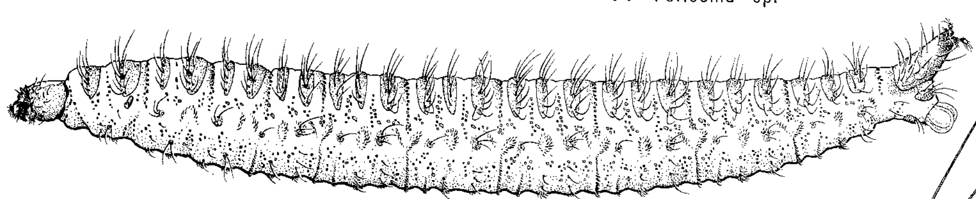
12 Maruina sp. ♂



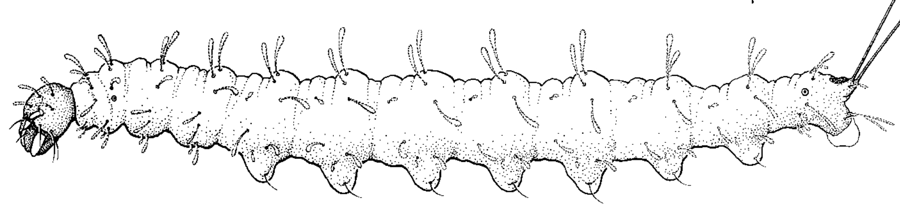
13 Trichomyia nuda ♀



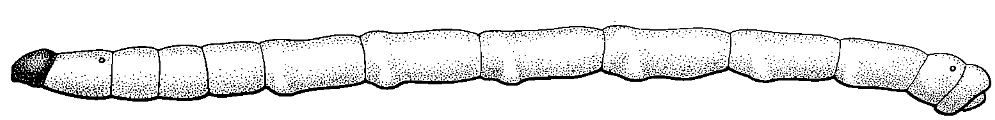
14 Pericoma sp.



15 Pericoma sp.



16 Lutzomyia vexator



17 Trichomyia urbica

Figs. 17.10–17. Wings and larvae: wing of (10) *Lutzomyia* sp., (11) *Pericoma marginalis* (Banks), (12) *Maruina* sp., and (13) *Trichomyia nuda* (Dyar); (14) dorsal view of larva of *Pericoma* sp.; left lateral view of larva of (15) *Pericoma* sp., (16) *Lutzomyia vexator* (Coquillett), and (17) *Trichomyia urbica* Haliday (not Nearctic).

Abbreviation: fk, fork.

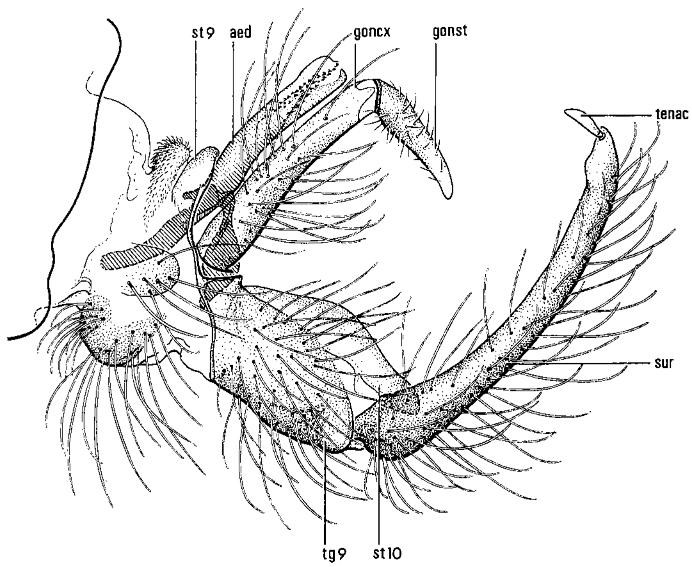


Fig. 17.18. Left lateral view of male terminalia of *Psychoda phalaenoides* (Linnaeus).
Abbreviations: aed, aedeagus; goncx, gonocoxite; gonst, gonostylus; st, sternite; sur, surstylus; tenac, tenaculum; tg, tergite.

Head with only simple setae; thorax and abdominal segments 1–7 with brush-like setae; abdominal segment 8 with two pairs of long setae each divided nearly to its base; most of integument covered with short strong spines. Abdomen without creeping welts. Antenna one-segmented, not projecting from head capsule.

In Trichomyiinae (Fig. 17) body cylindrical, slender; segments not annulated; setae simple and very small; integument finely pilose. Small creeping welts present on abdominal segments 1–7. Antenna one-segmented, projecting.

In Psychodinae (Figs. 14, 15) body usually cylindrical, tapering slightly or strongly posteriorly; thoracic segments and first abdominal segment each divided into two annuli; abdominal segments 2–7 each divided into three annuli; each annulus usually with a broad dorsal sclerotized plate, but plates sometimes reduced by fusion or loss, sometimes present only on abdominal segments 5–7. Setae usually simple, often rather long, on both dorsal plates and membrane; plumose setae present only on lobes of respiratory siphon; dorsal plates with slender to very stout short setae arising from distinct plaques; membrane with minute setae or spinose sclerotized plaques. Creeping welts absent. Antenna small, unsegmented, composed of two or more small rods and setae or a group of sensory processes covered by a domed vesicle. In *Maruina* Müller form broad, convex above, flat below, tapering at both ends; ventral surface with a median row of eight sucking discs, with the first disc positioned on the thorax and the others on abdominal segments 1–7.

In Sycoracinae (widespread but not Nearctic) and Horaiellinae (eastern Asia) habitus similar to that of *Maruina*; most segments with dorsal sclerotized plates but only one or two on each segment. Antenna long, slender. In Sycoracinae most body segments with several prominent lateral lobes fringed with long setae, but lacking a definite ventral sucker. In Horaiellinae segments lacking lateral lobes; ventral surface with a single large sucker over most of its length margined by a membrane formed of very fine agglutinated hairs.

Pupa. Subcylindrical or tapering posteriorly, strongly depressed in *Maruina.* Wing sheaths reaching the middle of the body, slightly beyond ends of leg sheaths; leg sheaths straight toward apices and lying one above another. Abdominal segments with one or more rows of short spines above and below. Anterior spiracular horn usually slender and elongate, in Phlebotominae very short; one pair of functional abdominal spiracles present only in Phlebotominae (from Hennig 1950).

Biology and behavior. Psychodids are widely distributed in many niches, but the immature stages require at least moderate amounts of moisture. Adults are mainly nocturnal and in daytime are found resting in shaded places such as tree or rock crevices, in caves, or under bridges. Most species are found in wooded areas near streams or marshes.

Larvae of Phlebotominae breed in soil, often in semidesert areas. The blood-sucking adults (sand flies) are usually associated with reptiles or small burrowing mammals in North America. However, many tropical species are of major importance as vectors, particularly of leishmaniasis but also of bartonellosis and of viruses; Lewis (1973) gives a useful brief summary. The larva of one species of *Trichomyia* has been found in rotting wood; larvae of one species of *Bruchomyia* have been reared in the same medium. Larvae of Psychodinae live in various habitats, most of them moist or subaquatic; Vaillant (1971–1976, pp. 44–45) gives a classification of larval habitats. A few occupy man-made niches rich in organic matter, such as compost heaps and sewage disposal systems. The larvae of *Maruina* (Psychodinae) and of Sycoracinae and Horaiellinae are associated with fast streams and waterfalls where they live on rocks near the surface or in the splash zone.

Classification and distribution. The monophylety of the Psychodidae is suggested by the following apparently synapomorphic characters: the dense vestiture of hairs or scales on most parts of the body, the presence of ascoids on most or all flagellar segments (unless secondarily lost), the presence of at least one break in C very near its base, the great reduction of the anal area of the wing and of A_1, and the almost universal absence of crossvein m-m (present only in some specimens of one species of *Nemopalpus).* Some recent authors recognize six subfamilies: Phlebotominae, Bruchomyiinae, Psychodinae, Trichomyiinae, Sycoracinae, and Horaiellinae. The last two are not Nearctic, and are often included in the Trichomyiinae. Some authors have treated the Phlebotominae as a separate family; unless it is demonstrated that the Phlebotominae are more closely related to another group than to the rest of the Psychodidae such a treatment serves no good purpose. Hennig (1972) has discussed at length the monophylety of the family and the relationships of its subgroups.

Most authors now consider New World Phlebotominae to be generically distinct from those of the Old World. Martins *et al.* (1978) review the matter; their opinion is followed here and the Nearctic species are referred to *Lutzomyia* França.

A recent, not yet completed treatment of the Palaearctic Psychodinae (Vaillant 1971–1976) recognizes 25 genera compared with nine (plus one subgenus) recognized below. Both Vaillant (1971–1976) and Duckhouse (1966) refer to genera in the Nearctic region which are not recognized here. A reassessment of the generic classification of the Nearctic fauna would be desirable. Vaillant treats both adults and larvae in detail; his work is important to any future student of Nearctic Psychodinae. Satchell (1953) has given a good comparison of the larvae of several subfamilies.

Ninety-one species have been recorded from America north of Mexico. Of these, 77 are Psychodinae; the presence of 76 species of this subfamily in Great Britain suggests that many species await discovery in the Nearctic region. The Nearctic larvae are very poorly known. Keys to Nearctic species were given by Quate (1955, 1960); only two later references are given in the key below.

The family is nearly world wide and both the Psychodinae and Trichomyiinae occur on oceanic islands, Hawaii for example. In the Nearctic region the largest subfamily, the Psychodinae, occurs from the treeline southward. The other subfamilies are predominantly tropical to warm temperate in distribution. Only one subfamily, the Horaiellinae with a few species in eastern Asia, has a restricted distribution.

The oldest fossils definitely referable to the Psychodidae are two species of Phlebotominae from Lower Cretaceous amber from Lebanon. An undescribed species, almost certainly of the genus *Sycorax*, is known from Upper Cretaceous amber from Canada. Species of Bruchomyiinae, Phlebotominae, Trichomyiinae, and Psychodinae are known from Baltic amber (probably upper Eocene). Quate (1961, 1963) has described 12 species from Miocene amber from Mexico; they are referred to *Phlebotomus* Rondani, *Trichomyia* Haliday, *Telmatoscopus* Eaton, *Brunettia* Annandale, *Philosepedon* Eaton, and *Psychoda* Latreille. These fossil species differ only slightly from contemporary ones and indicate that most, if not all, of the higher taxa were well differentiated by the middle Tertiary. Hennig (1972) gives an extensive review of fossil Psychodidae.

Key to genera

Adult

1. Eyes without eye bridge, although eyes sometimes closely approximated above (Figs. 2, 4). Flagellomeres of antenna pyriform or subcylindrical (Figs. 5, 6) 2

   Eyes with eye bridge complete or incomplete (Fig. 3). Flagellomeres strongly nodiform or fusiform (Figs. 7–9) .... PSYCHODINAE 4

2. Rs three-branched; only one longitudinal vein between radial and medial forks (Fig. 13) .... TRICHOMYIINAE .... ***Trichomyia*** Haliday

   3 spp.; widespread

   Rs four-branched; two longitudinal veins present between radial and medial forks (Fig. 10) 3

3. Mouthparts much longer than height of head (Fig. 2). A_1 absent (Fig. 10) .... PHLEBOTOMINAE .... ***Lutzomyia*** França

   9 spp.; widespread

Mouthparts shorter than height of head. A_1 short but distinct .... BRUCHOMYIINAE.... ***Nemopalpus*** Macquart
1 sp., *nearcticus* Young; Florida

4. Wing broad or moderately so, at most three times as long as wide (Fig. 11) 5
Wing very narrow, lanceolate, more than three times as long as wide, with apex acute (Fig. 12) .. .. ***Maruina*** Müller
3 spp.; western U.S.A.; Vaillant 1963, Hogue 1973

5. Flagellomeres nodiform, with basal part globular or spherical and distal part a slender internode; flagellar verticils cupuliform; antenna longer than width of wing (Fig. 7). R_5 ending in wing apex 6
Flagellomeres fusiform or barrel-shaped; flagellar verticils sparse; antenna shorter than width of wing (Fig. 9). R_5 usually ending beyond wing apex (Fig. 11) 13

6. Terminal flagellomeres not reduced in size, subequal to or larger than preceding segments (as in Fig. 9). Species often brightly colored 7
One, two, or three of the terminal flagellomeres reduced in size, about half size of preceding segments (Figs. 7, 8). Species usually uniformly gray or yellowish gray 8

7. Rs not pectinate (as in Fig. 11); wing generally of moderate width, about 2.5 times as long as wide; membrane without scales. Antennal sensilla variable, but seldom consisting of a single anterior branch. Tenacula of male surstylus not clavate or racket-shaped .... ***Telmatoscopus*** Eaton
17 spp.; widespread
Rs pectinate, i.e. R_3 and R_4 branching separately from Rs; wing broad; membrane sometimes covered with scales. Antennal sensilla consisting of a single anterior branch. Tenacula of male surstylus clavate or racket-shaped .... ***Brunettia*** Annandale
2 spp.; eastern

8. Wing vestiture on membrane as well as veins 9
Wing vestiture confined to veins 10

9. R_3 and M_2 absent at bases, thus radial and medial forks incomplete........ ***Trichopsychoda*** Tonnoir
1 sp., *insulicola* (Quate); southeastern
Radial and medial forks complete, or only one incomplete................. ***Philosepedon*** Eaton, in part
5 spp.; widespread

10. Antennal sensilla rod-like or U-shaped 11
Antennal sensilla Y- or trident-shaped (Fig. 7)...12

11. Antennal sensilla rod-like .... ***Threticus*** Eaton
2 spp.; eastern
Antennal sensilla U-shaped, with pair of broad leaf-like elements .... ***Eurygarka*** Quate
1 sp., *helicis* (Dyar); southeastern

12. Labella bulbous. Flagellum always with 14 flagellomeres .... ***Philosepedon*** Eaton, in part
see couplet 9
Labella flattened. Flagellum with 12, 13, or 14 flagellomeres .... ***Psychoda*** Latreille
21 spp.; widespread

13. Scape longer than pedicel. Radial fork on same level as medial fork or only slightly distal to it (Fig. 11).. ***Pericoma*** Walker....14
Scape shorter than pedicel. Radial fork distal to medial fork by distance equal to one-fifth wing length .... ***Breviscapus*** Quate
1 sp., *trilobus* (Kincaid); western U.S.A.

14. First flagellomere of male unmodified or with a row or cluster of bristles, without wavy tuft of long hairs (Fig. 9). Cell br short (Fig. 11) or elongate............... ***Pericoma*** (***Pericoma*** Walker)
23 spp.; widespread
First flagellomere of male with a tuft of long wavy hairs. Cell br elongate, with distance between base of R_{2+3} and base of R_5 at least twice width of cell br .... ***Pericoma*** (***Clytocerus*** Eaton)
1 sp., *americana* Kincaid; widespread

Key to subfamilies

Larva

1. Abdomen not terminating in tubular siphon; posterior spiracles on sides of abdominal segment 8 (Figs. 16, 17) 2
   Abdomen terminating in tubular siphon with a pair of fan-like brushes at apex; posterior spiracles close together at apex of siphon (Figs. 14, 15) .... **Psychodinae**
2. No conspicuous body setae, those present simple (Fig. 17) .... **Trichomyiinae**
   Many conspicuous body setae, most of them brush-like 3
3. Head with some brush-like setae. Each side of tergite 8 with two very long undivided setae (Fig. 16) .... **Phlebotominae**
   Head with only simple setae. Each side of tergite 8 with two long divided setae (*Bruchomyia* only; *Nemopalpus* unknown) .... **Bruchomyiinae**

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TRICHOCERIDAE 18

C. P. ALEXANDER

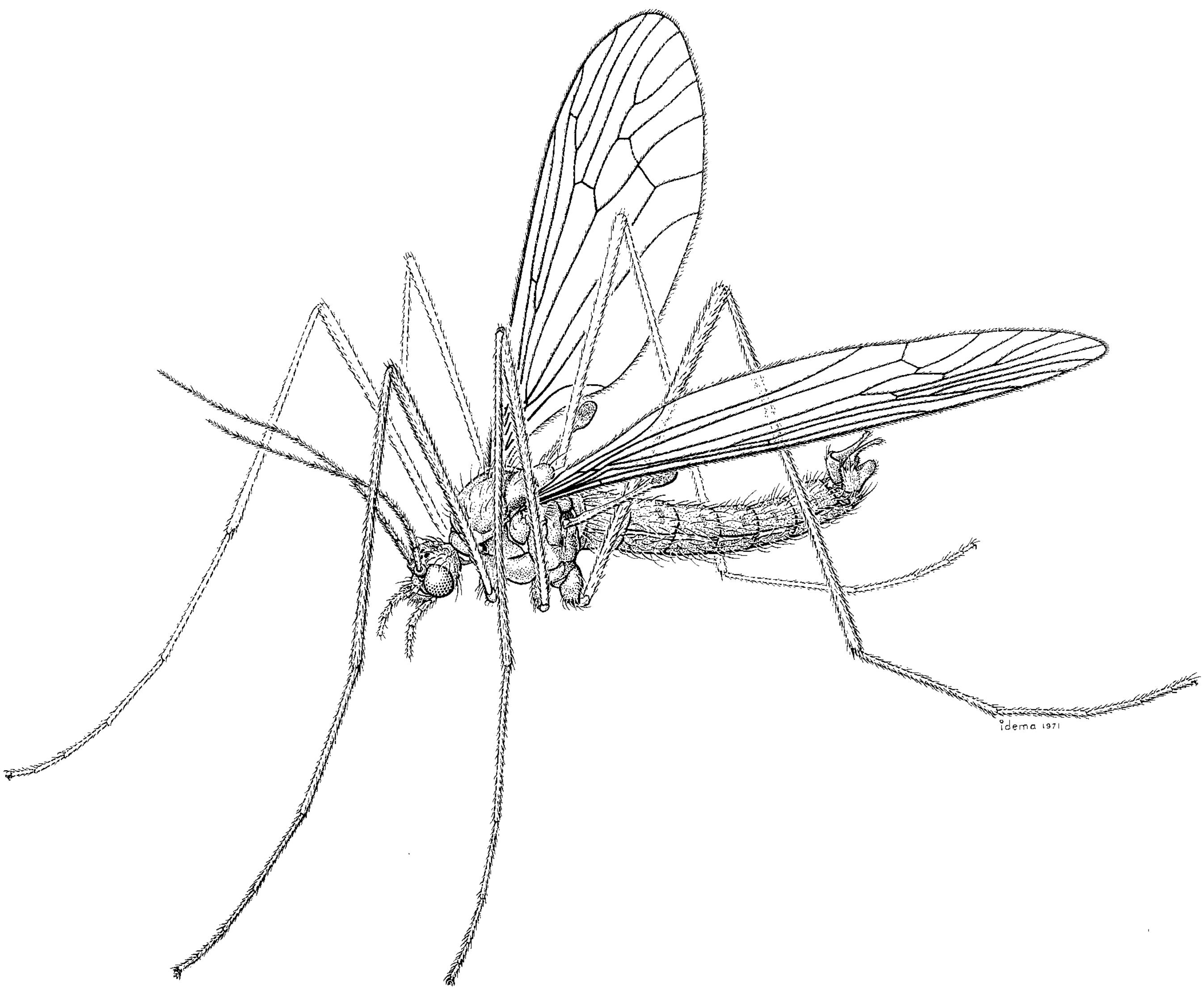


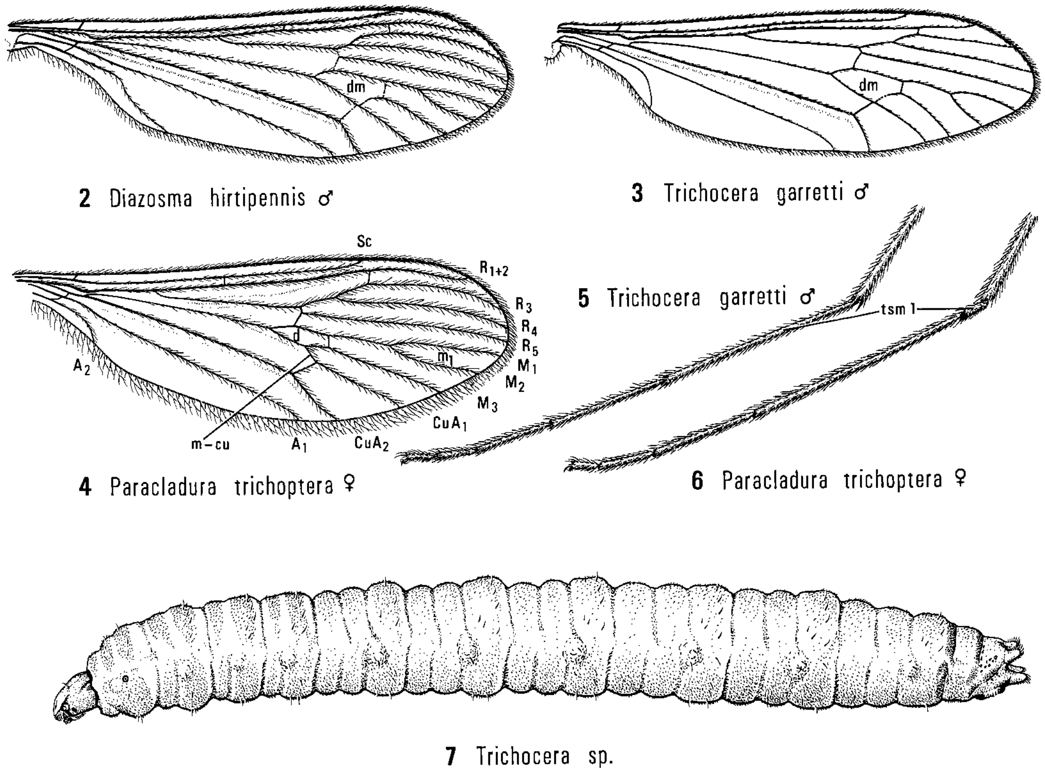
Fig. 18.1. Male of *Trichocera garretti* Alexander.

Small to medium-sized slender flies, with long slender legs (Fig. 1); wing to 10 mm in *Trichocera gigantea* Dahl.

Adult. Head: labrum reduced. Three ocelli present. Flagellum 16-segmented, elongate, setaceous, with segmentation of distal segments obscure.

Thorax: scutum flat, with a V-shaped suture, not separated from scutellum by a suture. Legs long and slender, but not falling off readily as in Tipulidae; tibial spurs present or absent; first tarsomere elongate (Fig. 5) except in *Paracladura* Brunetti (Fig. 6). Wing (Figs. 2–4) with Sc long; M_2 always present; cell m_1 petiolate in the Trichocerinae; crossvein m-cu or basal section of CuA_1 meeting cell dm in its distal half; A_2 short and curved in *Trichocera* Meigen (Fig. 3) and *Paracladura* (Fig. 4), more extended in *Diazosma* Bergroth (Fig. 2); MA (arculus) nearly lost by atrophy, shortened by a caudal bend of R; calypter with setal fringes.

Abdomen: gonostylus of male terminalia (Figs. 2.113–115) single, usually simple and cylindrical, and in *Trichocera* (*Metatrichocera* Dahl) complicated by basal



Figs. 18.2–7. Wings, fore tarsi, and larva: wing of (2) *Diazosma hirtipennis* (Siebke), (3) *Trichocera garretti* Alexander, and (4) *Paracladura trichoptera* (Osten Sacken); fore tarsus of (5) *Trichocera garretti* and (6) *Paracladura trichoptera*; (7) larva of *Trichocera* sp.
Abbreviation: tsm, tarsomere.

tubercles or processes. Female ovipositor (Figs. 2.80–82) with cerci sclerotized or fleshy; when cercus elongate, curved downward, not bent upward as normal for Tipulidae.

Larva. Cylindrical, soft-bodied, amphipneustic, with a well-developed fully exposed head capsule and 11 body segments; each segment secondarily divided, with the terminal segment ending in four lobes (Fig. 7).

Head capsule convex dorsally, completely encircling occipital opening, tapering anteriorly to a laterally compressed conical labrum. Short papilla-like antenna and small eyespot present on each side of labrum above base of mandibles. Mandible bipartite, moving in an oblique downward direction, with a stout base and apical toothed portion having associated tufts of hairs; maxilla oblong and fleshy, comprising two parts, the maxilla proper and a dorsolateral fleshy palpal lobe having a round apical sensory area; small fleshy lobe-like labrum present between maxillae ventrally.

Thoracic segment and the first and terminal abdominal segments with two secondary annular divisions; the remaining abdominal segments each with three divisions. Integument covered with fine pubescence among which project longer systematically placed hairs. Anterior and posterior spiracles similar in that spiracular openings encircle a central ecdysial scar; posterior spiracles situated at base of upper two of four terminal lobes; these lobes moderately sclerotized on median face and fringed with short fine setae. Anus opening in a longitudinal slit on a well-defined round anal pad.

Pupa. Obtect. Head small; antennal sheaths close together at base, curving posteriorly to slightly surpass wing bases.

Pronotum narrow, lenticular; mesonotum about one-fifth length of body; metanotum divided into two units. Thoracic respiratory horn short, club-shaped, with spiracle linear on posterior apical third of horn. Wing and leg sheaths reaching to abdominal segment 3; leg sheaths superposed. Eight abdominal segments visible; all but the terminal segment fringed posteriorly by a closely grouped row of short small spines; segments 1–6 secondarily divided into three annular units each and segment 7 into two units. Abdominal spiracles small, situated laterally on middle subdivision of segments 1–6, bordered posteriorly by two or three small spines. Pairs of spine-tipped conical tubercles dorsally and posteriorly on terminal abdominal segment; in male both pairs of tubercles short and of about equal length; additional blunt anal tubercles prominent ventrally in male; in female posterior tubercles lengthened to about four times that of dorsal ones and distinctly annulated; anal tubercles very small in female.

Biology and behavior. The family includes the familiar winter crane flies, so named from their occurrence during the colder spring and fall months. They are common especially on sunny days in swarms of primarily male flies. The adults often occur in caverns, mine shafts, cellars, hollow trees, and similar darkened places. The early stages are scavengers found in a variety of habitats, especially in decaying leaves and vegetables, manure, fungi, stored roots and tubers, burrows of rodents, and other comparable materials.

Detailed accounts of the habits of adults and early stages can be found in Alexander (1920), Brindle (1962), Dahl (1966, 1967*a*, 1967*b*, 1970*a*, 1970*b*), Karandikar (1931), Keilin (1912), Keilin and Tate (1940), Laurence (1956), and Rhynehart (1925).

Classification and distribution. All known members of the family belong to the subfamily Trichocerinae with the exception of the remarkably distinct *Kawasemyia* Alexander from Japan (Alexander 1969). Females of this genus are nearly apterous, the wings of the male are very reduced, and the wing venation is entirely different from that of all other Trichoceridae. The Trichoceridae as known at present includes about 100 species. More than 65 are in the genus *Trichocera* and are chiefly Holarctic in distribution. A few species have been widely transported, however, presumably by commerce. Some have been found even in remote parts of the southern hemisphere. *Trichocera regelationis* (Linnaeus) was recorded on the island of South Georgia in the south Atlantic by Dahl (1970*b*), and Alexander (1969) recorded *Trichocera maculipennis* Meigen on Kerguelen Island in the Indian Ocean. The genus *Paracladura* has approximately 25 species; several occur in Asia and New Zealand, a few are found in extreme southern South America, and a single species is found in western North America. A third Nearctic genus is *Diazosma*, which is represented by a single Holarctic species. The remaining genus in the family is *Nothotrichocera* Alexander; at present five species are known to occur in southeastern Australia and one other is found in the subantarctic islands of New Zealand. The proposed genus *Metatrichocera* Dahl (Dahl 1966) is considered here to be a subgenus of *Trichocera*. Nearctic species referred to here include *alexanderi* (Dahl) (Dahl 1976*a*), *colei* Alexander, *garretti* Alexander, *salmani* Alexander, *ursamajor* Alexander, and *mackenzie* (Dahl) (Dahl 1967*a*). Dahl and Alexander (1976) have recently reviewed the Trichoceridae and provided an updated catalog of this family with synonomies.

Two fossil species of Trichoceridae are known, both from Baltic amber (Dahl 1971).

Key to genera

1. Tarsi with first tarsomere very short, about one-eighth as long as the second (Fig. 6). Wing with crossvein m-cu present (Fig. 4) .... ***Paracladura*** Brunetti
   1 sp., *trichoptera* (Osten Sacken); western North America

   Tarsi with first tarsomere longer than the second (Fig. 5). Wing with crossvein m-cu absent 2

2. A_2 subsinuous, not curved evenly into margin of wing (Fig. 2). Eye glabrous. Tibial spurs lacking. Ovipositor with cerci short–oval and fleshy .... ***Diazosma*** Bergroth
   1 sp., *hirtipennis* (Siebke); transcontinental

   A_2 short, curved evenly to margin of wing (Fig. 3). Eye with hairs between ommatidia. Tibial spurs present. Ovipositor with downward-curved elongate sclerotized cerci (Figs. 2.81–82) .... ***Trichocera*** Meigen
   27 spp.; widespread; Alexander 1966 and 1967, Dahl 1967*a*

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ANISOPODIDAE 19

B. V. PETERSON

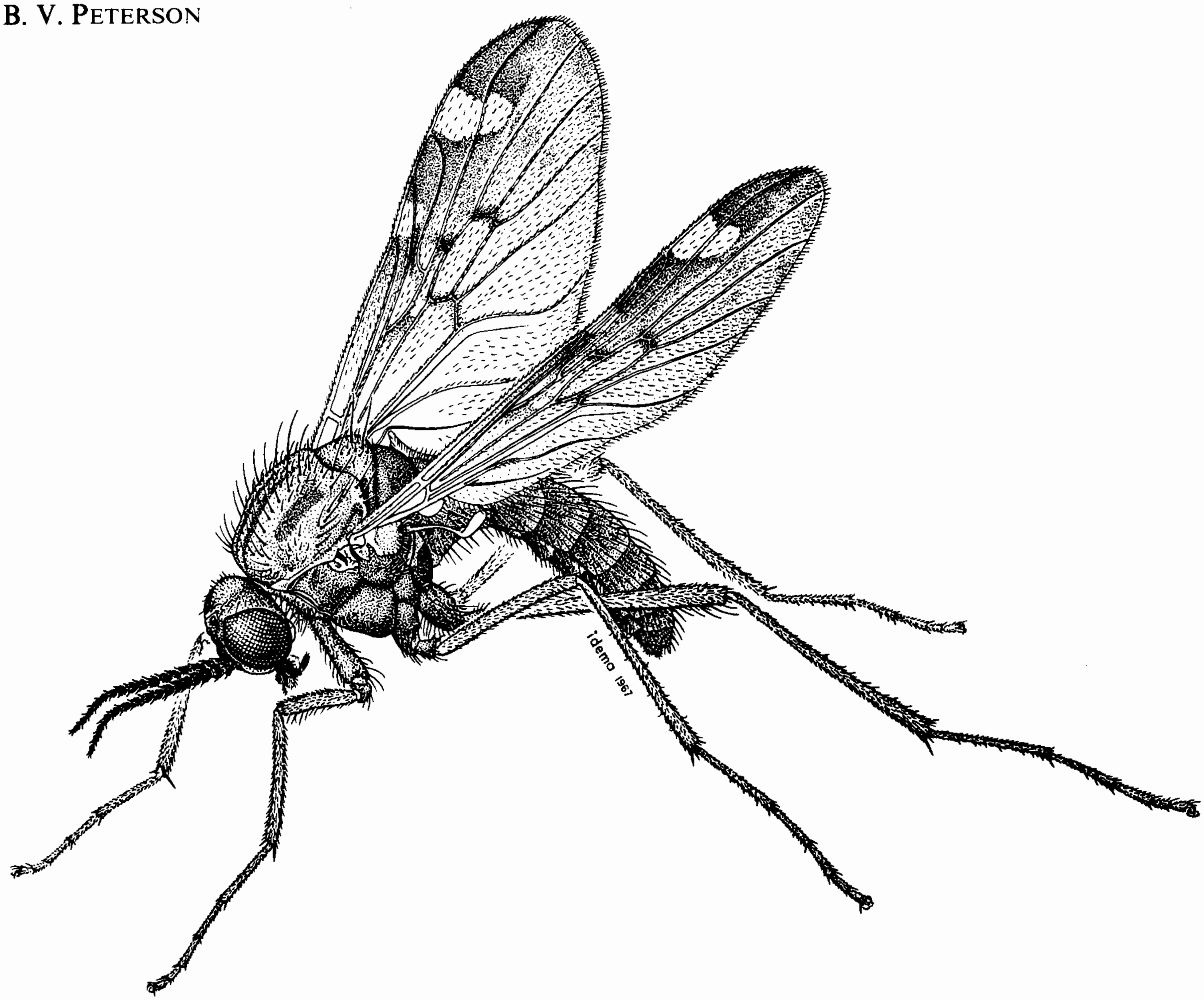
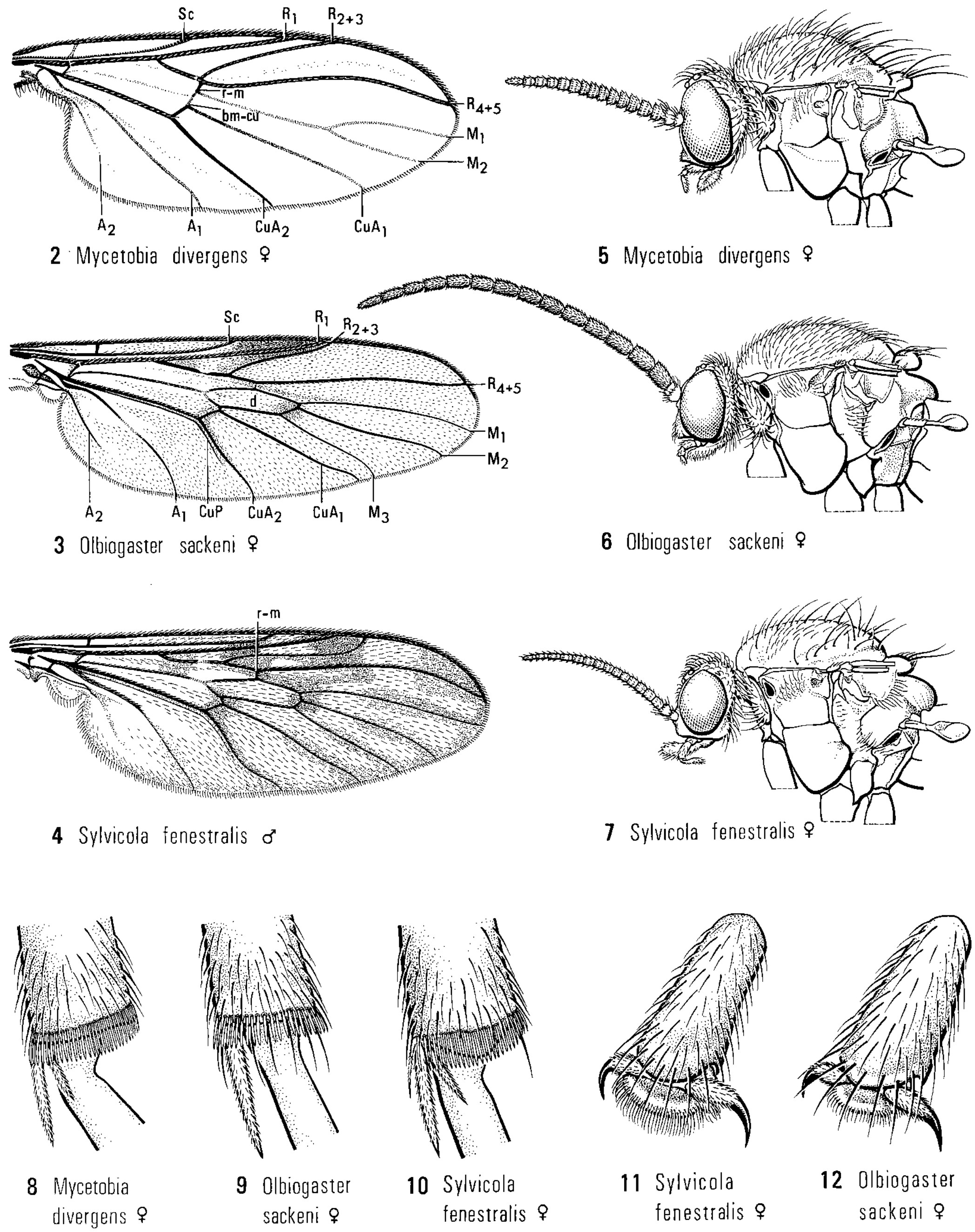


Fig. 19.1. Female of *Sylvicola alternatus* (Say).

Small to medium-sized flies (Fig. 1), 2.0–10.0 mm long with some Neotropical species as much as 18.0 mm long. Body slender and elongate, with long slender legs. Head with three ocelli and moderately long antennae.

Adult. Head: small, rounded, usually somewhat flattened or, at least, not noticeably produced posteriorly (Figs. 5–7). Eyes moderately large, rounded to ovoid, bare or hairy, holoptic or dichoptic in male; three ocelli situated closely together in a nearly equilateral triangle. Frons short, varying from distinctly narrower to slightly wider than face, glabrous or with a few short fine setae. Antenna about as long as head and thorax combined (Figs. 5–7); scape and pedicel short; flagellum composed of 14 uniformly cylindrical flagellomeres. Face not separated by frontoclypeal suture, slightly convex to distinctly swollen, with a few short fine setae or bare (Fig. 2.48). Labrum reduced, membranous; mandible absent in both sexes; hypopharynx free; lacinia of maxilla well-developed but not dentate; palpus rather short, three- or four-segmented, with basal segment in three-segmented forms or second segment in four-segmented forms having a sensory vesicle that opens externally by an apical pore.

Thorax: convex (Figs. 5–7). Pronotum greatly reduced, usually evident as a pair of lateral lobes; postpronotal lobe small. No distinct transverse suture separating presutural and postsutural regions of scutum; scutellum small, somewhat semicircular. Postnotum well-developed. Pleural sutures distinct especially between anepisternum and katepisternum, with a small pit at junction of latter sclerites with anepimeron. Chaetotaxy: scutum setose, with setae varying in stoutness, length, and density among genera; bristles of scutum sparse and weak, with some genera having zero or one postpronotal bristle, zero to two notopleural bristles, zero to seven intra-alar bristles, one to ten dorsocentral bristles, and zero to five postalar bristles; scutellum bare or setose, with zero to four fine bristles; postnotum often setose; proepisternum usually setose; sclerites of lateral portion of thorax variously bare or setose.



Figs. 19.2–12. Wings, thoraces, and legs: wing of (2) *Mycetobia divergens* Walker, (3) *Olbiogaster sackeni* Edwards, and (4) *Sylvicola fenestralis* (Scopoli); lateral view of thorax of (5) *Mycetobia divergens*, (6) *Olbiogaster sackeni*, and (7) *Sylvicola fenestralis*; apical comb of bristles on inside of hind tibia of (8) *Mycetobia divergens*, (9) *Olbiogaster sackeni*, and (10) *Sylvicola fenestralis*; apical tarsomere showing claws and empodium of (11) *Sylvicola fenestralis* and (12) *Olbiogaster sackeni*.

Legs long and slender, without strong spines. Fore coxa long; mid and hind coxae short or long. Fore tibia usually with one apical spur; mid and hind tibiae (Figs. 8–10) usually with two apical spurs, with fine pubescence on all spurs. Claws of all legs small, uniform, and simple; pulvilli absent; empodia pad-like, small or large, always hairy (Figs. 11, 12).

Wing (Figs. 2–4) moderately large and broad, both lying flat over abdomen in resting position; anal lobe well-developed; alula strongly differentiated in *Olbiogaster* Osten Sacken and *Sylvicola* Harris. Membrane hyaline or with pattern of dark markings; pterostigma present or absent; membrane densely covered with microtrichia; macrotrichia present in *Sylvicola*. C ending at or slightly beyond tip of R_{4+5}; Sc ending in C at about middle of wing and distal to base of Rs; stem of R straight but sometimes with a minute interruption or weakening below crossvein h; Rs arising near but proximal to middle of wing, with two branches; R_{4+5} long, ending near tip of wing; crossvein r-m situated near or distal to fork of Rs; M with two or three branches; cell d present or absent; CuA_2 straight or sinuous distally; CuA_1, CuA_2, and A_1 reaching wing margin; CuP when present variably distinct; A_2 present but evanescent apically. Calypter fringed with fine hairs. Halter moderately large.

Abdomen: elongate and cylindrical, slightly convex dorsally, more flattened ventrally, with eight pregenital segments. Segment 1 long, with a pair of variably sized tubercles or prominences at base dorsolaterally. Segment 8 small.

Female terminalia as in Figs. 13 and 15; cercus free and well-developed, rather short in *Sylvicola* and *Mycetobia* Meigen, but often very large in *Olbiogaster*. Tergite 9 reduced, sclerotized laterally, connected ventrally with sternite 9, the genital fork. Sternite 8 subquadrate; hypogynial valves (ovipositor lobes) varying from very short and weakly separated to long, distinct, and well-separated. Sternite 9, or genital fork, somewhat Y-shaped, moderately sclerotized, with arms of fork connecting dorsolaterally to lateral portions of tergite 9; spermathecal openings situated between arms of genital fork; one to three spermathecae present, small, heavily sclerotized. Hypoproct lying posteroventral to cerci, conical or triangular, sometimes notched apically.

Male terminalia (Figs. 14, 16–18) complex, varying from small and more or less retracted to large and exserted, exhibiting up to 180° of rotation. Tergite 10 sometimes sclerotized, with a variably developed rod-like or setose flap-like surstylus; sternite 10 often membranous and delineated by a row or patch of setae, but sometimes sclerotized plate-like or with two small sclerotized tubercle-like or elongate rod-like processes; hypoproct lying posteroventral to cerci, fleshy but well-developed, somewhat conical, usually notched apically. Tergite 9 reduced, not sclerotized; gonocoxites relatively large, sometimes fused medially forming a capsule-like structure; a variably developed aedeagal guide present ventromedially between gonocoxites; gonostylus usually well-developed but variable in size and shape, except rudimentary or absent in *Mycetobia*; aedeagus simple to complex in structure; aedeagal apodeme small; parameres varying from two small rod-like processes to a heavily sclerotized sheath-like and often very complex structure.

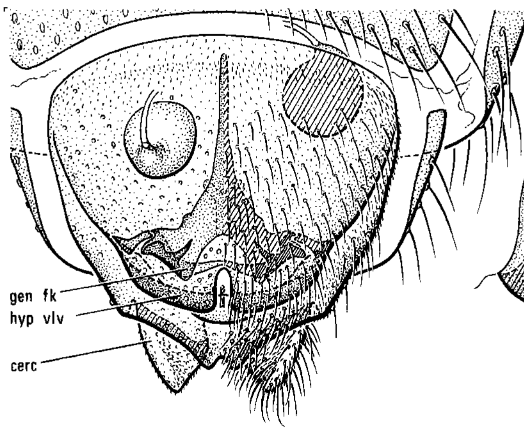
Egg. Small, pear-shaped, surrounded by a gelatinous substance when laid.

Larva. Slender, fusiform, white to yellowish orange, often with dark markings, and varying from about 10–16 mm in length with large Neotropical species somewhat longer. Respiratory system amphipneustic. Head distinct; three thoracic segments; eight abdominal segments; cuticle glabrous, without setae (Fig. 19).

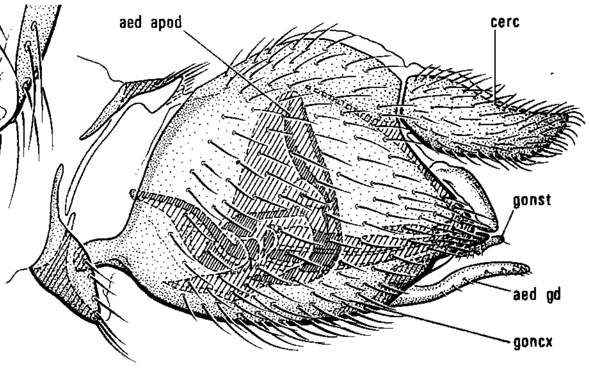
Head capsule small but distinct, subconical, with a pair of anterior tentorial arms evidenced externally by two well-marked pits; head heavily sclerotized dorsally, usually pale and weakly sclerotized ventrally, with or without setae; eyespots small, dorsal. Antenna small and usually visible only in dorsal view, but that in *Olbiogaster* longer and also visible in ventral view with a terminal rod-like sensory process or special sensory organ supposedly corresponding to bell-shaped organ of other dipterous larvae and with a series of small sensory papillae. Labrum with anterior and posterior midventral fleshy protuberances covered with fine setae; posterior protuberance also covered with sensory papillae, with a sclerotized torma and comb-like premandible sometimes present on either side. Mandible variously sclerotized; basal portion large, either simple or with a sclerotized dentate process; apical portion heavily sclerotized, bearing several strong teeth and often a brush-like group of setae. Maxilla soft and fleshy, lobate, bearing various setae and sensory papillae; palpus short, lobate, and transparent, with various sensory papillae, often with a sensory pit, and sometimes with two sensory vesicles. Labium well-developed, sometimes soft and fleshy; glossa when developed sometimes produced as a short conical process; labial palpus tiny, with two circular sensory organs or sensory papillae, and often with a basal fringe of setae.

Thoracic segments longer than broad; prothorax with a narrow anterior intercalary segment; each segment with two ventral circular sensory organs bearing two long and two short pale setae that are commonly considered remnants of thoracic legs and are thought to have locomotor function. Anterior spiracle small but distinct, with three to nineteen openings.

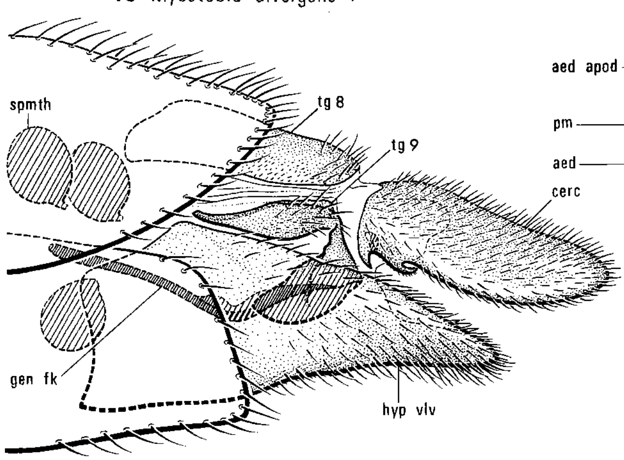
Abdomen with eight segments, each with an anterior intercalary segment. Segment 8 composed of two to five secondary annulations, with terminal annulus ending in a short conical process (Figs. 20, 21) or in five variably developed fleshy lobes (Fig. 22). Anus ventral, lying between first two secondary annulations, and sometimes surrounded by a shield-like perianal thickening. Posterior spiracles lateral and proximal to anus, slightly raised



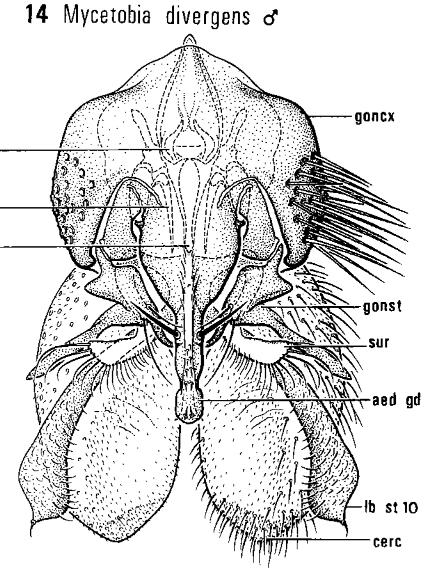
13 Mycetobia divergens ♀



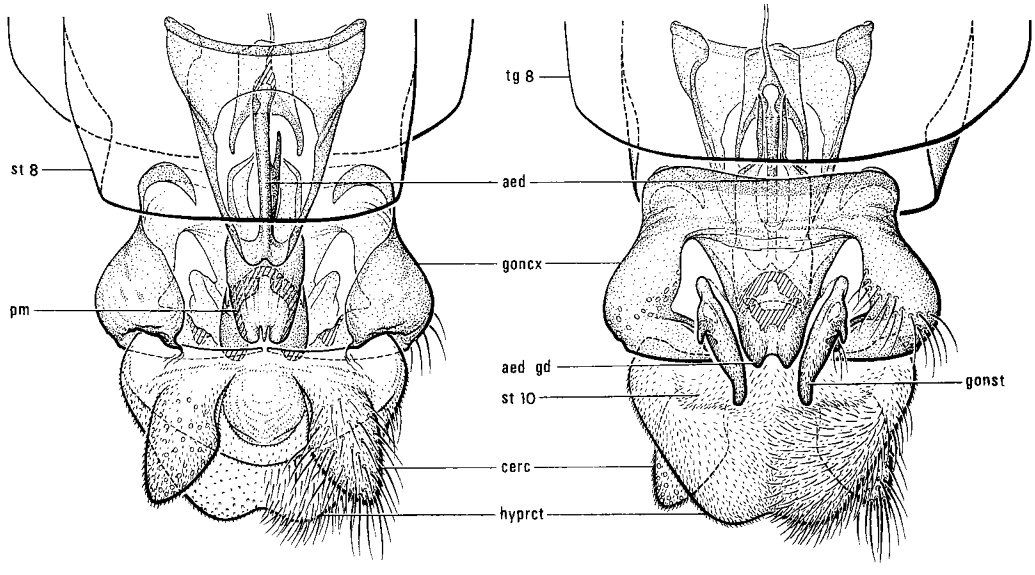
14 Mycetobia divergens ♂



15 Olbiogaster sp. ♀



16 Olbiogaster taeniata ♂



17 Sylvicola fenestralis ♂

18 Sylvicola fenestralis ♂

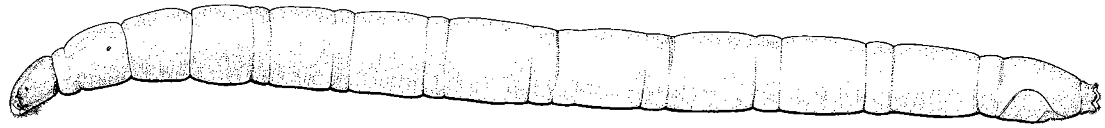
Figs. 19.13–18. Terminalia: (13) female of *Mycetobia divergens* Walker, ventral view; (14) male of *M. divergens*, lateral view; (15) female of *Olbiogaster* sp., lateral view; (16) male of *Olbiogaster taeniata* (Bellardi), ventral view; (17) dorsal view and (18) ventral view of male of *Sylvicola fenestralis* (Scopoli).

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; cerc, cercus; gen fk, genital fork; goncx, gonocoxite; gonst, gonostylus; hyprct, hypoproct; hyp vlv, hypogynial valve; lb st 10, lobe of sternite 10; pm, paramere; spmth, spermatheca; st, sternite; sur, surstylus; tg, tergite.

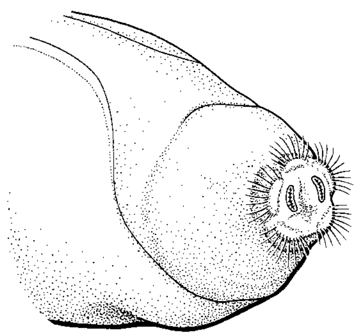
and crescent-shaped, with 25 primary openings in *Olbiogaster* (Fig. 21), or terminal, crescent- or oval-shaped, with 12–23 primary openings in *Sylvicola* (Fig. 22) and *Mycetobia* (Fig. 20).

Pupa. Strongly sclerotized, slender, shorter than corresponding larva (Fig. 23). Head near dorsal margin of frontoclypeal apotome, with two small tubercles, each bearing a long or short seta or bare (Figs. 24, 25). Antenna moderately long, curved in front of and over dorsal margin of eye, and extending to near base of wing. Palpal sheaths broadly L-shaped; apical portions straight and directed laterally.

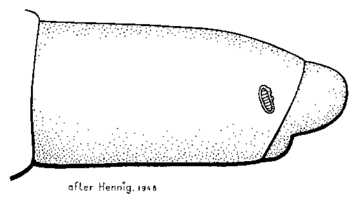
Thorax variously setose dorsally and laterally; respiratory organ small, slightly elevated, sessile; legs superposed, with foreleg shortest and ventralmost, hindleg dorsalmost; foreleg not reaching apex of wing, but midleg and hindleg extending beyond wing.



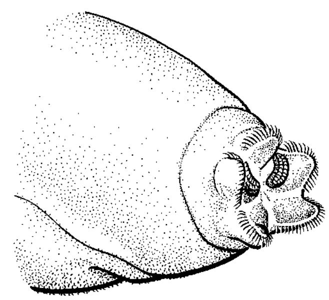
19 Sylvicola punctatus



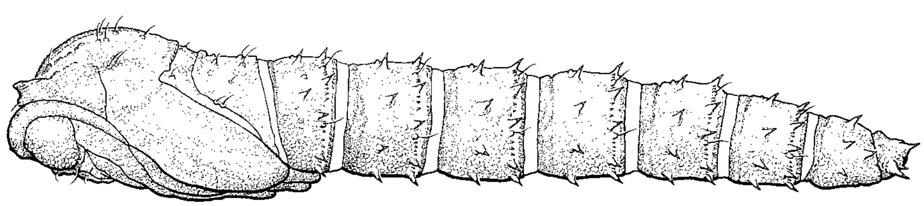
20 Mycetobia divergens



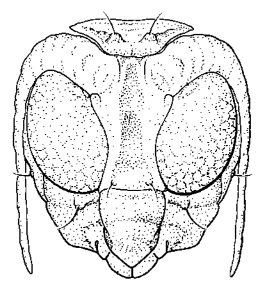
21 Olbiogaster africanus



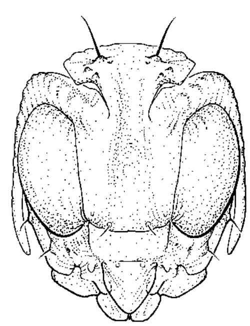
22 Sylvicola punctatus



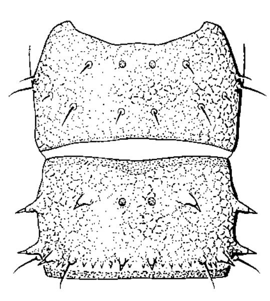
23 Mycetobia divergens



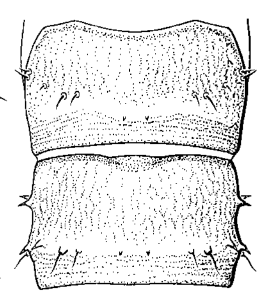
24 Mycetobia divergens



25 Sylvicola punctatus



26 Mycetobia divergens



27 Sylvicola punctatus

Figs. 19.19–27. Immature stages: larva of (19) *Sylvicola punctatus* (Fabricius) in lateral view; terminal segment of larva of (20) *Mycetobia divergens* Walker, (21) *Olbiogaster africanus* Edwards (not Nearctic), and (22) *Sylvicola punctatus*; (23) lateral view of pupa of *Mycetobia divergens*; frontal view of head capsule of pupa of (24) *M. divergens* and (25) *Sylvicola punctatus*; dorsal view of abdominal segments 7 and 8 of pupa of (26) *M. divergens* and (27) *S. punctatus*.

Abdominal segments with varying armature of short spines in transverse series along anterior and posterior borders (Figs. 26, 27); some spines with long apical sensory hairs; segments sometimes with a pair of divergent spines dorsolaterally on each side; apex of terminal segment with three to seven pairs of variably sized stout spines; some spines occasionally serrated. Abdominal spiracles small but distinct.

Keilin and Tate (1940) give good detailed descriptions and figures of the immature stages of this family.

Biology and behavior. According to Keilin (1919) and Keilin and Tate (1940), the egg is so small and the developing embryo is so confined within it that the embryo is doubled upon itself within the egg shell. The immature stages of representative species of four of the six world genera are known. The larvae are saprophagous and are found in areas with moist to wet decaying and fermenting organic matter such as manure, rotting potatoes, decaying leaves and roots, honeycombs, moldy and decaying cardboard, sewage filter beds, exudates from trees such as bleeding elms, fermenting leaves and sap in tree holes, rotting wood, and even in homemade ciders and wines. Edwards (1928) reported larvae living in partly exposed, moldy liver that had been preserved in 10% Formalin for 7 yr. Shrewsbury (1930) reported a case of intestinal myiasis involving larvae of *Sylvicola* (as *Anisopus*) *fenestralis* (Scopoli) in a 3-yr-old girl. Smith and Taylor (1966) documented a case of urinogenital myiasis, involving larvae of *S. fenestralis*, in a pregnant woman, and Morris (1968) reported a case in which larvae of the same species were passed in the urine of a 2-yr-old boy from St. John's, Nfld. The larvae move in a serpentine manner or by using their mandibles (Keilin 1919, Keilin and Tate 1940). Snow (1949) reported that *Sylvicola alternatus* (Say) and *Mycetobia divergens* Walker were found to overwinter as mature larvae frozen in debris at the bottom of tree holes. Pupation occurs in the larval habitat without the formation of a cocoon; pharate adults actively wriggle about and make their way to the surface for emergence. Females oviposit on almost any moist surface. Males form large or small mating swarms and are reported to execute various types of aerial dances to attract females into the swarms. Mating readily occurs in laboratory-reared colonies of *S. fenestralis*, and often several males may attempt to copulate with the same female, including those that have just emerged with bodies still soft and wings not fully expanded (Keilin and Tate 1940). Adults can be found near the larval habitats, often on bleeding tree trunks, and sometimes on the insides of windows. They apparently feed on nectar and other liquid substances (Malloch 1917).

Classification and distribution. This family has had an unsettled history both taxonomically and nomenclaturally. Some of its species have been shifted around among different families including the Tipulidae, Bibionidae, and Mycetophilidae. It has contained species, such as *Axymyia furcata* McAtee (Axymyiidae), which are now assigned elsewhere, and some of its current species have appeared under such family names as Phryneidae, Rhyphidae, Sylvicolidae, Mycetobiidae, and Olbiogastridae.

The Anisopodidae is a small, primitive family with a worldwide distribution but is apparently quite rare in the Ethiopian region. The family consists of six genera with about 100 described species in the world fauna. Three of these genera and nine species occur in the Nearctic region. Traditionally, the family has been divided into the subfamilies Anisopodinae and Mycetobiinae. The genera of Anisopodinae are *Sylvicola* Harris (=*Anisopus* Meigen), *Olbiogaster* Osten Sacken, *Lobogaster* Philippi, and *Carreraia* Corrêa; the genera of Mycetobiinae are *Mycetobia* Meigen and *Mesochria* Enderlein (Alexander 1942, 1965; Papavero 1967; Stone 1973). However, Hennig (1973) placed *Olbiogaster* and *Lobogaster* in the subfamily Olbiogastrinae, and *Sylvicola, Mycetobia*, and *Mesochria* in the Anisopodinae; he did not mention *Carreraia*. The traditional subfamily classification is followed here, although that of Hennig might be more correct especially when considering larval characters. One character, the apical comb of bristles on the inside of the hind tibia, has been used by several authors to separate *Sylvicola* from other genera. Because this character appears in most, if not all, species of the family and differs only in the degree of development of the pectinate bristles (Figs. 8–10), the feature has little value in classification of the genera.

The comprehensive work of Edwards (1928) placed the classification of the Anisopodidae on a firm basis. Important works on the Nearctic fauna, besides that of Edwards, include those of Malloch (1917), Alexander (1942), Lane and d'Andretta (1958), Stone (1965, 1966), and Pratt and Pratt (1980). Other useful extralimital works include those of Lindner (1930) and Corrêa (1947).

Fossil species directly assigned to the Anisopodidae apparently are few. Edwards (1928) listed 11 species in three extant genera for the family, including one species in each of these three genera from Eocene or Oligocene formations of Colorado and Wyoming. McAlpine and Martin (1969) reported the presence of an unnamed member of this family in Cretaceous Canadian amber. In 1964, Rohdendorf provided a list of ten species in five genera from four related families that he grouped under the superfamily Rhyphidea. Of these species, *Protolbiogaster rhaetica* Rohdendorf, family Protolbiogastridae, from the upper Triassic of Central Asia, is possibly the nearest of these ancient fossil relatives to the Anisopodidae. However, the current placement of some of these fossil species remains doubtful and more work is needed to amplify their true relationships.

Keys to genera

Adult

1. Wing without cell d; M with two branches; fork of M_1 and M_2, at most, slightly longer than its petiole, often much shorter. Wing membrane clear, without dark markings, and without macrotrichia although it is covered with microtrichia (Fig. 2). Antenna short (Fig. 5) .... MYCETOBIINAE....***Mycetobia*** Meigen

   1 sp., *divergens* Walker; widespread in U.S.A. and eastern Canada; Stone 1966

   Wing with cell d; M with three branches; fork of M_1 and M_2 nearly or more than twice as long as its petiole. Wing membrane clear or with dark markings; macrotrichia present or absent in addition to microtrichia (Figs. 3, 4). Antenna long or short (Figs. 6, 7) .... ANISOPODINAE....2

2. Wing membrane, except for pterostigma, clear or, at most, with faint clouding on crossveins and at apex of cell d; C extending well beyond tip of R_{4+5}; membrane without macrotrichia (Fig. 3). Face narrower than frons; antenna much longer than head and thorax combined (Fig. 6); eyes widely separated in both sexes. Empodia small in both sexes (Fig. 12) .... ***Olbiogaster*** Osten Sacken

   3 spp.; southern U.S.A.; Lane and d'Andretta 1958

   Wing membrane, in addition to pterostigma, variably patterned with dark markings; C ending at or very near tip of R_{4+5}; membrane with macrotrichia (Fig. 4). Face wider than frons; antenna about as long as head and thorax combined (Fig. 7); eyes well-separated in female but more approximate and often touching in male. Empodia large in both sexes (Fig. 11) ...... ***Sylvicola*** Harris

   5 spp.; widespread in Canada and U.S.A.; Stone 1965, Pratt and Pratt 1980

Larva

(after Hennig 1948)

1. Posterior spiracles situated on lateral surface of abdominal segment 8 (Fig. 21). Base of mandible ventrally without a denticulated process. Antenna long, visible both in dorsal and ventral views of head capsule .... ***Olbiogaster***

   Posterior spiracles situated terminally on abdominal segment 8. Base of mandible ventrally with a denticulated process. Antenna short, visible only in dorsal view of head capsule 2

2. Anterior spiracle with 19 openings; posterior spiracle with 12 openings; terminal segment with only very small processes, which are difficult to see, around spiracular disc (Fig. 20). Prementum with glossae developed as two conical processes .... ***Mycetobia***

   Anterior spiracle with three openings; posterior spiracle with 23 or more openings; terminal segment with five short but distinct processes around spiracular disc (Fig. 22). Prementum with glossae not developed, but bearing a fringe of fine setae .... ***Sylvicola***

Pupa

(after Hennig 1948)

1. Head without frontal setae. Abdominal segment 1 without spines, segment 2 with one spine on each side, segments 3–7 each with two divergent lateral spines, and remaining segments each with three pairs of long stout serrate spines .... ***Olbiogaster***

   Head with one pair of long or short frontal setae. Abdominal segments without distinct spines, having only rings of variably sized hooks 2

2. Head with short frontal setae (Fig. 24). Anterior margins of abdominal segments with many large hooks (Fig. 26) .... ***Mycetobia***

   Head with long frontal setae (Fig. 25). Only posterior margins of abdominal segments with hooklets (Fig. 27) .... ***Sylvicola***

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SCATOPSIDAE 20

EDWIN F. COOK

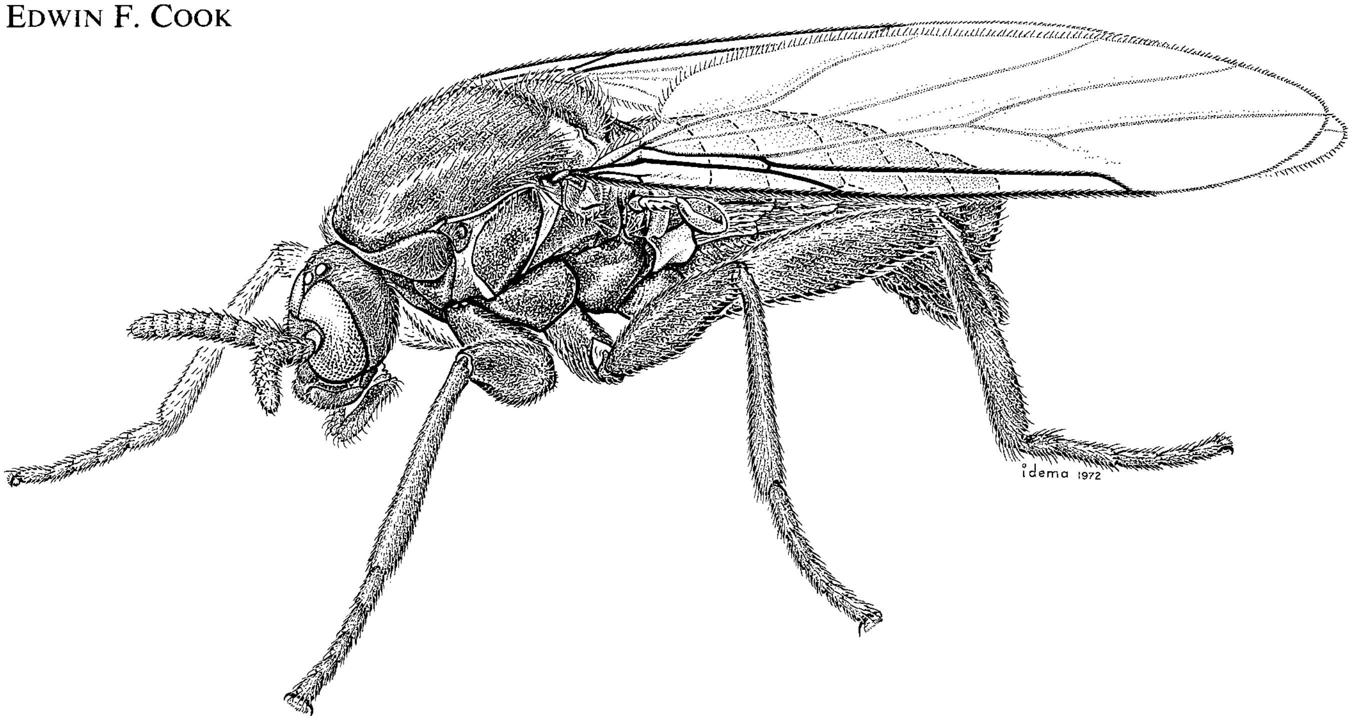


Fig. 20.1. Male of *Scatopse notata* (Linnaeus).

Rather sturdy but small flies, 0.62–4.10 mm long, black, dark gray, or brown, shining or dull, a few with some yellow (Fig. 1). Antenna (Figs. 11–13) with five to ten rather short flagellomeres. Palpus one-segmented. Postnotal phragma long, sometimes extending as far as abdominal segment 2. Wing (Figs. 2–10) with rather reduced venation; Rs (R_{4+5}) usually unbranched; veins posterior to R usually faint. Abdominal membranes longitudinally ridged, setose.

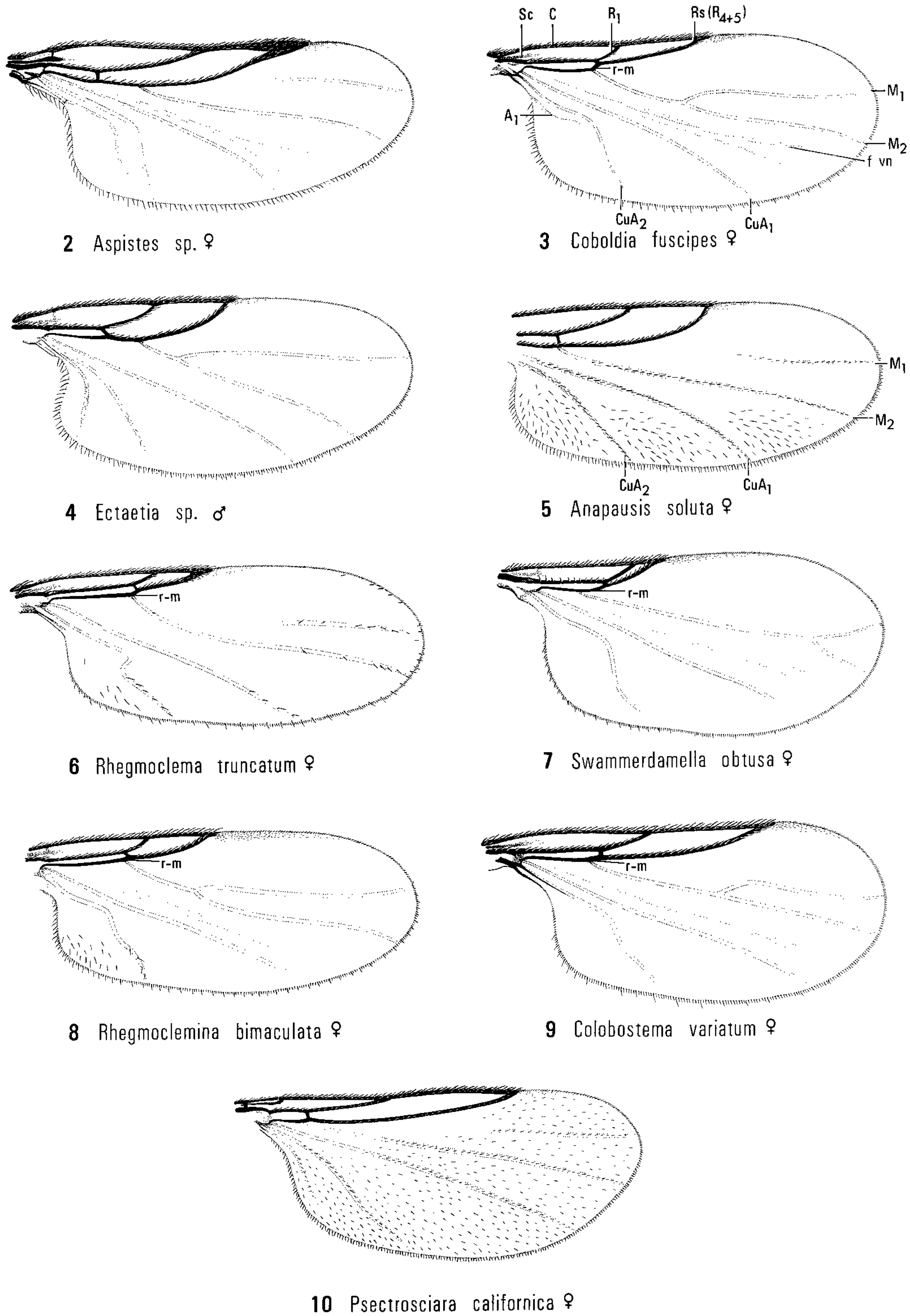
Adult. Head: laterally compressed, setose, convex behind eyes; anterior half of head occupied by eyes. Face and clypeus narrow; clypeus with a few setae on upper surface. Eyes holoptic except in known females of *Colobostema* Enderlein, thickly or sparsely beset with setae; three ocelli present. Antenna (Figs. 11–13) with five to ten flagellomeres; scape, pedicel, and flagellomeres short, often wider than long, usually pedicellate, covered with setae and microtrichia. Mouthparts reduced; palpus with a single segment; labella large, obvious, with one pseudotrachea on each lobe in Ectaetiinae.

Thorax: laterally compressed and elongate in most Scatopsinae except *Holoplagia* Enderlein, *Colobostema*, and *Parascatopse* Cook, very elongate and narrow in Psectrosciarinae, but not especially narrow in Aspistinae or Ectaetiinae. Anterior spiracle on separate anterior sclerite of anepisternum in Scatopsinae (Figs. 20, 21), but on anepisternum in other subfamilies (Fig. 15). Postnotal phragma (phragma 2) well-developed, often extending into abdominal segment 2. Scutum rather sparsely covered with short setae, with a regular row of supra-alar setae present in several genera; anepisternal setae also present, having some taxonomic value. Legs generally unremarkable; coxae as long as fore femur in all but Scatopsinae; tibial spurs absent; empodia setose.

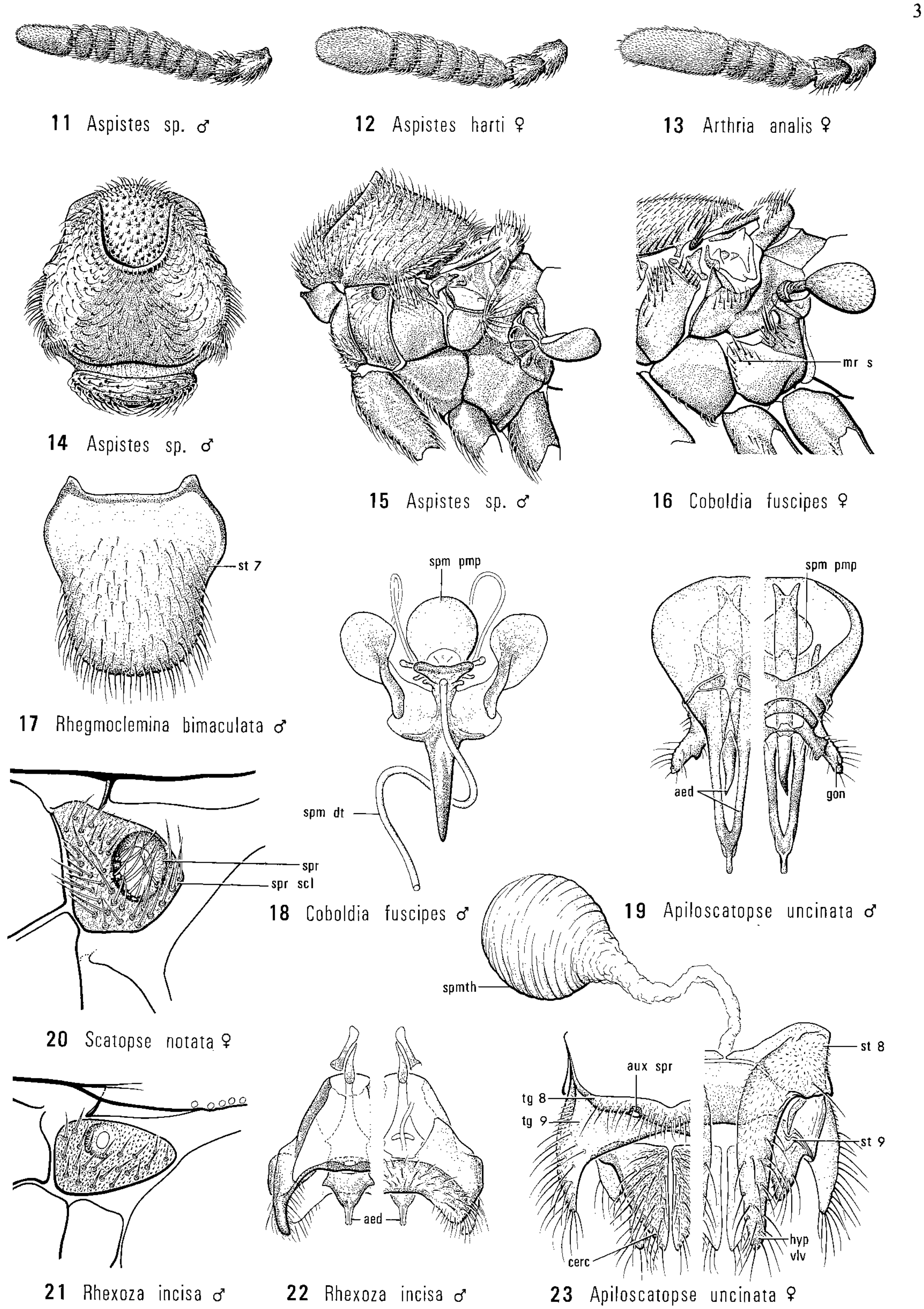
Wing with reduced venation (Figs. 2–10); only C, R_1, R_{4+5}, and sometimes base of M obvious and pigmented; Rs (R_{4+5}) unbranched; M_2 and often M_1 evident; base of M_1 sometimes absent; a concave fold or false vein often present between M_2 and CuA_1 (this false vein has been wrongly referred to as M_3 or M_{3+4}); A_1 present or absent, and when present variably developed; crossvein r-m present in several genera, but usually short. Wing membrane covered with microtrichia, sometimes very thickly; membrane and veins sometimes with obvious setae. Halter (Figs. 15, 16) covered with microtrichia; some setae on knob and a few setae on stem in most genera.

Abdomen: with seven obvious pregenital segments in all species. Seven pairs of spiracles plus one pair of auxiliary spiracles present on segment 8 (Fig. 23). Most tergites and sternites single sclerotized plates; tergites 1 and 2 often subdivided; sternites 1 and 2 often absent; sternites 7 and 8 sometimes modified and incorporated as part of terminalia. Intersegmental membrane longitudinally ribbed, beset with setae.

Male terminalia complex, capsule-like, sometimes rotated through 180°; gonopod and paramere present or



Figs. 20.2–10. Wings: (2) *Aspistes* sp.; (3) *Coboldia fuscipes* (Meigen); (4) *Ectaetia* sp.; (5) *Anapausis soluta* (Loew); (6) *Rhegmoclema truncatum* Cook; (7) *Swammerdamella obtusa* Cook; (8) *Rhegmoclemina bimaculata* (Melander); (9) *Colobostema variatum* Cook; (10) *Psectrosciara californica* (Cole).
Abbreviation: f vn, false vein.



Figs. 20.11–23. Antennae, thoraces, and abdomens: antenna of (11) *Aspistes* sp., (12) *Aspistes harti* Malloch, and (13) *Arthria analis* Kirby; (14) dorsal view of thorax of *Aspistes* sp.; (15) lateral view of thorax of *Aspistes* sp.; (16) lateral view of thorax of *Coboldia fuscipes* (Meigen); (17) ventral view of sternite 7 of male of *Rhegmoclemina bimaculata* (Melander); (18) dorsal view of sperm pump of male of *Coboldia fuscipes*; (19) dorsal three-fifths (*left*) and ventral three-fifths (*right*) of male terminalia of *Apiloscatopse uncinata* (Melander); lateral view of spiracular sclerite of anepisternum of (20) *Scatopse notata* (Linnaeus) and (21) *Rhexoza incisa* Cook; dorsal three-fifths (*left*) and ventral three-fifths (*right*) of terminalia of (22) male of *Rhexoza incisa* and (23) female of *Apiloscatopse uncinata*.

Abbreviations: aed, aedeagus; aux spr, auxiliary spiracle; cerc, cercus; gon, gonopod; hyp vlv, hypogynial valve; mr s, meral seta; spm dt, sperm duct; spm pmp, sperm pump; spmth, spermatheca; spr, spiracle; spr scl, spiracular sclerite; st, sternite; tg, tergite.

absent; aedeagus often highly modified; well-developed sperm pump (vesica) present (Figs. 18, 19). Female terminalia (Fig. 23) with genital chamber (atrium); hypogynial valve (valvifer) present in several genera; cerci fused together or to tergite 9 in many species; single spermatheca present.

Egg. Small, ovoid, and white in *Coboldia* Melander. Laid in clusters containing approximately 200 eggs.

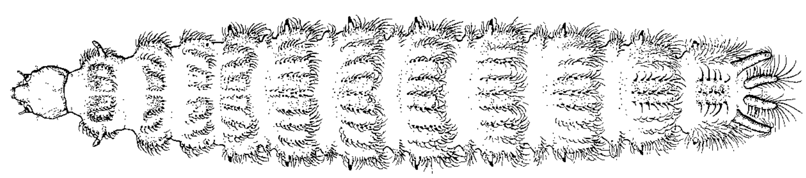
Larva. Dorsoventrally flattened, gray brown, setose. Head free, nonretractile; premandible present. Respiratory system peripneustic, with spiracles on short processes in *Scatopse* Geoffroy, *Coboldia*, and *Rhexoza* Enderlein, but not on processes in *Ectaetia* Enderlein; spiracles of segment 8 larger, on longer processes (Fig. 24).

Pupa. Often in last larval cuticle (puparium), with branched thoracic respiratory horns. Six abdominal segments each with spiracles (Figs. 25, 26).

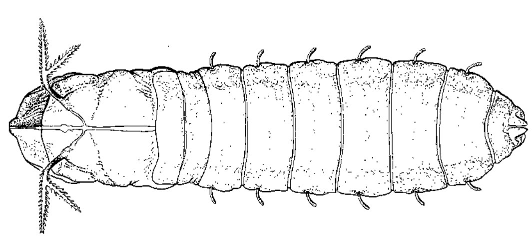
Biology and behavior. The immature stages of only four or five species are known. Larvae of two species, *Coboldia fuscipes* (Meigen) and *Scatopse notata* (Linnaeus), are found in all kinds of decaying plant and animal material. They have been reported living in decaying bulbs and onions, wastes from fruit canneries and wineries, and animal excreta. *Rhexoza similis* (Beekey) is found in the decaying bark of dead or dying deciduous trees. The biology of *Coboldia fuscipes* has been briefly described by Meade and Cook (1961).

Classification and distribution. The family has 18 genera and 73 known North American species. It has a worldwide distribution and is found on all continents. Most species described have been from the North Temperate zone (Melander 1916, Duda 1928*a*, Cook 1963), Africa, and Australia (Cook 1971*a*); little has been done with the Neotropical fauna.

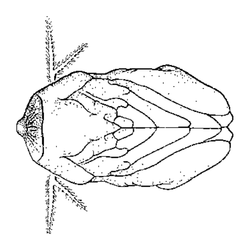
Scatopsidae consists of four subfamilies, of which Scatopsinae is the largest. It is divided into three tribes. The tribe Rhegmoclematini consists of *Rhegmoclema* Enderlein and *Rhegmoclemina* Enderlein, genera that are found in the Holarctic, Neotropical, Australian, and Ethiopian regions; and *Parascatopse* Cook, which inhabits the Holarctic and Ethiopian regions. No immature stages are known. The tribe Swammerdamellini consists of the genera *Swammerdamella* Enderlein, *Rhexoza* Enderlein, *Akorhexoza* Cook, *Quateiella* Cook, and *Coboldia* Melander. *Swammerdamella* is mainly distributed like *Rhegmoclema* but is also found in the Oriental region. *Rhexoza* is typically Holarctic, Australian, and Ethiopian. *Rhexoza incisa* Cook has been reared from larvae taken from beneath the bark of dead American elm (*Ulmus americana*), box-elder (*Acer negundo*), and cottonwood (*Populus*). *Akorhexoza* contains two species from Mexico and southwestern United States. *Quateiella* contains a southwestern species and a southeastern species. *Coboldia* contains only the cosmopolitan *C. fuscipes* (Meigen). The larva of *Coboldia* has been described and is found in all kinds of decaying plant and animal material. The tribe Scatopsini consists of six genera. *Scatopse* Geoffroy has a worldwide distribution and contains one cosmopolitan species, *S. notata*, whose larval stages have been described. *Reichertella* Enderlein is Holarctic and Australian, *Colobostema* Enderlein is found in all zoogeographic regions, *Holoplagia* Enderlein is absent from the Nearctic and Ethiopian regions, *Ferneiella* Cook is Palaearctic and Australian, and *Apiloscatopse* Cook is Holarctic and Ethiopian.



24 Rhexoza sp.



25 Rhexoza sp.



26 Rhexoza sp.

Figs. 20.24–26. Immature stages of *Rhexoza* sp.: (24) dorsal view of larva; (25) dorsal view of pupa; (26) ventral view of head and thorax of pupa.

The subfamily Psectrosciarinae consists of only two genera. *Psectrosciara* Kieffer is found in the Oriental, Australian, Ethiopian, and Neotropical regions and in western North America. Biology and immature stages are not known. *Anapausis* Enderlein is found mainly in the Holarctic and Ethiopian regions, and a single species occurs in southern Chili. Most species are European. Nothing is known of the larvae.

The subfamily Aspistinae is very distinctive among scatopsids. They are quite stout and some species are among the largest members of the family. The subfamily is believed to be exclusively Holarctic. It is composed of two genera, *Aspistes* Meigen and *Arthria* Kirby. *Arthria analis* Kirby is found in both Europe and North America. The immature stages are entirely unknown.

The subfamily Ectaetiinae contains only *Ectaetia* Enderlein, which is Holarctic and Neotropical. The larva of *E. clavipes* (Loew) has been briefly described by Laurence (1953).

Four fossil species of Scatopsidae from Baltic amber (Meunier 1907) and a single fossil scatopsid from Aix-en-Provence, France, have been described. Tertiary amber of Chiapas, Mexico, has provided two species of *Scatopse*, one species of *Swammerdamella*, and four species of *Procolobostema* Cook. The species of *Procolobostema* were described by Cook (1971*b*). Specimens of at least one undescribed Cretaceous species from Canadian amber have been recently found.

Key to genera

1. Scutum with an elevated U-shaped ridge (Figs. 14, 15). Fore tibia produced, spine-like. C swollen at junction with R_{4+5} (Fig. 2). Eyes dichoptic in both sexes ....ASPISTINAE....2

   Scutum without a U-shaped ridge (Fig. 16). Fore tibia not produced apically. C not swollen at junction with R_{4+5}. Eyes holoptic in both sexes, except in female *Colobostema* 3

2. Base of M with no more than two or three setae (Fig.2). Male antenna with 8–10 flagellomeres (Fig. 11); female antenna with six flagellomeres (Fig. 12) ....***Aspistes*** Meigen
   4 spp.; widespread, boreal; Cook 1965

   Base of M with numerous setae. Antenna of male and female with only five flagellomeres (Fig. 13) ....***Arthria*** Kirby
   3 spp.; boreal; Cook 1965

3. Wing with false vein present midway between M_2 and CuA_1 (Fig. 3). Male with sperm pump attached to structures of terminalia only by elongate sperm duct (Fig. 18) ....SCATOPSINAE....4

   Wing with false vein absent (Figs. 4, 5). Male with sperm pump attached directly to structures of terminalia 9

4. Stem of halter with setae; wing without setae on CuA_2 5

   Stem of halter without setae; wing usually with setae on CuA_2 (Figs. 6, 8) ....RHEGMOCLEMATINI....6

5. Palpus small, ovoid or obovate. Anterior spiracular plate about as long as high, with spiracle relatively large (Fig. 20). Stem of M_{1+2} always shorter than its fork (Fig. 3); CuA_2 not sharply bent along its course; R_{4+5} extending beyond middle of wing. Thorax without meral setae ....SCATOPSINI....11

   Palpus large, reniform, sometimes distally acute. Anterior spiracular plate triangular, longer than high, with spiracle relatively small (Fig. 21). Stem of M_{1+2} longer than its fork (Fig. 7) or CuA_2 with two sharp bends (except in *Coboldia*); R_{4+5} usually not extending beyond middle of wing. Thorax often with meral setae ....................SWAMMERDAMELLINI....17

6. Some macrosetae on M_1 or M_2, or on both; M_1 usually incomplete basally (Fig. 6). Antenna with 10 flagellomeres ....***Rhegmoclema*** Enderlein
   6 spp.; widespread, boreal; Cook 1955

   No setae on M_1 or M_2; M_1 always complete. Antenna with 8 or 10 flagellomeres 7

7. Sternite 7 of male shield-shaped (Fig. 17). In both sexes, distinct supra-alar row of setae present. Spiracular sclerite triangular ....***Rhegmoclemina*** Enderlein....8

   Sternite 7 of male not shield-shaped. In both sexes, no distinct supra-alar row of setae. Spiracular sclerite rounded ....***Parascatopse*** Cook
   3 spp.; southeastern U.S.A., California; Cook 1955

8. Antenna with 8 flagellomeres. Wing with macrosetae on CuA_2 and on membrane behind CuA_2 (Fig. 8) .... ***Rhegmoclemina*** (***Rhegmoclemina*** Enderlein)
3 spp.; widespread; Cook 1955

Antenna with 10 flagellomeres. Wing sometimes with setae on CuA_2 but never on membrane behind CuA_2 .... ***Rhegmoclemina*** (***Neorhegmoclemina*** Cook)
2 spp.; U.S.A. from Iowa to east coast; Cook 1955

9. Wing membrane without setae; stem of M_{1+2} arising distal to base of R_{4+5} (Fig. 4). Labella with pseudotracheae .... ECTAETIINAE.... ***Ectaetia*** Enderlein
2 spp.; widespread

Wing membrane and veins with obvious setae; base of M_2 arising at base of R_{4+5} (Figs. 5, 10). Labella without pseudotracheae .... PSECTROSCIARINAE....10

10. Anterior spiracle situated on anepisternum. R_{4+5} long, extending beyond middle of wing, not strongly curved, intersecting C at an acute angle (Fig. 10); stem of halter without setae .... ***Psectrosciara*** Kieffer
10 spp.; western and southwestern U.S.A.; Cook 1958

Anterior spiracle situated on a separate anepisternal sclerite. R_{4+5} strongly curved to C, intersecting C almost at right angles (Fig. 5); stem of halter with a single seta near knob .... ***Anapausis*** Enderlein
3 spp.; widespread north of 38°; Cook 1965

11. Thorax stout, as wide as long; wing with dense microtrichia, appearing pubescent 12

Thorax narrow, longer than wide; wing hyaline 13

12. M_1 with a supernumerary crossvein connecting dorsally with R_{4+5} .... ***Holoplagia*** Enderlein
not yet recorded in the Nearctic; Cook 1957

M_1 usually without a supernumerary crossvein, but if rarely present, then short and not connecting with R_{4+5} (Fig. 9) .... ***Colobostema*** Enderlein
4 spp.; eastern, southeastern, and western U.S.A.; Cook 1956, 1978

13. R_{4+5} terminating in C at or before middle of wing. Palpus large, reniform, dorsally concave, sometimes apically acute; proboscis about half as long as height of head. Male terminalia with simple aedeagus (Fig. 22). Female terminalia usually without appendages (except cerci). Anterior spiracular sclerite triangular, much larger than spiracles (Fig. 21)........17

R_{4+5} terminating in C beyond middle of wing. Palpus usually small, not dorsally concave, never apically acute; proboscis less than half height of head. Male terminalia with large and often highly modified aedeagal complex (Fig. 19). Female terminalia usually with one or two pairs of appendages besides cerci (Fig. 23). Spiracular sclerite usually not much larger than spiracles (Fig. 20)........14

14. Cluster of spiniform setae on sternite 7 posteriorly, besides usual setae. Wing infuscate, dull........ ***Ferneiella*** Cook
not yet recorded in the Nearctic; Cook 1974

No spiniform setae on sternite 7. Wing hyaline, shining 15

15. M_1 near base with an anterodorsally directed supernumerary crossvein that sometimes nearly reaches R_{4+5}. Tarsomere 1 of male hindleg shorter than or no longer than tarsomere 2 (Fig. 1) .... ***Scatopse*** Geoffroy
3 spp.; widespread; Cook 1957, 1972, 1974

M_1 without a supernumerary crossvein. Tarsomere 1 of male hindleg longer than tarsomere 2 16

16. Male with tergite 7 produced posteriorly, with small or large paramere, and with gonocoxite either absent or unarticulated. Female without hypogynial valves .... ***Reichertella*** Enderlein
3 spp.; boreal; Cook 1957, 1974

Male without tergite 7 produced posteriorly, and with two pairs of articulated appendages on terminalia. Female with one or two pairs of obvious hypogynial valves ... ***Apiloscatopse*** Cook
3 spp.; widespread; Cook 1974

17. Fork of M shorter than or no longer than stem of fork; R_{4+5} terminating very near end of R_1 (Fig. 7). Male with only six abdominal segments visible externally .... ***Swammerdamella*** Enderlein
10 spp.; widespread; Cook 1956

Fork of M longer than stem; R_{4+5} terminating in C far from R_1 (Fig. 3). Male with seven visible abdominal segments 18

18. Male with tergite 7 produced posteriorly as a narrow spatulate process; aedeagus elongate and coiled. Female with small hypogynial valves on sternite 8, and with rounded bare emargination on posterior margin of sternite 7 .... ***Coboldia*** Melander
1 sp., *fuscipes* (Meigen); cosmopolitan

Male with tergite 7 not produced posteriorly as a narrow spatulate process; aedeagus small, never coiled. Female with or without hypogynial valves, and without posterior emargination on sternite 7 19

19. Male terminalia laterally compressed; tergite 9 produced ventrally as a beak-like process. Female with tergite 8 medially divided by a short longitudinal suture .... ***Quateiella*** Cook
2 spp.; southern and western Nearctic; Cook 1975

Male terminalia not laterally compressed; tergite 9 not produced ventrally. Female with tergite 8 not divided by a short suture 20

20. Male with tergite 7 produced posteriorly, triangular, truncate, or notched; tergite 8 not evident; female without hypogynial valves .... ***Rhexoza*** Enderlein
10 spp.; widespread; Cook 1956, 1975

Male with tergite 7 not produced posteriorly; tergite 8 evident, darkly pigmented; female with acute or rounded hypogynial valves .... ***Akorhexoza*** Cook
2 spp.; southwestern Mexico; Cook 1978

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SYNNEURIDAE 21

B. V. PETERSON AND EDWIN F. COOK

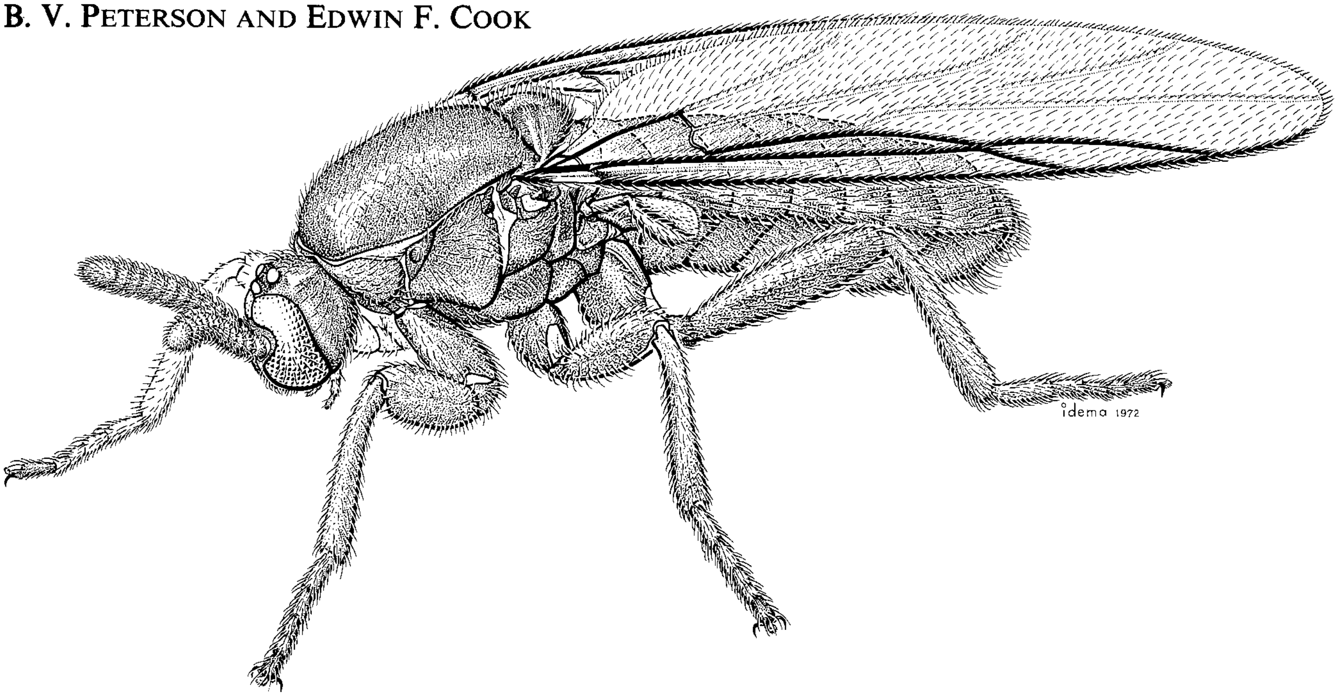


Fig. 21.1. Female of *Synneuron decipiens* Hutson.

Small slender heavily sclerotized shiny dark brown to black flies, 2.0–3.5 mm long, resembling Scatopsidae except palpus with four segments and flagellum of antenna with 10–14 simple bead-like flagellomeres. Thorax rather slender, longer than high (Fig. 1).

Adult. Head: eyes holoptic, variably surrounding bases of antennae, narrowly separated to almost contiguous ventrally (Fig. 2.79), covered with short setae; three ocelli present. Antenna with 10–14 simple bead-like flagellomeres; flagellomeres slightly increasing in size distally; apical flagellomere largest. Clypeus small, short, and narrow. Mouthparts reduced; palpus with four segments; second palpal segment in *Synneuron* Lundström and third in *Exiliscelis* Hutson largest, with a tiny sensory vesicle; labella with a single pseudotrachea on each lobe.

Thorax: pronotum reduced medially but with conspicuous postpronotal lobes. Scutum narrow, strongly arched, slightly tapering and more narrow anteriorly, sparsely covered with short stiff setae; scutellum triangular, sparsely covered with short setae; postnotum varying from rather small to moderately large, narrowly arched along midline in *Synneuron*, sometimes with very fine pubescence laterally; postnotal phragma (phragma 2) very long, extending into abdominal segment 1; paratergite narrow but conspicuous. Anterior spiracle rather large, situated on a small setose sclerite variably isolated from rest of anepisternum. Pleural sclerites well-developed including meron and katepimeron, although meron small in *Exiliscelis*; anepisternum and katepisternum sparsely covered with short stiff setae.

Legs moderately long and stout; fore tibia with a small but distinct single spur; other tibiae with two short spurs. Claws small, simple or with a basal tooth; empodia small and slender, with fringe of setae; pulvilli absent.

Wing long and slender, with anal lobe scarcely developed if at all, and without an alula; membrane and veins covered with microtrichia. Veins well-developed, but posterior veins often pale (Figs. 2, 3); C strong, not reaching tip of wing, but extending beyond posterior branch of Rs; Sc short, evanescent distally; R_1 free, or possibly fused with R_{2+3}, or R_{2+3} absent or present as a short dorsal branch of Rs; R_{4+5} reaching wing margin; base of M fused with stem of Rs (and possibly including crossvein r-m); M_1 and M_2 distinct, but basal portion of M_2 sometimes missing; crossvein bm-cu present, but probably including portion of stem of M; CuA_1 and CuA_2 distinct, reaching wing margin; CuP and A_1 variably distinct or absent. Halter short, with a large ovate knob that is usually more than twice as long as its stem; both knob and stem sparsely covered with setae.

Abdomen: long and slender, somewhat flattened dorsoventrally, narrower anteriorly, widening posteriorly; segments 1–7 in *Synneuron* each with a conspicuous narrow setose pleural sclerite below which are situated small but conspicuous spiracles on segments 2–7; both tergites and sternites with short stiff setae.

Female with tergite 8 reduced, only about half as long as tergite 7; tergite 9 shorter than or about as long as tergite 8 but somewhat narrower, with two very small submedial auxiliary spiracles in *Synneuron* (apparently absent in *Exiliscelis*) corresponding to those of male in *Synneuron* (the exact nature of these auxiliary spiracles has yet to be investigated); tergite 10 membranous in *Synneuron* but well-developed and sclerotized in *Exiliscelis*. Cercus free, moderately large, well-developed, setose, one-segmented in *Synneuron*, two-segmented in *Exiliscelis*. Sternite 8 large, sometimes extending dorsolaterally to slightly above ventrolateral margins of tergites 8 and 9, with hypogynial valves separated by a U-shaped space; sternite 9, or genital fork, somewhat Y-shaped, moderately sclerotized, with arms of fork variously developed, sometimes greatly expanded, and connecting dorsally with tergite 9; sternite 10 in *Exiliscelis* a slender setose inverted U-shaped structure whose arms broaden dorsally uniting with tergite 10. One large or two smaller sclerotized spermathecae present, and a pair of small sclerotized accessory glands present in *Exiliscelis*.

Male with tergite 8 well-developed in *Exiliscelis*, but in *Synneuron* with tergite 8 probably represented by a small triangular area between bases of and fused with plates of epandrium, or tergite 9. Epandrium in *Synneuron* enlarged, divided into two subrectangular plates fused along midline and anteromedially with tergite 8; epandrium, or tergite 9 (commonly referred to as tergite 8 by previous authors), with a pair of small auxiliary spiracles bearing a closely associated minute seta on each; epandrium in form of a single well-developed plate in *Exiliscelis*, with tergite 10 represented as a somewhat triangular digitiform surstylus situated on each side (Figs. 4, 5). Cercus large or small but conspicuous, setose. Sternite 8 well-developed in *Exiliscelis*, but in *Synneuron* lightly sclerotized, largely retracted under sternite 7, and bearing a patch of short spinules along distal margin. Hypandrium, or sternite 9, in *Synneuron* broad, U-shaped, with lateral arms somewhat angulate, and with a slender somewhat spade-shaped sparsely setose aedeagal guide arising posteromedially; guide variably produced laterally as a short or long angulate process; a short rounded process that probably represents remnant of gonopod (gonocoxite and gonostylus) present lateral to aedeagal guide. Hypandrium in *Exiliscelis* narrow, heavily sclerotized, and ring-like; gonocoxites greatly enlarged, fused medially, with posteromedial margin produced posteriorly as a rather broad V-shaped aedeagal guide; gonostylus short, with broad basal half, and tapering distally as a slender curved process. Sperm pump in *Synneuron* large, tapering distally, discharging through a very short slender simple aedeagus; sperm pump in *Exiliscelis* smaller, short, and closely associated with base of aedeagus; sperm pump in both genera with large variously shaped ejaculatory apodemes. Aedeagus in *Exiliscelis* moderately long, heavily sclerotized, broadening basally, tapering distally, partially fused with two parameral processes, and with entire structure dividing apically into three slender dorsally curving tube-like structures each with its own opening; aedeagus with an enlarged aedeagal apodeme. Paramere in *Synneuron* large, well-developed, F-shaped or inverted-L-shaped; paramere in *Exiliscelis* a short bilobate structure associated with base of aedeagus. Sternite 10 and hypoproct sclerotized, and variable in size but distinct.

Larva. The following description is modified from that of Teskey (1976) which was based on a single specimen of S. *decipiens* Hutson (as S. *annulipes* Lundström).

Slender cylindrical body tapering anteriorly and posteriorly, peripneustic, about 5 mm long (Fig. 6).

Head segment small, membranous, without sclerotized skeletal parts, but bearing dorsally a pair of short two-segmented antennae. Three thoracic and nine abdominal segments clearly delineated. Anterior and posterior spiracles (Fig. 8) enlarged and with numerous spiracular pores arranged in a circle on margin of each spiracle; integument below each of these spiracles with a smaller circular area that is faintly divided in half; spiracles on abdominal segments 1–7 small. Dorsal and ventral surfaces of cuticle of mesothoracic and metathoracic segments and abdominal segments 1–7, and ventral surface of abdominal segment 8, with transverse bands of minute pubescence that impart an iridescent luster. Terminal abdominal segment with a pair of sclerotized upturned spine-like hooks posteriorly; integument of most of this segment lightly sclerotized.

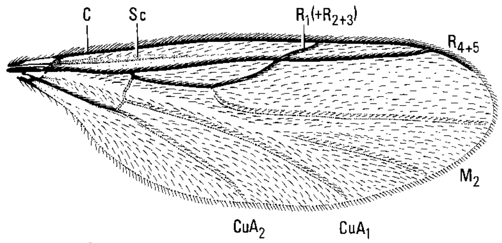
Mamaev and Krivosheina (1969) described the larvae of the two Palaearctic species of *Synneuron*, i.e. *annulipes* Lundström and *silvestre* Mamaev & Krivosheina; the description of these species closely approximates that of *S. decipiens* by Teskey (1976) and that given above.

Pupa. The following description is based on three pupal skins of *S. decipiens*.

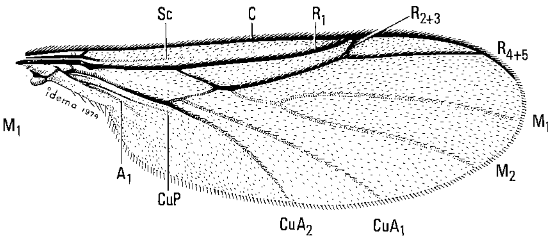
Obtect, cylindrical, strongly sclerotized, not enclosed in last larval skin as are scatopsid pupae, and 4.0–4.5 mm long (Fig. 7). Cuticle apparently without setae, but finely granulate on intersegmental areas.

Head ventral to and flexed beneath thorax; frons short, broader than long, subovate. Antennal sheath extending posteriorly to about half length of thorax to base of wing sheath, faintly annulate, with short angulate projection at point of posterior flexion. Clypeal plate prominent. Palpal sheath short but broad.

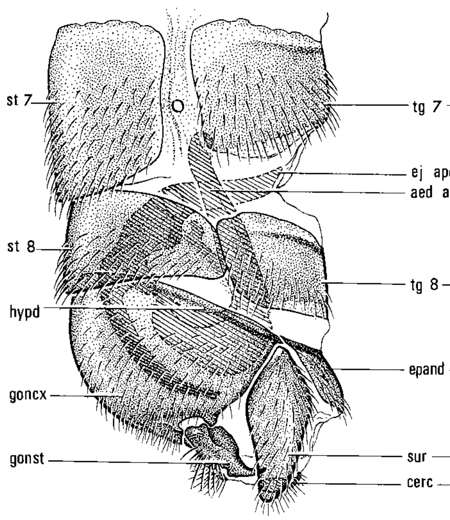
Thorax strongly arched, narrower dorsally than ventrally, with a small spiracle-like pit near each anteroventral corner, and with a larger respiratory tubercle laterally before mid length of thorax. Wing sheath large, extending posteriorly to just beyond posterior margin of sternite 2; anterior leg sheath not reaching tip of wing sheath; middle leg sheath subequal to wing sheath; posterior leg sheath longer than wing sheath.



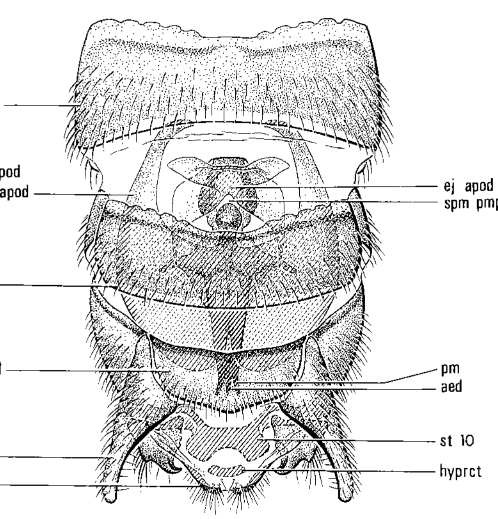
2 Synneuron decipiens ♀



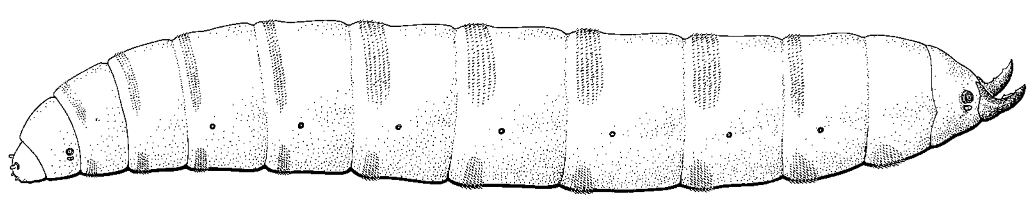
3 Exiliscelis californiensis ♂



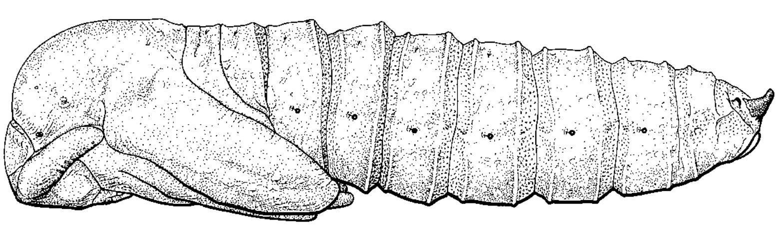
4 Exiliscelis californiensis ♂



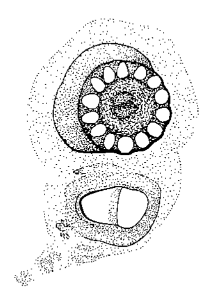
5 Exiliscelis californiensis ♂



6 Synneuron decipiens



7 Synneuron decipiens



8 Synneuron decipiens

Figs. 21.2–8. *Synneuron decipiens* Hutson and *Exiliscelis californiensis* Hutson: wing of (2) *S. decipiens* and (3) *E. californiensis*; male terminalia of *E. californiensis*, (4) in lateral view and (5) in dorsal view; lateral view of (6) larva and (7) pupa of *S. decipiens*; (8) posterior spiracle of larva of *S. decipiens*.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; goncx, gonocoxite; gonst, gonostylus; hypd, hypandrium; hyprct, hypoproct; pm, paramere; spm pmp, sperm pump; st, sternite; sur, surstylus; tg, tergite.

Abdominal segments 2–7 each with a lateral spiracle. Segments 2–8 each with a shiny narrow transverse ridge near anterior and posterior margins; these ridges weakening lateroventrally then slightly strengthening ventrally, so they essentially ring entire segment. Segment 9 with two dorsal spiracles situated in front of two dorsal spine-like processes.

Biology and behavior. Very little is known about the life history and habits of these novel little flies. For a long time only a few adult specimens were known. However, the recent discovery of larvae living in various kinds of decaying wood permeated by mycelia of various fungi (Krivosheina and Mamaev 1967, Teskey 1976) provides an opportunity for investigating the details of the life cycle and habits of the immature and adult stages.

Classification and distribution. Cook (1963) first recorded the presence of *Synneuron* (as *S. annulipes*) in North America. Teskey (1976) reared several adults from larvae and published the first description of the larva of this species (also as *annulipes*). Hutson (1977) revised the genera previously grouped under the family name Hyperoscelidae. Of these genera he assigned *Synneuron* and *Exiliscelis* to the family Synneuridae, and the remaining genera to the family Canthyloscelidae. For a historical review of the taxa included in these two families the paper by Hutson (1977) should be consulted.

The family Synneuridae is composed of two genera and four species. *Synneuron* is Holarctic and contains the two Palaearctic species *annulipes* and *silvestre*, and the Nearctic *decipiens*. *Exiliscelis* is monotypic and its only described species, *californiensis* Hutson, occurs in western North America. No fossils are known.

Key to genera

1. Antenna with 14 flagellomeres. Rs forked apically so that branches R_{2+3} and R_{4+5} are both present; base of M_2 not interrupted so that fork of M is complete (Fig. 3) .... ***Exiliscelis*** Hutson

   1 sp., *californiensis* Hutson; California, Oregon

   Antenna with 10 flagellomeres. Rs not forked so that only R_{4+5} is present; base of M_2 interrupted so that fork of M is not complete (Fig. 2) .... ***Synneuron*** Lundström

   1 sp., *decipiens* Hutson; Quebec to British Columbia, Colorado to Alaska

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PTYCHOPTERIDAE 22

C. P. ALEXANDER

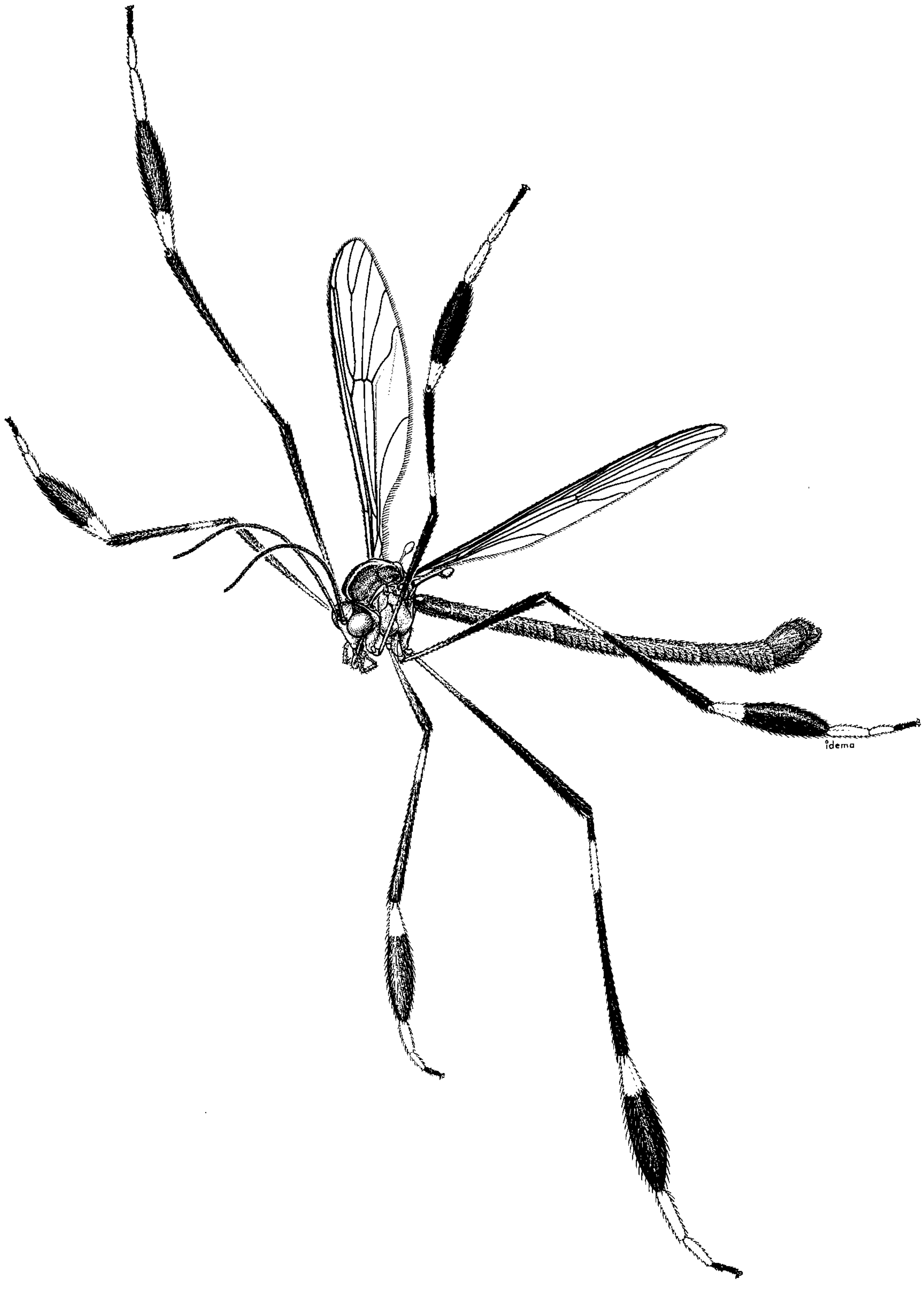


Fig. 22.1. Male of *Bittacomorpha clavipes* (Fabricius).

Slender flies of moderate size (Fig. 1). Ocelli lacking. Antenna long; flagellum multisegmented. Legs long, sometimes conspicuously banded with white. Wing slender, with nine or ten longitudinal veins including a four-branched radius and one anal vein reaching margin (Figs. 2–4). Abdomen long.

Adult. Head: transverse, closely applied to thorax. Palpus long, five-segmented, with terminal palpal segment the longest. Flagellum in Ptychopterinae 13-segmented, in Bittacomorphinae 18- or 19-segmented with indications of a further very reduced terminal flagellomere; flagellomeres long–cylindrical. Vestiture conspicuous in *Ptychoptera* Meigen, delicate and inconspicuous in Bittacomorphinae.

Thorax: mesonotum with transverse suture bent strongly toward posterior end in region of scutum to form a deep loop; presutural area with parallel longitudinal furrows on either side of median. Tibiae spurred. Wing (Figs. 2–4) with Sc_2 lacking; Rs short; R_{2+3} close to R_1, narrowing cell r_1; cell r_4 present; M_2, and therefore cell m_1, preserved in Ptychopterinae (Fig. 4), but lacking in Bittacomorphinae (Figs. 2, 3); distal section of CuA_2 strongly sinuous; a longitudinal fold in cell cu*p* extending from A_1 outwardly to near the bend in distal section of CuA_2, most evident in *Ptychoptera*. Halter with peculiar prehalter.

Abdomen: long and slender, especially in male of Bittacomorphinae. Male terminalia with gonopods distinctly separate from well-developed sternite 9 and tergite 9; sternite 9 with accessory apical appendages that are particularly large and trough-shaped in *Ptychoptera*; surstylus on tergite 10, which is closely associated with tergite 9, well-developed in Bittacomorphinae, smaller and overshadowed by large lateral composite tergal horn in *Ptychoptera*. Ovipositor of female with tergites 8–10 fused; cercus either a simple fleshy lobe (Bittacomorphinae) or a sclerotized slightly downwardly curved tapering structure presumably functioning as an egg guide (*Ptychoptera*).

Detailed accounts of adult morphology found in Crampton (1926), Alexander (1927), Anthon (1943), Kramer (1954), and Peus (1958).

Larva. Eucephalic, metapneustic. Body segments with serially arranged hairs sometimes arising from small papillae (Figs. 5, 6). Abdominal segments 1–3 with a pair of prolegs ventrally; prolegs each with a single hook-like spine. Posterior end of larva produced into a fairly long retractile respiratory siphon (Fig. 5).

Pupa. Obtect. Mesonotal breathing horns very unequal; one very long and slender, exceeding body in length; the other small and degenerate. Sheaths of at least two pairs of legs lying side by side and exceeding length of wing pads. Abdominal segments with transverse rows of spicules (Fig. 7).

Biology and behavior. The immature stages are aquatic or nearly so, inhabiting saturated mud at the margins of streams or in swales. Alexander (1920) has summarized many of the references to the early stages. Other discussions include Brindle (1962), Stubbs (1972), and Hodkinson (1973).

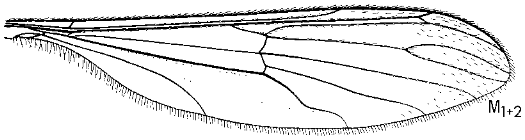
Classification and distribution. At present more than 60 world species are known. Two are members of *Bittacomorpha* Westwood, and both are Nearctic. One of these is the familiar *B. clavipes* (Fabricius), the so-called phantom crane fly. This species is one of the most conspicuous and interesting of all Nearctic Diptera. The first tarsomere of the legs of this species is dilated and filled with tracheae, a characteristic which enables the flies to drift in the wind with their long legs extended to catch the breeze (Alexander 1920). The genus *Bittacomorphella* Alexander has seven species. Four are Nearctic, one occurring in eastern North America and the others in the far west; the remaining three species are from eastern Asia. All other species in the family are in the genus *Ptychoptera* Meigen, which has representatives in all biotic regions except the Australasian and the Neotropical regions. In the Nearctic fauna there are 10 described species, the majority in the west.

The only undoubted fossils of Ptychopteridae are *Ptychoptera deleta* Novak (upper Oligocene), whose strict generic position is doubtful, and *Bittacomorphella miocenica* (Cockerell) from the Florissant Miocene (Alexander 1927). A much older fossil, *Eolimnobia geinitzi* Handlirsch from Lower Jurassic deposits of western Europe, has been placed near the base of the evolutionary stem of Ptychopteridae by Rohdendorf (1974).

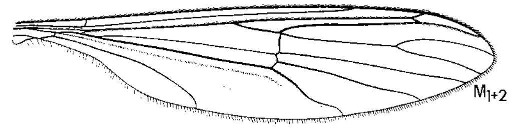
Keys to genera

Adult

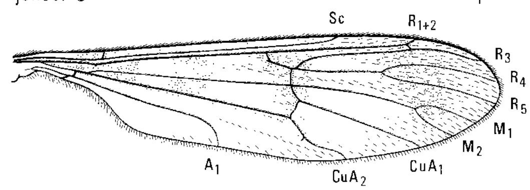
1. Flagellum with 13 segments. Wing with M branched (Fig. 4) .... PTYCHOPTERINAE....***Ptychoptera*** Meigen
   10 spp.; widespread; Alexander 1942, 1967
   Flagellum with 18 or 19 segments. Wing with M unbranched........BITTACOMORPHINAE....2
2. Wing with distal radial and medial cells with macrotrichia (Fig. 2). First tarsomere of all legs not dilated .... ***Bittacomorphella*** Alexander
   4 spp.; widespread; Alexander 1942, 1967



2 Bittacomorphella jonesi ♂



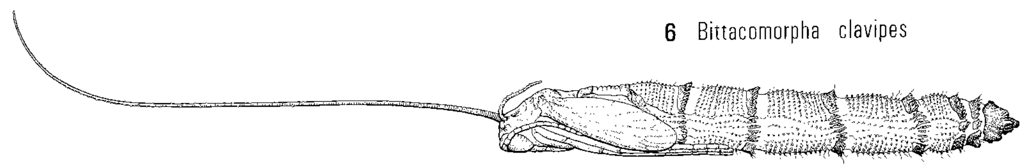
3 Bittacomorpha clavipes ♂



4 Ptychoptera quadrifasciata ♂

5 Ptychoptera sp.

6 Bittacomorpha clavipes



7 Ptychoptera lenis

Figs. 22.2–7. Wings and immature stages: wing of (2) *Bittacomorphella jonesi* (Johnson), (3) *Bittacomorpha clavipes* (Fabricius), and (4) *Ptychoptera quadrifasciata* Say; (5) larva of *Ptychoptera* sp.; (6) first two abdominal segments of larva of *Bittacomorpha clavipes*; (7) pupa of *Ptychoptera lenis* Osten Sacken.

Wing without macrotrichia in these cells (Fig. 3). First tarsomere of all legs conspicuously dilated (Fig. 1) .... ***Bittacomorpha*** Westwood
2 spp.; widespread; Alexander 1942, 1967

Larva

1. Hypostoma absent or fused with hypostomal bridge that closes head capsule ventrally; mandible with a single outer tooth. Prolegs prominent ventrally on first three abdominal segments, each with a conspicuous curved claw (Fig. 6). Coloration rusty red or black 2

   Hypostoma separated from hypostomal bridge; mandible with three large outer teeth. Prolegs and apical curved claws small and inconspicuous (Fig. 5). Coloration yellow or brown .... ***Ptychoptera***

2. Predominantly blackish in color. Respiratory siphon light yellow, entirely retractile. Very long projections encased in a black horny substance, covering entire body. Mandible with an inner comb of teeth .... ***Bittacomorphella***

   Rusty red in color. Body tapering gradually to a long slender partly retractile respiratory siphon. Transverse rows of shorter stellate tubercles covering entire body (Fig. 6). Mandible without an inner comb of teeth .... ***Bittacomorpha***

Pupa

1. All tarsi lying parallel. Wing pads with M branched .... ***Ptychoptera***

   Fore tarsus lying above mid tarsus. Wing pads with M unbranched 2

2. Right breathing horn small, degenerate; left horn very long. Abdominal tubercles weak, tipped with several strong setae .... ***Bittacomorphella***

   Right breathing horn elongate; left horn short and degenerate (Fig. 7). Abdominal tubercles strong, elongate, crowned by a circlet of four or five spines and tipped with setiferous papillae .... ***Bittacomorpha***

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DIXIDAE 23

T. MICHAEL PETERS

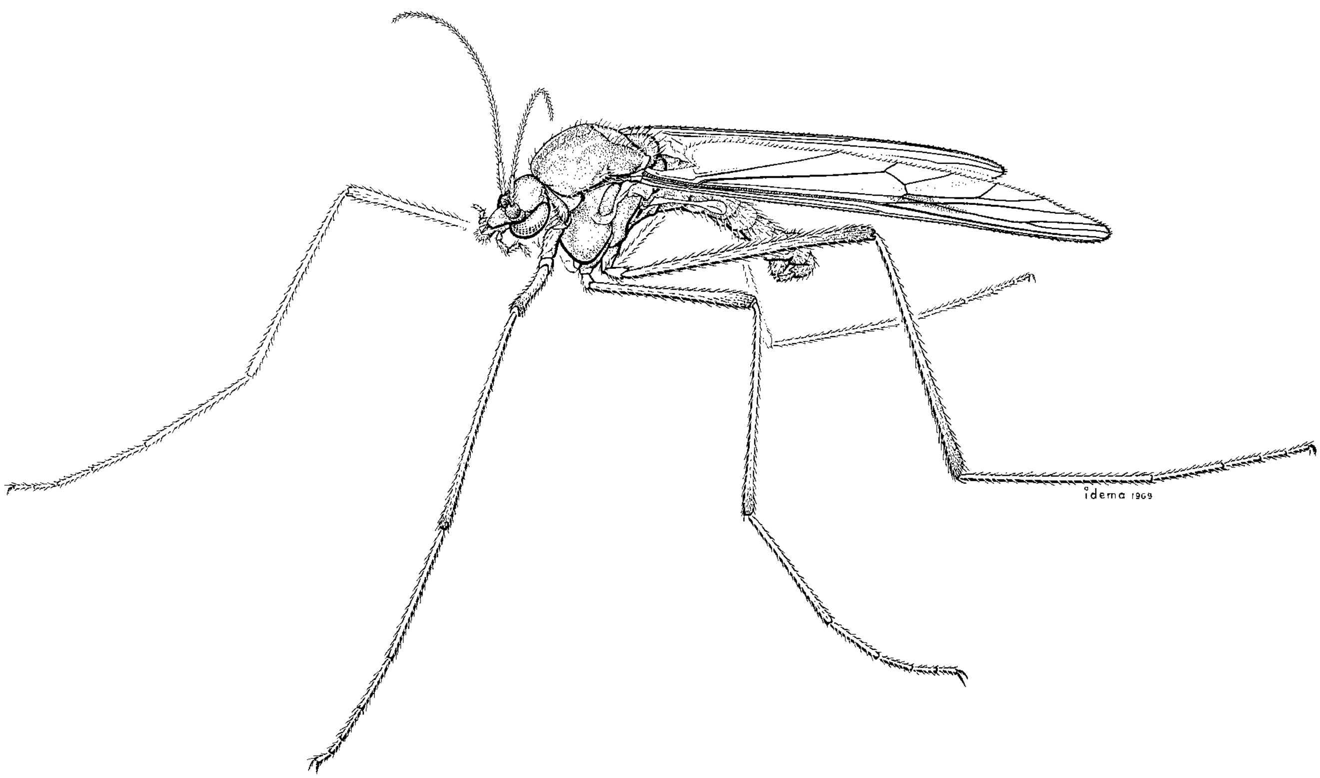


Fig. 23.1. Male of *Dixa* sp.

Slender frail flies (Fig. 1), brown, black, or yellow. Wing (Fig. 4) with R_{2+3} strongly arched; halter large. Legs and antenna long. Adult short-lived.

Adult. Head: as dark as or darker than body. Compound eyes large, more widely separated dorsally than ventrally, giving head a subtriangular appearance in frontal aspect; ocelli absent; one to five long postocular setae dorsally. Antennal socket large; pedicel enlarged; flagellum 14-segmented; flagellomeres elongate (Figs. 2, 3). Mouthparts reduced, forming a weak proboscis; labrum triangular; mandible short, thin, scimitar-shaped, nonfunctional, with single articulation; palpus long, five-segmented; lacinia weak; prementum triangular; labella short, wide.

Thorax: scutum large, with or without vittae; scutellum with transverse row of setae, with or without intersecting median row of setae longitudinally; antepronotum and postpronotum well-differentiated; katepisternum well-developed, with or without central group of setae. Wing large, hyaline or variously pigmented; R_{2+3} strongly arched (Fig. 4); crossvein m-cu broken or complete. Halter long; knob seamed. Legs long, thin; hind tibia slightly to markedly expanded distally; tarsi frequently with a distal spiniform seta on some tarsomeres, often with a basal recurved spiniform seta on tarsomere 5 of at least one leg in male but uncommon in female; hind tarsus in male smaller than other tarsi and simple, or as large as others and bearing ventral teeth; claws of at least one leg of male with two or more ventral teeth; claws of female simple.

Abdomen: unmodified anteriorly, with four pairs of spiracles. Male with terminalia inverted 180°, the rotation occurring between segments 5 and 8; gonocoxite with apical lobe and usually with basal lobe (Figs. 7–9); basal lobe usually simple, setose, small; apical lobe short to very long, variously formed; gonostylus short to long, variously formed; sclerotized sperm duct very long to lacking; cercus free or fused with tergite 10. Female with large lightly sclerotized cerci; sternite 9 narrowed midventrally, frequently expanded laterally into short lobes; sternite 10 slightly to markedly bilobate medially, with lateral edges sometimes expanded into long posterior lobes; single spermatheca sclerotized, round to elliptical, infrequently with small sclerotized neck; bursa frequently with sclerotized structures taking the form of cones, spinose bodies, or one to three groups of variously formed setae that project into lumen (Figs. 5, 6).

Egg. Ovoid, with ratio of width to length about 1:1.75. Micropyle at more tapered end. Chorion transparent. Yolk yellow, white, or green.

Larva. Elongate, cylindrical (Fig. 10). Head distinct, highly mobile. Thoracic segments distinct, slightly enlarged. One or two anterior abdominal prolegs; ventral ambulatory combs on some abdominal segments; caudal respiratory apparatus complex.

Head capsule complete. Ocular area large, clear, circular, posterior to and slightly below antennal base. Antenna one-segmented, curved with concave surface dorsally, and arising from tubercle. Frontoclypeal apotome a convex subtrapezoidal sclerite, narrowed anteriorly, comprising most of dorsum of head. Labrum subtriangular, with apex directed anteriorly; labral brush consisting of many hairs that are shorter anteriorly and progressively elongate posteriorly. Mandible subquadrangular, with two articulations; stout apical seta on distal outer angle; inner surface complex, with comb of hairs on incisor area, and with teeth distally and small uniform pegs proximally on molar area. Maxilla with weak basal sclerite; endite lobe elongate, triangular, with apex directed distally; maxillary palpus one-segmented, with shape similar to antenna. Labium complex, subtriangular; oral surface covered with pegs and short spiniform setae.

Thoracic segments each distinct, without spiracles, sparsely setose. Mesothoracic segment largest; pro- and metathoracic segments subequal.

Abdomen 10-segmented; segments 1–7 subequal. Pair of retractile crochet-bearing prolegs on venter of segment 1 or segments 1 and 2. Ambulatory comb, with or without median triangular plate, present on venter of each of segments 5–7. Dorsum of anterior abdominal segments with or without complex plumose hairs sometimes arranged as a corona (Figs. 11, 12). Segment 8 with pair of spiracles on dorsum; each spiracle with postspiracular process extending laterally from attachment immediately behind spiracle, fringed with single row of hairs; pairs of branched or palmate paraspiracular hairs arranged in a row between and frequently slightly anterior to spiracles, with some frequently attached to anterior margin of variously formed median plate. Segment 9 with one unpaired median sclerite, a pair of posterolateral processes, and a pair of anterolateral plates; unpaired median sclerite variously formed, frequently with microtrichia, and frequently fused to posterolateral process near its dorsal anteromedial seta; posterolateral process frequently pointed, fringed with a single row of short to long hydrofuge setae; anterolateral plate subrectangular, frequently fused dorsoposteriorly to the posterolateral processes, and bearing a pecten on posterior margin; this pecten variously formed, consisting of either spiniform setae, or small lobes bearing dendritic hairs or setae; three-pronged spine frequently ventralmost structure of pecten. Segment 10 partially to completely encircled by strongly sclerotized saddle that extends posteriorly beyond segment as postanal process; paired subtriangular ventrolateral plate beneath lateral margin of saddle bearing three very long setae; anus and eversible anal papillae located at apex of segment; ventral anal comb situated at edge of anus, and consisting of single or double row of compound spines or spiniform setae; postanal process cylindrical, strongly sclerotized, frequently pointed posteriorly, separated from saddle by sharp break in sclerotization, and bearing two or three pairs of very long posteriorly projecting caudal setae at its apex.

Pupa. Generally similar to pupa of Culicidae. Respiratory trumpets widely separated, arising from fairly distinct lateral cephalic tubercles; spiracular-closing mechanism within thorax, with trachea-like tube continuing into trumpet; trachea-like tube constricted at or beyond middle before forming funnel-like or flask-like inner wall, provided distally with complex spiculi that apparently close lumen; apex of trumpet wide. Halter case long.

Abdomen long and slender, strongly curved under cephalothorax. Segments poorly sclerotized, without lateral border; tergites 2–7 with submedian transverse ridges and angular processes. Spiracular sensilla present on tergites 1–7, very large on tergite 1; dorsal sensilla present on tergites 2–7; all hairs single and simple. Tergite 1 very short. Tergite 8 almost as long as tergite 7, with its caudal border indistinctly emarginate; sternite 8 as large as sternite 7. Tergite 9 represented by broad fused bases of paddles; sternite 9 distinct, broader than long; paddle long, triangular, not basally articulated and not movable, continuous with tergite 9, without supporting sclerotizations. Anal lobe of female single, slightly cleft apically, with lateral parts probably representing cerci; anal lobe of male consisting of a pair of ventrolateral lobes containing developing gonopods and a dorsomedial lobe representing proctiger and aedeagus. Belkin (1962) should be consulted for larval and pupal chaetotaxy.

Biology and behavior. The biology of most dixid species is unknown. *Dixella californica* (Johannsen) has been studied by Hubert (1953), and the biology of dixids, in general, has been discussed by Nowell (1951).

Larval Dixidae inhabit lakes, streams, ponds, rivers, swamps, marshes, and bogs; the adults are found nearby. During the day, adults rest on vegetation or soil at the water's edge. The insect usually rests on a vertical plane with its head up. Hubert (1953) concluded that adults feed and drink. He also states that they assume a particular position while drinking. No one has examined the alimentary tract for traces of food, and consequently, consumption of food has not been proven.

The mating behavior of Dixidae follows two distinct patterns, often within the same species. The literature often reports that mating follows swarming, which is characteristic of most Dixidae. The swarm, occurring only at dusk and comprising one to many males, forms along the bank of streams or ponds, below or near overhanging vegetation. Nowell (1951) and Hubert (1953) reported that mating is initiated within the swarm. Nowell observed females flying into the swarm and, subsequently, falling out with a male to complete copulation on the ground. Hubert (1953) described the second type of mating behavior. It usually occurs during daylight and is not accompanied by swarming.

After mating, the female oviposits in the water. Nowell (1951) has described the process whereby the female inserts the tip of her abdomen into the water and deposits the eggs beneath the surface. The ovoid eggs, numbering 16 to 107, are enclosed within a heavy gelatinous matrix. The mass sinks until it touches a substrate to which it adheres.

Hatching occurs four or more days after oviposition. The matrix surrounding the eggs at oviposition disintegrates before the larvae hatch. The doubled-up larva escapes from the egg through a hole that is formed at one end just before the egg hatches. Part of the chorion evidently dissolves to create the hole.

Larvae spend most of their lives at the edge of the water just below the water–air interface. The head and caudal respiratory structures of the larva are partially covered by water and the rest of the body remains in air, resting on some solid substrate. The resting larva thus assumes a typical inverted U-shaped position. The larva breathes atmospheric air through its two posterior spiracles. Swimming, accomplished by alternate lateral movements of the anterior part of the body, is generally restricted to the surface, although larvae usually submerge when disturbed.

Larvae feed on microorganisms and decayed organic material. Movement of the labral brushes sets up currents bringing food to the mouth, where it is strained out. Older larvae also dive and scrape microorganisms from submerged vegetation and rocks. Length of the larval stage depends on the abundance of food. The insect may pass through the four larval instars in as little as 18 days when food is abundant.

The pupal stage occurs near the water rather than in it. The fourth instar larva crawls 1–4 cm out of the water onto the bank or emergent vegetation. The insect remains in a vertical position and pupates. The pupal stage lasts from 17 h to 5 days.

The newly emerged adult is ready to fly in about 1 h, after the wings have expanded and the exoskeleton has hardened. The male terminalia rotate 180° in the first 4 h. During this time copulation probably does not occur.

Classification and distribution. All but one of the 43 species currently recognized as the Nearctic dixid fauna have been recently described or redescribed (Peters and Cook 1966). In this monograph the subgenera recognized by Hubert (1965) are raised to generic rank following Nowell (1951, 1963). One genus, *Dixapuella* Dyar & Shannon, has been synonymized with *Dixella* Dyar & Shannon. Eleven species recognized by Hubert (1965) are synonymized and 11 new species are described. Only two species, *Dixella naevia* (Peus) and *Dixella dyari* (Garrett), have been shown to be Holarctic. Sources of the type material for all dixids originally described from North America are presented by Peters (1968). The most recent addition to the fauna of the Nearctic dixids is a new species, *Dixella alexanderi* Peters, in which larva, pupa, and both sexes of adult have been described (Peters and Barbosa 1970). No fossil dixids have been reported from the Nearctic region.

Keys to genera

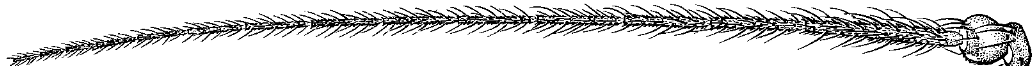
Adult

1. First flagellomere of antenna cylindrical (Fig. 2), rarely slightly fusiform. Katepisternal setae lacking. Sclerotized inflections of bursa in female, if present, consisting of a pair of solid cones or spinose areas. Apical lobe of gonocoxite in male elongate, at least one-half as long as gonostylus (Fig. 7), variously formed, rarely triangular .... ***Dixella*** Dyar & Shannon
   19 spp.; Peters and Cook 1966, Peters and Barbosa 1970

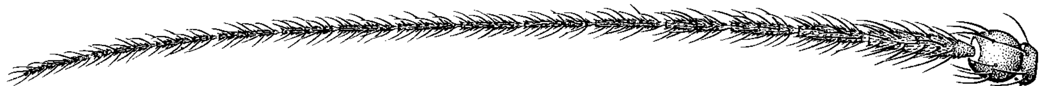
   First flagellomere of antenna slightly fusiform (Fig. 3). Katepisternal setae frequently present. Sclerotized inflections of bursa in female, if present, consisting of groups of spines with bases contiguous but not originating from a single sclerotized unit. Apical lobe of gonocoxite less than half as long as gonostylus (Figs. 8, 9) 2

2. Gonostylus subrectangular in dorsal aspect, truncate apically (Fig. 9). Hind claw of male without ventral teeth. Sclerotized inflections of bursa consisting of one pair of spines and two groups of three spines; all spines with wide thick bases, tapering sharply to elongate thick processes (Fig. 6) .... ***Meringodixa*** Nowell
   1 sp., *chalonensis* Nowell; coastal region of western U.S.A.; Nowell 1951

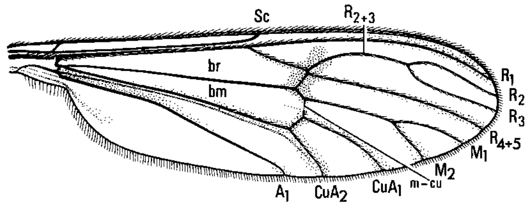
   Gonostylus tapering in dorsal aspect, pointed or rounded apically (Figs. 7, 8). Hind claw of male with or without ventral teeth. Sclerotized inflections of bursa, if present, consisting of one to three groups of setae (Fig. 5) .... ***Dixa*** Meigen
   22 spp.; Peters and Cook 1966



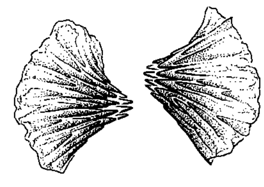
2 *Dixella nova* ♂



3 *Dixa brevis* ♂

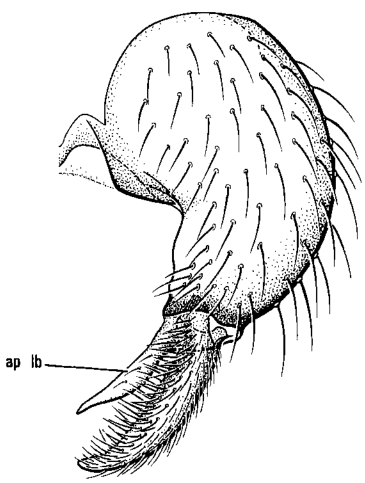


4 *Dixella nova* ♂

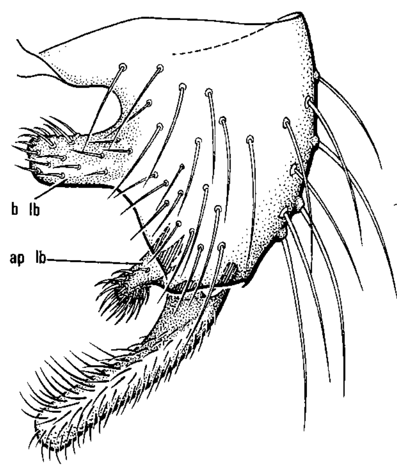


5 *Dixella nova* ♀

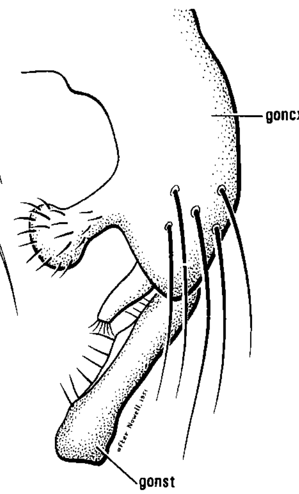
6 *Meringodixa chalonensis* ♀



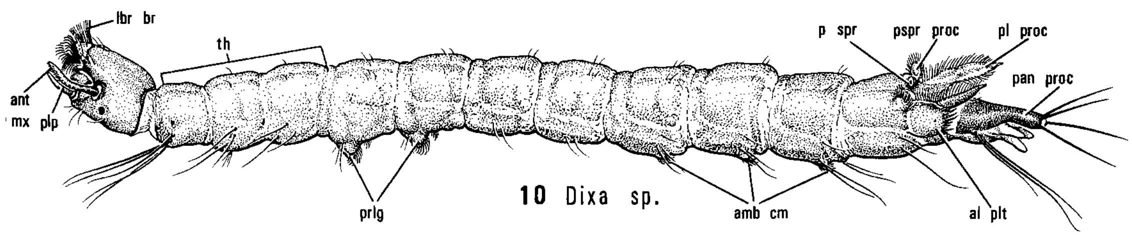
7 *Dixella clavata* ♂



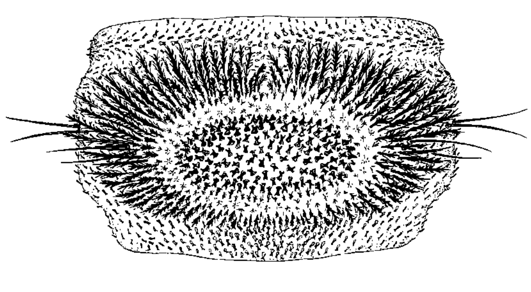
8 *Dixa brevis* ♂



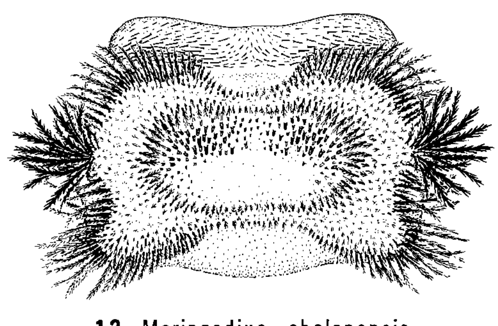
9 *Meringodixa chalonensis* ♂



10 *Dixa* sp.



11 *Dixa* sp.



12 *Meringodixa chalonensis*

Larva

1. One pair of abdominal prolegs; tuft of long hairs on each side of abdominal segments 2–6 (Fig. 12) .... ***Meringodixa***

   Two pairs of abdominal prolegs; tuft of long hairs on abdominal segments absent 2

2. Abdominal segments 2–7 each with a dorsal corona (Fig. 11) .... ***Dixa***

   Abdominal segments each without a dorsal corona .... ***Dixella***

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Figs. 23.2–12. Antennae, wing, abdomen, and larvae: antenna of (2) *Dixella nova* (Walker) and (3) *Dixa brevis* Garrett; (4) wing of *Dixella nova*; sclerotized inflections of bursa in female of (5) *Dixella nova* and (6) *Meringodixa chalonensis* Nowell; left gonopod of male of (7) *Dixella clavata* (Loew), (8) *Dixa brevis*, and (9) *Meringodixa chalonensis* [redrawn from Nowell (1951)]; (10) lateral view of left side of larva of *Dixa* sp.; dorsal view of an abdominal segment of larva of (11) *Dixa* sp. and (12) *Meringodixa chalonensis*.

Abbreviations: al plt, anterolateral plate of segment 9; amb cm, ambulatory comb; ant, antenna; ap lb, apical lobe; b lb, basal lobe; goncx, gonocoxite; gonst, gonostylus; lbr br, labral brush; mx plp, maxillary palpus; pan proc, postanal process; pl proc, posterolateral process; prlg, proleg; p spr, posterior spiracle; pspr proc, postspiracular process; th, thorax.

CHAOBORIDAE 24

EDWIN F. COOK

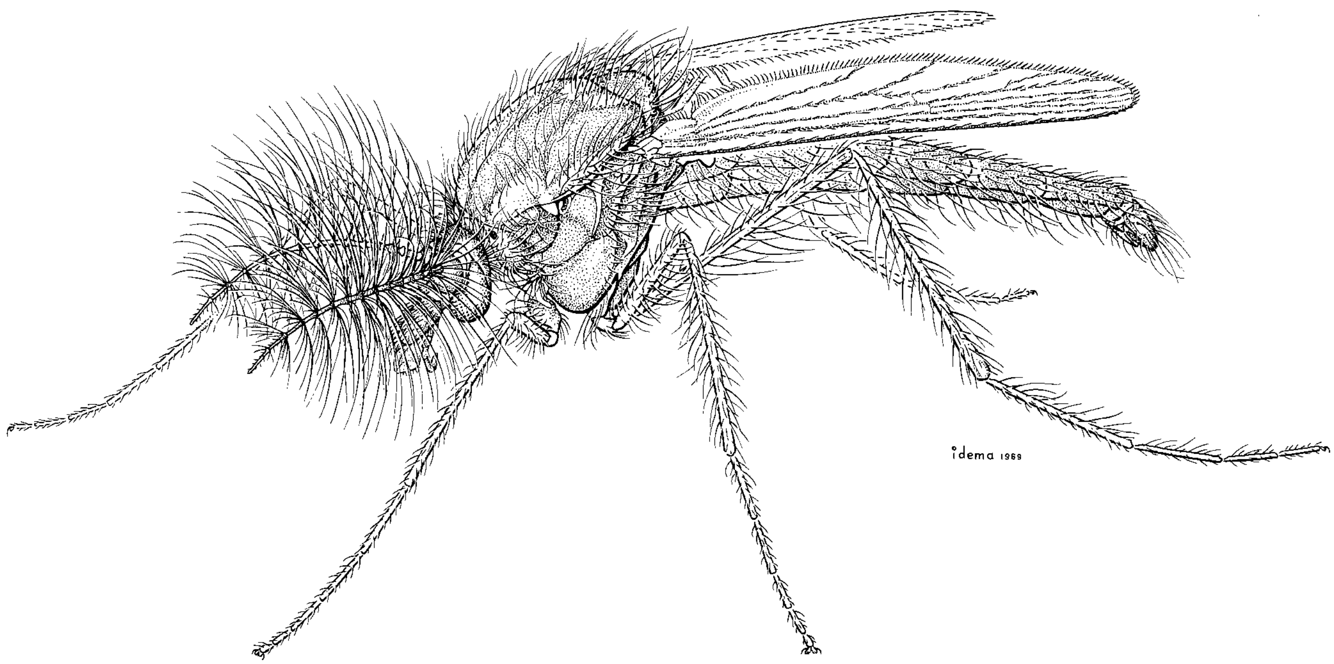


Fig. 24.1. Male of *Chaoborus* (*Chaoborus*) *americanus* (Johannsen).

Family very close to Culicidae. Adult small to medium (Fig. 1), 1.4–10 mm long, delicate, usually pale yellow, gray, or brown; ocelli absent; antenna plumose in male, with pedicel greatly enlarged; most veins covered with slender scales. Larva aquatic, with distinct head capsule, prehensile antennae, and greatly reduced labral brushes; thorax enlarged; respiratory siphon sometimes present.

Adult. Head: ocelli absent; eyes separated in both sexes (Fig. 4). Antenna with globular pedicel that is nearly twice as large in male as in female; flagellum plumose in male, merely setose in female. Clypeus elongate, conspicuous. Proboscis fairly short, with only labella extending beyond tip of labrum; mandible well-sclerotized, with less-sclerotized serrate edges in female Corethrellinae and simple edges in others; lacinia present, not heavily sclerotized; palpus five-segmented; labium with conspicuous prementum and well-developed labella. Most cranial sclerites setose.

Thorax: a few to many setae on scutum and scutellum (Fig. 5); a few setae on episternum and epimeron; two pairs of bare stripes on scutum. Legs unmodified, with simple or pectinate claws; claws either equal or asymmetric.

Wing with culicid-like venation (Figs. 2, 3); Sc present; R four-branched; M two-branched; Cu two-branched; branches of Rs almost straight and parallel to one another. Slender scale-like setae on most veins and on posterior margin; wing sometimes patterned by light and dark scales or by pigment in membrane; membrane covered with microtrichia. Halter with at least a few setulae on knob.

Abdomen: eight simple pregenital segments, each bearing a pair of small spiracles; tergites and sternites bearing setae and microtrichia. Female terminalia consisting of well-developed tergite 9, narrow and sometimes fragmented sternite 9, gonopore in atrium between segments 8 and 9, pair of setose cerci, and three spermathecae except in Corethrellinae, which have only one. Male terminalia shown in Figs. 6–8; tergite 9 well-developed, often laterally lobate, and produced medially into one or two acute or rounded lobes; sternite 9 reduced; gonocoxite well-developed, setose, with subapically median thumb-like projection in some species of *Chaoborus* (*Sayomyia* Coquillett); gonostylus slender, with or without apical spiniform seta; parameres unarmed or each with claw-like apical spine, medially fused in Corethrellinae; aedeagus inconspicuous, membranous.

Larva. Head capsule complete, fully exposed (Figs. 9, 10). Larval and developing adult eyes both visible in last instar. Antennae prehensile, either approximated or widely separated, with three to five long blade-like setae at apex. Frontoclypeal apotome obvious, large, with two to twelve modified setae at apex or between clypeus and labrum except in Corethrellinae. Labrum well-developed but lacking well-developed labral brushes; mandible well-developed, bearing spines; maxilla reduced to stipes and palpus, bearing blade-like, spatulate, serrate, or otherwise modified setae; labium reduced, but with elaborately modified setae.

Thorax enlarged, with the three segments fused into a single unit, bearing numerous simple and multiple setae (Fig. 10).

Abdomen consisting of eight obvious segments, a reduced ninth segment, and a tenth or anal segment (Fig. 14). Anterior segments 1–7 similar. Segment 8 bearing a long or short respiratory siphon except in *Chaoborus* Lichtenstein; tracheal system in *Chaoborus* reduced to dorsally pigmented air sacs in thorax and abdominal segment 7, but normal in *Mochlonyx* Loew, with enlargements in thorax and abdominal segment 7. Anal segment bearing four long or short papillae and several setae and setal clusters; fan-like row of pectinate setae on ventral side except in Corethrellinae; row of hooked or blade-like spines often around each side of anus.

Pupa. All but those of Corethrellinae generally resembling culicid pupa; cephalothorax less than one-third total length of pupa; abdomen hanging straight down or only slightly curved under thorax. Thoracic respiratory organ (Figs. 12, 13) either spindle-shaped or open and trumpet-like. Pair of swimming paddles at end of abdomen in *Corethrella* Coquillett (Fig. 11) fused basally and pointed apically like those at apex of ceratopogonid pupa, or larger, rounded, and separated from one another in other subfamilies.

Biology and behavior. Immature Chaoboridae are found in standing, freshwater habitats. The larvae prey on other aquatic organisms, including the larvae of mosquitoes. The larva of *Chaoborus punctipennis* (Say) has been the subject of much limnological research in North America (Juday 1921, Eggleton 1932, Miller 1941). The bionomics of *Eucorethra underwoodi* Underwood and *Mochlonyx* have been discussed by Lake (1960, 1969), and that of *Chaoborus* by Borkent (1979) and Saether (1972). An extensive bibliography of *Chaoborus* was published by Roth and Parma (1970).

Classification and distribution. Three subfamilies are recognized, and all are found in the Nearctic region. The Corethrellinae is mainly tropical with only five species of two genera in the Nearctic region. Eucorethrinae is monotypic and is found only in the Nearctic region. Chaoborinae has a nearly worldwide distribution and is represented by five genera, only two of which (*Chaoborus* with ten species and *Mochlonyx* with three species) occur in the Nearctic region. *Chaoborus* contains six subgenera, including *Sayomyia* which is mainly tropical, but five species are found in the Nearctic.

Several fossil Chaoboridae from the Oligocene are known from Europe and North America (Borkent 1979). These include one named species of *Mochlonyx* and one of *Chaoborus* in Baltic amber; pupae and larvae of *Chaoborus tertiarius* (von Heyden) in paper coal deposits from Germany; and two unnamed *Chaoborus* from Aix-en-Provence, France. *Chaoborus exita* (Scudder) from White River, Colo., is probably not a species of Chaoboridae.

Keys to genera

Adult

1. Clypeus long, nearly as long as height of rest of head capsule (Fig. 4). Halter with numerous setae on stem and knob. Postpronotum undivided medially, i.e. its lateral lobes connected to one another by a narrow transverse band between antepronotum and scutum. Tergite 9 of male produced into two posteriorly directed spine-like processes .... EUCORETHRINAE....*Eucorethra* Underwood

   1 sp., *underwoodi* Underwood; boreal, extending southward into eastern and western U.S.A.; Cook 1956

   Clypeus shorter, no more than two-thirds height of rest of head capsule. Halter with or without numerous setae. Lateral lobes of postpronotum separated medially by scutum and antepronotum. Tergite 9 of male with only one median process or none 2

2. R_1 terminating in C nearer to Sc than to R_2 (Fig. 3). Clypeus with very few setae .... CORETHRELLINAE....3

   R_1 terminating in C near wing apex, nearer to R_2 than Sc (Fig. 2). Clypeus with numerous setae .... CHAOBORINAE....4

3. Wing and legs without pattern. Gonocoxite with one to three foliaceous setae medially .... ***Lutzomiops*** Lane

   1 sp., *kerrvillensis* Stone; Kerrville, Tex.

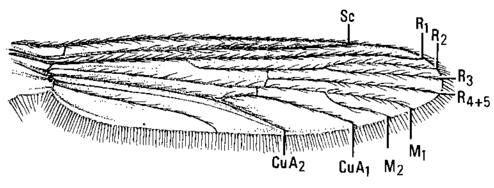
Wing and legs usually with spots or other pigmented pattern. No foliaceous setae on gonocoxite .... ***Corethrella*** Coquillett

4 spp.; eastern and southwestern U.S.A., southeastern Canada; Stone 1968

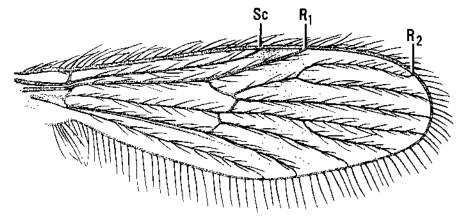
4. First tarsomere shorter than second. Halter with numerous setae on stem and knob. Gonostylus with spiniform seta at apex (Fig. 6). Anteponotum of female resembling a broad collar anterior to scutum .... ***Mochlonyx*** Loew

3 spp.; boreal, extending southward into eastern and western U.S.A.; Cook 1956

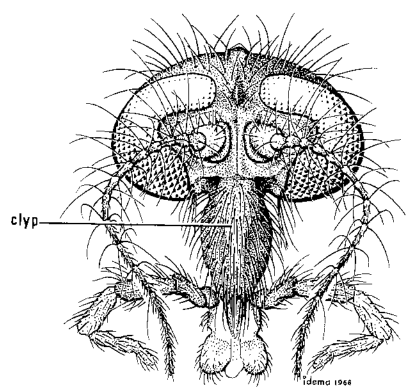
First tarsomere longer than second. Halter with two groups of two to five setae on knob (Fig. 5). Gonostylus without apical spiniform seta at apex (Figs. 7, 8). Female antepronotum reduced to slender band medially .... ***Chaoborus*** Lichtenstein....5



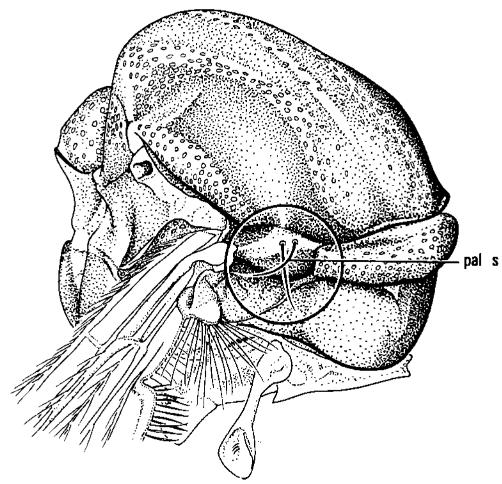
2 C. (Chaoborus) americanus



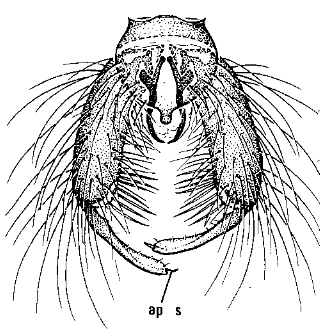
3 Corethrella sp.



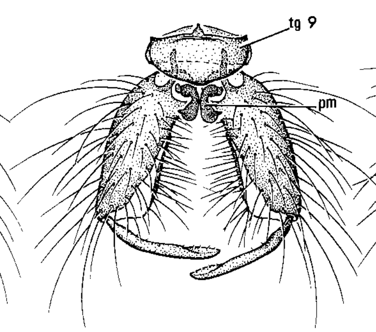
4 Eucorethra underwoodi ♀



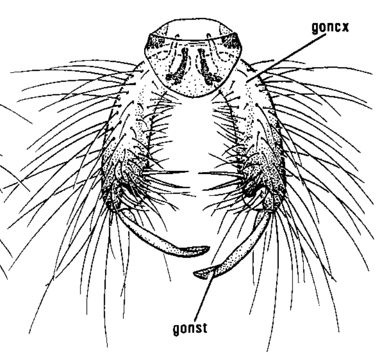
5 C. (Chaoborus) americanus ♂



6 Mochlonyx cinctipes ♂



7 C. (Chaoborus) americanus ♂



8 C. (Sayomyia) punctipennis ♂

Figs. 24.2–8. Wings, head, thorax, and male terminalia: wing of (2) *Chaoborus* (*Chaoborus*) *americanus* (Johannsen) and (3) *Corethrella* sp.; (4) anterior view of head of adult of *Eucorethra underwoodi* Underwood; (5) posterolateral view of thorax of *Chaoborus* (*Chaoborus*) *americanus*, showing postalar setae (*circled*); dorsal view of male terminalia of (6) *Mochlonyx cinctipes* (Coquillett), (7) *Chaoborus* (*Chaoborus*) *americanus*, and (8) *Chaoborus* (*Sayomyia*) *punctipennis* (Say).

Abbreviations: ap s, spiniform seta at apex of gonostylus; clyp, clypeus; goncx, gonocoxite; gonst, gonostylus; pal s, postalar setae; pm, paramere; tg, tergite.

5. Wing spotted. Legs with or without spots or rings. Postalar setae absent 6
   Wing unspotted. Legs unmarked. Postalar setae present (Fig. 5) ....**Chaoborus (Chaoborus** Lichtenstein)

   3 spp.; mainly north of 36° N lat.; Saether 1970, 1972

6. Pulvilli at least half as long as claws. Gonocoxite without subapicomedial lobe or stout paired setae; paramere with large claw-like apex ....***Chaoborus*** (***Schadonophasma*** Dyar & Shannon)

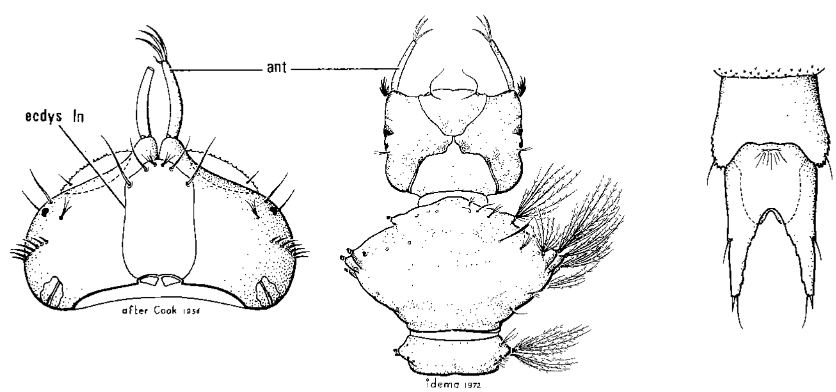
   2 spp.; boreal, extending southward into eastern and western U.S.A.; Borkent 1979

   Pulvilli minute, less than one-fourth as long as claws. Gonocoxite either with an apicomedial lobe or with paired stout setae on apical half (Fig. 8); paramere with small apex..***Chaoborus*** (***Sayomyia*** Coquillett)

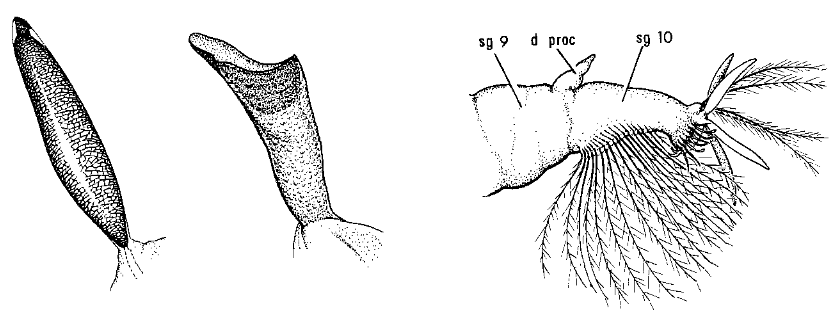
   5 spp.; widespread; Saether 1970, 1972

Fourth instar larva

1. A transverse row of spiniform setae on each side of head. Antennae approximated. Ecdysial line on dorsum of head distinct (Fig. 9). Anal segment with a tuft of long bristles ventrally instead of a fan ....**Corethrellinae**
   No transverse row of setae on side of head. If antennae approximated, ecdysial line indistinct. Anal segment with longitudinal fan-like row of bristles (Fig. 14) 2



9 Corethrella brakeleyi **10** Eucorethra underwoodi **11** Corethrella brakeleyi



12 C. (Chaoborus) americanus **13** Eucorethra underwoodi **14** C. (Sayomyia) punctipennis

Figs. 24.9–14. Immature stages: (9) head of larva of *Corethrella brakeleyi* (Coquillett); (10) dorsal view of head, thorax, and abdominal segment 1 of larva of *Eucorethra underwoodi* Underwood; (11) dorsal view of terminal two abdominal segments of pupa of *Corethrella brakeleyi*; thoracic respiratory organ of pupa of (12) *Chaoborus* (*Chaoborus*) *americanus* (Johannsen) and (13) *Eucorethra underwoodi*; (14) lateral view of abdominal segments 9 and 10 of larva of *Chaoborus* (*Sayomyia*) *punctipennis* (Say).

Abbreviations: ant, antenna; d proc, dorsal process; ecdys ln, ecdysial line; sg, segment.

2. Thorax diamond-shaped in dorsal view (Fig. 10). Siphon of segment 8 short, stout, terminating in conspicuous flat spiracular apparatus .... EUCORETHRINAE.... ***Eucorethra***

   Thorax rounded laterally. Siphon absent or as long as anal segment, with pointed apex .... CHAOBORINAE....3

3. Antennae widely separated at base. Head broad. Ecdysial line on dorsum of head distinct. Siphon present .... ***Mochlonyx***

   Antennae approximated. Head narrow. Ecdysial line not obvious. No siphon or spiracles .... ***Chaoborus***....4

4. Dorsal process of apparent segment 9 with subapical constriction (Fig. 14). Subordinate tooth on second mandibular tooth hair-like. Labrum with pair of long setae on anterior surface near middle .... ***Chaoborus*** **(*Sayomyia*)**

   Dorsal process of apparent segment 9 without subapical constriction (process sometimes absent). Subordinate tooth on second mandibular tooth distinctly thickened. Labrum with only short setae anteromedially 5

5. Larva large, 11–20 mm. Anal fan large, with 21–38 setae; tentorium thick, pigmented .... ***Chaoborus*** **(*Schadonophasma*)**

   Larva smaller, not exceeding 16 mm. Anal fan smaller with 20–28 setae; tentorium thin, indistinct .... ***Chaoborus*** **(*Chaoborus*)**

Pupa

1. Swimming paddles basally fused, rigid, acutely pointed (Fig. 11) .... **Corethrellinae**

   Swimming paddles free, moveable, broadly rounded apically 2

2. Thoracic respiratory organ trumpet-shaped, wide open at apex (Fig. 13) .... EUCORETHRINAE.... ***Eucorethra***

   Thoracic respiratory organ spindle-shaped, with small apical opening (Fig. 12) .... CHAOBORINAE....3

3. Swimming paddle with rigid membrane, weak marginal ribs, and a median reinforcing rib .... ***Mochlonyx***

   Swimming paddle with membrane reinforced by median and strong marginal ribs ...... ***Chaoborus***

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ALAN STONE

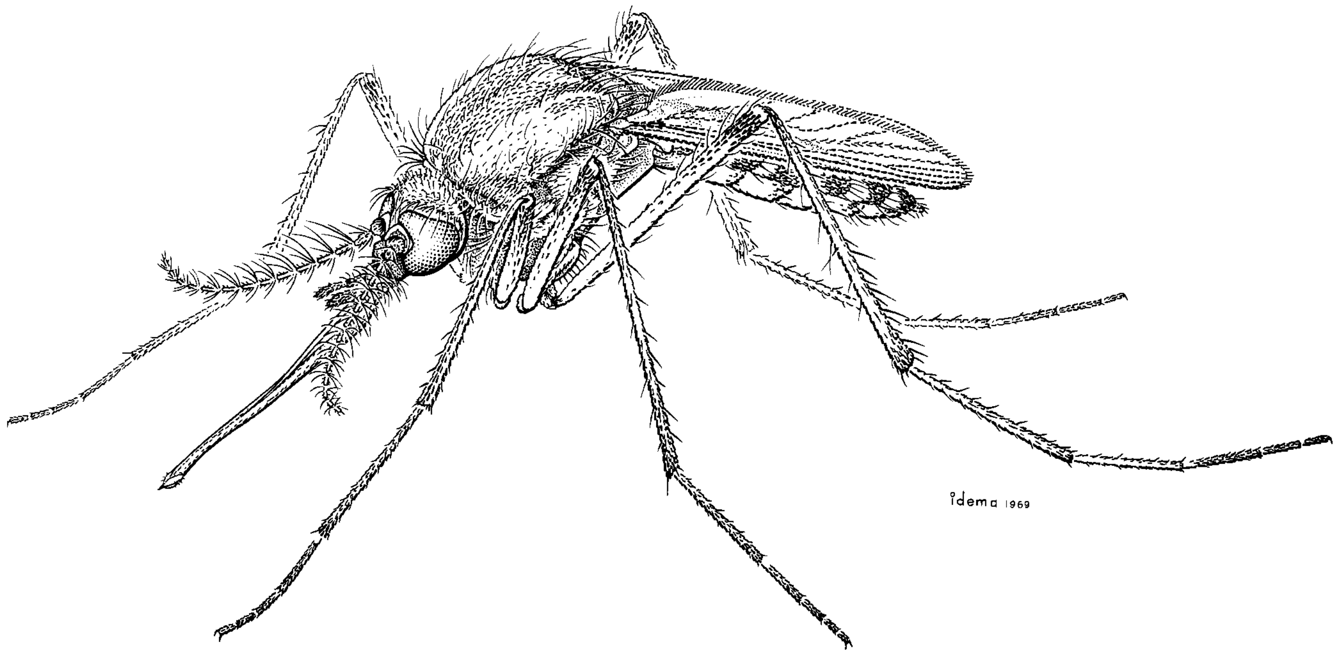


Fig. 25.1. Female of *Aedes sticticus* (Meigen).

Slender delicate flies, 3–9 mm long (Fig. 1). Legs slender. Proboscis slender, much longer than head (Figs. 2–4); labrum, mandibles, laciniae, and hypopharynx greatly elongate, stylet-like, enclosed in sheath formed by labium; palpus of male usually about as long as proboscis, with terminal segments often bearing dense tufts of long setae. Wing veins and usually most of the body and legs clothed with scales.

Adult. Head: small, subspherical (Figs. 2–4). Eye reniform, with facets of equal size, similar in both sexes; ocelli absent. Antenna with very small scape, enlarged globose pedicel, and 13 long slender flagellomeres; each flagellomere with a whorl of hairs that are much longer and more abundant in male than in female.

Thorax: ovoid, broadest dorsally, usually heavily scaled above but less so laterally (Figs. 12–18). Scutellum short, evenly arched or trilobate; postnotum rather large, usually bare. Wing (Fig. 5) narrow, elongate, lying flat above abdomen when at rest; at least 10 veins reaching wing margin; cells br and bm reaching to near middle of wing; C continuing around wing, but weaker posteriorly. Scales (Fig. 6) usually abundant on wing veins; fringe of long scales along posterior margin of wing; knob of halter usually bearing scales.

Abdomen: narrow, slender, subcylindrical (Figs. 19, 20). Male terminalia (Figs. 2.116–120; 21, 22) usually highly modified, not greatly enlarged, rotated 180° between segments 7 and 8 soon after emergence.

Larva. Freely swimming 'wriggler' with well-defined subquadrate head, enlarged thorax composed of three fused segments, and rather slender abdomen (Figs. 33, 34). Antennae well-separated, one-segmented, arising from anterolateral margins of head (Figs. 23, 27). Labral brush (Figs. 23, 26, 27) usually consisting of many very fine hairs, but sometimes reduced to about 10 stout curved rods (Fig. 26).

Thorax a broad mass bearing various setae particularly as lateral tufts.

Abdomen with 10 segments, distinctly narrower than thorax. Segments 1–7 each with up to 13 pairs of setae. Segment 8 with dorsal respiratory organ; spiracles flush with body surface, surrounded by plates or flaps in Anophelinae (Fig. 33); spiracles at end of a siphon in other subfamilies (Figs. 28–32). Segment 10 with sclerotized dorsal saddle or sclerotized ring, long dorsal hairs, and usually a prominent ventral brush; two or four membranous anal papillae present.

Biology and behavior. The immature stages of Culicidae are aquatic. Larvae and pupae are active swimmers in quiet water and live in many habitats, such as swamps, marshes, snowmelt pools, rain puddles, man-made containers, tree holes, and plant axils. Eggs are laid singly or in rafts either directly on water or in places that are later flooded. Some larvae prey on other mosquito larvae and are beneficial to man. The female of most species, however, sucks blood from vertebrates and is a painfully annoying pest, sometimes also transmitting disease organisms to man and other animals. Serious disease organisms transmitted by mosquitoes are those causing malaria, filariasis, yellow fever, dengue, and the encephalitides.

Classification and distribution. Although dixids and chaoborids are sometimes included in the Culicidae, these are treated here as separate families. Recently *Coquillettidia* Dyar has been raised from a subgenus of *Mansonia* Blanchard to generic rank, and this change is adopted here. *Kompia* Aitken is also retained as a valid subgenus rather than continuing it as a synonym of *Ochlerotatus* Lynch Arribálzaga. The subgenus *Mochlostyrax* Dyar & Knab is returned to synonymy under *Culex* (*Melanoconion* Theobald). Three species of *Aedes* Meigen are lone representatives of the Old World subgenera *Aedes*, *Stegomyia* Theobald, and *Aedimorphus* Theobald; and the subgenus *Nyssorhynchus* Blanchard and the genera *Deinocerites* Theobald and *Haemagogus* Williston are intrusions from the Neotropical fauna.

Three fossil species have been described in the genus *Culex* from North America. Two from the Eocene of Wyoming and Colorado are mosquitoes, probably of the genus *Culex*; the third, from the Tertiary of Utah, probably belongs to the family Psychodidae.

Useful keys to Nearctic species are found in the references listed at the end of this chapter.

Keys to genera

Adult

1. Abdomen without scales, or sparsely scaled with tergites not covered (Fig. 19). Palpus of female nearly as long as proboscis (Fig. 2). Scutellum with evenly rounded hind margin .... ANOPHELINAE...***Anopheles*** Meigen....2

   Abdomen densely scaled, at least beyond tergite 1 (Fig. 20). Palpus of female not more than three-fourths length of proboscis, usually much shorter (Figs. 3, 4). Scutellum trilobate except in *Toxorhynchites* Theobald 3

2. Hind tarsus all dark. Gonocoxite with one internal and two parabasal spines (Fig. 21) .... ***Anopheles*** (***Anopheles*** Meigen)
   13 spp.; widespread

   Hind tarsus with at least tarsomeres 3 and 4 entirely white. Gonocoxite with one internal, one parabasal, and two accessory spines (Fig. 22) .... ***Anopheles*** (***Nyssorhynchus*** Blanchard)
   1 sp., *albimanus* Weidemann; subtropical

3. Proboscis rigid, with basal half thickened and apical half strongly curved downward and backward (Fig. 4). Scutellum rounded on posterior margin .... TOXORHYNCHITINAE....***Toxorhynchites*** Theobald (***Lynchiella*** Lahille)
   1 sp., *rutilus* (Coquillett); eastern U.S.A.

   Proboscis in life not rigid, nearly uniformly thick, not curved downward and backward on apical half. Scutellum trilobate on posterior margin, with bristles in three groups (Figs. 15–18) .... CULICINAE....4

4. Base of hind coxa in line with or above upper margin of meron (Fig. 12). Postnotum with median tuft of bristles (Fig. 12) .... SABETHINI....***Wyeomyia*** (***Wyeomyia*** Theobald)
   4 spp.; Saskatchewan and Nova Scotia south to Florida

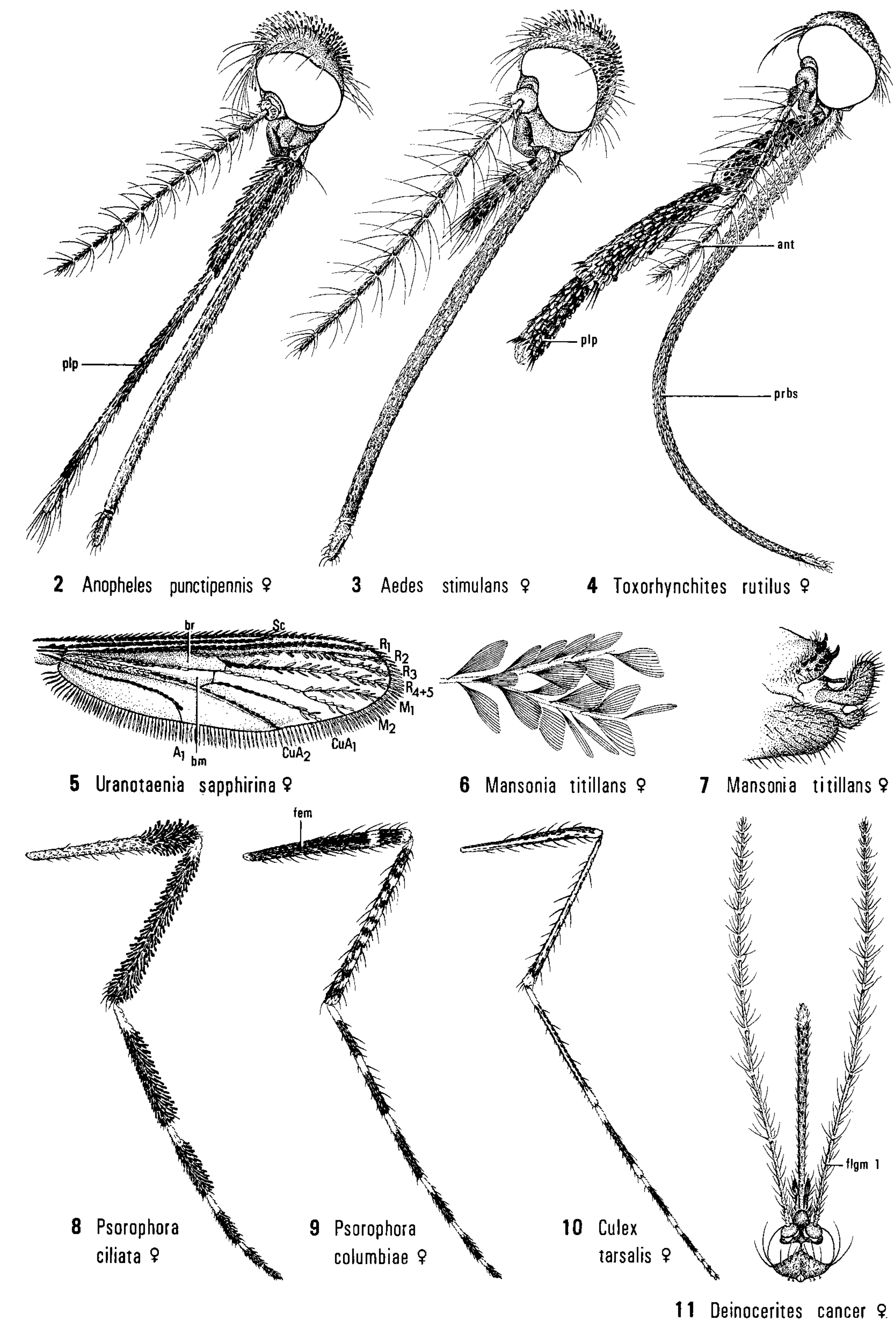
   Base of hind coxa below upper margin of meron (Figs. 13, 14). Postnotum without median bristles .... CULICINI....5

5. Cell r_2 of wing much shorter than vein R_{2+3}; A_1 reaching wing margin at or before level of forking of CuA (Fig. 5) .... ***Uranotaenia*** Lynch Arribálzaga
   3 spp.; southeastern Canada to California and Florida

   Cell r_2 of wing as long as or longer than vein R_{2+3}; A_1 reaching wing margin well beyond level of forking of CuA 6

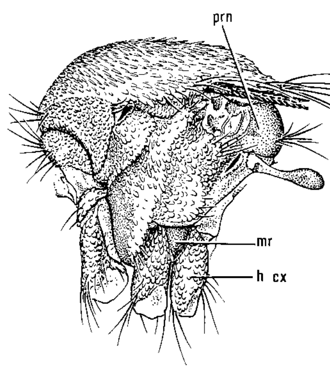
6. Spiracular bristles present (Fig. 14) 7

   Spiracular bristles absent (Fig. 13) 10

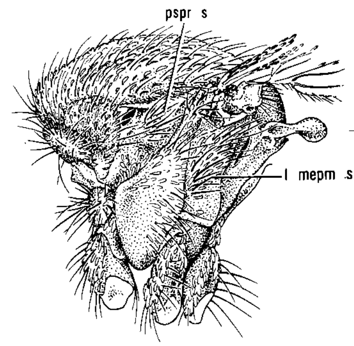


Figs. 25.2–11. Adult female: lateral view of head of (2) *Anopheles punctipennis* (Say), (3) *Aedes stimulans* (Walker), and (4) *Toxorhynchites rutilus* (Coquillett); (5) wing of *Uranotaenia sapphirina* (Osten Sacken); (6) scales on dorsal surface of wing of *Mansonia titillans* (Walker); (7) lateral view of left side of apex of abdomen of *Mansonia titillans*; hindleg of (8) *Psorophora ciliata* (Fabricius), (9) *Psorophora columbiae* (Dyar & Knab), and (10) *Culex tarsalis* Coquillett; (11) dorsal view of head of *Deinocerites cancer* Theobald.

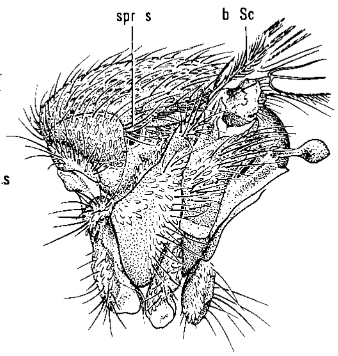
Abbreviations: ant, antenna; fem, femur; flgm, flagellomere; plp, palpus; prbs, proboscis.



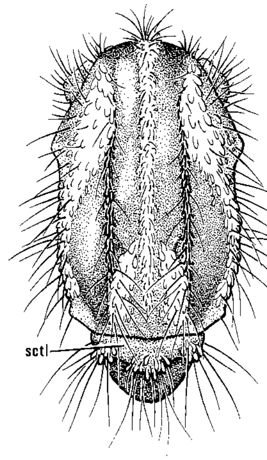
12 Wyeomyia smithii ♀



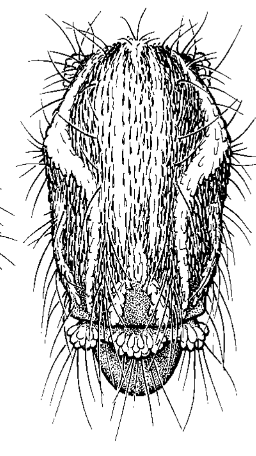
13 Aedes stimulans ♀



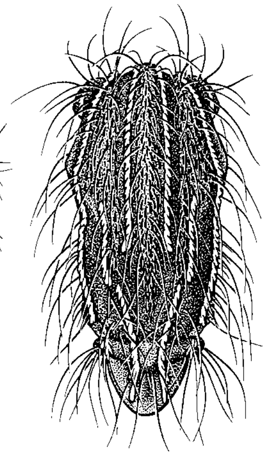
14 Culiseta impatiens ♀



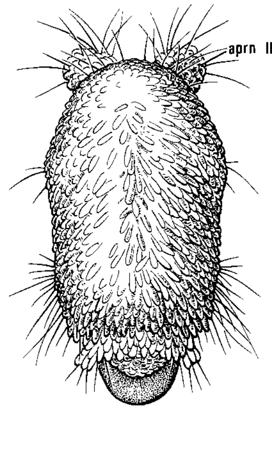
15 Psorophora ciliata ♀



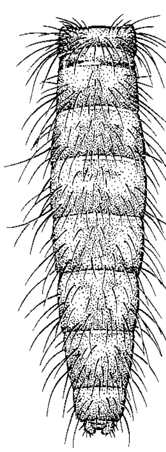
16 Aedes aegypti ♀



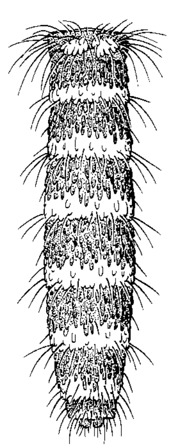
17 Orthopodomyia signifera ♀



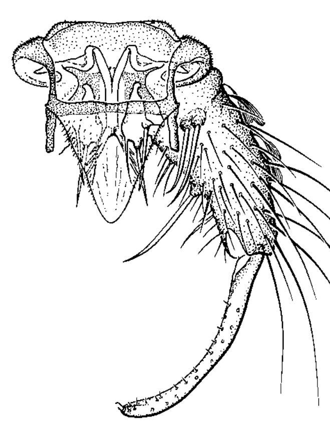
18 Haemagogus equinus ♀



19 Anopheles punctipennis ♀



20 Culex territans ♀



21 Anopheles (Anopheles) punctipennis ♂

22 Anopheles (Nyssorhynchus) albimanus ♂

Figs. 25.12–22. Thoraces and abdomens: lateral view of female thorax of (12) *Wyeomyia smithii* (Coquillett), (13) *Aedes stimulans* (Walker), and (14) *Culiseta impatiens* (Walker); dorsal view of female thorax of (15) *Psorophora ciliata* (Fabricius), (16) *Aedes aegypti* (Linnaeus), (17) *Orthopodomyia signifera* (Coquillett), and (18) *Haemagogus equinus* Theobald; dorsal view of female abdomen of (19) *Anopheles punctipennis* (Say) and (20) *Culex territans* Walker; dorsal view of male terminalia minus left gonopod of (21) *Anopheles* (*Anopheles*) *punctipennis* and (22) *Anopheles* (*Nyssorhynchus*) *albimanus* Wiedemann.

Abbreviations: aprn lb, antepronotal lobe; b Sc, base of subcosta; h cx, hind coxa; l mepm s, lower mesepimeral seta; mr, meron; prn, pronotum; pspr s, postspiracular bristle; sctl, scutellum; spr s, spiracular bristle.

7. Postspiracular bristles present (as in Fig. 13). Underside of base of Sc without setae but sometimes with scales. Tip of female abdomen pointed ....***Psorophora*** Robineau-Desvoidy....8

Postspiracular bristles absent. Underside of base of Sc with a group of setae (Fig. 14). Tip of female abdomen blunt (as in Fig. 20) ....***Culiseta*** Felt
9 spp.; widespread

8. Scutum with smooth bare areas (Fig. 15). Hindleg, including apical part of femur, with long erect scales giving shaggy appearance (Fig. 8). Very large species ....***Psorophora*** (***Psorophora*** Robineau-Desvoidy)
2 spp.; eastern U.S.A., southeastern Canada

Scutum uniformly though sometimes sparsely scaled. Hindleg usually without erect scales, particularly on femur. Smaller species 9

9. Wing scales all dark or with only a few inconspicuous paler scales. Hind femur without subapical ring of white scales ....***Psorophora*** (***Janthinosoma*** Lynch Arribálzaga)
7 spp.; central and eastern U.S.A.

Wing scales mixed dark and pale. Hind femur with fairly distinct narrow subapical ring of white scales (Fig. 9) ....***Psorophora*** (***Grabhamia*** Theobald)
4 spp.; central, eastern, and southwestern U.S.A.

10. Postspiracular bristles present (Fig. 13)..11

Postspiracular bristles absent 16

11. Wing scales very broad and asymmetric (Fig. 6). Tip of female abdomen blunt; tergite 8 bearing heavy teeth (Fig. 7) ....***Mansonia*** (***Mansonia*** Blanchard)
2 spp.; subtropical

Wing scales narrow, or broad but not strongly asymmetric. Tip of female abdomen acute at least in dorsal view; tergite 8 without heavy teeth ....***Aedes*** Meigen (except subgenus *Kompia*)....12

12. Palpus of male not more than one-fourth length of proboscis. Gonostylus furcate and inserted well before apex of gonocoxite. Small dark species with broad dark scales on vertex; scutum entirely dark-scaled; fore coxa with central patch of dark scales...........***Aedes*** (***Aedes*** Meigen)
1 sp., *cinereus* Meigen; widespread

Palpus of male longer than one-half length of proboscis. Gonostylus not deeply furcate, inserted at apex of gonocoxite. If scutum entirely dark-scaled, fore coxa lacking a central patch of dark scales..13

13. Claws of female all simple. Scutum with conspicuous lyre-shaped pattern of silvery white scales (Fig. 16); clypeus with white scales..***Aedes*** (***Stegomyia*** Theobald)
1 sp., *aegypti* (Linnaeus); southern U.S.A.

Claws of female toothed on foreleg and midleg. Scutum not so patterned with scales; clypeus without scales 14

14. Cercus of female short; sternite 8 larger, not completely retractile. Tarsi banded; many pale scales on side of scutum anterior to wing base ....***Aedes*** (***Finlaya*** Theobald)
5 spp.; widespread

Cercus of female long; sternite 8 short, completely retractile. Tarsi and scutum variable in color..15

15. Claspette filament of male absent; spine of gonostylus subapical. Tarsi with very narrow bands at base of each tarsomere. Lower mesepimeral bristles absent. Tergite 7 mostly dark-scaled ....***Aedes*** (***Aedimorphus*** Theobald)
1 sp., *vexans* (Meigen); widespread

Claspette filament of male present; spine of gonostylus apical. Tarsi usually not banded or with broad bands; if with narrow bands then lower mesepimeral bristles present (as in Fig. 13). Tergite 7 mostly pale-scaled......................................***Aedes*** (***Ochlerotatus*** Lynch Arribálzaga)
59 spp.; widespread

16. Mid lobe, at least, of scutellum with broad flat metallic scales. Legs and abdomen purplish or blue 17

Mid lobe of scutellum with narrow scales. Legs and abdomen not purplish or blue 18

17. Antepronotal lobes close together (Fig. 18); scutum without bristles. Abdomen bright blue .... ***Haemagogus*** Williston (***Longipalpifer*** Levi-Castillo)
   1 sp., *equinus* Theobald; Texas

   Antepronotal lobes widely separated; scutum with many bristles. Abdomen mixed yellowish, brown, and purplish .... ***Aedes*** (***Kompia*** Aitken)
   1 sp., *purpureipes* Aitken; Arizona

18. Antenna much longer than proboscis; combined length of first three flagellomeres in female close to half length of antenna (Fig. 11) .... ***Deinocerites*** Theobald
   3 spp.; Florida, Texas; Belkin and Hogue 1959

   Antenna shorter than proboscis; first three flagellomeres about same length as succeeding ones 19

19. Tarsomere 4 of foreleg very short, scarcely longer than wide. Scutum dark brown, with narrow lines of white scales (Fig. 17) .... ***Orthopodomyia*** Theobald
   4 spp.; eastern and southwestern U.S.A.

   Tarsomere 4 of foreleg distinctly longer than wide. Scutum not dark with narrow lines of white scales 20

20. Tarsomeres with broad basal bands; hind tibia with subapical pale band .... ***Coquillettidia*** (***Coquillettidia*** Dyar)
   1 sp., *perturbans* (Walker); widespread

   Tarsomeres dark and without bands, or with very narrow basal bands, or with broader bands both basally and apically (Fig. 10); hind tibia without subapical pale band .... ***Culex*** Linnaeus....21

21. Wing scales narrow on R_2 and R_3; occiput usually lacking broad appressed scales dorsally. Sternite 10 of male usually crowned mostly with acute spines 22

   Wing scales slightly or distinctly broadened on R_2 and R_3; occiput usually with broad appressed scales dorsally, with scales sometimes limited to narrow border near eye margin. Sternite 10 of male crowned with comb-like row of blunt teeth .... ***Culex*** (***Melanoconion*** Theobald)
   9 spp.; central, southwestern, and eastern U.S.A.

22. Abdominal tergites, at least on posterior segments, each with pale scales on posterior margin (Fig. 20); sternite 10 of male without laterobasal arm .... ***Culex*** (***Neoculex*** Dyar)
   5 spp.; widespread

   Abdominal tergites with basal pale scales or entirely dark-scaled; sternite 10 of male with laterobasal arm .... ***Culex*** (***Culex*** Linnaeus)
   13 spp.; widespread

Larva

1. Abdominal segment 8 without elongate dorsal siphon (Fig. 33) .... ANOPHELINAE....***Anopheles***....2

   Abdominal segment 8 with dorsal siphon that is longer than broad (Figs. 28–32, 34) 3

2. Abdominal segments 1–7 with a pair of palmate hairs; separate leaflets of all hairs with smooth margins (Fig. 24) .... ***Anopheles*** (***Nyssorhynchus***)

   Abdominal segment 1 without palmate hairs and segment 2 only rarely with palmate hairs; leaflets of palmate hairs on segments 3–7 with serrated margins (Fig. 25) .... ***Anopheles*** (***Anopheles***)

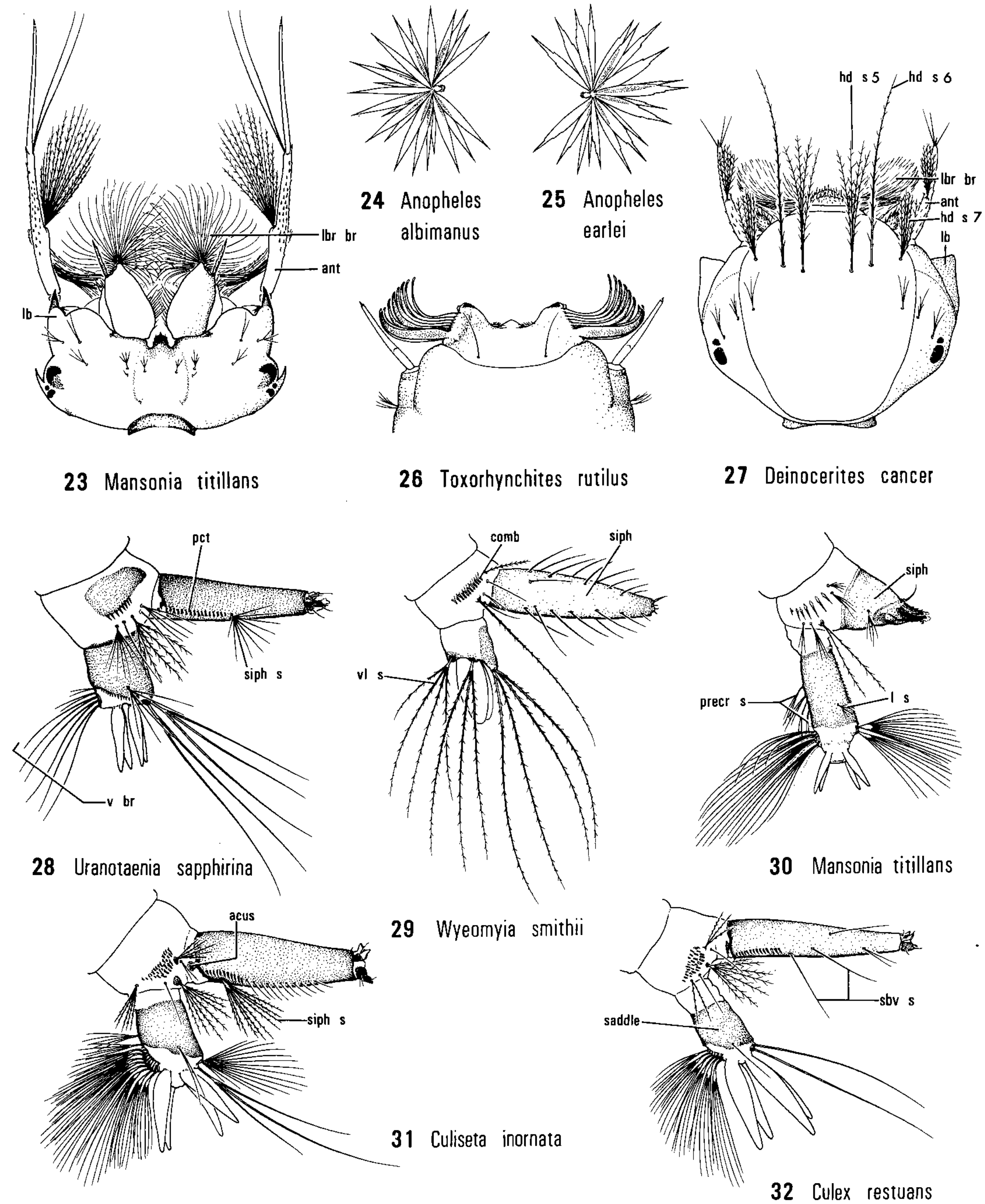
3. Labral brush prehensile, composed of about 10 stout curved rods (Fig. 26) .... TOXORHYNCHITINAE....***Toxorhynchites*** (***Lynchiella***)

   Labral brush prehensile only in subgenus *Psorophora*, composed of 30 or more hairs .... CULICINAE....4

4. Anal segment without median ventral brush but with a pair of ventrolateral branched setae; siphon without pecten (Fig. 29) .... SABETHINI....***Wyeomyia*** (***Wyeomyia***)

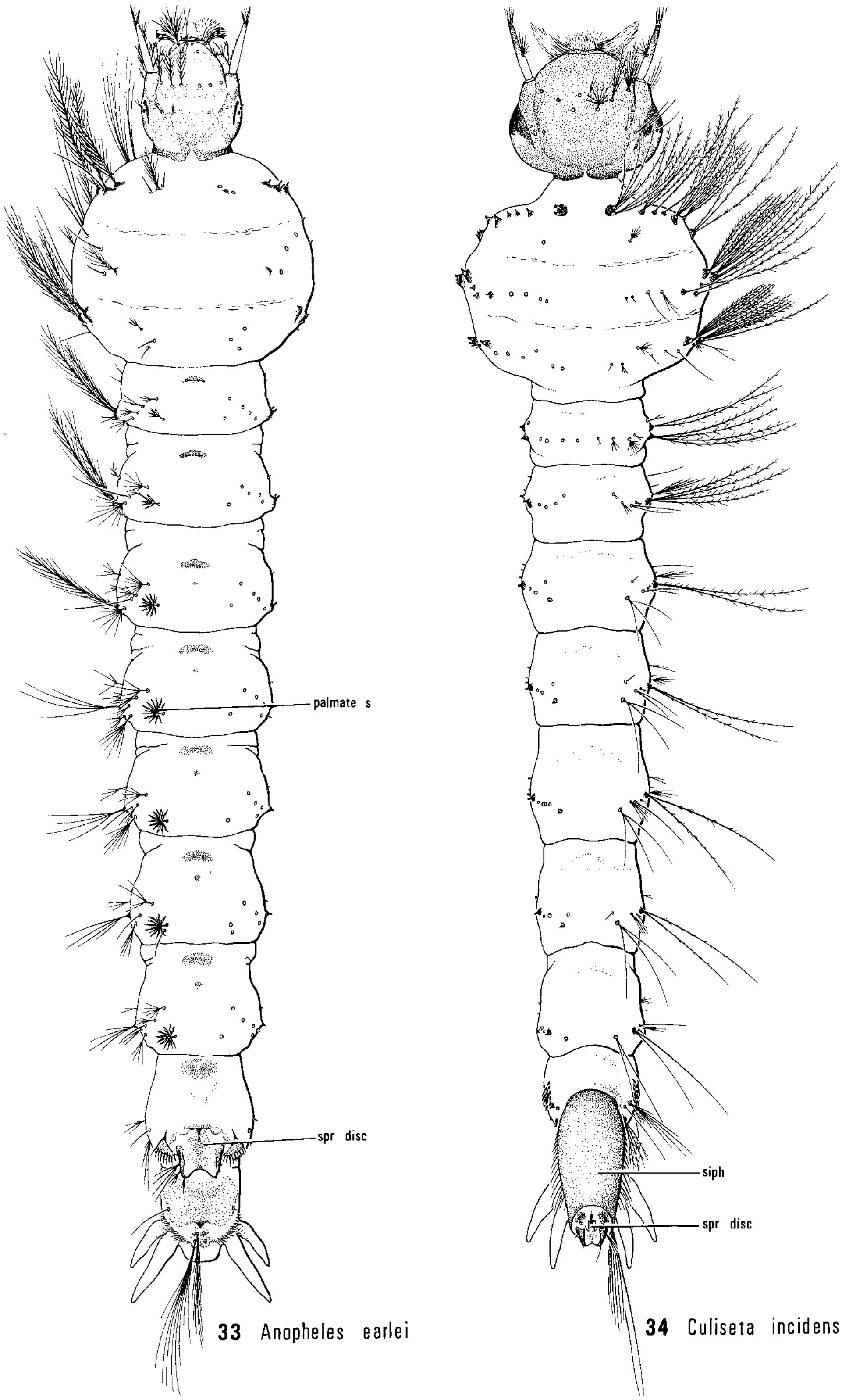
   Anal segment with median ventral brush; siphon usually with pecten (Figs. 28, 31, 32) .... CULICINI....5

5. Distal half of siphon strongly attenuated, adapted for piercing plant tissue (Fig. 30) 6
   Siphon cylindrical or fusiform, not adapted for piercing plant tissue 7
6. Head with stout acute lobe below base of antenna (Fig. 23). Anal segment with about four strong precratal setae; lateral seta of anal segment short, not reaching apex of saddle (Fig. 30) ....***Mansonia* (*Mansonia*)**



Figs. 25.23–32. Larvae: (23) ventral view of head of *Mansonia titillans* (Walker); palmate seta of abdominal segment 4 of (24) *Anopheles* (*Nyssorhynchus*) *albimanus* Wiedemann (seta of left side) and (25) *Anopheles* (*Anopheles*) *earlei* Vargas (seta of right side); (26) dorsal view of anterior part of head of *Toxorhynchites rutilus* (Coquillett); (27) dorsal view of head of *Deinocerites cancer* Theobald; lateral view of terminal segments of (28) *Uranotaenia sapphirina* (Osten Sacken), (29) *Wyeomyia smithii* (Coquillett), (30) *Mansonia titillans*, (31) *Culiseta inornata* (Williston), and (32) *Culex restuans* Theobald.

Abbreviations: ant, antenna; b s, basal seta; hd s, head seta; lb, lobe; lbr br, labral brush; l s, lateral seta of saddle; pct, pecten; precr s, precratal seta; sbv s, subventral seta; siph, siphon; siph s, siphonal seta; v br, ventral brush; vl s, ventrolateral seta.



Figs. 25.33–34. Larvae: dorsal view of (33) *Anopheles earlei* Vargas and (34) *Culiseta incidens* (Thomson). Abbreviations: s, seta; siph, siphon; spr disc, spiracular disc.

Head without acute lobe below base of antenna. Anal segment with no more than two much smaller precratal setae; lateral seta of anal segment longer, ending well beyond apex of saddle .... ***Coquillettidia*** (***Coquillettidia***)

7. Siphon without pecten .... ***Orthopodomyia***
Siphon with pecten (as in Fig. 28) 8

8. Head longer than wide. Abdominal segment 8 with large sclerotized plate bearing comb on posterior margin (Fig. 28) .... ***Uranotaenia***
Head at least as wide as long. Segment 8 with no lateral plate or with very small one 9

9. Head with large ventrolateral pouch behind antenna (Fig. 27). Anal segment with dorsal and ventral sclerotized areas separated by lateral membranous area. Species found in crab-holes .... ***Deinocerites***
Head without lateral pouch behind antenna. Anal segment with dorsal saddle, broken only ventrally. Species rarely found in crabholes 10

10. Siphon with pair of large branched siphonal setae near base (Fig. 31) or with small setae and comb consisting of single row of about 25 bar-like scales .... ***Culiseta***....11
Siphon without pair of branched setae near base (Fig. 32) 13

11. Comb scales in patch of more than one row; basal siphonal seta large (Fig. 31) 12
Comb scales in a single row; basal siphonal seta small .... ***Culiseta*** (***Climacura***)

12. Pecten not followed by row of single hairs. Antenna long, with branched seta well beyond middle .... ***Culiseta*** (***Culicella***)
Pecten followed by a row of single hairs (Fig. 31). Antenna short, with branched seta near middle .... ***Culiseta*** (***Culiseta***)

13. Siphon with one pair of subventral branched or single setae 14
Siphon with several pairs of subventral branched or single setae (Fig. 32) 18

14. Anal segment completely ringed by saddle and pierced on midventral line by setae of ventral brush .... ***Psorophora***....15
Anal segment not completely ringed by the saddle, or ringed but not pierced on midventral line by setae of ventral brush 17

15. Pecten teeth numerous (18 or more), each terminating in a hair-like filament; last tooth followed by a long unbranched siphonal seta .... ***Psorophora*** (***Psorophora***)
Pecten teeth few (less than 10), not prolonged into hair-like filaments; last tooth followed by a branched siphonal seta 16

16. Head setae 5 and 6 double or triple, or single with siphonal seta small or head seta 7 double .... ***Psorophora*** (***Janthinosoma***)
Head setae 5 and 6 single, or multiple with each comprising more than three hairs, siphonal seta very large and multiple or head seta 7 multiple .... ***Psorophora*** (***Grabhamia***)

17. Comb in a single row, with each scale lacking lateral spinules; saddle of anal segment broadly broken ventrally and with strong spines on apical margin dorsally; no precratal setae; siphon without acus (as in Fig. 30) .... ***Haemagogus*** (***Longipalpifer***)
Not with this combination of characters .... ***Aedes***

18. Head seta 6 long, single or double. Siphon lacking small subdorsal branched setae; pecten tooth with one to four long coarse side teeth .... ***Culex*** (***Neoculex***)
Not with this combination of characters 19

19. Head seta 6 long, single. Pecten tooth fringed on one side nearly to apex .... ***Culex*** (***Melanoconion***)
Head seta 6 with three or more branches. Pecten tooth with one to seven coarse side teeth .... ***Culex*** (***Culex***)

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THAUMALEIDAE 26

ALAN STONE AND B. V. PETERSON

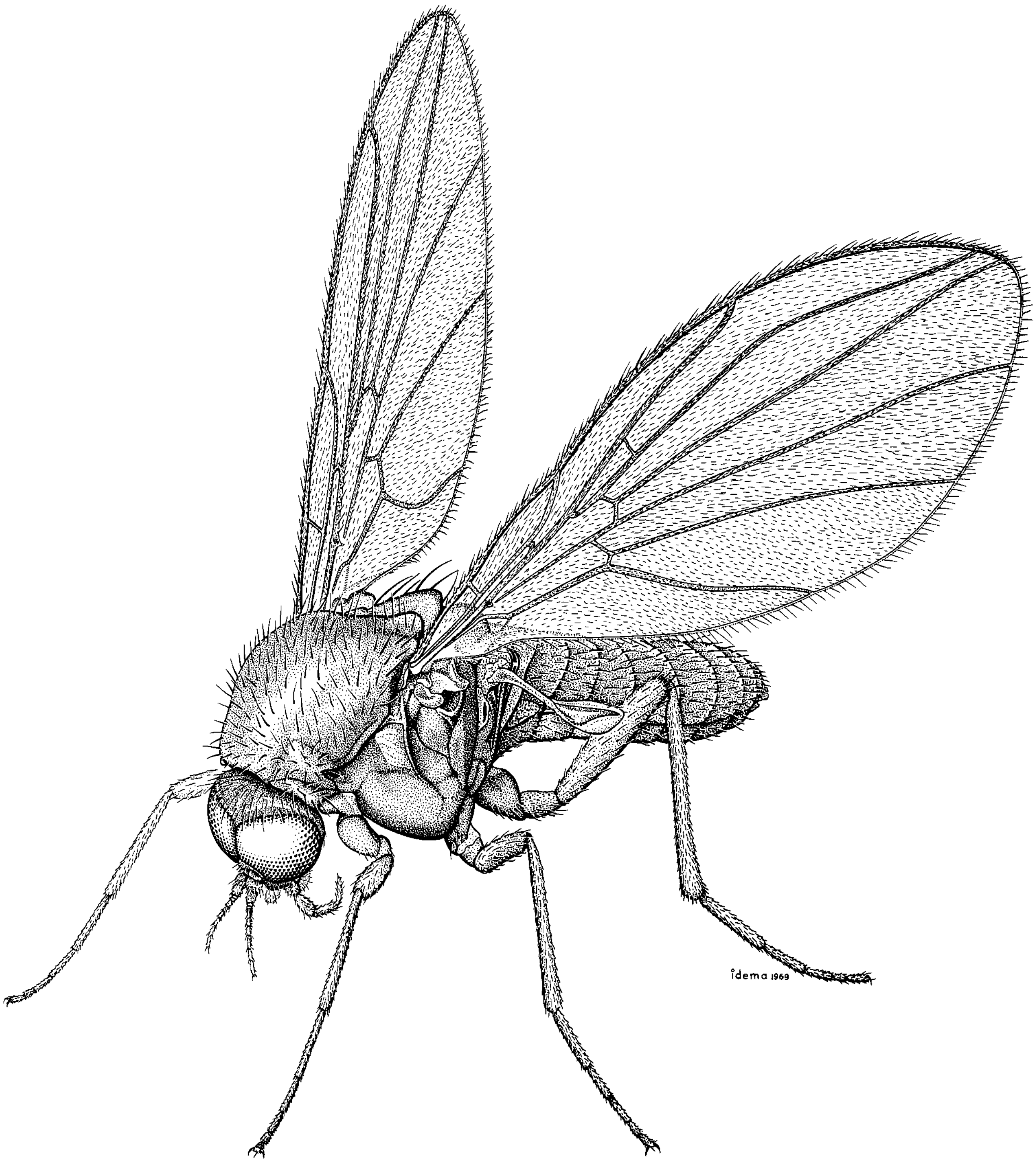


Fig. 26.1. Female of *Thaumalea americana* Bezzi.

Rather small flies, about 2.0–3.0 mm long; body stocky, shiny yellow to dark brown (Fig. 1). Flagellum of antenna slender and arista-like. Eyes holoptic in both sexes.

Adult. Head: small, round. Eyes holoptic in both sexes; ocelli absent. Frons small, somewhat triangular in shape. Antenna projecting forward, evenly clothed with short setae; scape and pedicel spherical, with pedicel larger; flagellum slender, arista-like; flagellomeres 1–3 subquadrate, rapidly decreasing in size; flagellomeres 4–10 slender, cylindrical, and progressively elongate (Fig. 2.19). Clypeus small, rounded, and convex. Proboscis short; palpus with five segments; first and second greatly expanded in male of Palaearctic species *Androprosopa larvata* Mik.

Thorax: stout, somewhat compressed laterally. Postpronotal lobe small; scutum rather strongly arched dorsally, without transverse suture; scutellum large, acute apically; postnotum strongly convex in profile. Anepisternum with a prominent anepisternal membrane; katepisternum large and triangular, but not strongly demarcated. Anterior and posterior spiracles small.

Wing (Figs. 2, 3) broad, often with a slight downward curvature near apex of Sc; membrane clothed with macrotrichia (*Trichothaumalea* Edwards), or bare and with macrotrichia confined to veins. C reaching wing tip; Sc short and incomplete, or complete and ending in C; R_1 relatively long; Rs usually forked to produce a very short variably distinct nearly vertical crossvein-like R_{2+3} and a long curving R_{4+5} reaching wing margin; R_{2+3} joining R_1 to form cell r_1; M_1, M_2, CuA_1, and CuA_2 strong and reaching wing margin, although M_2 occasionally evanescent distally or even absent; CuP and A_1 variably distinct, sometimes absent. Halter about as long as first two abdominal segments combined, with a large ovate knob.

Legs rather short, slender; tibiae without spurs. Claws rather elongate, simple; empodia minute; pulvilli absent.

Abdomen: cylindrical, slightly narrower than thorax, with seven pairs of spiracles; spiracles of segments 5–7 larger than others; sternites of both sexes sclerotized; pleural membrane of segments 3–8 with two to four longitudinal rows of short stout setae.

Female tergite 9 with posteroventral corners round, truncate, or produced as short to long processes; cercus large and compressed, divided ventrally. Sternite 8 with a pair of short subtruncate to subtriangular hypogynial valves. Sternite 9, or genital fork, a slender Y- or T-shaped sclerite whose arms are variously expanded plate-like; hypoproct conspicuous, membranous, and setose.

Male terminalia not rotated. Tergite 9, or epandrium, large, in dorsal view sometimes completely obscuring gonostyli, simple or with a long forked antler-like posterodorsal process on each side (*A. larvata*); cercus large, densely setose. Sternite 9, or hypandrium, slender, heavily sclerotized, and uniting with tergite 9; gonocoxite short and stout; gonostylus usually shorter, tapering distally, with a variable number of apical spines; paramere sclerotized, elongate, curved, smooth, and usually slender; aedeagus short and broad, with lateral margins and apex variably sclerotized.

Larva. Elongate, cylindrical (Fig. 4), with broad unpaired prolegs on prothorax and at end of abdomen; each proleg armed with a series of stout curved hooks. Head well-developed, nonretractile, not divided into lobes or rods posteriorly; mandibles opposed; hypostoma elongate, tapering anteriorly, pointed upward in relation to long axis of head, giving the head a truncate appearance; tip of hypostoma armed with teeth. Each thoracic segment sclerotized dorsally; prothorax with a pair of short respiratory tubes dorsolaterally; mesothorax and metathorax each with a pair of stout erect setae. Each abdominal segment sclerotized dorsally, bearing several long stout dark setae laterally; abdominal segment 8 with a transverse respiratory opening near hind margin, flanked by a pair of sclerotized finger-like processes bearing several longer dark setae apically.

Pupa. Free, subcylindrical, not in cocoon. Leg sheaths projecting just slightly beyond wing sheaths; thoracic respiratory organ rather short, subcylindrical, truncate apically, with apical opening encircled by papillae. Abdominal segments angulate laterally, with anterolateral and posterolateral corners of tergites acute; each tergite with a short posterolateral papilla on each corner bearing one or two stout setae; usually anterolateral corners of each sternite just in front of spiracle with similar papillae; short erect tube-like spiracles present on all but first and terminal abdominal segments; apex of abdomen with two long spine-like processes dorsolaterally and one or more shorter coarse setae laterally.

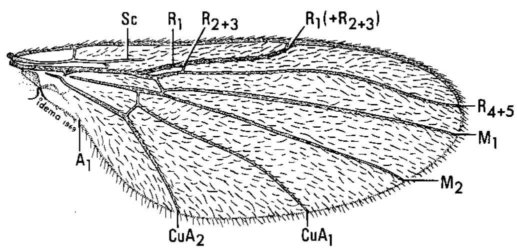
Biology and behavior. Larvae are found on wet rocks, most frequently on the vertical surfaces, and always where the surface is covered with a film of water thin enough not to submerge them. The rocks are located in cold streams, usually in the shade. When larvae are disturbed, they glide rapidly over the film of water on the rock surface; they feed mostly on diatoms found on the rocks (Leathers 1922). Pupae are found in wet moss or leaves, or buried in mud. Adults fly only a short distance from the larval habitat. The immature stages of this family are known only for the genus *Thaumalea* Ruthe.

Classification and distribution. This family contains about 60 described species in five genera. They are mainly Holarctic in distribution, with only two genera and about eight species known from the temperate areas of the Southern Hemisphere. All species apparently have a restricted distribution and none is known from more than one continent. These flies are infrequently encountered, and the species limits are not clear. Although Dyar and Shannon (1924), Vaillant (1959), and Stone (1964) treated the Nearctic fauna and new species were described by Schmid (1970) and Brothers (1972), further taxonomic study of the family is needed. No fossil species have been described.

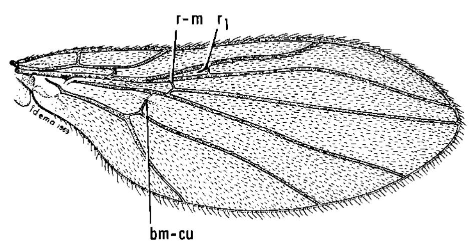
Key to genera

1. Sc reaching C; macrotrichia confined to veins (Fig. 3) ....***Thaumalea*** Ruthe
   6 spp.; mostly western but 2 spp. in eastern North America

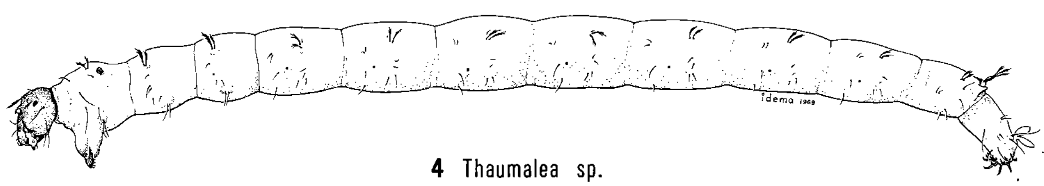
   Sc not reaching C; macrotrichia on membrane of wings as well as on veins (Fig. 2) ....***Trichothaumalea*** Edwards
   1 sp., *pluvialis* (Dyar & Shannon); British Columbia



2 Trichothaumalea pluvialis ♀



3 Thaumalea americana ♂



4 Thaumalea sp.

Figs. 26.2–4. Wings and larva: wing of (2) *Trichothaumalea pluvialis* (Dyar & Shannon) and (3) *Thaumalea americana* Bezzi; (4) larva of *Thaumalea* sp.

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SIMULIIDAE 27

B. V. PETERSON

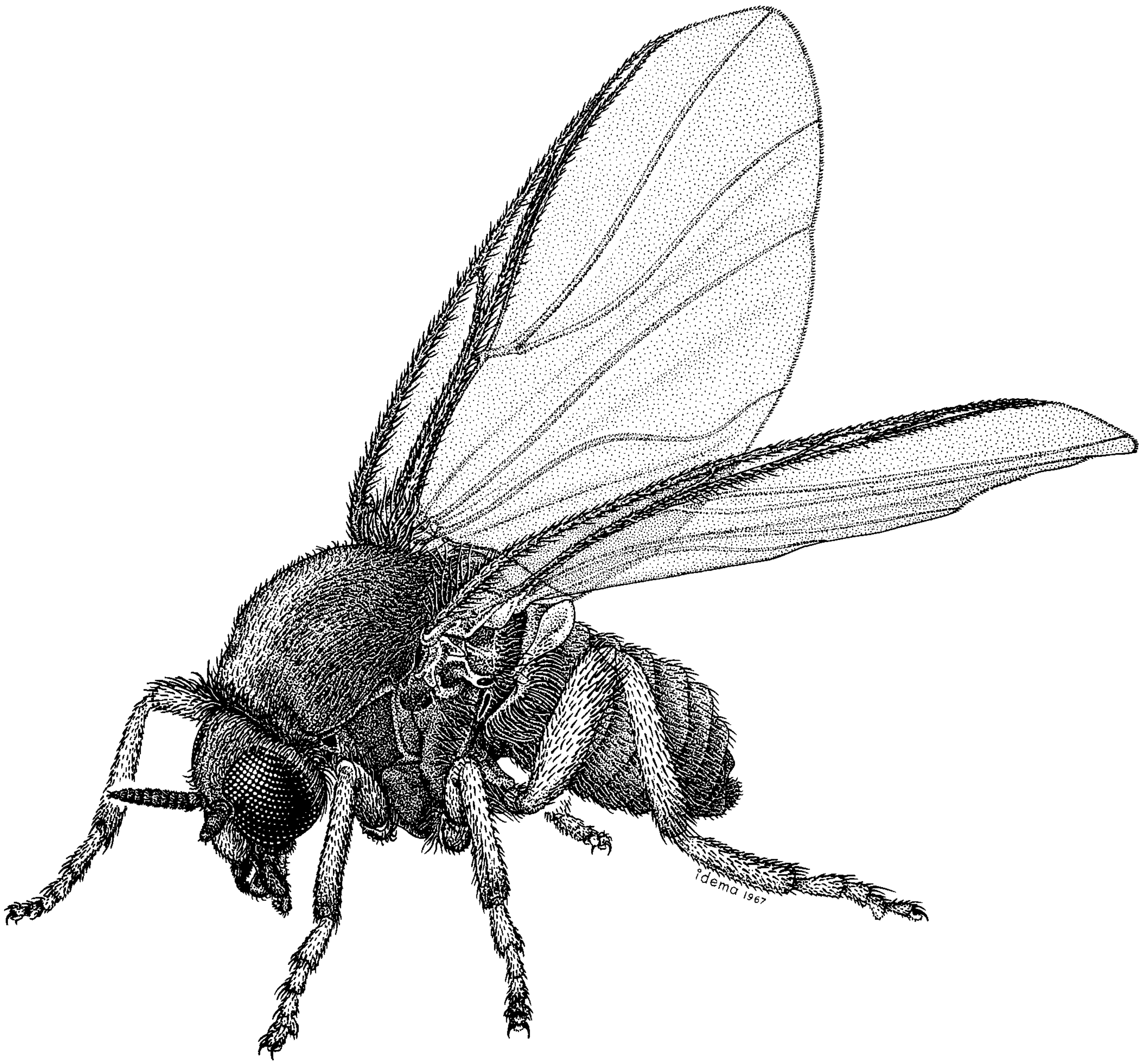


Fig. 27.1. Female of *Prosimulium mixtum* Syme & Davies.

Small stout flies, 1.2–5.5 mm long, usually black or dark brown in color, but sometimes reddish brown, gray, orange, or yellow. Legs short. Wing broad; anterior veins strong; posterior veins weak (Fig. 1).

Adult. Head: moderately large, rounded. Female (Figs. 2, 4, 5) dichoptic; male (Figs. 3, 6) usually holoptic, with facets of upper half of eye usually distinctly larger than facets of lower half, but with all facets similar in size in a few species, or rarely with only a few larger facets present near middle of anterior margin of eye (*Parasimulium* Malloch) (Fig. 6); posterior margin of eye near middle with a slightly raised and variously prominent shiny stemmatic bulla in a few species (Fig. 2); ocelli absent. Frons in female varying from about four times longer than wide to less than twice as long as wide, usually small in male but moderately large and broad in *Parasimulium*, usually covered with short fine setae in both sexes. Antenna short, rather stout, erect, with seven to nine flagellomeres; all segments bead-like; pedicel usually largest of segments. Clypeus moderately large in female, small in male, more or less convex, with some short setae.

Proboscis short and thick; mouthparts of female (Fig. 8) usually adapted for cutting skin and sucking blood, but weak and suitable only for taking in liquids such as water and nectar in female of some species and in male of all species. Labrum of female broad, hinged to clypeus, sclerotized, somewhat gutter-like, with a pair of strong apical trifid hooks, and deeply channeled on its undersurface. Mandible blade-like, with variously serrated margins. Lacinia of maxilla longer and more slender than mandible, usually with a series of retrorse teeth along its margins (Fig. 7). Palpus moderately long, five-segmented, with somewhat swollen third segment containing an internal sensory vesicle (Fig. 7); this organ varying somewhat in size and shape, opening to exterior through a small neck or directly by a small pore. Hypopharynx broad, somewhat flattened, sclerotized, blade-like in form, having anterior surface continuous with floor of cibarial pump, and with a salivary pump at its base. Labium short, broad, fleshy, with a pair of basal thecal plates ventrally; labial trough enclosing mandibles and maxillary laciniae, concealed beneath labrum. Cibarial pump (buccopharyngeal apparatus) well-developed, sclerotized trough-like, with dorsal (proximal) arms or cornua; space between these arms of varying depth and shape, sometimes bearing a series of minute teeth in varying patterns (Figs. 8, 9).

Thorax: usually high, often strongly arched dorsally especially in male, rarely weakly arched or flattened (Figs. 11–13, 15–17). Antepronotum reduced; postpronotal lobe well-developed. Scutum usually rather uniformly convex, but with slightly raised strip-like median portion between lower lateral portions in some species of *Gymnopais* Stone, usually rather densely covered with short fine recumbent setae but sometimes with sparse erect setae, and sometimes with flattened scales [Hannay and Bond (1971*b*) briefly discuss the nature of the fine pubescence on the scutum]; scutellum moderately large, subtriangular in shape, densely covered with long setae; postnotum (Fig. 14) moderately large, rather strongly convex, usually bare, occasionally with a varyingly conspicuous median longitudinal ridge or line, and rarely with two dorsolateral patches of short appressed scale-like setae. Anepisternum with a characteristic membrane that is usually bare but in some species bearing a patch of fine setae (Figs. 10, 13); katepisternum usually large and well-developed, although varying in size among some genera, usually divided into an upper and a lower part by a narrow deep katepisternal (mesepisternal) sulcus (Fig. 10); sulcus more or less complete anteriorly, but in a few genera broad, shallow, and virtually absent. Mesepimeron usually with a variably extensive tuft of setae, which is absent in *Parasimulium*.

Legs short, moderately stout. Fore tibia with one apical spur; mid and hind tibiae with two apical spurs. First tarsomere of all legs elongate; first tarsomere of hindleg swollen in male of some species, often with an anterior process called the ***calcipala*** on inner apical surface (Figs. 20–23); second tarsomere of hindleg often with a variably deep notch called the ***pedisulcus*** in posterior margin (Figs. 20, 22, 23); claws short, simple or with a variably sized basal or subbasal tooth (Figs. 18, 19, 20); pulvilli absent; empodia minute, setose [Sutcliffe and McIver (1974, 1976) discuss the cleaning setae and sensory setae on the legs of black flies].

Wing broad; membrane usually hyaline but sometimes fumose, covered with microtrichia and regularly spaced submicroscopic raised wax 'buttons' (Hannay and Bond 1971*a*). Anterior veins strong; posterior veins weak; C, R, and Rs often with short stout spinules variously interspersed among usual setae (Figs. 29, 30); Rs simple, or with a long fork, or more rarely with a short obscure apical fork; basal section of R setose or bare; Sc sometimes setose ventrally, occasionally with a few setae on dorsal surface especially near apex; characteristic submedian false vein (m-cu fold) present, usually forked apically, but simple in *Parasimulium*; CuA_2 usually with a strong sigmoid curvature but straight in *Gigantodax* Enderlein; branches of A variously developed, not usually reaching wing margin; MA (arculus) and base of A_2 variously pale or darkened in color; a small cell bm sometimes present. Several small sensory pores present on stem vein and crossvein r-m.

Abdomen: first segment modified as a collar-like basal scale bearing a fringe of long fine setae and first abdominal spiracle (Figs. 34, 35). Tergites 2–6 of female variously reduced; sternite 1 small, sclerotized; sternites 2–7 usually membranous but sclerotized in a few species. Tergites of male large; sternites moderately large and sclerotized. Tergites and sternites sparsely covered with short fine setae; pleural membranous areas variously setose; scales sometimes present on both tergites and pleural areas.

Female terminalia as in Figs. 36–50. Tergite 9 well-developed, connected ventrolaterally to lateral arms of sternite 9, or genital fork. Tergite 10 consisting of a tiny plate situated anterodorsally between bases of cerci and with a variously shaped but well-developed lateral sclerite or anal lobe on each side; cercus one-segmented, free, small but well-developed. Sternite 8 somewhat shield-shaped; hypogynial valve (ovipositor lobe, gonapophysis) varying from a short truncate lobe to an elongate blade-like lobe reaching to or extending beyond tip of cercus. An apparent sternite 10 present in some species (Fig. 40). Spermatheca single, bag-like, and variously shaped, patterned, and sclerotized.

Male terminalia (Figs. 51–73) not rotated. Tergite 9, or epandrium, large, continuous ventrally with sternite

9, or hypandrium; sternite 9 slender, heavily sclerotized. Tergite 10 and cercus small. Gonocoxite fairly large, subconical, never fused with its gonostylus or with gonocoxite of other side; gonostylus well-developed, moderately long, flattened to subtriangular in cross section, with simple apex, or with internal apical margin narrowly sclerotized, or with one or more apical spinules. Ventral plate of aedeagus a large heavily sclerotized plate-like structure situated between and dorsal to gonopods, usually of characteristic shape for each species and probably functioning much like aedeagal guide of other Nematocera; anterolateral corners produced arm-like, with each arm usually attached to or articulating with gonocoxite or paramere or both; distal margin of ventral plate often produced into a ventrally directed lip often bearing short fine setae in specific patterns; median sclerite usually moderately long, slender, flattened, and basically Y-shaped, lying immediately dorsal to ventral plate of aedeagus, articulated with it mediobasally, and forming distal portion of floor of aedeagus; aedeagal membrane broad, often beset with minute cuticular setulae or ridges, and occasionally with a flattened dorsal plate-like sclerite in dorsal wall of aedeagus; paramere typically a large subtriangular to subquadrate plate-like sclerite, with a dorsal arm sometimes bearing a variety of subapical or apical spines or both, usually articulated basally with anterodorsal corner of gonocoxite and apex of arm of ventral plate; aedeagal complex, in some species at least, adapted for forming and passing a spermatophore during copulation.

Egg. Small, varying from about 0.18 to 0.46 mm long, asymmetrically ovoid varying from triangular or reniform in one aspect to more oval in another. Under lower magnifications shell appearing smooth and without pattern or external structural specializations, but under scanning electron microscope magnifications eggs of some species showing several forms of sculpturing and pitting, and those of others featureless or slightly dimpled (Williams and MacDonald 1974). Color pale white when laid but gradually darkening with age and embryonic development to dark brown.

Larva. Slender, somewhat cylindrical, varying from about 5.0 to 15.0 mm long, apneustic, pale whitish brown to blackish brown. Head prognathous, well-developed. Thoracic segments stout, indistinctly delineated, with a single ventral proleg. Abdomen with eight segments; anterior segments slender; posterior segments somewhat enlarged (Fig. 76).

Head: head capsule (Figs. 78–82, 87, 88) rather large, subcylindrical, heavily sclerotized, ranging in color from pale yellowish white to blackish brown, composed of two sclerites; first of these sclerites a dorsal frontoclypeal apotome, which is separated by a U-shaped cephalic ecdysial line (epicranial suture) from second sclerite; second sclerite a larger lateral and ventral plate consisting of a gena on each side united ventrally by a hypostomal bridge; this bridge variable in length, usually incised on posterior margin by a hypostomal cleft; cleft varying in size and shape, sometimes absent; anteroventral margin of hypostomal bridge with a heavily sclerotized flattened double-walled wedge-shaped or subtriangular hypostoma that is separated from hypostomal bridge by a hypostomal groove. Hypostoma with smooth or variously serrated lateral margins, and with a series of heavily sclerotized teeth along anterior margin; these teeth arranged in a central group with another group on either side; central group consisting of one usually long median tooth with one smaller tooth on each side; lateral groups each composed of several variably sized sublateral teeth and one larger strong outer lateral or corner tooth; size, shape, and arrangement of teeth in lateral groups variable; a sublateral row of setae of varying lengths usually borne on each side of hypostoma. Posterolateral margins of head bordered by a narrow sclerotized postocciput; postocciput terminating ventrally in a small occipital condyle just behind posterior tentorial pit, and usually terminating dorsally near posterolateral corners of frontoclypeal apotome leaving cervical sclerites free, but sometimes nearly complete dorsally and enclosing cervical sclerites. Head capsule with a variable pattern of pale or dark spots representing muscle attachment sites; spots of frontoclypeal apotome usually consisting of an anteromedial group, a posteromedial group, an anterolateral group (usually in two subgroups), and a posterolateral group (also in two subgroups, one of which is arranged transversely near posterior margin of frontoclypeal apotome); a fuscous area of varying extent sometimes present, surrounding dorsal spots; spots less numerous on rest of head capsule; eyespot double, nearly uniform in size, surrounded by a clear or colorless area of variable size.

Pair of labral fans present on head capsule, arising at anterolateral corners of frontoclypeal apotome, and derived from lateral wall of labrum; stalk of each fan consisting of a small subrectangular somewhat horizontally situated basal sclerite and a larger rigid somewhat tubular sclerite; dorsal wall of larger sclerite convex, and ventral wall mostly membranous and flexible. Distal half of ventral wall of larger sclerite reinforced by a two-part sclerotized rod that forms a fulcrum for rotation of rays of primary fan; a second rod present forming ventrobasal wall of stalk, and a third thinner rod present, supporting median lobe of this stalk. Each labral fan composed of three well-developed fans: a large primary fan arising from apex of stalk, a smaller secondary fan inside and below primary fan, and a small median fan situated on median side of stalk. Primary fan composed of a series of long slender tapering flattened curved rays, variously pectinate on underside. Secondary fan composed of rays essentially like those of primary fan but with longer hairs; rays of secondary fan when erected arranged in two patterns, either as a small triangular fan with tips forming a straight line (*Prosimulium* Roubaud), or as a small cupped fan (*Simulium* Latreille). Median fan composed of straight flexible rays lying parallel to each other in a straight line, not spreading out when entire fan is opened, with bulbous membranous bases, and bearing setae. Labral fans absent in species of *Gymnopais* and *Twinnia* Stone & Jamnback (Fig. 82), much reduced and specialized in *Crozetia crozetensis* (Womersley) (Crozet Islands) and *Simulium oviceps* Edwards (Tahiti).

Antenna (Fig. 85) variously pigmented or patterned, basically with four segments with all but tiny apical segment varying considerably in length; basal two segments sometimes weakly separated; second segment sometimes subdivided into two to seven secondary annulations; third segment usually narrower than basal two segments, and separated by a distinct flexible joint bearing two minute conical papillae; terminal segment a small conical tip. Basal two segments often weakly sclerotized; distal two segments usually well-sclerotized.

Labrum an enlarged lobe or beak-like structure lying anteroventral to and continuous medially with ventral surface of stalks of labral fans, and joined dorsally by a membrane to frontoclypeal apotome; main areas of labrum densely covered by various short setae, and bearing a medioventral somewhat spindle-shaped patch of stout blunt setae; a somewhat spade-shaped labral sclerite present ventrally, with apex forming tip of ventral wall of labrum; anterior margin of this sclerite with a series of short peg-like teeth, three to five lateral blade-like lobes, and a dense brush of long thick compound setae; a patch of variable setae also occurring midway between labrum and stalk of labral fan. Mandible (Figs. 83, 84) heavily sclerotized, broadly rectangular, somewhat flattened laterally, with three to five large apical teeth, a series of smaller more basal comb teeth, and a series of 0–22 small, single, or double serrations all borne on inner subapical margin; a series of variously sized simple or compound bristles also present, arranged in eight basic groups or brushes; mandible articulating with a heavily sclerotized phragma at anterolateral margin of head capsule; ventral arm of phragma occasionally produced ventrally to laterobasal margin of hypostoma. Maxilla situated ventral to mandible and dorsolateral to labiohypopharyngeal apparatus (Figs. 78, 79), and consisting of a large median lobe and a smaller laterobasal lobe or cardo; median lobe having two sclerotized areas usually considered to bear elements of galea and lacinia, and bearing a series of five groups of bristles or brushes and some bristle-like teeth; laterobasal lobe having a ventral patch of stiff setae, and bearing a single segmented digitiform palpus; this palpus pigmented, bearing several scattered setae and four to six apical papillae. Hypopharynx and labium apparently fused into a complex labiohypopharyngeal structure bearing various setae and sensory areas.

Body: thoracic segments broader than anterior abdominal segments; prothorax with a ventral two-segmented proleg bearing an apical ring of minute hooks arranged in rows, and bearing a lateral sclerite varying in size and shape on each side (Fig. 76). Developing pupal respiratory filaments visible under epidermis of later instars; histoblast of legs, wings, and halteres also visible in later instars, with venational patterns sometimes visible in developing histoblasts of wing and halter.

Abdomen with eight usually poorly defined segments (Fig. 76); in a few species subconical dorsolateral tubercles present on segments 1–5; segments gradually increasing in size posteriorly with segment 7 stoutest, or segments rather abruptly expanding at segment 5, or in a few species lateral margins of segment 5 markedly expanding and projecting ventrally far beyond central portions of segments 4 and 5. A pair of conical tubercles of varying size sometimes present ventrally on segment 8 (Figs. 92, 93), or sometimes fused medially to form a single midventral bulge (Fig. 94); a ring of many rows of minute hooks also present posteriorly (structure of this ring of hooks suggests it might represent a fusion of two abdominal prolegs); anal sclerite usually present anterodorsal to ring of hooks (Figs. 89, 90), usually X-shaped, but sometimes Y-shaped (*Gymnopais, Twinnia*), subrectangular (some *Prosimulium*), or absent (*Ectemnia* Enderlein), and sometimes with various elaborations or struts present on either or both anterodorsal or posteroventral arms (*Simulium, Austrosimulium* Tonnoir, *Gigantodax, Crozetia* L. Davies); small lateral sclerites sometimes present between anal sclerite and posterior ring of hooks. Cuticle of abdomen sometimes ornamented with fine setae or scales.

One prothoracic and eight abdominal spiracles present (Fig. 76) but none functional (apneustic). Rectum with colorless extrusible anal papillae (anal gill, rectal gill) that arise from ventral wall of rectum (Headlee 1906) (Figs. 90, 91), and composed either of three simple digitiform lobes sometimes bearing a few small secondary lobules, or of three compound lobes each with many secondary lobules; anal papillae apparently osmoregulatory in function.

Pupa. Obtect (Figs. 74, 75, 77). Head anteroventral to and flexed beneath thorax; frons (cephalic plate, cephalic apotome) of female fairly short and broad, with antennal sheaths extending to hind margin of head or slightly beyond onto thorax; frons of male relatively long and slender, with antennal sheaths extending about one-half to three-quarters distance to hind margin of head; clypeal, antennal, and palpal sheaths distinct; integument of head usually with one or more pairs of setae situated about mid length of frons, near bases of antennal sheaths, laterally near hind (dorsal) margin of eye, and near or above bases of palpal sheaths. Thorax enlarged and strongly arched dorsally, usually with two to five pairs of dorsal and one or two lateral pairs of specialized setae, often called ***trichomes***, on each half, but sometimes very densely setose; trichomes varying from simple or bifurcate (Fig. 75) to multibranched to flattened and scale-like; integument of dorsal part of head and thorax sometimes smooth with a faint reticulate pattern, or densely rugose, and sometimes with a series or pattern of flattened to noticeably raised granules of varying sizes, shapes, and density; wing and leg sheaths distinct laterally and ventrally; a respiratory organ (gill) present at each anterolateral corner of thorax, varying in shape from one to many short or long slender filaments (Figs. 74, 75), to an enlarged club-like or antler-like structure, to various combinations of these forms, and sometimes quite bizarre; head and thorax relatively rigid. Abdomen rather flexible (Fig. 77); abdominal tergites 5–9 often with a single complete or broken row of short fine closely set posteriorly directed spines along their anterior margins, and tergites 3–4 often with four to eight larger anteriorly directed hooks along their posterior margins, but tergites sometimes without any or all of these spines and hooks; tergite 9 usually bearing a pair of very short to long terminal spines; sternites 3–7 variously armed with two to four slender hooks; tergite, sternite, and pleural membrane of each segment sometimes with a few other fine simple curved or multibranched setae or hooks. Cocoon of pupa varying in discreteness and modification of form, and in density and texture of weave, ranging from nearly no cocoon at all, to an irregular shapeless sleeve covering part or all of pupa (Fig. 74), to a well-formed pocket- or slipper-shaped structure tapering posteriorly from a large open anterior end having no connection medioventrally between opposite sides (Fig. 75), to a shoe- or boot-shaped structure with an anterior opening raised above substrate by a short or variously elongate anterior collar, to nearly circular and flattened; one or more anterolateral apertures or windows sometimes present, or various long or short, single or double anterodorsal projections sometimes present; strands composing cocoon rather coarse and loosely woven or finer and tightly woven, homogeneous in construction or incorporating small pieces of debris; a floor of varying length also sometimes present.

For additional descriptions of the immature stages of this family see Sommerman (1953), Rubtzov (1959), Crosskey (1960), Dumbleton (1962), Wood *et al.* (1963), L. Davies (1965*a*, 1974), Chance (1970), and Craig (1974, 1975).

Biology and behavior. The general biology of black flies is reasonably well known, but the peculiarities of most individual species have yet to be investigated. All black fly larvae are aquatic. They attach to various submerged objects in many types of lotic environments ranging from large rivers to tiny spring-fed trickles and from swift currents to barely moving water. Choice of habitat usually varies with the species, although some species, e.g. *Simulium vittatum* Zetterstedt, are able to tolerate widely differing conditions. One African species, *S.* (*Meilloniellum*) *adersi* Pomeroy, has been recorded on rocks and tree roots in water on the wave-washed shores of a small island in Lake Victoria, Uganda (Gibbins 1934), and on vegetation attached to wharf piles in brackish water where a small stream discharged into the sea near Victoria, Cameroon (Crosskey 1960). Some African species are phoretic on mayfly nymphs, prawns, and river-crabs (Disney 1971).

After eclosion, larvae often remain at the site of hatching if suitable attachment sites are available and the food supply is adequate; otherwise, they may drift downstream on silken strands until they find a suitable environment. Larvae pass through a series of four to nine molts, usually seven, the actual number apparently varying among species. The rate of larval growth fluctuates with water temperature and the amount of available food. The larval period lasts from about 1 month in species that hatch in the spring or summer to 6 months or more in species that overwinter as larvae. Most larvae possess a pair of labral fans and are filter feeders; those without such fans feed by grazing on the organic debris found around their attachment sites.

The last-stage larvae (pharate pupae) feed and spin cocoons of various shapes that serve to protect and anchor the developing pupae. The pupal stage usually lasts 4–7 days, but the duration varies with water temperature. The emerging adult pulls itself out of the pupal skin through a T-shaped slit that originates at the back of the head and extends along the median longitudinal line of the thorax. As the adult emerges, its wings expand and it rises to the surface of the water in an air bubble. On reaching the surface the adult flies to a nearby support to rest and allow its cuticle to harden.

The female is ready to mate and oviposit usually after the maturation of her eggs, for which a blood meal is often required. However, mating can occur shortly after emergence or just before oviposition and takes place in flight or while landed, depending on the species. In some species, at least, the male transfers the sperm to the female in a spermatophore (L. Davies 1965*b*).

Most females produce 200–500 eggs in a single gonotrophic cycle. Various species oviposit in different manners. Some females freely distribute the eggs while tapping their abdomens on the water surface during flight. Others oviposit while landed on wet surfaces such as blades of grass trailing in the water. Sometimes, some females even crawl under water to deposit their eggs. Perhaps the most unique method of egg dissemination is that reported by Carlsson (1962) for certain northern females of *Prosimulium ursinum* (Edwards). Females of this species sometimes fail to emerge from their pupae, and when these pharate females disintegrate, their fully matured eggs are shed into the streams and hatch parthenogenetically the following spring. Depending on the species and water temperature, incubation time for the eggs varies from 4 to about 30 days, and even much longer in those species whose eggs pass through diapause. The egg burster on the head of the first-stage larva can be seen through the eggshell when the larva is ready to hatch.

Simuliid females are among the most serious insect pests of man and homoiothermic animals in many parts of the world because they are vectors of certain parasitic disease organisms and because their bite produces severe initial irritation often accompanied by toxic and allergic manifestations. Not all female black flies bite man; some species feed strictly on birds or other animals, and some species do not feed on blood at all. Adults of both sexes imbibe nectar as a source of energy.

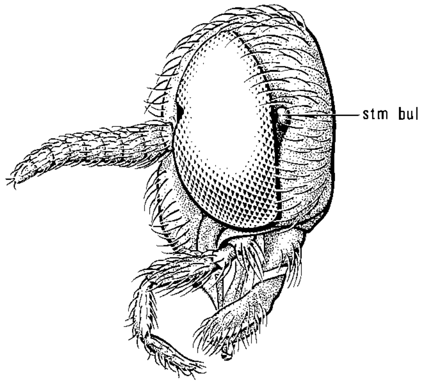
The economic importance of female black flies is difficult to estimate accurately, but certainly they have a marked impact on the economy of many regions of the world. Their greatest public health importance lies in their role as vectors of the filarial nematode *Onchocerca volvulus* Leuckart, the causitive organism of human onchocerciasis in tropical Africa, Central America, northern South America, and Yemen where between 20 and 30 million people are infected (R. Pal 1977, personal commun.). The main vectors, as now known, include several species of the *Simulium damnosum* Theobald complex in Africa, and *S. metallicum* Bellardi, *S. ochraceum* Walker, *S. sanguineum* Knab, and *S. callidum* (Dyar & Shannon) in the New World tropics. Other species serve as vectors of other filarial nematodes of man, cattle, ducks, loons, and possibly deer and moose. In addition to filarial nematodes, some black flies are known to transmit various avian blood protozoans including *Trypanosoma* and several species of *Leucocytozoon*, as well as certain viruses pathogenic to various animals. Crosskey (1973) tabulated our present knowledge of the role of black flies as vectors of pathogenic organisms.

All black flies that feed on blood can be considered pests. Such species in various parts of the world have been responsible for illness and mortality in both humans and various domestic and wild animals, strictly as a result of their bites. Loss of weight, reduced production of commercial animals and animal products, and death have been documented by a number of authors including Millar and Rempel (1944), Rempel and Arnason (1947), Edgar (1953), Anderson and Voskuil (1963), Fallis (1964), Hunter and Moorhouse (1976), El Bashir *et al.* (1976), and Fredeen (1969, 1977). Because of the vast economic importance of black flies, they have been and continue to be the subject of much intensive research.

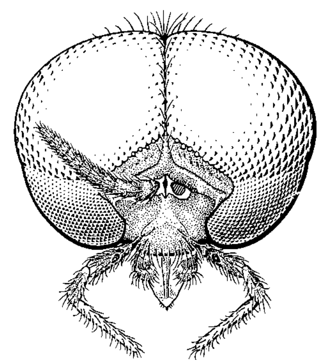
Classification and distribution. The family Simuliidae is small compared with many other families of Diptera. It is also one of the most homogeneous and easily recognized families. This homogeneity often makes generic and especially specific determinations difficult and also severely reduces the number of distinctive morphological characters available for delimiting various taxonomic categories and constructing a completely satisfactory family classification. Despite this limitation, the taxonomic literature on the Simuliidae, like that on the biological aspects of the family, is extensive.

For more than a century before 1906, the 30 or more described world species were all assigned to the genus *Simulium*. In 1906, Roubaud divided the genus into the subgenera *Prosimulium* and *Eusimulium*. Edwards in a series of papers (1915*a*, 1915*b*, 1920, 1923, 1931) maintained a very conservative view by retaining all species in the genus *Simulium* and recognizing all other named generic segregates as subgenera at most. In 1921, Enderlein segregated the family into tribes and genera (1921*a*), and later (1930) revised and elaborated his classification into six subfamilies and 30 genera. In later papers, Enderlein (1934–1936) expanded the number of genera to 50, created a seventh subfamily, and again used tribal categories in two of his subfamilies. Although Edwards held an over-simplified view in recognizing an absolute minimum of genera, some of which contained several hundred species, Enderlein went to the opposite extreme in distributing the species among numerous small genera allocated to several tribes and subfamilies. Smart (1945) provided a much needed review of the classification of the Simuliidae and recognized two subfamilies and six genera. Shortly after Smart's paper appeared, Vargas (1945) published his catalog of the New World Simuliidae, in which he included all species in the genus *Simulium*. More recently, Stone (1963) compiled all the genus-group names that had previously been used in the family and suggested the systematic status of each of these nominal groups. He presented a synonymical list of 11 genera and 26 subgenera (23 plus three nominate subgenera) that he considered valid on a world basis. Rubtzov (1956, 1959–1964) treated the Palaearctic fauna, among which he distinguished 17 supraspecific (generic) taxa and more than 400 species. Crosskey (1967, 1969) reviewed the classification of the black flies of the Australian region and Africa; the latter work is particularly significant. The most recent synthesis on the evolution, phylogeny, and classification of the Simuliidae is that of Rubtzov (1974), in which he details the history of the classification of the family. In this work, Rubtzov divided the family into four subfamilies, five tribes, and 59 genera. After Rubtzov's paper was submitted for publication, descriptions of about 10 new and valid genera and subgenera were published. The classification adopted here for the Nearctic black fly fauna consists of two subfamilies, 11 genera, and 17 subgenera, with about 137 described species and more than 22 known but as yet undescribed species. The validity of a few of the subgenera included in the key below is questionable, pending further study. The key is designed to be used mainly for the Nearctic fauna, but it may be useful for a few Neotropical subgenera of *Simulium*.

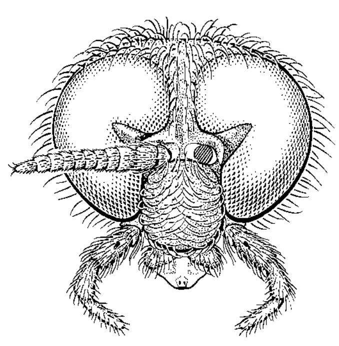
The above summary mentions only some of the most important papers dealing primarily with the higher classification of the family. However, a few other works that had a direct impact on black fly taxonomy at the specific level deserve mention. Lundström (1911) was the first to use characters of the male terminalia for the separation of species, and Edwards (1920) was among the first to utilize the diagnostic characters of the immature stages. Peterson (1978) provided a list of papers useful in determining North American species.



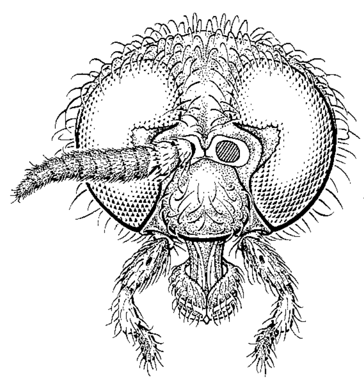
2 Twinnia sp. ♀



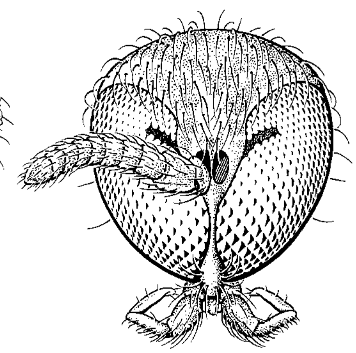
3 Simulium decorum ♂



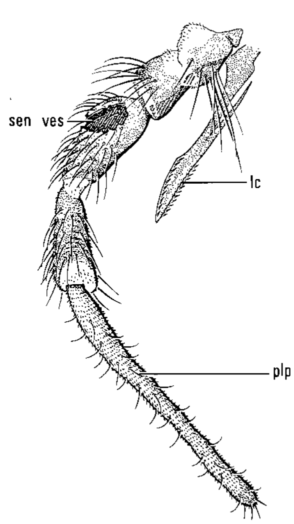
4 Ectemnia taeniatifrons ♀



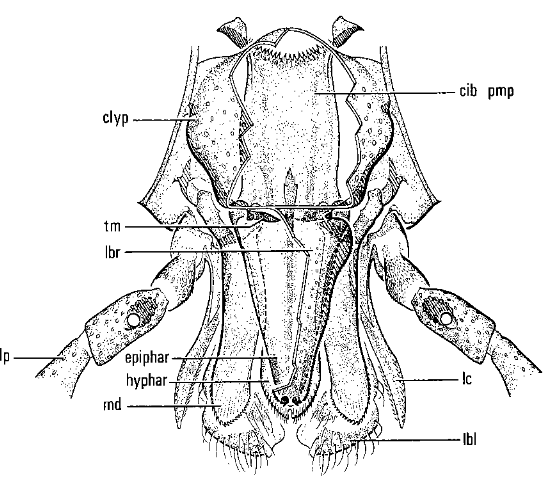
5 Cnephia dacotensis ♀



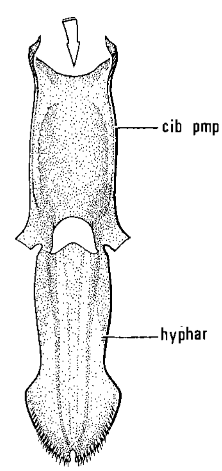
6 Parasimulium stonei ♂



7 Simulium vittatum ♀



8 Simulium vittatum ♀



9 Prosimulium mixtum ♀

Figs. 27.2–9. Heads and mouthparts: head of (2) *Twinnia* sp., (3) ***Simulium decorum*** Walker, (4) ***Ectemnia taeniatifrons*** (Enderlein), (5) *Cnephia dacotensis* (Dyar & Shannon), and (6) ***Parasimulium stonei*** Peterson; (7) palpus and lacinia of maxilla of *Simulium vittatum* Zetterstedt; (8) anterior cutaway view of mouthparts of *S. vittatum*, showing relationship of parts; (9) cibarial pump and hypopharynx of ***Prosimulium mixtum*** Syme & Davies.

Abbreviations; cib pmp, cibarial pump; clyp, clypeus; epiphar, epipharynx; hyphar, hypopharynx; lbl, labellum; lbr, labrum; lc, lacinia; md, mandible; plp, palpus; sen ves, sensory vesicle; stm bul, stemmatic bulla; tm, torma.

Karyotype and chromosomal polymorphism studies have had considerable impact on recent taxonomic work on the Simuliidae. Geitler (1934) began these studies with work on an unidentified European species and was closely followed by Painter and Griffen (1937*a*, 1937*b*) with work on the North American species *Simulium virgatum* Coquillett. Although several similar papers appeared during the next two decades, such as those of Montalenti (1947), Kunze (1952, 1953), and Rothfels and Dunbar (1953), they had little if any direct effect on black fly taxonomy. The first real impact of such chromosomal work on simuliid taxonomy came with the publication of Rothfels' 1956 paper. Since that time, several papers by Rothfels and his students have appeared that helped refine the thinking of North American black fly systematists and altered the course of their taxonomic studies. Similar European studies are beginning to appear, particularly from the Soviet countries, which should produce a like impact on the treatment of Old World species. Rothfels (1979) reviewed the current state of knowledge on the cytotaxonomy of black flies throughout the world.

Reports on fossil black flies are few. Handlirsch (1906–1908) compiled a list of six unnamed and five named species of fossil simuliids dating from lower Oligocene to middle Miocene. Seven of these are from Baltic amber, one is from Sicilian amber, and three are from other formations. Enderlein (1921*b*) and Rubtzov (1936) each described one additional species from Baltic amber, bringing the total number of described fossil species to 13, all in the genus *Simulium*. Larsson (1965) reported the presence of 13 unidentified specimens from Baltic amber in the collection of the Zoological Museum, Copenhagen. A thorough study of all this material is needed before the correct placement and true relationship of the species can be determined. A recent reexamination of *Pseudosimulium humidum* (Westwood) (Craig 1977) has made it clear that this fossil species does not belong to the Simuliidae.

Keys to genera

Adult

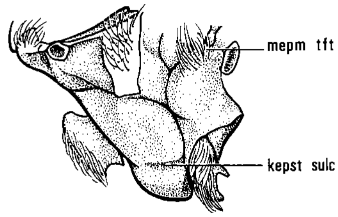
1. R_1 joining C slightly beyond middle of wing; branches of Rs conspicuously separated by membrane, with posterior branch ending well before terminus of C; C, Sc, and branches of R with moderately long setae on dorsal and ventral surfaces; false vein (m-cu fold) not forked apically; cell bm absent (Figs. 24, 25). Facets of eye all similar in size except for a few larger facets near middle of anterior margin of eye; eyes broadly separated by frons dorsally, touching or nearly so below antennae (Fig. 6). Calcipala and pedisulcus absent. Mesepimeral tuft absent (Fig. 11). Gonostylus without an apical spinule, but with internal apical margin sometimes sclerotized (Figs. 51–54). Male only, female unknown .... PARASIMULIINAE.... ***Parasimulium*** Malloch....2
Peterson 1977

R_1 joining C well beyond middle of wing; if Rs forked, then branches lying closer together, with posterior branch ending near terminus of C; C, Sc, and branches of R with short setae sometimes present on one surface only; false vein (m-cu fold) distinctly forked apically; cell bm present or absent (Figs. 26–30). Facets of dorsal half of male eye usually conspicuously larger than those of ventral half; eyes usually touching or nearly so at middle of head above antennae, with frons usually small (Fig. 3). Calcipala and pedisulcus present or absent. Mesepimeral tuft present (Figs. 10, 12, 13). Gonostylus of male usually with one or more apical spinules (Figs. 55, 58) .... SIMULIINAE....3

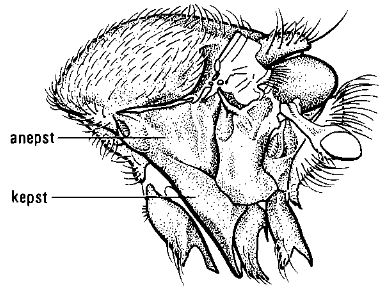
2. Stem of Rs shorter than or at most subequal to posterior branch (R_{4+5}) of fork; false vein (m-cu fold) faint, becoming evanescent at about level of distal end of anterior branch (R_{2+3}) of Rs; A_2 absent or very faint (Fig. 25). Halter entirely yellow. Gonostylus yellow, narrowing distally and somewhat rounded, or pointed, or with inner distal corner produced as a short rounded upturned lobe (Figs. 51–53); ventral plate of aedeagus, in ventral view, broad,

Figs. 27.10–23. Thoraces and hind tarsi: thorax of (10) *Metacnephia jeanae* (DeFoliart & Peterson), (11) *Parasimulium stonei* Peterson, (12) *Prosimulium mixtum* Syme & Davies, and (13) *Gymnopais holopticus* Stone; (14) dorsal view of scutellum and postnotum of *G. holopticus*; thorax of (15) *Simulium* (*Ectemnaspis*) sp. in dorsal view, (16) S. (*Parabyssodon*) *transiens* Rubtzov, and (17) S. (*Phosterodoros*) *jenningsi* Malloch; hind tarsus and claw of (18) *Prosimulium decemarticulatum* (Twinn), (19) *Prosimulium ursinum* (Edwards), (20) *Simulium arcticum* Malloch, (21) *Stegopterna mutata* (Malloch), (22) *Simulium* (*Psilozia*) *vittatum* Zetterstedt, and (23) *S.* (*Byssodon*) *meridionale* Riley.

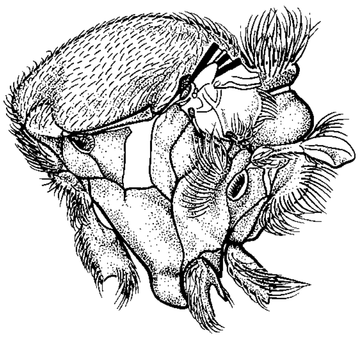
Abbreviations: anepst, anepisternum; anepst memb, anepisternal membrane; b tth, basal tooth of claw; clcp, calcipala; clw, claw; kepst, katepisternum; kepst sulc, katepisternal sulcus; mepm tft, mesepimeral tuft; pdsl, pedisulcus; pn, postnotum; sbb tth, subbasal tooth of claw; sctl, scutellum.



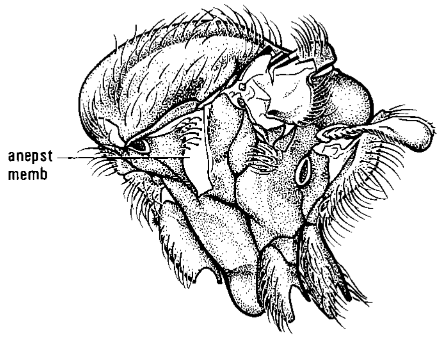
10 Metacnephia jeanae ♀



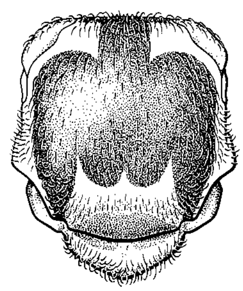
11 Parasimulium stonei ♂



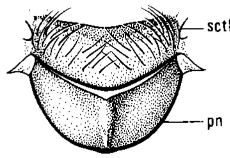
12 Prosimulium mixtum ♀



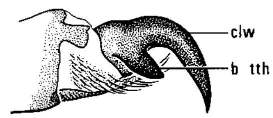
13 Gymnopais holopticus ♀



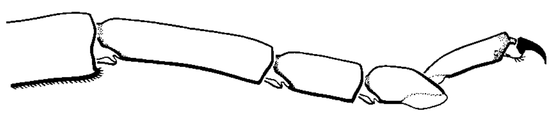
15 S. (Ectemnaspis) sp. ♀



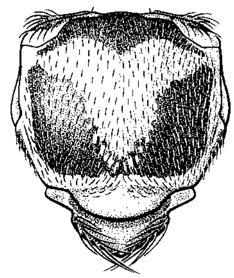
14 Gymnopais holopticus ♀



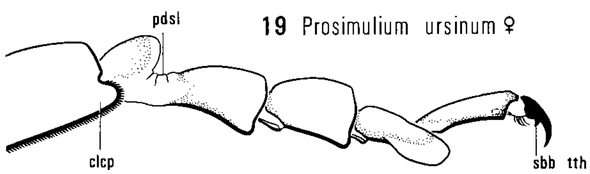
18 Prosimulium decemarticulatum ♀



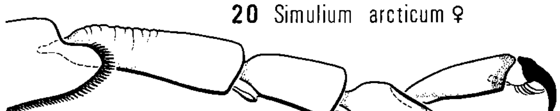
19 Prosimulium ursinum ♀



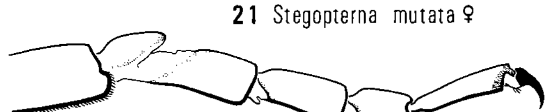
16 S. (Parabyssodon) transiens ♂



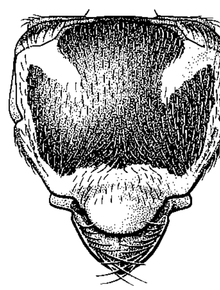
20 Simulium arcticum ♀



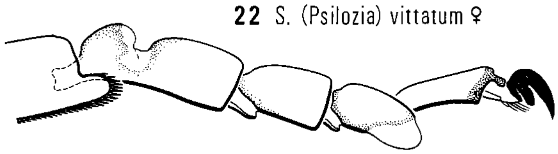
21 Stegopterna mutata ♀



22 S. (Psilozia) vittatum ♀



17 S. (Phosterodoros) jenningsi ♂



23 S. (Byssodon) meridionale ♀

dorsoventrally flattened, and somewhat H-shaped (Fig. 52) .... ***Parasimulium*** (***Parasimulium*** Malloch)
3 spp.; California, Oregon

Stem of Rs distinctly longer than posterior branch (R_{4+5}) of fork; false vein (m-cu fold) weak but extending more nearly to wing margin; A_2 present and distinct (Fig. 24). Halter entirely brownish black. Gonostylus black, broad, with apex broadly rounded, and with a short median sclerotization (Fig. 54); ventral plate of aedeagus, in ventral view, a narrow subquadrate structure with a short bulbous apical lip-like projection, and with basal arms extending laterally at right angles beyond its margins (Fig. 54) .... ***Parasimulium*** (***Astoneomyia*** Peterson)
1 sp., *melanderi* Stone; Washington

3. Rs with a long distinct fork that is conspicuously longer than its petiole; C with fine setae only, without spinules interspersed among them; basal section of R always setose (Fig. 31); cell bm present, although sometimes very small. Katepisternum divided by a wide shallow katepisternal sulcus that is sometimes evanescent anteriorly; lower portion of katepisternum in profile about as deep as or deeper than long (Fig. 12). Calcipala and pedisulcus absent (Fig. 19) 4

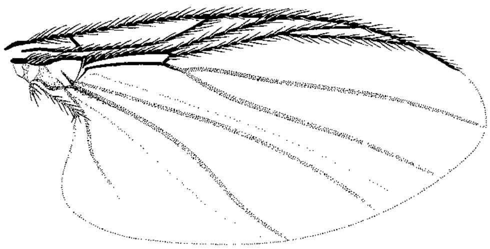
Rs unforked, or with a short usually obscure apical fork that is conspicuously shorter than its petiole; C often with spinules interspersed among its fine setae; basal section of R setose or bare; small cell bm present or absent (Figs. 27–30). Katepisternum usually divided by a narrow deep more or less complete katepisternal sulcus; lower portion of katepisternum, in profile, often longer than deep (Fig. 10). Calcipala and pedisulcus present or absent (Figs. 20–23) 13

4. Wing fumose, sometimes nearly opaque; petiole of M at least twice as long as Rs from its base to crossvein r-m (Fig. 26). Head, body, coxae, and femora sparsely covered with rather coarse semierect to erect setae, without fine recumbent setae (Fig. 13); clypeus bare except for a few erect setae near lateral margins. Postnotum rather small and strongly arched, sometimes with a varyingly conspicuous median longitudinal ridge or line (Fig. 14); anepisternal membrane usually with some setae dorsally (apparently absent in one species). Anal lobe and cercus of female fused into a single heavily sclerotized piece; spermatheca globular, sclerotized, with a long neck (Fig. 37). Gonostylus of male usually with two or more minute apical spinules that cannot easily be seen under a dissecting microscope.. ***Gymnopais*** Stone
5 spp.; northwestern North America from British Columbia to Alaska; Wood 1978

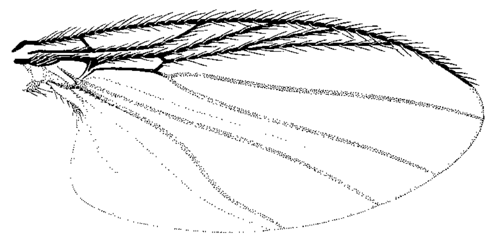
Wing usually hyaline, but if slightly fumose or tinted then distinctly transparent; petiole of M less than twice as long as Rs from its base to crossvein r-m (Figs. 27–30). Head, body, coxae, and femora entirely covered with rather dense fine recumbent setae, with a few erect setae sometimes evident especially posteromedially on scutum; clypeus entirely covered with setae. Postnotum larger, rather evenly arched, without a median longitudinal ridge or line; anepisternal membrane setose or bare. Anal lobe and cercus of female clearly separated by membrane, usually lightly to moderately sclerotized; spermatheca of various shapes, but if sclerotized then without a long sclerotized neck. Gonostylus of male with a variable number of apical spinules that are visible under a dissecting microscope.. 5

5. Antenna with seven flagellomeres (Fig. 2), rarely with eight. Posterior margin of eye near middle with a slightly raised but prominent shiny stemmatic bulla (Fig. 2). Claws of female simple. Hypogynial valve of female rather truncate, short, not reaching anal lobe; spermatheca short, broader than long, with a large differentiated area at junction with spermathecal duct (Fig. 36). Gonostylus of male with a single (rarely two) apical spinule; lateral margins of ventral plate of aedeagus strongly emarginate near junction with basal arms (Fig. 58).. ***Twinnia*** Stone & Jamnback
3 spp.; western and northeastern U.S.A. and Canada; Wood 1978

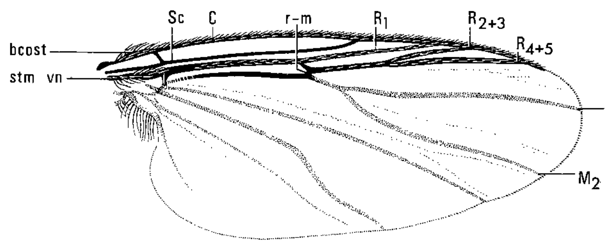
Antenna usually with nine flagellomeres (Figs. 4, 5), but sometimes with seven or eight. Posterior margin of eye near middle without a prominent stemmatic bulla, but in some species with a weak indication of a bulla. Claws of female variable. Hypogynial valve of female short or elongate, but if valve short and rather truncate then claws having a variably sized but usually conspicuous basal or subbasal tooth; spermatheca variable. Gonostylus of male often with more than one apical spinule; ventral plate of aedeagus variable, but not exactly as above .... ***Prosimulium*** Roubaud....6
Peterson 1970



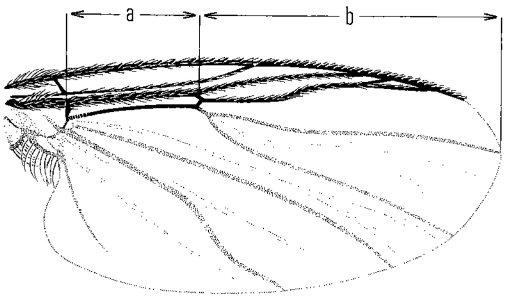
24 P. (Astoneomyia) melanderi ♂



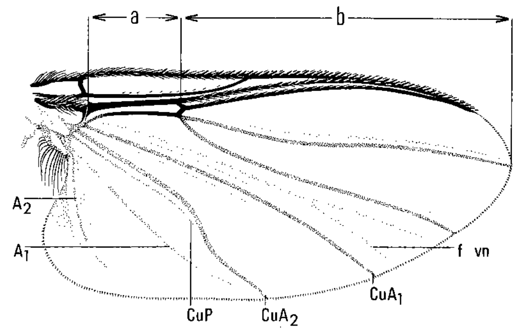
25 P. (Parasimulium) stonei ♂



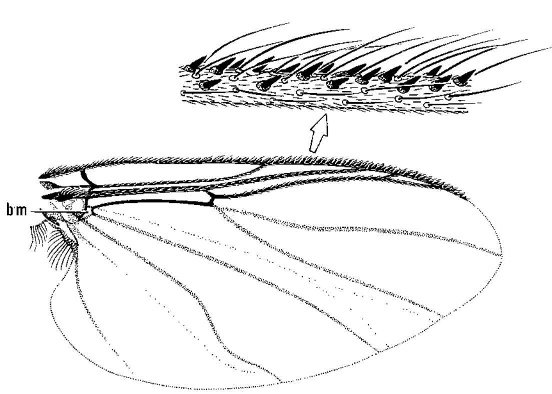
26 Gymnopais holopticus ♀



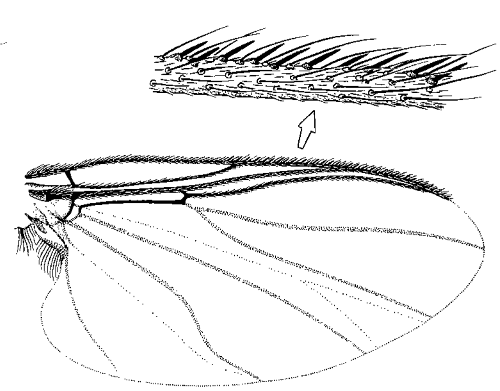
27 Cnephia dacotensis ♀



28 Simulium venustum ♀



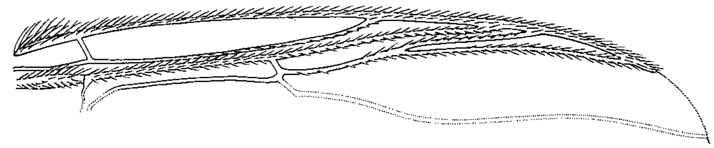
29 Mayacnephia sp. ♀



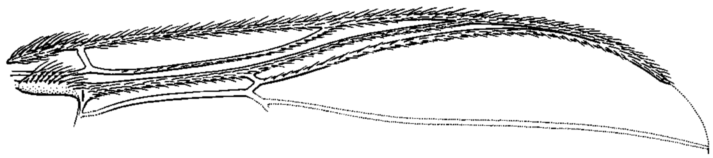
30 Greniera sp. ♀

Figs. 27.24–30. Wings: (24) ***Parasimulium*** (***Astoneomyia***) ***melanderi*** Stone; (25) ***P.*** (***Parasimulium***) ***stonei*** Peterson; (26) *Gymnopais holopticus* Stone; (27) *Cnephia dacotensis* (Dyar & Shannon); (28) ***Simulium venustum*** Say; (29) *Mayacnephia* sp.; (30) *Greniera* sp.

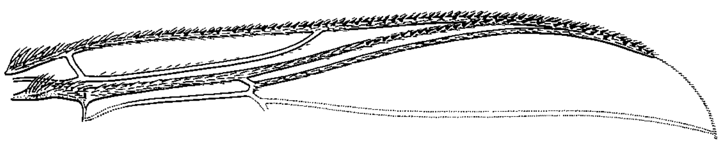
Abbreviations: a, basal section of R; b, base of Rs to apex of wing; bcost, basicosta; f vn, false vein; stm vn, stem vein.



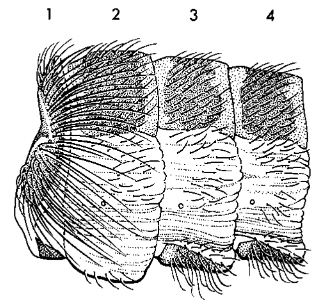
31 Prosimulium ursinum ♀



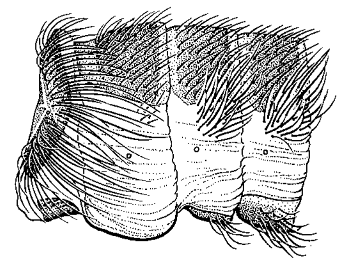
32 Greniera abdita ♀



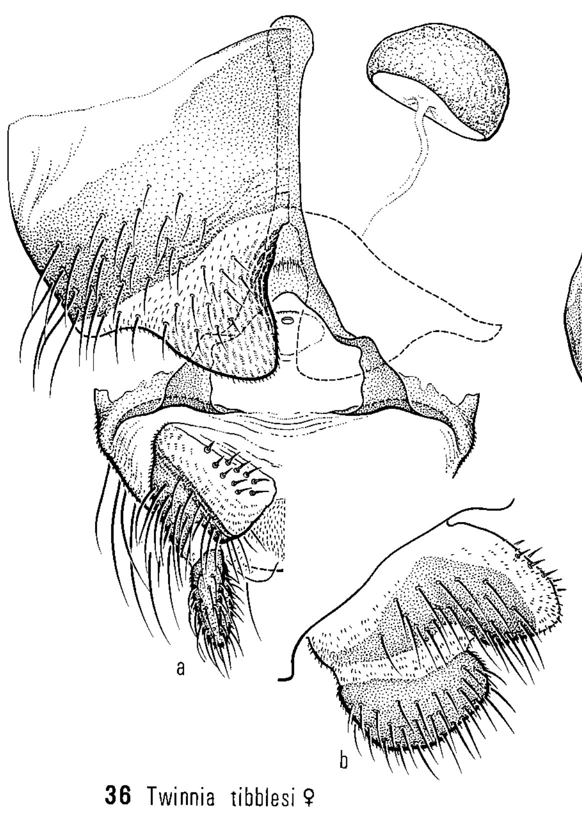
33 Metacnephia saileri ♀



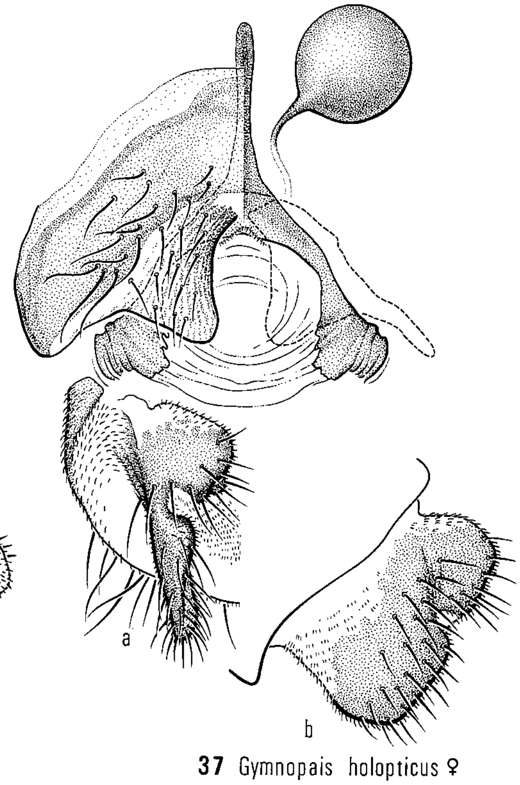
34 Cnephia daçotensis ♂



35 Greniera sp. ♂



36 Twinnia tibblesi ♀



37 Gymnopais holopticus ♀

Figs. 27.31–37. Anterior veins of wing and abdominal features: anterior veins of (31) *Prosimulium ursinum* (Edwards), (32) *Greniera abdita* (Peterson), and (33) *Metacnephia saileri* (Stone); abdominal segments 1–4 of (34) *Cnephia dacotensis* (Dyar & Shannon) and (35) *Greniera* sp.; female terminalia (*a*, ventral view with left hypogynial valve removed; *b*, right lateral view at right angles to plane of ventral view) of (36) *Twinnia tibblesi* Stone & Jamnback and (37) *Gymnopais holopticus* Stone (*continued*).

6. Female 7
   Male 10

7. Hypogynial valve long, narrowly rounded or pointed distally, reaching or extending beyond anal lobe so that abdomen appears rather pointed posteriorly; anteromedial corner of each hypogynial valve produced nipple-like (Fig. 38). Spermatheca with a large differentiated circular area at junction with spermathecal duct. Claw simple, or at most with a small inconspicuous subbasal tooth (Fig. 19) .... ***Prosimulium*** (***Prosimulium*** Roubaud), in part
   32 spp.; widespread

   Hypogynial valve short, broadly rounded or truncate distally, not reaching anal lobe so that abdomen appears rounded or truncate posteriorly; anteromedial corner of each hypogynial valve not produced nipple-like (Figs. 39–41). Spermatheca with only a small differentiated circular area, or none, at junction with spermathecal duct. Claw with a variably sized but usually conspicuous basal or subbasal tooth (Figs. 20, 23) 8

8. Anepisternum with a small patch of fine setae both anterior and posterior to anepisternal membrane. Two sclerotized plates bearing short setae present posterior to hypogynial valves, and continuous laterally with a prominent protuberance on each side of segment 9 (Fig. 39). Spermatheca a greatly enlarged rounded thin delicate bag, neither pigmented nor patterned (often difficult to see, and therefore sometimes seemingly absent) (Fig. 39) ....
   ....***Prosimulium*** (***Distosimulium*** Peterson), in part
   1 sp. *pleurale* Malloch; Canada, Alaska

   Anepisternum without a small patch of setae on both sides of anepisternal membrane. Sclerotized plates posterior to hypogynial valves absent, and without a prominent lateral protuberance on each side of segment 9. Spermatheca not greatly enlarged, at least lightly pigmented, often patterned 9

9. Spermatheca subcircular to pear-shaped, heavily sclerotized. Arm of genital fork slender at base, greatly expanded distally into a weakly sclerotized plate that is sometimes wrinkled or denticulate and sometimes bearing a basal denticulate median process (Fig. 40) ....
   ....***Prosimulium*** (***Parahelodon*** Peterson), in part
   3 spp.; northeastern U.S.A., Canada, Alaska

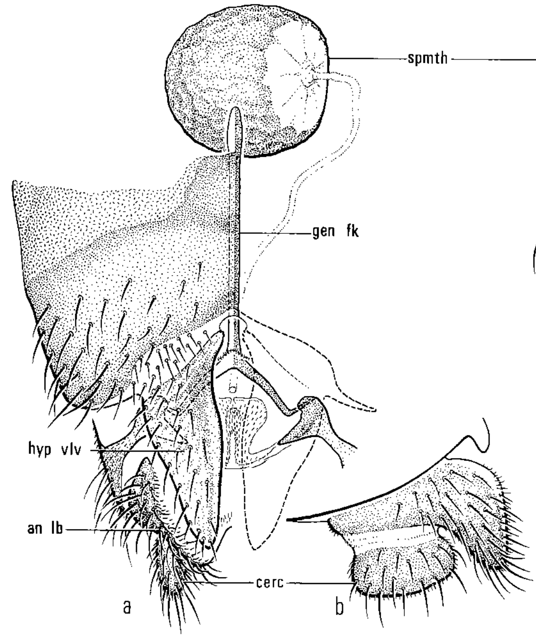
   Spermatheca usually elongate, always lightly sclerotized. Arm of genital fork rather thick at base, gradually expanding distally into a large heavily sclerotized plate that sometimes bears a sharply pointed posteromedial process (Fig. 41) but never bearing a wrinkled or a denticulate basal median process ....***Prosimulium*** (***Helodon*** Enderlein), in part
   6 spp.; northwestern and northern North America

10. Anepisternum with a small patch of fine setae both anterior and posterior to anepisternal membrane. Ventral plate of aedeagus deeply cleft and basal arms long, so that entire structure appears H-shaped; median sclerite Y-shaped, with its stem and basal portion of arms heavily sclerotized, and remainder of arms membranous and prolonged, projecting posteriorly and ventrally beyond margin of ventral plate. Gonostylus thin, pointed, bending at nearly a right angle, with one subterminal and two terminal spinules; paramere with a strong spiniform process that curves ventrally and posteriorly to meet tip of gonostylus (Figs. 55–57)...***Prosimulium*** (***Distosimulium*** Peterson), in part
    see couplet 8

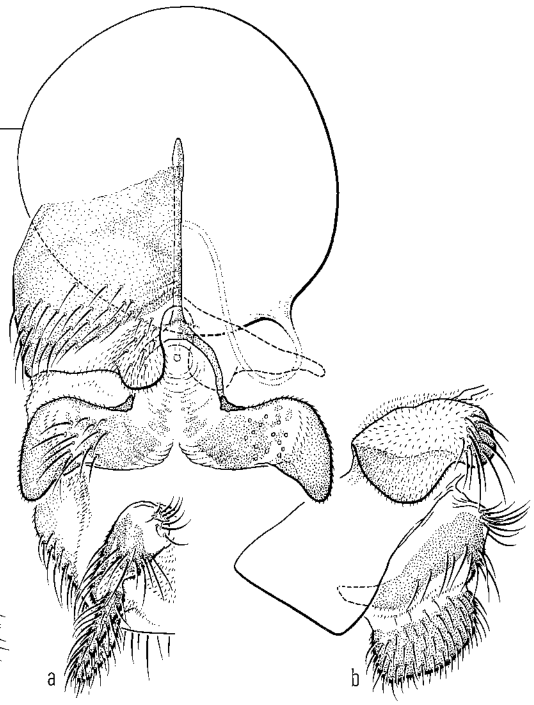
    Anepisternum without a small patch of setae on both sides of anepisternal membrane, except for *P. neomacropyga* Peterson, in which a few setae are sometimes present anterior to ventral edge of anepisternal membrane. Ventral plate of aedeagus not deeply cleft nor H-shaped; median sclerite variable but arms not prolonged. Gonostylus variable; paramere expanded plate-like distally but not as a spiniform process curving to meet tip of gonostylus 11

11. Ventral plate of aedeagus broad, flattened dorsoventrally, with anterior margin of dorsal surface produced medially beyond tips of basal arms as a long slender tube-like process or a similar somewhat flattened grooved process to which base of median sclerite is fused; basal arms short, slender, pointed; median sclerite of modified structure, not Y-shaped. Paramere free, not connected to basal arms of ventral plate; gonostylus with a single apical spinule (Fig. 59)
    ....***Prosimulium*** (***Parahelodon*** Peterson), in part
    see couplet 9

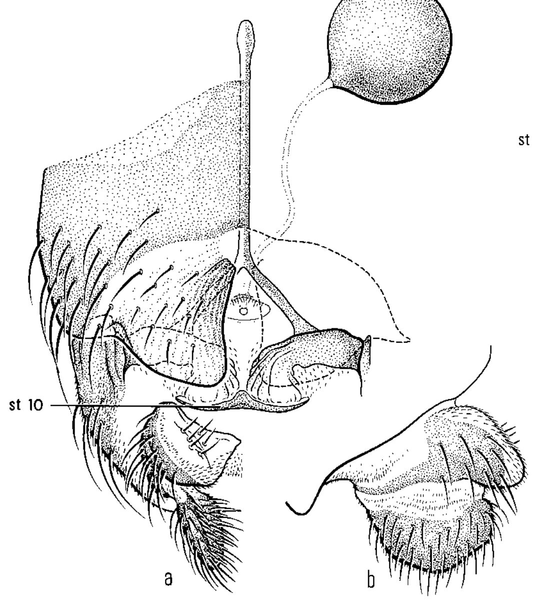
    Ventral plate of aedeagus not flattened dorsoventrally, but if somewhat compressed then dorsal surface broadly convex; anteromedial margin of dorsal surface not produced tube- or groove-like; basal arms usually longer and broader; median sclerite Y-shaped. Paramere connected to basal arms of ventral plate; gonostylus variable 12



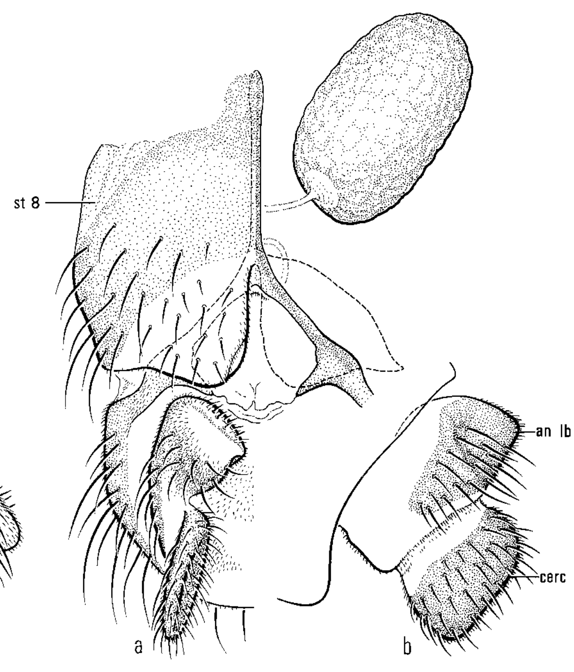
38 P. (Prosimulium) mixtum ♀



39 P. (Distosimulium) pleurale ♀



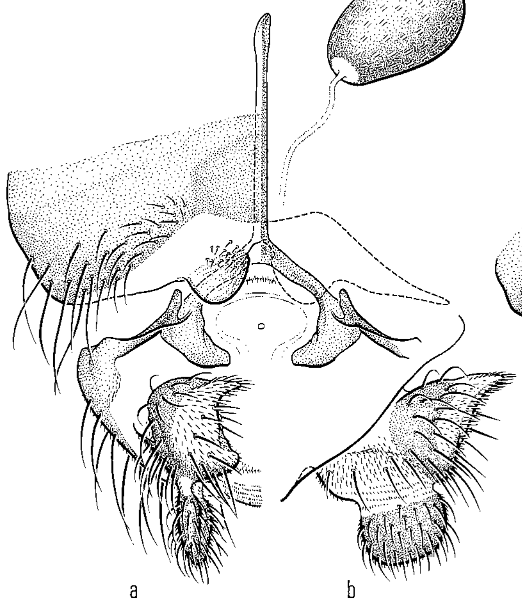
40 P. (Parahelodon) decemarticulatum ♀



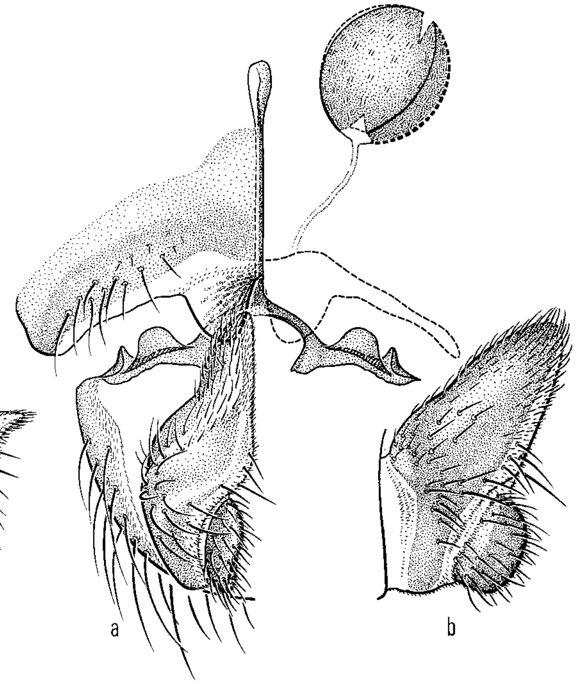
41 P. (Helodon) onychodactylum ♀

Figs. 27.38–41. Female terminalia (*continued*; *a* and *b* as in Figs. 36 and 37): (38) ***Prosimulium (Prosimulium) mixtum*** Syme & Davies; (39) ***P. (Distosimulium) pleurale*** Malloch; (40) ***P. (Parahelodon) decemarticulatum*** (Twinn); (41) ***P. (Helodon) onychodactylum*** Dyar & Shannon (*continued*).

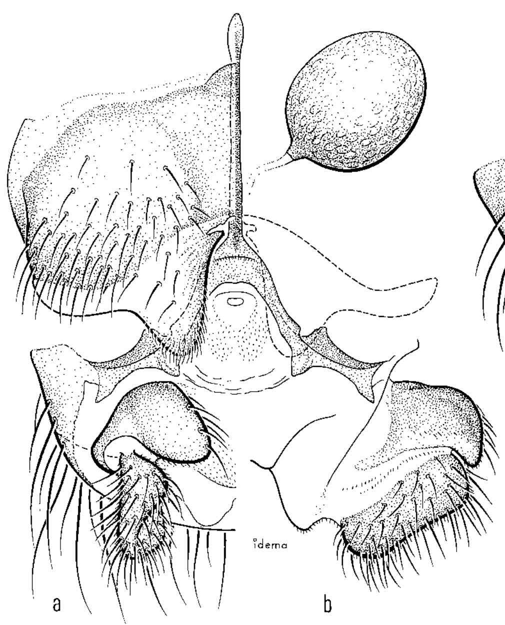
Abbreviations: an lb, anal lobe of tergite 10; cerc, cercus; gen fk, genital fork; hyp vlv, hypogynial valve; spmth, spermatheca; st, sternite.



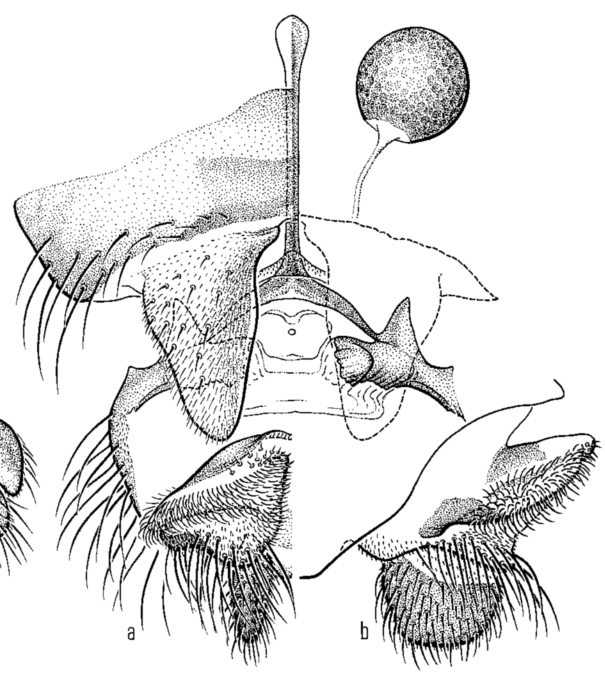
42 S. (Psilopelmia) bivittatum ♀



43 S. (Ectemnaspis) sp. ♀



44 S. (Eusimulium) aureum ♀



45 S. (Hemicnetha) virgatum ♀

Figs. 27.42–45. Female terminalia (*continued*; *a* and *b* as in Figs. 36 and 37): (42) ***Simulium*** (***Psilopelmia***) ***bivittatum*** Malloch; (43) *S.* (***Ectemnaspis***) sp.; (44) *S.* (***Eusimulium***) ***aureum*** Fries; (45) *S.* (***Hemicnetha***) *virgatum* Coquillett (*continued*).

12. Ventral plate of aedeagus broad, compressed dorsoventrally, but with dorsal surface broadly convex and having either a shallow medial depression, or furrow, or a median dorsal convexity; apical margin with at most a short narrow ventrally directed lip, or none (Fig. 60). Gonostylus rounded or pointed apically, with two to five apical spinules (Fig. 60) .... **_Prosimulium_ (_Helodon_** Enderlein), in part
see couplet 9

Ventral plate of aedeagus variably broad or narrow, but not noticeably compressed dorsoventrally, with dorsal surface conspicuously concave at least proximally; apical margin usually with a prominent ventrally directed lip or emargination (Fig. 61). Gonostylus variable .... **_Prosimulium_ (_Prosimulium_** Roubaud), in part
see couplet 7

13. Length of basal section of R (*a*, Fig. 28) equal to much less than one-third distance from base of Rs to apex of wing (*b*, Fig. 28); R with or without setae dorsally; cell bm absent or greatly reduced. Calcipala usually well-developed (Figs. 20, 23), although sometimes reduced (e.g. *Psilozia* Enderlein, Fig. 22); pedisulcus present, usually deep and distinct (Figs. 20, 22, 23), rarely a shallow depression .... ***Simulium*** Latreille....25
Peterson 1960, Davies *et al.* 1962, Stone and Snoddy 1969

Length of basal section of R (*a*, Fig. 27) rarely less than one-third distance from base of Rs to apex of wing (*b*, Fig. 27); R setose dorsally; cell bm present and distinguishable. Calcipala present, but sometimes reduced; pedisulcus absent, or if present very shallow 14

14. C with fine uniformly colored setae, some of which are sometimes short and stiff but not spiniform nor darker in color (Fig. 32) .... ***Greniera*** Doby & David....15

C with short stout black spinules interspersed among longer and paler setae (Figs. 29, 30) 16

15. Antenna with eight flagellomeres .... ***Greniera*** Doby & David, in part
1 sp., *denaria* (Davies, Peterson & Wood); Ontario, British Columbia

Antenna with nine flagellomeres .... ***Greniera abdita*** (Peterson) group
2 spp.; northeastern U.S.A., eastern Canada

16. Rs with a short but distinct apical fork, with branches narrowly separated by membrane (Fig. 29); Sc of male bare ventrally .... ***Mayacnephia*** Wygodzinsky & Coscaron
4 spp.; western North America

Rs simple, or with a short indistinct apical fork whose branches are closely appressed and scarcely or not separated by membrane; Sc of male bare or setose ventrally 17

17. Calcipala large and prominent, lamellate, rounded apically, in posterior view overlapping and sometimes concealing base of second tarsomere (Fig. 21); claw of female simple. Sc of male setose ventrally .... ***Stegopterna*** Enderlein
2 spp.; widespread especially in northern North America; Davies *et al.* 1962

Calcipala absent, or if present, small and bluntly pointed, in posterior view not concealing base of second tarsomere; claw of female with a small subbasal tooth or a large basal thumb-like projection. Sc of male bare or setose ventrally 18

18. Female 19
Male 22

19. R_1 dorsally with scattered black spinules on distal half (Fig. 33). Anepisternal membrane usually with tuft of pale setae dorsally (Fig. 10) .... ***Metacnephia*** Crosskey, in part
7 spp.; western U.S.A., western Canada, Alaska

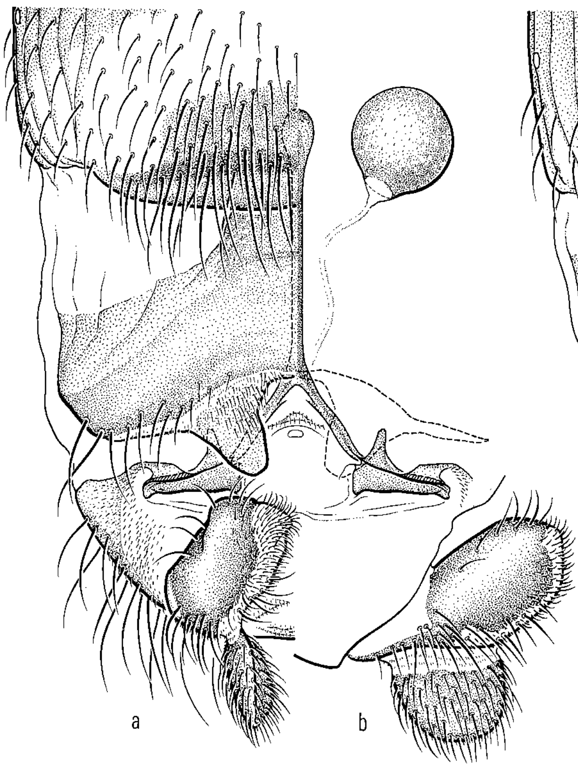
R_1 dorsally with setae only on distal half. If a few spinules present on R_1, then anepisternal membrane bare 20

20. Frons narrow, four times longer than wide, of nearly uniform width (Fig. 4) .... ***Ectemnia*** Enderlein, in part
2 spp.; New York to Michigan, Canada

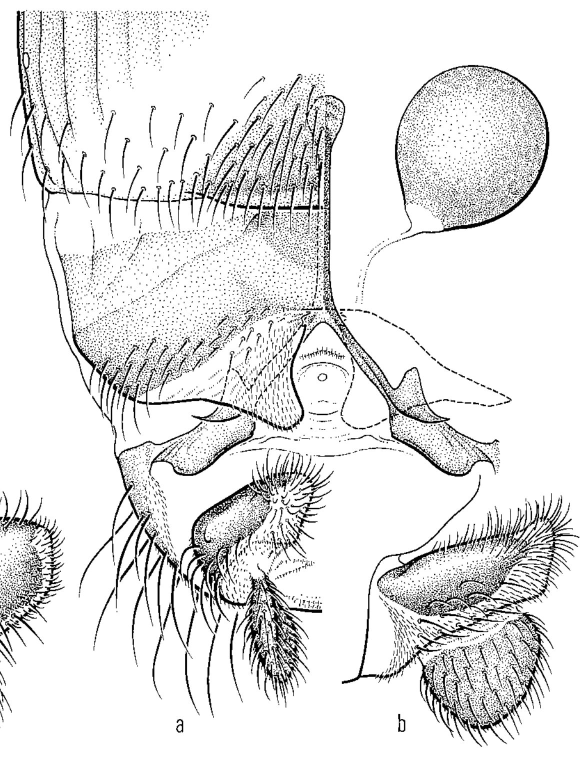
Frons wider, not more than twice as long as wide, or if narrower then noticeably widening above (Fig. 5) 21

21. Halter pale brown, with knob paler than stem. R_1 dorsally with a few spinules on distal half .... ***Cnephia*** Enderlein, in part
4 spp.; widespread in eastern half of North America

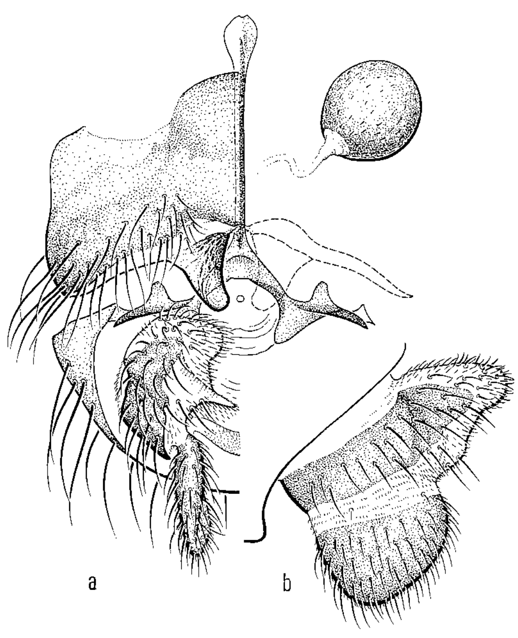
Halter entirely black. R_1 dorsally with setae only on distal half .. ***Greniera*** Doby & David, in part
1 sp., undescribed; British Columbia



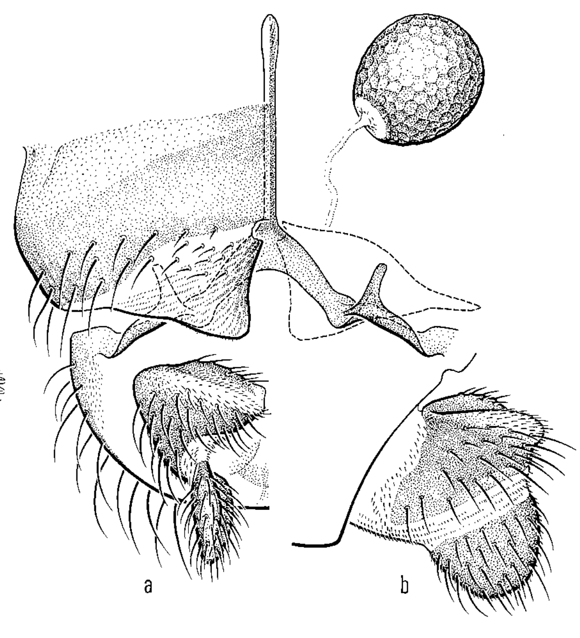
46 S. (Shewellomyia) pictipes ♀



47 S. (Hearlea) canadense ♀



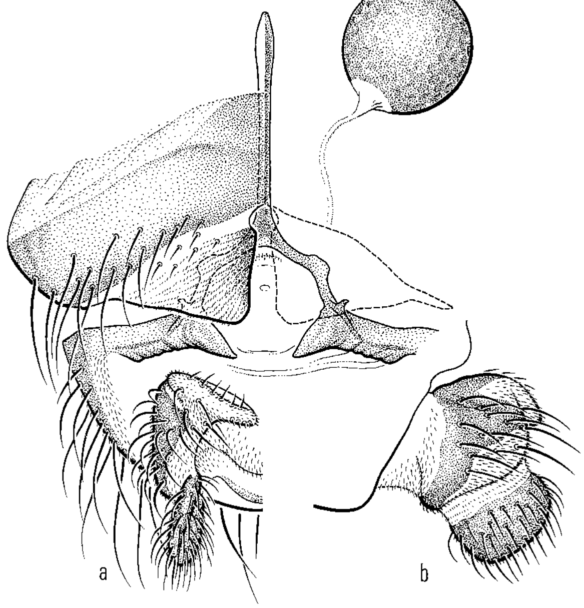
48 S. (Psilozia) vittatum ♀



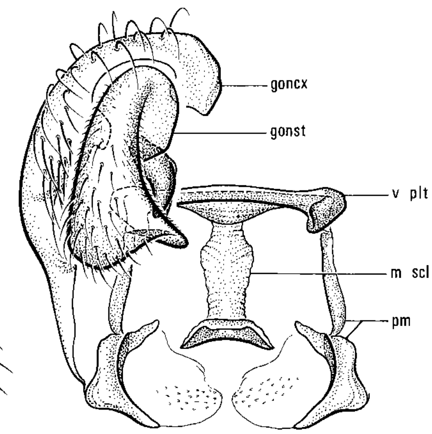
49 S. (Byssodon) meridionale ♀

Figs. 27.46–49. Female terminalia (*continued*; *a* and *b* as in Figs. 36 and 37): (46) *Simulium* (*Shewellomyia*) *pictipes* Hagen; (47) *S.* (*Hearlea*) *canadense* Hearle; (48) *S.* (*Psilozia*) *vittatum* Zetterstedt; (49) *S.* (*Byssodon*) *meridionale* Riley (*continued*).

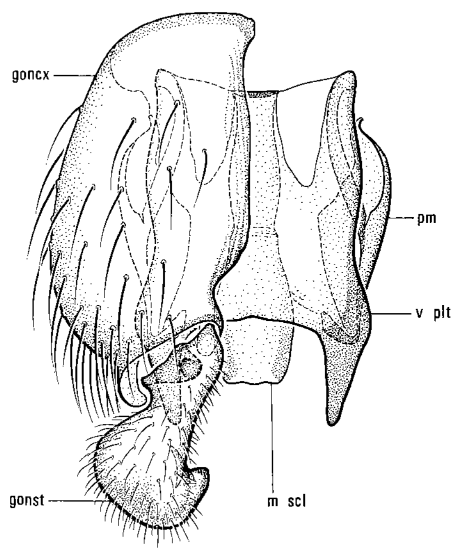
22. R_1 dorsally with scattered black spinules on distal two-thirds or more; these more numerous apically and as stout as spinules on C 23
R_1 dorsally usually with setae only; if spinules present on R_1, these confined to distal half or less and not as stout as spinules on C 24



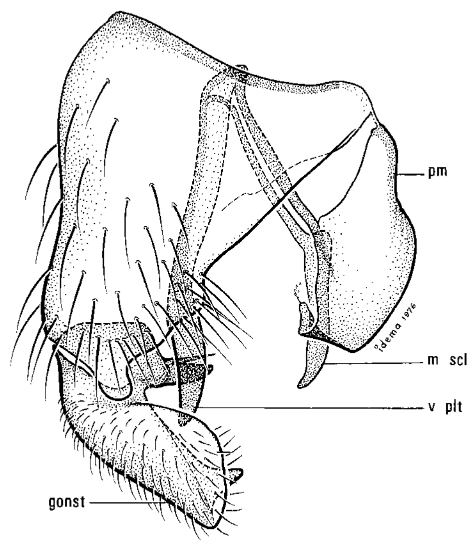
50 S. (Parabyssodon) transiens ♀



51 P. (Parasimulium) furcatum ♂



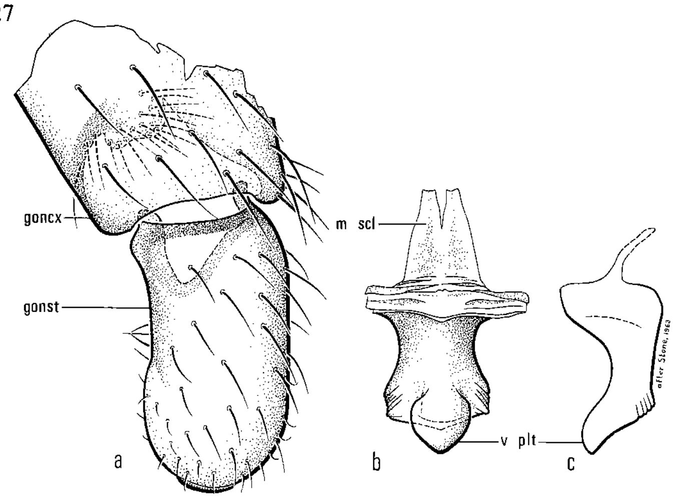
52 P. (Parasimulium) furcatum ♂



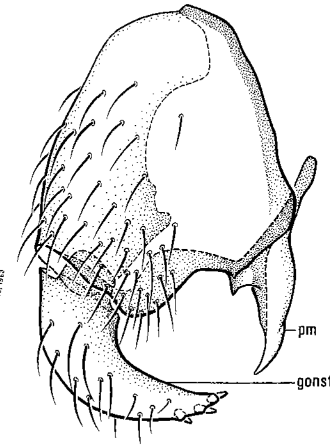
53 P. (Parasimulium) furcatum ♂

Figs. 27.50–53. Terminalia: (50) female terminalia (*concluded*; *a* and *b* as in Figs. 36 and 37) of ***Simulium*** **(*Parabyssodon*) *transiens*** Rubtzov; male terminalia of ***Parasimulium*** **(*Parasimulium*) *furcatum*** Malloch in (51) terminal (end) view, (52) ventral view, and (53) lateral view (*continued*).

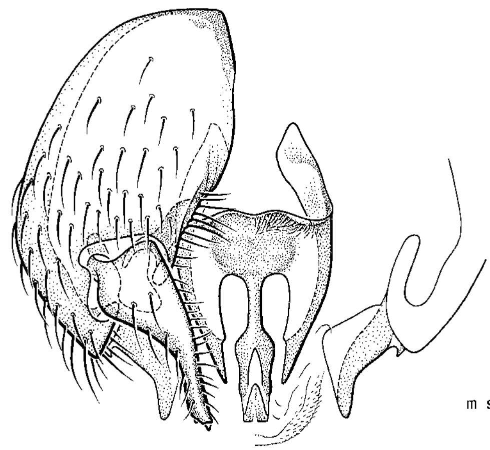
Abbreviations: goncx, gonocoxite; gonst, gonostylus; m scl, median sclerite of aedeagus; pm, paramere; v plt, ventral plate of aedeagus.



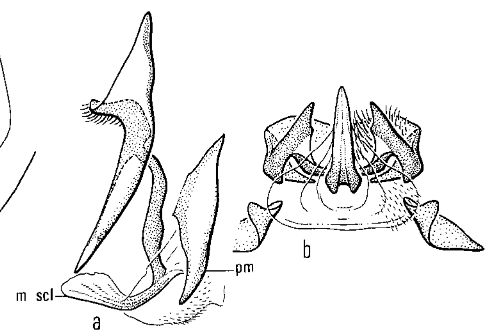
54 P. (Astoneomyia) melanderi ♂



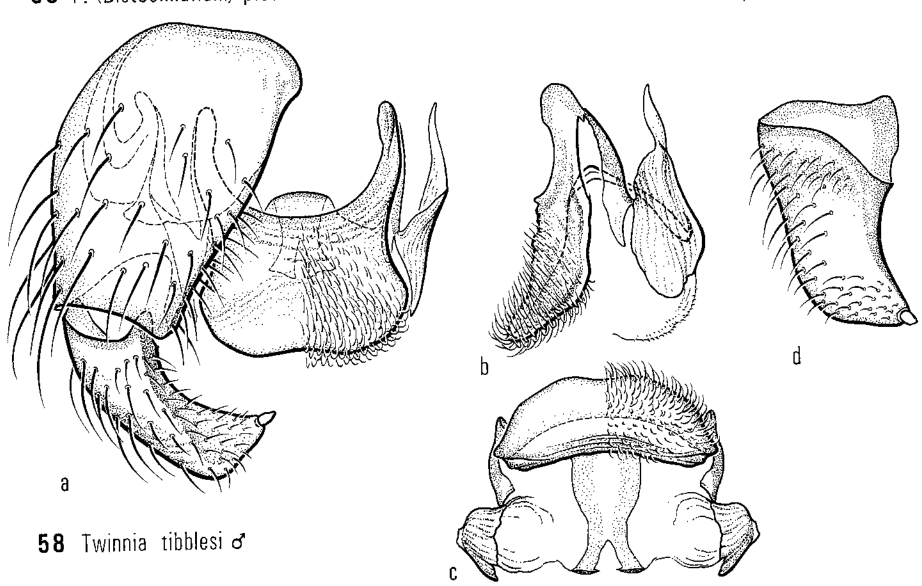
55 P. (Distosimulium) pleurale ♂



56 P. (Distosimulium) pleurale ♂



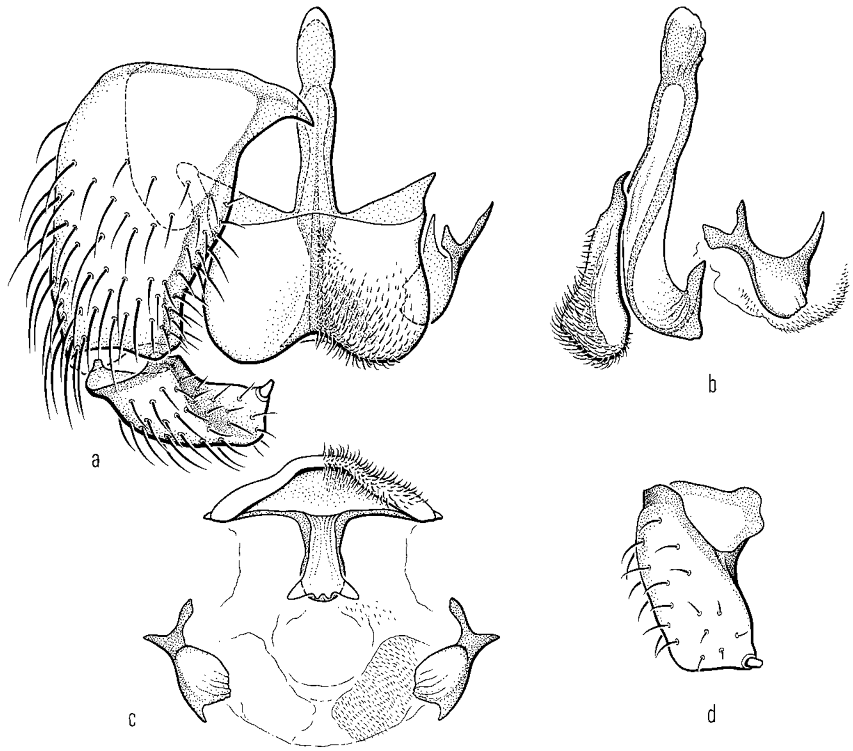
57 P. (Distosimulium) pleurale ♂



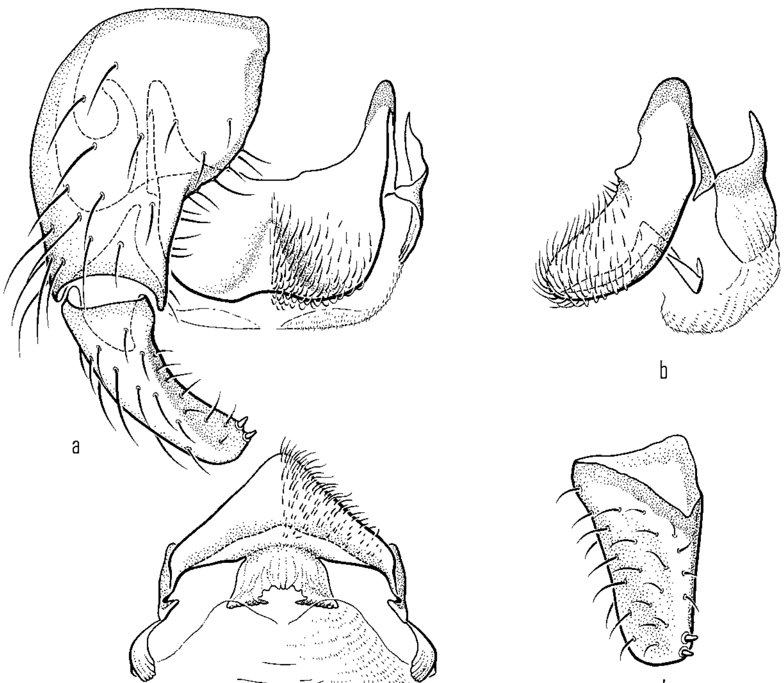
58 Twinnia tibblesi ♂

Figs. 27.54–58. Male terminalia (*continued*): (54) ***Parasimulium (Astoneomyia) melanderi*** Stone—***a*** ventral view, ***b*** ventral view, ***c*** lateral view; (55) ***Prosimulium (Distosimulium) pleurale*** Malloch, lateral view; (56) ***P. (D.) pleurale***, ventral view; (57) ***P. (D.) pleurale—a*** lateral view, ***b*** terminal view; (58) ***Twinnia tibblesi*** Stone & Jamnback—***a*** ventral view with left gonocoxite and gonostylus removed, ***b*** left lateral view of ventral plate, median sclerite, paramere, and aedeagal membrane, ***c*** terminal (end) view of same structures, ***d*** inner (dorsal) view of right gonostylus (*continued*).

Abbreviations: goncx, gonocoxite; gonst, gonostylus; m scl, median sclerite of aedeagus; pm, paramere; v plt, ventral plate of aedeagus.



59 P. (Parahelodon) decemarticulatum ♂

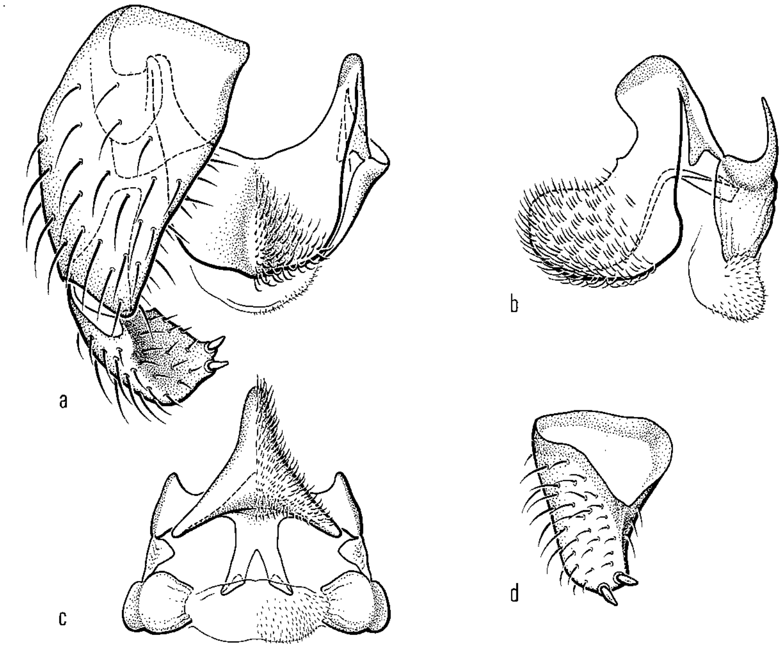


60 P. (Helodon) onychodactylum ♂

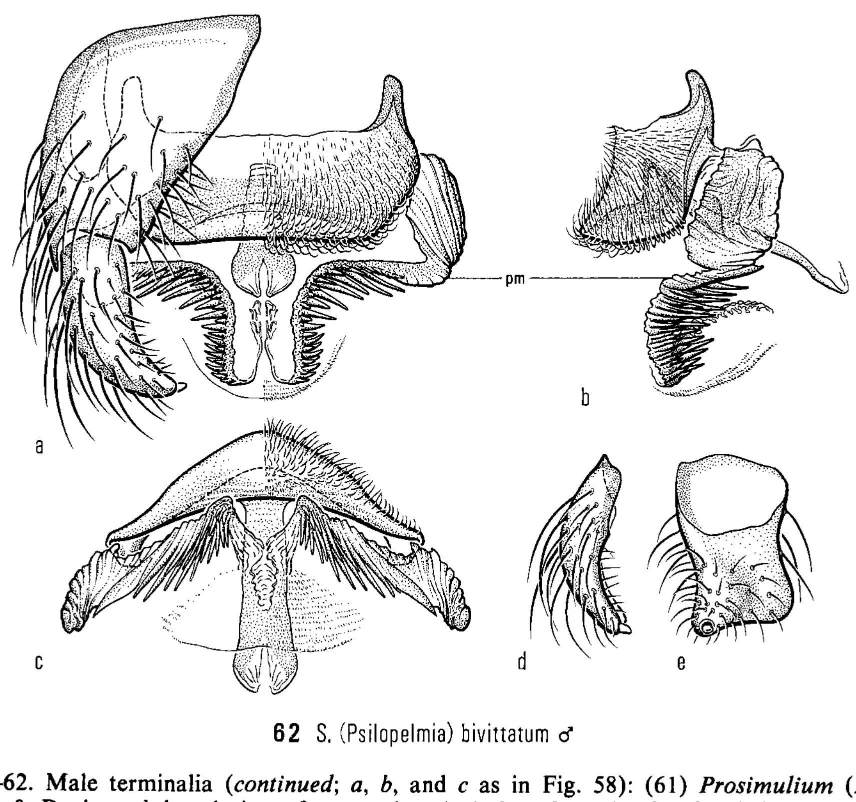
Figs. 27.59–60. Male terminalia (*continued*; *a*, *b*, *c*, and *d* as in Fig. 58): (59) ***Prosimulium*** (***Parahelodon***) ***decemarticulatum*** (Twinn); (60) ***P.*** (***Helodon***) ***onychodactylum*** Dyar & Shannon (*continued*).

23. Sc setose ventrally. Anepisternal membrane usually with tuft of pale setae dorsally (as in Fig. 10) .... ***Metacnephia*** Crosskey, in part
see couplet 19

Sc bare ventrally. Anepisternal membrane bare .... ***Ectemnia*** Enderlein, in part
see couplet 20



61 P. (Prosimulium) mixtum ♂



62 S. (Psilopelmia) bivittatum ♂

Figs. 27.61–62. Male terminalia (*continued*; *a*, *b*, and *c* as in Fig. 58): (61) ***Prosimulium*** (***Prosimulium***) ***mixtum*** Syme & Davies—*d* dorsal view of gonostylus; (62) ***Simulium*** (***Psilopelmia***) ***bivittatum*** Malloch—*d* lateral view of gonostylus, *e* dorsal view of gonostylus (*continued*).
Abbreviation: pm, paramere.

24. Halter brown, with knob distinctly paler than stem. Fine setae on pleural membrane of abdominal segments 3 and 4 not conspicuously long (Fig. 34) .... ***Cnephia*** Enderlein, in part
see couplet 21

Halter entirely black. Fine setae on pleural membrane of abdominal segments 3 and 4 long and erect (Fig. 35) .... ***Greniera*** Doby & David, in part
see couplet 21

25. Basal section of R setose dorsally (Fig. 31) 26

Basal section of R bare dorsally (Fig. 28) 28

26. Anal lobe of female attenuate or narrowly angulate ventrally, extending well below cercus (Fig. 42). Gonostylus of male shorter than gonocoxite, flattened, subquadrate, with inner distal angle prolonged and bearing a single spinule (Fig. 62). Pruinose species, often pale in color but sometimes black, usually with antenna and legs mostly yellow. Thorax usually with one or more straight longitudinal stripes in female, but usually patterned with simple gray or white pruinose stripes or anterior spots in male; prescutellar area without long setae .... ***Simulium*** (***Psilopelmia*** Enderlein), in part
6 spp.; mostly southwestern and western but extending to Alberta and Saskatchewan

Anal lobe of female, if angulate or extending well below cercus, more uniformly broadened and with a rounded ventral margin (Figs. 43, 45–48). Gonostylus of male variable in length, more or less cylindrical, or if flattened usually much longer than greatest width at base, and usually with a single apical spinule. Species, if pruinose, usually darker brownish to black in color, with antenna and legs mostly dark, but if legs bicolored then with conspicuous black areas. Thorax of both sexes usually unstriped or faintly striped; or if patterned then with conspicuous yellow and black markings; prescutellar area usually with long setae 27

27. Thorax of both sexes patterned with conspicuous yellow and black markings (Fig. 15). Claw of female with a small subbasal tooth. Anal lobe of female broad, extending well below cercus (Fig. 43); gonostylus of male tapering distally. Male of North American species unknown .... ***Simulium*** (***Ectemnaspis*** Enderlein)
1 sp., unnamed; New York; Wygodzinsky 1973

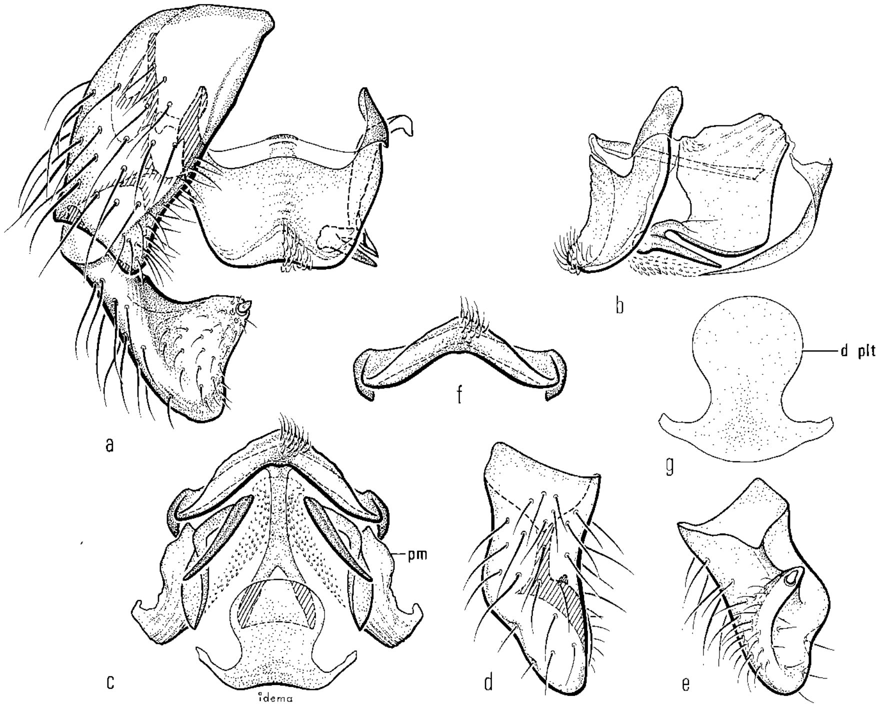
Thorax of both sexes brownish to black, not patterned, or at most with a faint narrow central stripe. Claw of female usually with a large basal thumb-like projection, rarely (two species) simple. Anal lobe of female not extending far below cercus (Fig. 44); gonostylus of male tapering distally or subtruncate with an internal triangular lobe (Figs. 63, 64) .... ***Simulium*** (***Eusimulium*** Roubaud)
20 spp.; widespread

28. Hypogynial valve of female elongate, usually reaching or extending beyond anterior margin of cercus; anal lobe extending well below cercus, but scarcely produced posteriorly and without a ventral notch in profile (Fig. 45). Frons of female narrow but widening dorsally. Scutum of female often slightly reddish with variably distinct pruinose vittae. Gonostylus of male usually broad and flattened, with lateral margins often sinuous; ventral plate of aedeagus broad, usually with a strong slender median projection that is sometimes nearly half as long as gonostylus (Fig. 65). Anepisternal membrane of both sexes bare or setose .... ***Simulium*** (***Hemicnetha*** Enderlein)
2 spp.; South Dakota south to Mexico and west to California, British Columbia

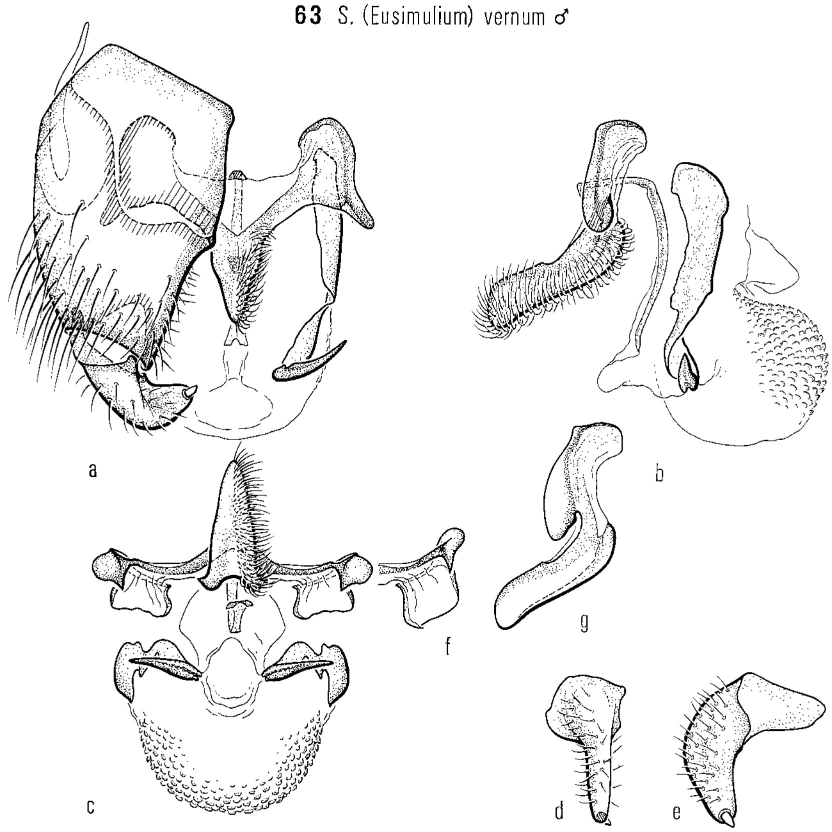
Hypogynial valve of female short, rarely reaching anterior margin of cercus; anal lobe variable, but often with a ventral notch in profile. Frons of female variable but usually wide. Scutum of female with or without pattern. Gonostylus of male variable in width but not unusually broad, with lateral margins more regular or not strikingly sinuous; ventral plate of aedeagus without a strong median projection. Anepisternal membrane always bare 29

29. Posterior margin of sternite 7 of female with a conspicuous fringe of long curved setae (Fig. 46); ventral portion of anal lobe greatly expanded, much wider than dorsal portion, subquadrate, highly polished (Fig. 46). Ventral plate of aedeagus of male large, with a deep median cleft so that entire structure in ventral view appears H-shaped, without denticles on margins of ventral lip; gonostylus without an apical spinule (Fig. 66) .... ***Simulium*** (***Shewellomyia*** Peterson)
2 spp.; eastern North America

Posterior margin of sternite 7 of female often setose but without a conspicuous fringe of long curved setae (Fig. 47); anal lobe variable in shape, usually without highly polished lateral surface, but if lateral surface polished then shaped as in Figs. 47 and 48. Ventral plate of



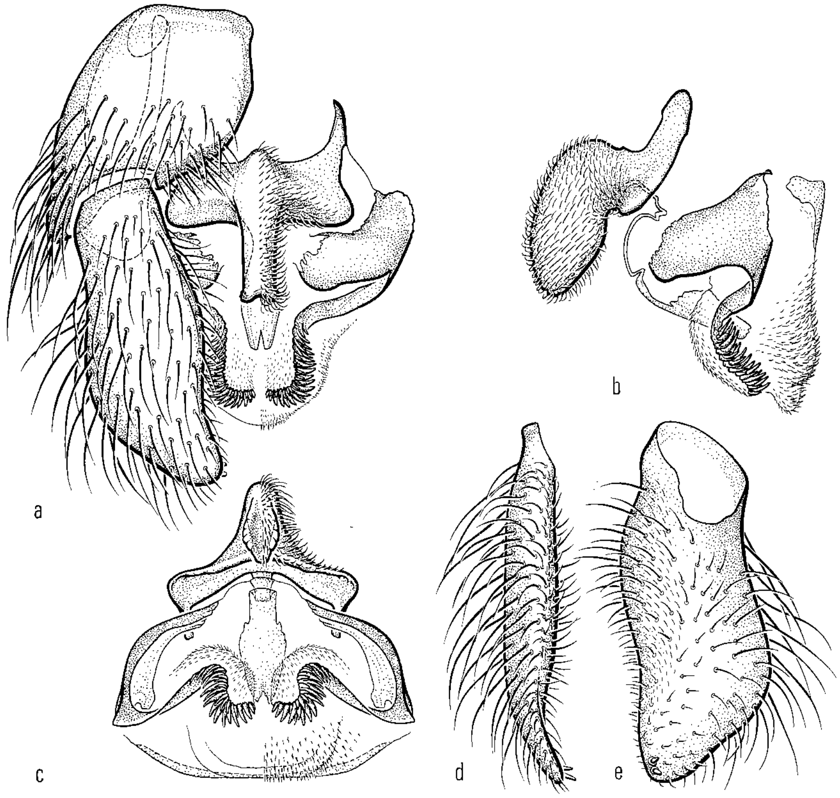
63 S. (Eusimulium) vernum ♂



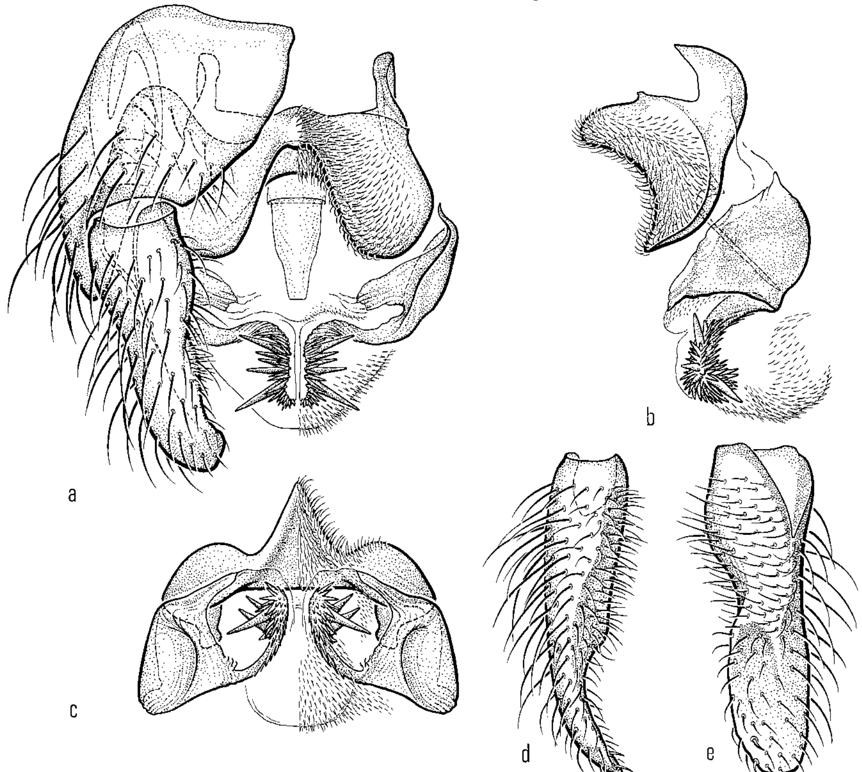
64 S. (Eusimulium) aureum ♂

Figs. 27.63–64. Male terminalia (*continued*; *a*, *b*, and *c* as in Fig. 58): (63) *Simulium* (*Eusimulium*) *vernum* Macquart—*d* ventral view of gonostylus, *e* dorsal view of gonostylus, *f* terminal view of ventral plate showing variation in development, *g* dorsal view of dorsal sclerite of aedeagus; (64) *S.* (*E.*) *aureum* Fries—*d* ventral view of gonostylus, *e* lateral view of inner surface of gonostylus, *f* lateral arm of ventral plate showing variation in development, *g* lateral view of ventral plate showing variation in development (*continued*).

Abbreviations: d plt, dorsal plate of aedeagus; pm, paramere.



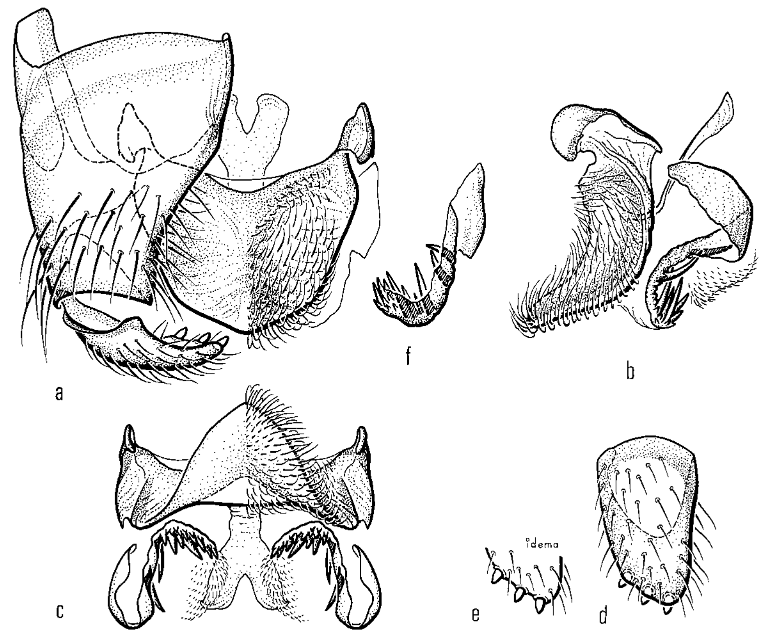
65 S. (Hemicnetha) virgatum ♂



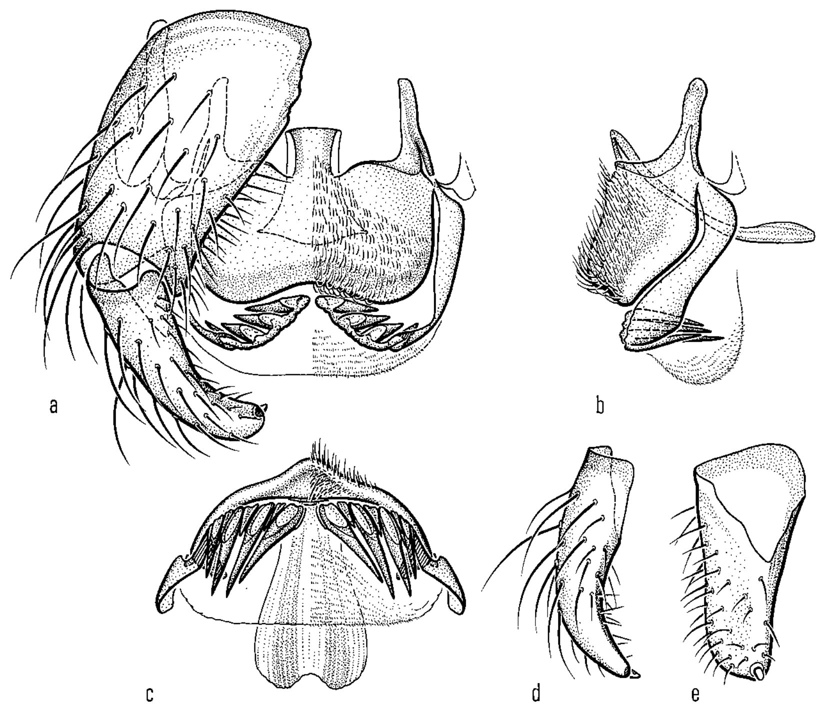
66 S. (Shewellomyia) pictipes ♂

Figs. 27.65–66. Male terminalia (*continued*; *a*, *b*, and *c* as in Fig. 58; *d* and *e* as in Fig. 62): (65) *Simulium* (*Hemicnetha*) *virgatum* Coquillett; (66) *S.* (*Shewellomyia*) *pictipes* Hagen (*continued*).

aedeagus of male variable, but not H-shaped nor with a deep median cleft, and with or without denticles on margins of ventral lip; gonostylus usually with one or more strong apical spinules 30

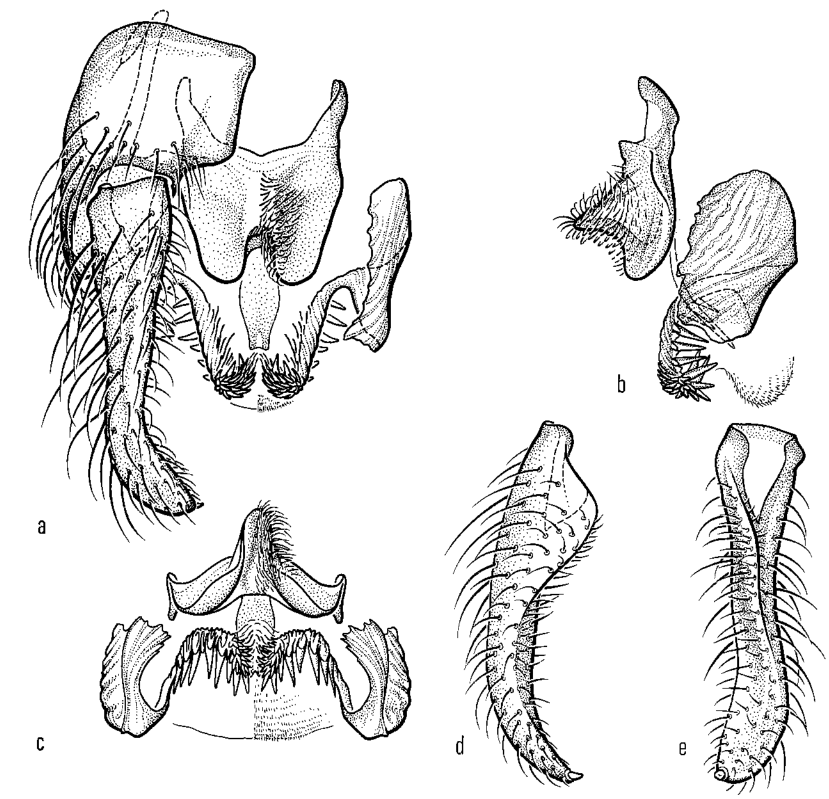


67 S. (Psilozia) vittatum ♂

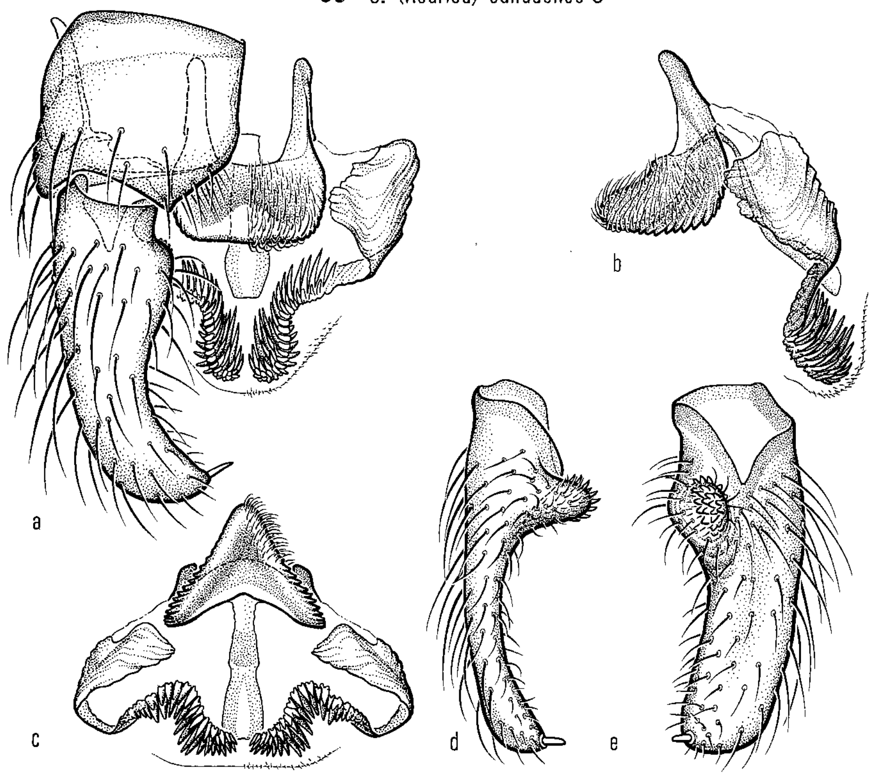


68 S. (Byssodon) meridionale ♂

Figs. 27.67–68. Male terminalia (*continued*; *a*, *b*, and *c* as in Fig. 58): (67) *Simulium* (*Psilozia*) *vittatum* Zetterstedt—*d* ventral view of gonostylus, *e* inner surface of tip of gonostylus, *f* lateral view of paramere; (68) *S.* (*Byssodon*) *meridionale* Riley—*d* and *e* as in Fig. 62 (*continued*).



69 S. (Hearlea) canadense ♂



70 S. (Simulium) tuberosum ♂

Figs. 27.69–70. Male terminalia (*continued*; *a*, *b*, and *c* as in Fig. 58; *d* and *e* as in Fig. 62): (69) ***Simulium* (*Hearlea*) *canadense*** Hearle; (70) *S.* (***Simulium***) ***tuberosum*** (Lundström) (*continued*).

30. Anal lobe of female attenuate or narrowly angulate ventrally, extending well below cercus (Fig. 42). Gonostylus of male shorter than gonocoxite, flattened, subquadrate with inner distal angle prolonged and bearing a single spinule (Fig. 62). Pruinose species, often pale in color but sometimes black, usually with antenna and legs mostly yellow. Thorax usually with one or more straight longitudinal stripes in female, but usually patterned with simple gray or white pruinose stripes or anterior spots in male; prescutellar area without long setae .... ***Simulium*** (***Psilopelmia*** Enderlein), in part

   see couplet 26

   Anal lobe of female, if angulate or extending well below cercus, more uniformly broadened and with a rounded ventral margin. Gonostylus of male variable in length, more or less cylindrical, or if flattened usually much longer than greatest width at base; number of apical spinules variable. Species, if pruinose, usually darker brownish to black in color, with antenna and legs variable in color. Thorax of both sexes variously patterned or unpatterned; prescutellar area usually with long setae 31

31. Calcipala small, ending well before pedisulcus (Fig. 22). Female black, with densely ashy gray pruinescence, with five dark vittae on scutum, and with a distinct black and gray pattern on abdomen; male velvety black, with two submedian stripes of varying length on scutum. Anal lobe of female extending well below cercus, broadly triangular in shape (Fig. 48). Gonostylus of male short, stout, somewhat flattened, subconical to subquadrate, with two to five apical spinules; ventral plate of aedeagus, in ventral view, broadly triangular, with short basal arms (Fig. 67) .... ***Simulium*** (***Psilozia*** Enderlein)

   3 spp.; one widespread, two western

   Calcipala large, distinct, ending near dorsal margin of pedisulcus (Fig. 23). Female, if black and grayish pruinose, with zero to three vittae on scutum and without a distinct black and gray pattern on abdomen; male variable in color, with or without two submedian stripes on scutum. Anal lobe of female usually not extending well below cercus, but if somewhat extended then not broadly triangular. Gonostylus of male long, more or less cylindrical, with variable number of apical spinules; ventral plate of aedeagus, in ventral view, variable in shape, but if somewhat triangular then narrower and with long basal arms 32

32. Fore tibia of female entirely brown to black, without a bright white patch anteriorly; fore coxa dark; claw with a large basal thumb-like projection (Fig. 23). Anal lobe of female shortly acuminate ventrally (Fig. 49). Ventral plate of aedeagus of male broad, lamellate, with distal margin nearly truncate, and lacking marginal denticles (Fig. 68). Scutum of male without anterolateral white or silvery spots .... ***Simulium*** (***Byssodon*** Enderlein)

   1 sp., *meridionale* Riley; widespread

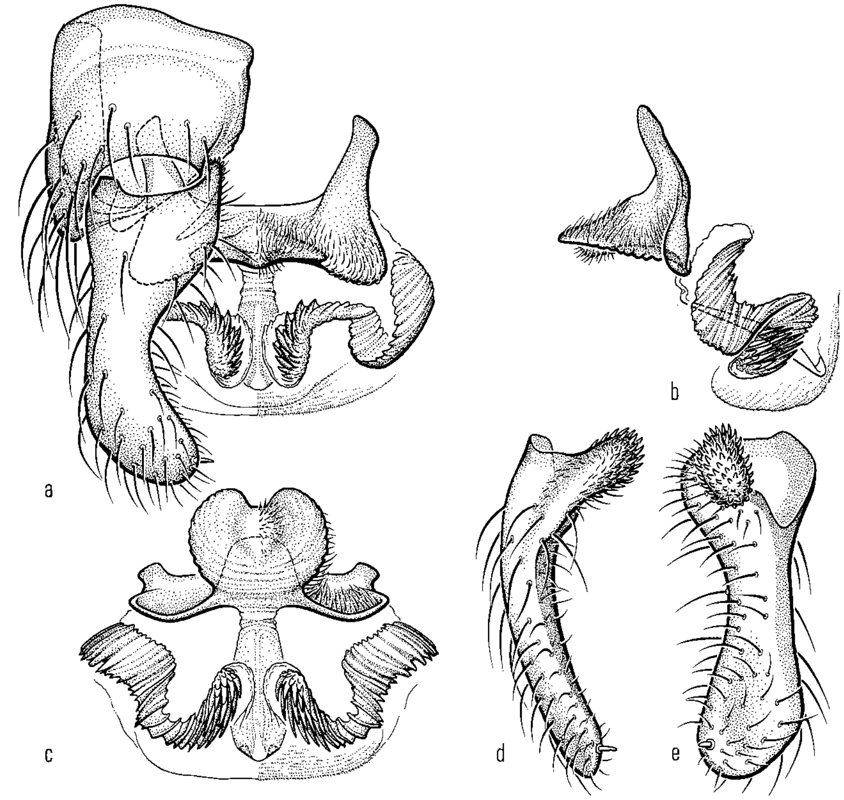
   Fore tibia of female usually with a bright white patch anteriorly; if fore tibia entirely brown or black, then anal lobe variable but not acuminate ventrally, at most with a very short rounded point. Ventral plate of aedeagus of male variable, if broad and lamellate then with a median notch and lip, and often with marginal denticles. Scutum of male usually with variably distinct anterolateral silvery or white spots, or with submedian stripes 33

33. Tarsomeres of foreleg of female slender; claw with a small subbasal tooth. Scutum of female with two distinct vittae. Outer surface of anal lobe of female mostly bare and polished; posterior and inner margins of hypogynial valve shallowly emarginate (Fig. 47). Gonostylus of male long and slender, narrowest at about mid length, with a small internal setose basal lobe and a single apical spinule; ventral plate of aedeagus, in ventral view, with a rounded distal margin, a median notch, and a short ventral lip without marginal denticles (Fig. 69) .... ***Simulium*** (***Hearlea*** Vargas, Martínez & Díaz)

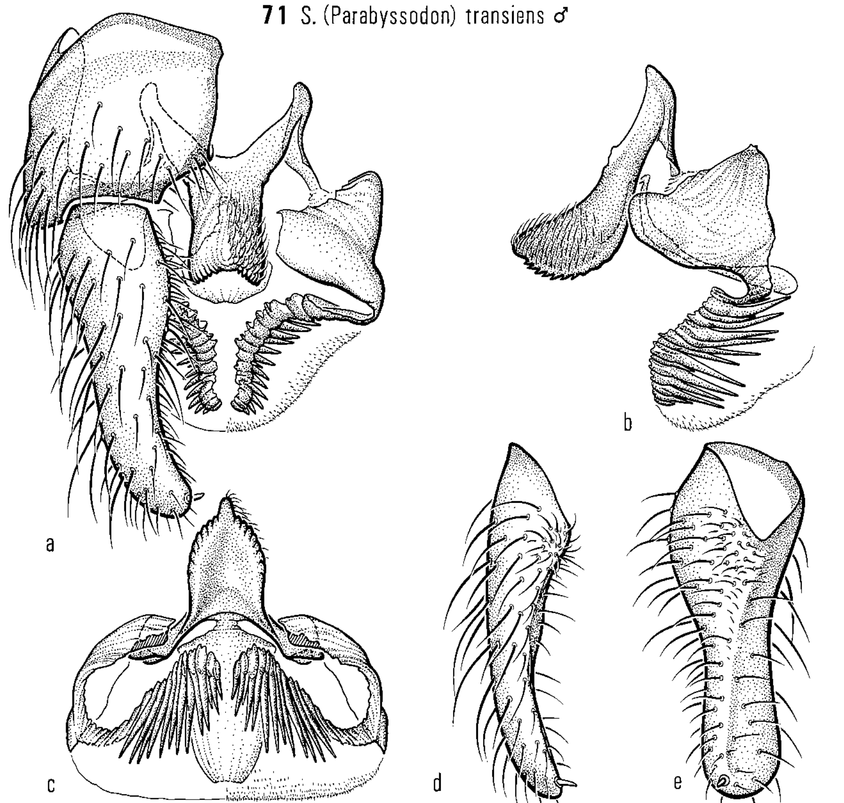
   1 sp., *canadense* Hearle; western

   Tarsomeres of foreleg of female variable but often noticeably widened and flattened; claw variable. Scutum of female patterned or unpatterned. Anal lobe of female variable, but outer surface usually setose and not polished; hypogynial valves short, with their posterior and inner margins nearly straight to rounded. Gonostylus of male variable, but if long then more uniformly widened (Figs. 70, 71); ventral plate of aedeagus, in ventral view, variable, but if somewhat rounded on distal margin then margins of ventral lip with denticles 34

34. Scutum of female semishining, covered with a light but even pruinescence allowing underlying integument to show through; scutum of male anteriorly with a V-shaped pruinose mark that is sometimes continuous anterolaterally with pruinose border encircling lateral and posterior margins (Fig. 16). Claw of female with a large basal thumb-like projection. Female

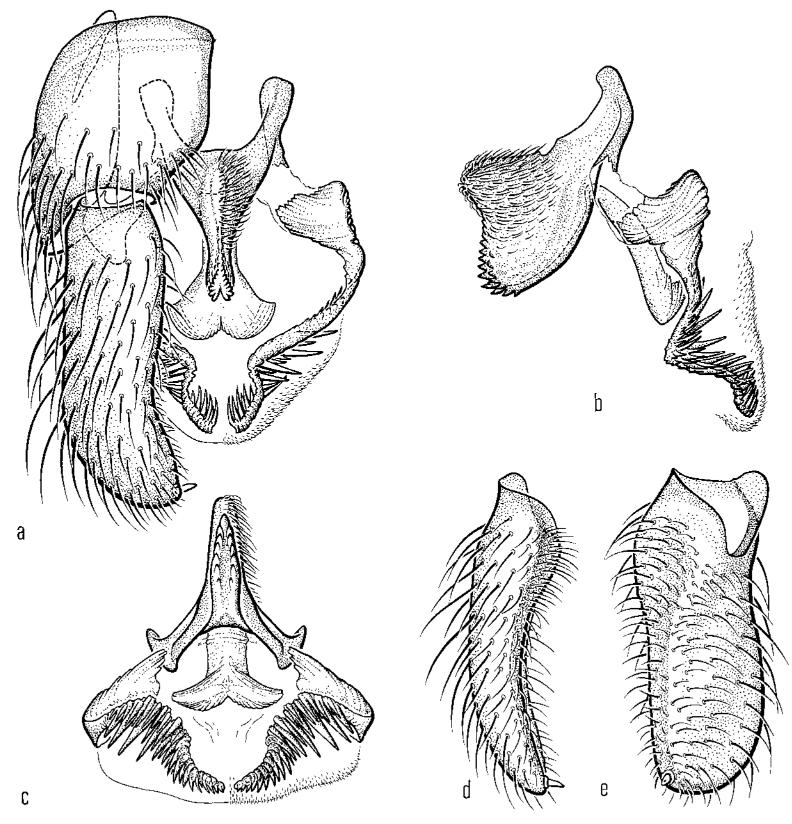


71 S. (Parabyssodon) transiens ♂

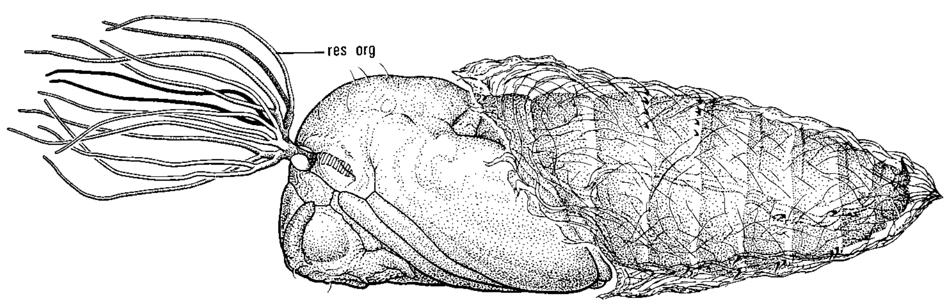


72 S. (Phosterodoros) jenningsi ♂

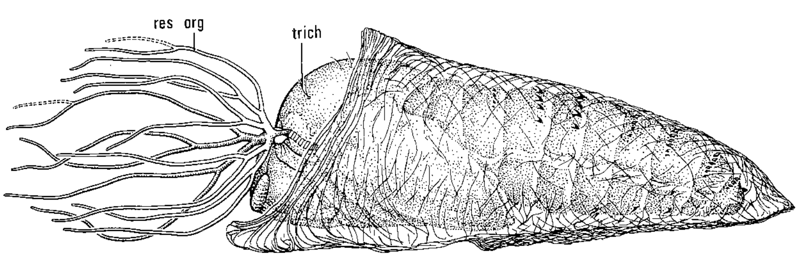
Figs. 27.71–72. Male terminalia (*continued*; *a*, *b*, and *c* as in Fig. 58; *d* and *e* as in Fig. 62): (71) ***Simulium (Parabyssodon) transiens*** Rubtzov; (72) *S.* (***Phosterodoros***) ***jenningsi*** Malloch (*continued*).



73 S. (Simulium) decorum ♂



74 Prosimulium ursinum



75 Simulium vittatum

Figs. 27.73–75. Male terminalia and pupae: (73) terminalia (*concluded*; *a*, *b*, and *c* as in Fig. 58; *d* and *e* as in Fig. 62) of *Simulium* (*Simulium*) *decorum* Walker; pupa of (74) *Prosimulium ursinum* (Edwards) and (75) *Simulium vittatum* Zetterstedt.

Abbreviations: res org, respiratory organ; trich, trichome.

terminalia as in Fig. 50. Ventral plate of aedeagus of male with apicolateral corners produced shoulder-like, and with a broad somewhat dorsoventrally flattened ventral lip bearing variably distinct denticles basally and with a medially notched apex; gonostylus with a densely spinulose internal lobe basally, and with a tiny subapical spinule (Fig. 71) .... ***Simulium*** **(*Parabyssodon*** Rubtzov)

1 sp., *transiens* Rubtzov; northwestern North America, Holarctic

Scutum of female variable, but usually distinctly shining or more densely pruinose; scutum of male unpatterned, or if patterned, then without an anterior V-shaped mark although anterolateral spots sometimes obliquely oriented. Claw of female usually simple or with a small subbasal tooth, rarely (two species) with a large basal thumb-like projection. Female terminalia not as in Fig. 50. Ventral plate of aedeagus of male variable but ventral lip, if present, not dorsoventrally flattened, and without distinct denticles on margins; gonostylus variable, but not exactly as above 35

35. Scutum of female viewed from front shining to subshining, often thinly covered with a slightly pearlaceous or iridescent pruinescence, and usually without a pair of distinct darker silvery spots anterolaterally, although vittae sometimes present; scutum of male with an anterolateral pair of oblique or triangular iridescent spots that are nearly devoid of setae (Fig. 17). Fore tarsus of female entirely dark; claw simple. Undersurface of Sc bare in female. Lateral margins of abdominal segments 2 and 5–7 in male each with an iridescent or pearlaceous spot. Ventral plate of aedeagus of male, in ventral view, rather narrow, with sides parallel or gradually widening distally; basal arms each with a sclerotized strap-like anterolateral projection (Fig. 72) .... ***Simulium*** **(*Phosterodoros*** Stone & Snoddy)

12 spp.; a few widespread, but most in southeastern U.S.A.

Scutum of female, viewed from front, variably shining to densely pruinose, usually with a pair of distinct widely separated dark or silvery spots anterolaterally, with or without vittae; scutum of male not patterned, or variably marked but without oblique or triangular iridescent bare spots anterolaterally. Fore tarsus of female bicolored; claw simple, with a small subbasal tooth, or rarely (two species) with a large basal thumb-like projection. Undersurface of Sc in female setose or bare. Abdominal segments in male usually unpatterned, but if patterned then without pearlaceous spots laterally on segments 2 and 5–7. Ventral plate of aedeagus in male, in ventral view, variously shaped but usually broad near basal arms and often tapering to a narrow beak-like apex, or broadly rounded apically; basal arms without a strap-like anterolateral projection (Figs. 70, 73) .... ***Simulium*** **(*Simulium*** Latreille)

about 17 spp.; widespread

Larva

(Larvae of *Parasimulium* are not known)

1. Lateral margins of head capsule strongly convex; labral fans absent (Fig. 82). Anal sclerite Y-shaped (Fig. 89) 2

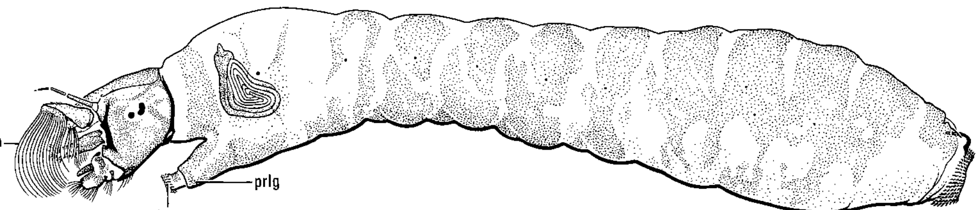
   Lateral margins of head capsule less convex; labral fans present (Figs. 80, 81). Anal sclerite X-shaped (Fig. 91), nearly rectangular, or absent 3

2. Outer (dorsal) apical surface of mandible with a series of short fine teeth and about 10 rows of distinct comb-like scales (Fig. 84) .... ***Gymnopais***

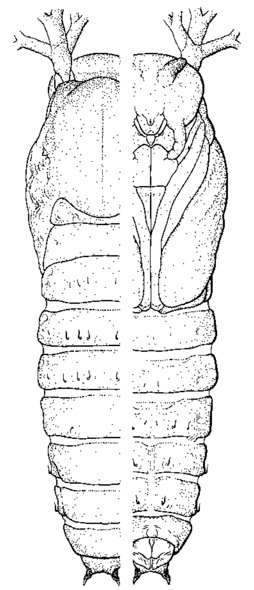
   Outer (dorsal) apical surface of mandible without a series of short fine teeth, and without comb-like scales (Fig. 83) .... ***Twinnia***

Figs. 27.76–81. Immature stages: (76) larva of *Simulium venustum* Say; (77) pupa of *Twinnia tibblesi* Stone & Jamnback–*left* dorsal three-fifths, *right* ventral three-fifths; larval head capsule of (78) *Cnephia dacotensis* (Dyar & Shannon), (79) *Simulium vittatum* Zetterstedt, (80) *Prosimulium ursinum* (Edwards), and (81) *Simulium vittatum*.

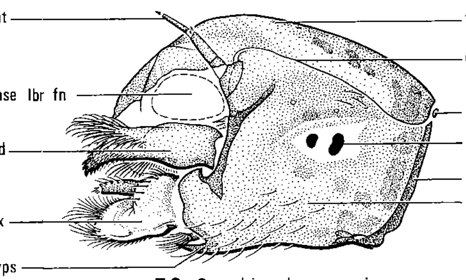
Abbreviations: al sp, anterolateral spot; am sp, anteromedial spot; ant, antenna; base lbr fn, base of labral fan; cerv scl, cervical sclerite; ecdys ln, ecdysial line; eyesp, eyespot; frclyp apot, frontoclypeal apotome; gn, gena; hyps, hypostoma; hyps brg, hypostomal bridge; hyps clft, hypostomal cleft; hyps grv, hypostomal groove; l plt prlg, lateral plate of proleg; lbr, labrum; lbr fn, labral fan; md, mandible; mx, maxilla; pl sp, posterolateral spot; pm sp, posteromedial spot; pocp, postocciput; prlg, proleg; p tnt pit, posterior tentorial pit; tnt pit, tentorial pit.



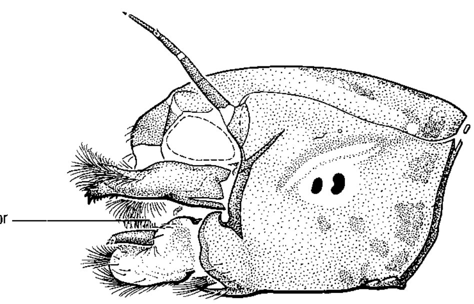
76 Simulium venustum



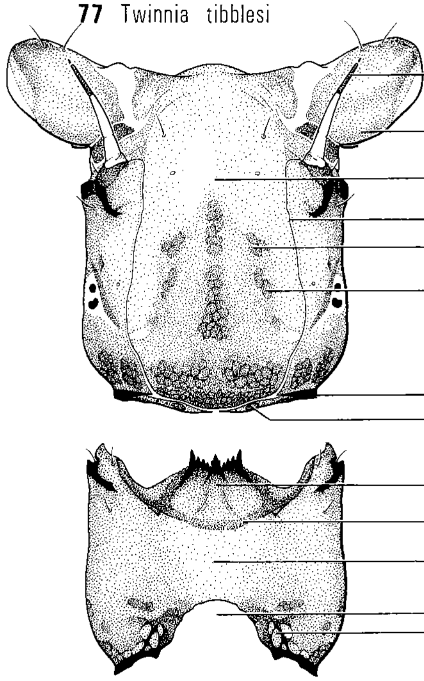
77 Twinnia tibblesi



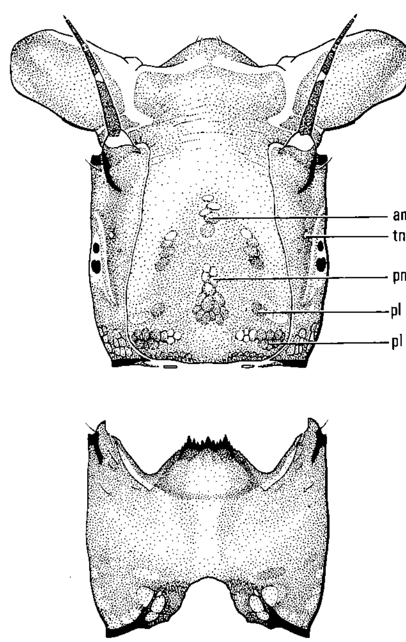
78 Cnephia dacotensis



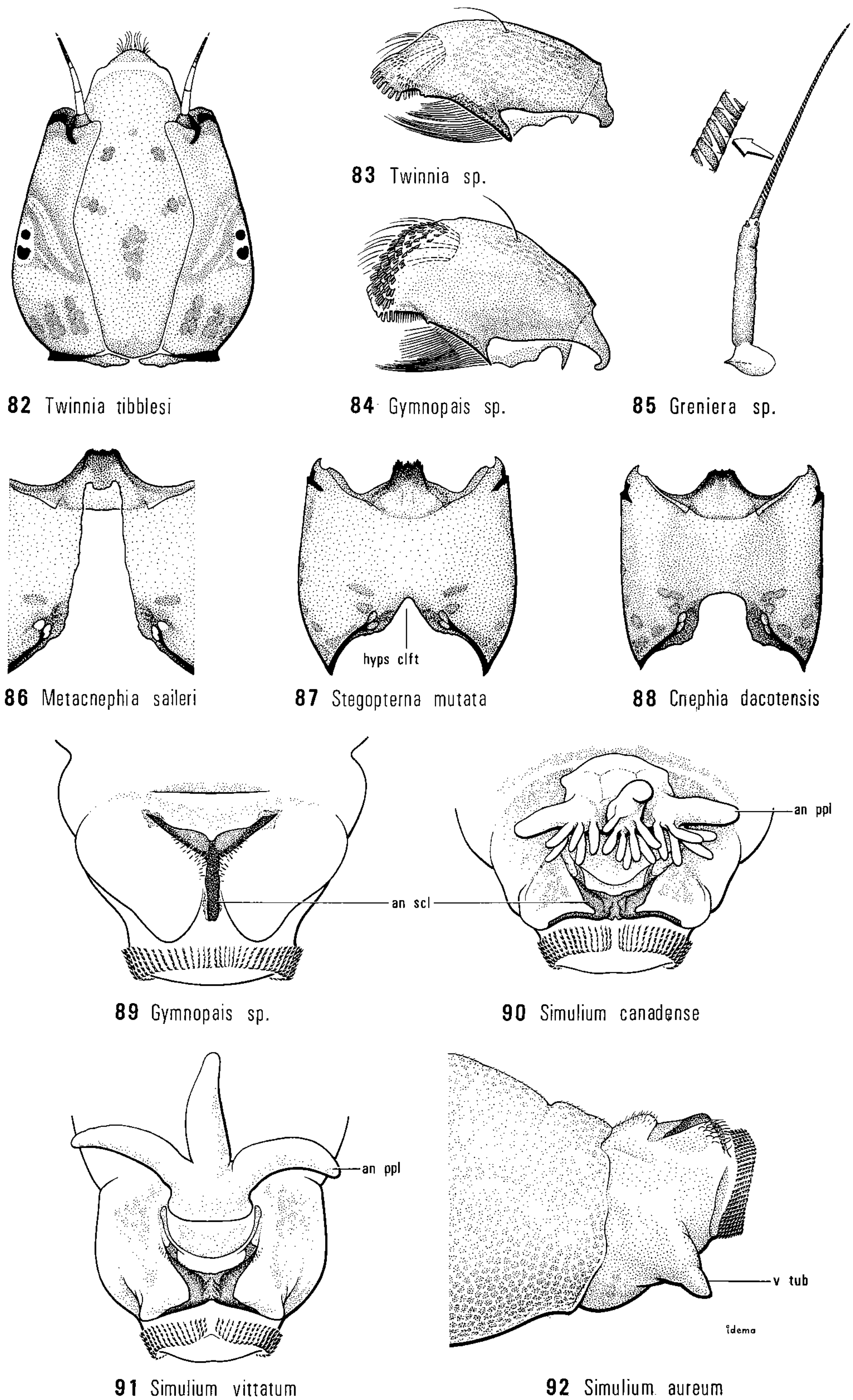
79 Simulium vittatum



80 Prosimulium ursinum

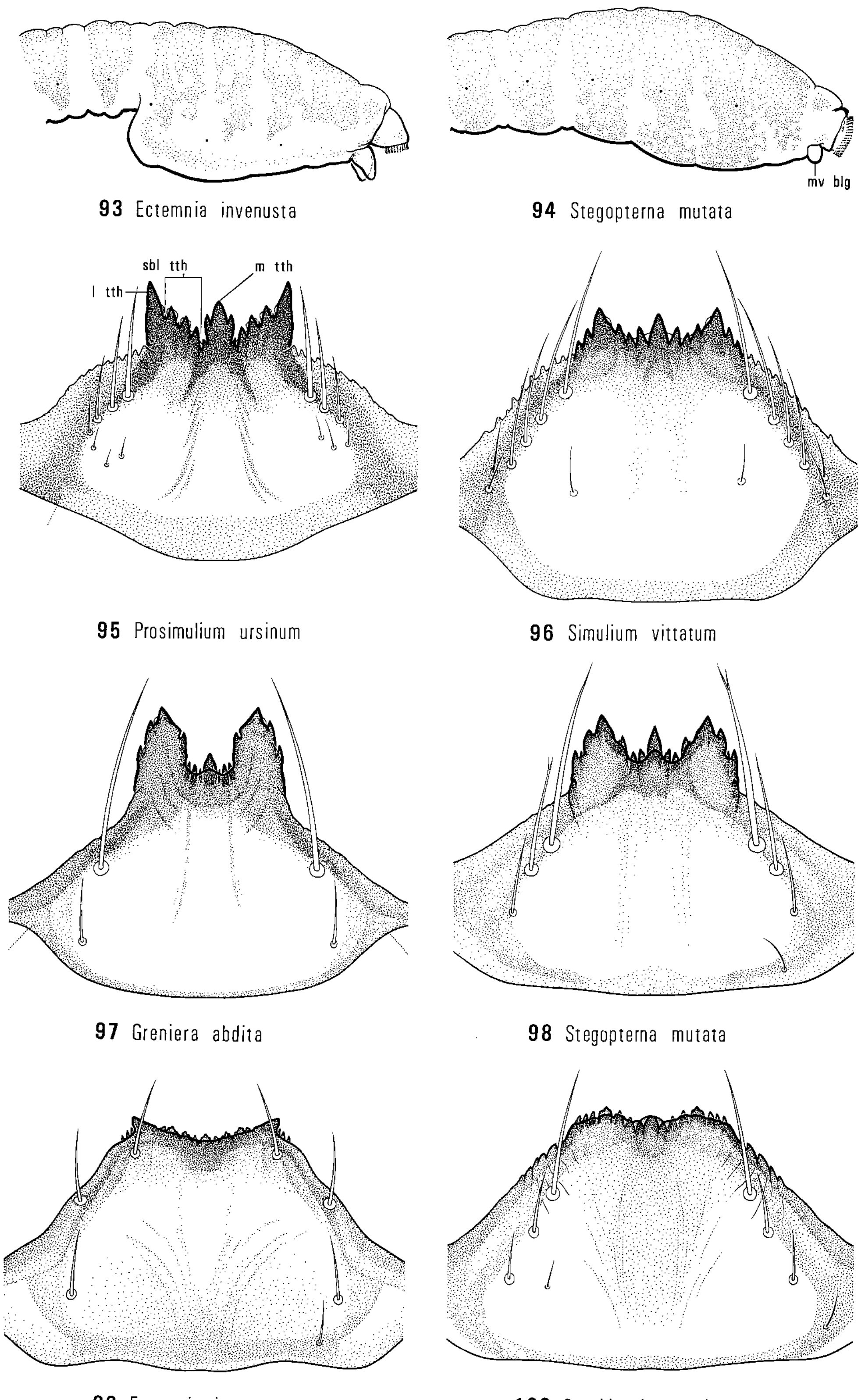


81 Simulium vittatum



Figs. 27.82–92. Details of larval head and abdomen: (82) head capsule of *Twinnia tibblesi* Stone & Jamnback; mandible in dorsolateral view of (83) *Twinnia* sp. and (84) *Gymnopais* sp.; (85) antenna of *Greniera* sp.; head capsule in ventral view of (86) *Metacnephia saileri* (Stone), (87) *Stegopterna mutata* (Malloch), and (88) *Cnephia dacotensis* (Dyar & Shannon); posterior portion of larval abdomen of (89) *Gymnopais* sp., (90) *Simulium canadense* Hearle, (91) *Simulium vittatum* Zetterstedt, and (92) *Simulium aureum* Fries.

Abbreviations: an ppl, anal papilla; an scl, anal sclerite; hyps clft, hypostomal cleft; v tub, ventral tubercle.



Figs. 27.93–100. Posterior portion of larval abdomen and hypostomal teeth: abdomen of (93) *Ectemnia invenusta* (Walker) and (94) *Stegopterna mutata* (Malloch); hypostomal teeth of (95) *Prosimulium ursinum* (Edwards), (96) *Simulium vittatum* Zetterstedt, (97) *Greniera abdita* (Peterson), (98) *Stegopterna mutata,* (99) *Ectemnia invenusta,* and (100) *Cnephia dacotensis* (Dyar & Shannon).

Abbreviations: l tth, lateral tooth; m tth, median tooth; mv blg, midventral bulge of segment 8; sbl tth, sublateral teeth.

3. Postocciput nearly complete dorsally, enclosing cervical sclerites. Basal two segments of antenna pale, strongly contrasting with darkly pigmented distal segments (Fig. 80). Median tooth of hypostoma distinctly trifid (Fig. 95). Anal papillae consisting of three simple finger-like lobes (Fig. 91) .... ***Prosimulium***

Postocciput with a distinct and usually wide gap dorsally, not enclosing cervical sclerites. Basal two segments of antenna at least partially pigmented, usually yellow to brown, not strongly contrasting in color with distal segments (Fig. 81). Median tooth of hypostoma single. Anal papillae consisting of three simple or compound lobes (Figs. 90, 91) 4

4. Hypostoma with median tooth and outer lateral (corner) teeth of each side moderately large and subequal in height, and with three variably smaller but nearly equal sublateral (intermediate) teeth on each side (Fig. 96). Anterodorsal portion of frontoclypeal apotome in lateral view not noticeably arched nor strongly convex (Fig. 79). Anal papillae usually consisting of three compound lobes, but lobes simple in species of subgenus *Psilozia* and in a few species of subgenus *Eusimulium* .... ***Simulium***

Hypostoma either with uniformly small teeth (Figs. 99, 100), with teeth on each side of median tooth confined to one large lobe (Fig. 97), or with teeth clustered in three prominent groups (Fig. 98). Anterodorsal portion of frontoclypeal apotome in lateral view often strongly convex (Fig. 78). Anal papillae consisting of three simple lobes 5

5. Hypostomal cleft reaching or extending anteriorly slightly beyond posterior margin of hypostoma, and broad throughout, with apex rather truncate. Hypostomal teeth all very small (Fig. 86) .... ***Metacnephia***

Hypostomal cleft not extending much more than about half distance to posterior margin of hypostoma, often much less, usually shaped like an inverted U or V (Fig. 87, 88). Hypostomal teeth variable, but often large and distinct (Figs. 97, 98) 6

6. Abdominal segment 8 with two ventral cone-shaped tubercles (Fig. 92) 7

Abdominal segment 8 without two ventral cone-shaped tubercles, but sometimes with a single transverse midventral bulge (Fig. 94) 10

7. Abdomen abruptly and greatly expanded at segment 5, with its lateral margins projecting ventrally beyond central portion of segment (Fig. 93). Anal sclerite absent. Anterior margin of hypostoma with small indistinct teeth (Fig. 99) .... ***Ectemnia***

Abdomen of normal shape, not abruptly nor greatly expanded at segment 5. Anal sclerite present. Anterior margin of hypostoma with minute lateral teeth borne on two large nearly parallel-sided lobes that are much longer than or subequal in length to median tooth (Fig. 97) 8

8. Third antennal segment much shorter than second segment, without spiral-like microannulations .... ***Greniera denaria***

Third antennal segment longer than combined lengths of segments 1 and 2, and with spiral-like microannulations (Fig. 85) 9

9. Median tooth of hypostoma slender and much shorter than large lateral toothed lobes so that hypostoma appears bidentate (Fig. 97) .... ***Greniera abdita*** group

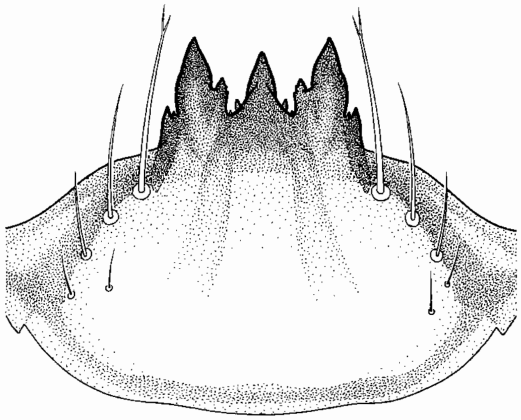
Median tooth of hypostoma rather stout, subequal in length to large lateral toothed lobes so that hypostoma appears tridentate (Fig. 101) .... ***Greniera***, in part

10. Hypostomal cleft moderately deep with its anterior margin rounded (Fig. 88). Hypostomal teeth uniformly small (Fig. 100) .... ***Cnephia***

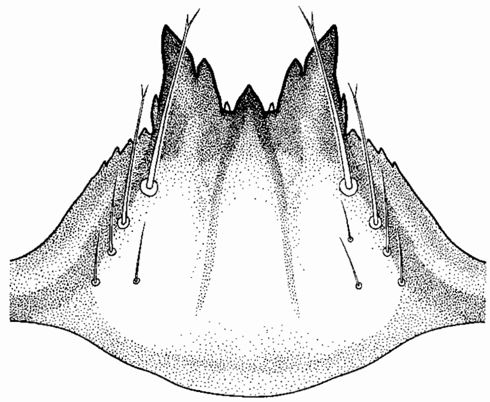
Hypostomal cleft narrow, shallow and acutely pointed or narrowly rounded, shaped much like an inverted V (Fig. 87). Hypostomal teeth larger and strong (Fig. 98) 11

11. Abdominal segment 8 with a single transverse midventral bulge (Fig. 94). Hypostomal teeth as in Fig. 98; outside margin of lateral cluster of teeth usually sloping inwardly. Labral fan with 40–60 rays .... ***Stegopterna***

Abdominal segment 8 simple, without a transverse midventral bulge (Fig. 76). Hypostomal teeth as in Fig. 102; outside margin of lateral cluster of teeth parallel or slightly sloping outwardly. Labral fan with 22–26 rays .... ***Mayacnephia***



101 Greniera sp.



102 Mayacnephia sp.

Figs. 27.101–102. Larval hypostomal teeth: (101) *Greniera* sp.; (102) *Mayacnephia* sp.

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CERATOPOGONIDAE 28

J. ANTONY DOWNES AND WILLIS W. WIRTH

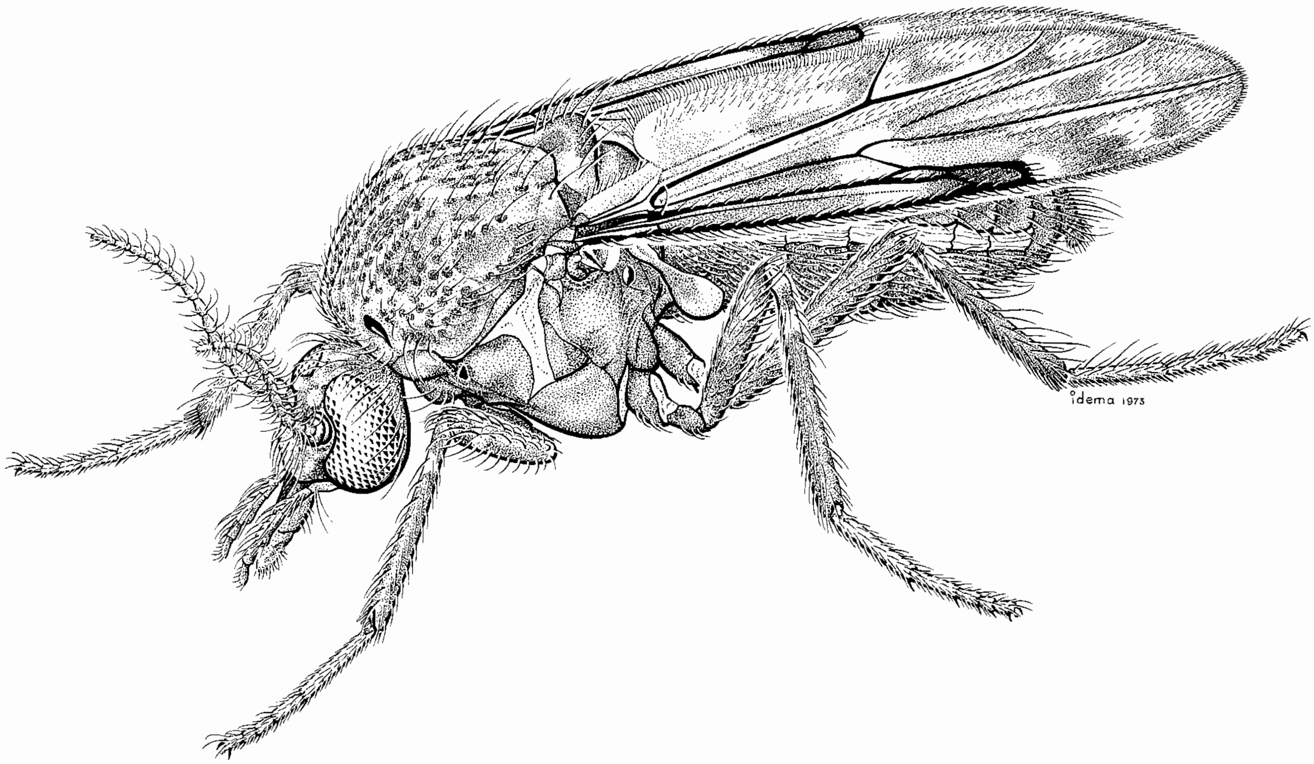


Fig. 28.1. Female of *Culicoides* (*Monoculicoides*) *variipennis* (Coquillett).

Small flies, 1–6 mm long, slender to moderately robust (Figs. 1, 2, 11–15). Female with biting and sucking mouthparts; bloodsucker of vertebrates or insects, or predator. Male with plumose antennae. Wings held horizontally at rest one above the other, sometimes strongly patterned. Early stages usually found in moist or aquatic habitats; larva apneustic, often elongate in form, and a strong swimmer (Wirth 1952*a*).

Adult. Adult forms of the three subfamilies Forcipomyiinae (Fig. 11), Dasyheleinae, and Ceratopogoninae (Figs. 12–15) fairly similar, and treated together in the general description. A fourth subfamily, Leptoconopinae (Fig. 2), differing from the others as described after the general account.

Head: eyes approximated or meeting at midline, usually bare, sometimes with fine pubescence; facets uniform in size. Ocelli perhaps represented by raised circular areas above antennae (Figs. 46, 47).

Antenna with 13 flagellomeres, and showing marked sexual dimorphism. Female (Figs. 13, 15, 63) with five distal flagellomeres elongated and differing from proximal flagellomeres in many details. Male (Figs. 12, 14, 64) with pedicel greatly enlarged and containing a specialized Johnston's organ; flagellomeres 1–8 usually bearing whorls of long setae giving characteristic plumose appearance; only three or four terminal flagellomeres elongated.

Proboscis (Figs. 46, 47) about as long as head; palpus slightly longer (Jobling 1928, Gad 1951). Female biting and sucking apparatus consisting of a rigid labrum, blade-like mandibles and laciniae, and a hypopharynx, each typically with apical armature; females in nonbiting species and all males with proboscis weaker and armature reduced. Palpus five-segmented; segments 1 and 2 sometimes poorly developed; segment 3 with sensory organ enclosed in a pit or on surface; segments 4 and 5 occasionally fused.

Thorax: mesonotum with a pair of prescutal pits near anterior margin in certain genera (Figs. 12, 13), sometimes with pattern of spots or shadings. Anepisternal cleft usually wide (Figs. 12, 13), but much narrower in some Ceratopogoninae (Figs. 14, 15). Postnotum without longitudinal division.

Wing (Figs. 12–15) narrower in male than in female; apex evenly rounded; anal lobe rarely prominent; calypter usually without fringe. Some genera with conspicuous pattern of dark spots or shadings or light spots. Macrotrichia sometimes dense and widespread, but absent in some Ceratopogoninae (Figs. 14, 15). Microtrichia usually distributed uniformly, occasionally apparently absent.

Venation (as in Fig. 13) characterized by compact radial system lying closely behind costal margin and meeting margin before apex of wing, often near or even before the midpoint. R_1 and Rs typically short, with Rs branching into R_{2+3} and R_{4+5}; R_{2+3} running forward and rejoining R_1 to form cell r_1 (usually termed first radial cell); R_{4+5} meeting C farther out to form cell r_{2+3}; one or both of these cells sometimes lost either by closure (approximation of upper and lower veins) or by becoming confluent through loss of R_{2+3}. Strong and characteristic crossvein r-m present. Posterior veins relatively weak; M_1 and M_2 usually arising beyond crossvein (Figs. 12, 13) (medial fork petiolate) but in some Ceratopogoninae before it (Figs. 14, 15) (medial fork sessile); M_2 sometimes incomplete basally or absent; crossvein m-cu absent; cubital fork well-developed; CuP and A weak, not reaching wing margin. A forked vein without complete stem, usually regarded as intercalary, often developed in cell r_{4+5} (Fig. 16). A false vein often evident in cell m_2, and sometimes also in cell m_1 (Fig. 13).

Legs moderately long; claws usually similar, average in size; empodia well-developed and branching in Forcipomyiinae (Figs. 65, 66), but slender or vestigial in Dasyheleinae and Ceratopogoninae. Females of predacious Ceratopogoninae usually having one or more pairs of specialized raptorial legs, with femur thickened and spiny or with claws enlarged, often unequally, and variously toothed. Male with small claws that are usually bifid at tips.

Abdomen: 10-segmented. Spiracles present on segments 2–7. Segment 1 somewhat reduced; tergites 1 and 2 sometimes fused (Figs. 14, 15).

In female (Figs. 120–128) sternite 8 with slightly bilobate hind margin extending below opening of spermathecal duct, and occasionally with diagnostic hair tufts or spines. Segment 9 with small tergite fused laterally to narrow band-like sternite; sternite usually dividing in midline around spermathecal opening; three spermathecae present, or two functional and one vestigial, or one only, usually oval dark-colored capsules, but in a few species of *Culicoides* Latreille elongate and thin-walled (Fig. 128). Segment 10 small; cercus rounded, on small dorsolateral basal plate.

In male (Figs. 98–119) segment 8 with normal tergite and sternite. Tergite 9 usually enlarged and prolonged backward to cover other elements of terminalia; gonopod two-segmented, conspicuous; aedeagus extending back from sternite 9 and articulated laterally with base of gonocoxite, often triangular with sclerotized lateral arms or ventral plate; paired parameres usually present above aedeagus, variously shaped, with shafts sometimes fused, asymmetric in many species of *Dasyhelea* Kieffer (Figs. 100, 101). Segment 10 weakly developed below tergite 9; cercus somewhat irregular in form; in some Ceratopogoninae, however, tergite 9 not greatly enlarged and segment 10 and cercus somewhat as in female. Terminalia inverted in some Ceratopogoninae; sperm transfer often by spermatophore, applied to spermathecal opening during mating.

Leptoconopinae: small dark-colored midges with pale wings, and differing from other Ceratopogonidae by several features (Figs. 2–10). Eyes widely separated in both sexes. Frons well-developed. Only the apical flagellomere elongated and sharply differentiated; 13 flagellomeres in male, 12 or 11 flagellomeres in female. Palpus with characteristic fusion of segments 4 and 5.

Wing lacking macrotrichia on membrane and veins. Radial system short, well-pigmented, but not developed as normal rib-like sclerotized veins; a long intercalary vein of uncertain origin present; crossvein r-m absent; posterior veins typical but faint.

In female cercus large, usually in form of an elongate triangular lamella (Fig. 2). In male gonocoxites approximated at base; gonostylus ending in small articulated denticle, unique in Ceratopogonidae (Figs. 9, 10).

Egg. Differing among subfamilies and genera. Oval to elongate, often black and glossy in Forcipomyiinae; horseshoe-shaped, enclosed in gelatinous cover in *Dasyhelea*; elongate, banana-shaped, with thin but often sculptured chorion in Ceratopogoninae. Loose groups of eggs laid on moist substrate (*Culicoides*), or strings or masses deposited with gelatinous coating (*Mallochohelea* Wirth, *Bezzia* Kieffer).

Larva. Head usually sclerotized; mandible strong, toothed, not apposed; pharyngeal apparatus conspicuous internally, with two strongly diverging arms and series of combs apparently serving to reduce and sort food. Short collar between head and thorax. Three thoracic and nine abdominal segments well-defined; no functional spiracles.

General habitus differing widely among subfamilies. In Forcipomyiinae (Figs. 130, 131), larva reminiscent of *Phlebotomus* Rondani (Psychodidae). Head hypognathous. Body segments with conspicuous setae, often complex, set on projecting tubercles; bilobate anterior proleg on prothorax; posterior proleg consisting of a group of hooklets just before anus. On pupation, larval skin usually retained over hind region of abdomen.

In Dasyheleinae (Fig. 132), head hypognathous or intermediate in shape. Body without conspicuous hairs or projections; anterior proleg absent; posterior hooklets much as those in *Forcipomyia* Meigen.

In Ceratopogoninae (Figs. 133, 134), head prognathous, pointed, and distinctively elongate. Body hairs minute, except on last segment; cuticle smooth, whitish or translucent; no prolegs (except for anterior proleg in first instar of some *Culicoides*).

In Leptoconopinae, larva white or yellow, elongate, smooth. Head prognathous; head capsule not fully sclerotized, with additional internal rod-like structures of uncertain morphology. Thorax and abdomen without evident setae; many segments divided transversely into two subsegments; anal segment with three short lobes.

Pupa. Relatively uniform in structure among subfamilies. Form compact, yellow brown to black. Prothoracic horns short, with many spiracular openings. Aquatic forms hanging at surface of water by nonwettable horns, and also supported by an air bubble beneath wing. Pupal stage of short duration. Pupal horn, operculum (vertex), tubercles bearing setae and spines, and apicolateral processes of abdomen with structural details that provide numerous diagnostic characters.

Biology and behavior. Adults live mainly in moist areas around the larval habitat. Some species, probably with fairly strict larval requirements, are characteristic of coastal marshes, inland saline sloughs, or heavily fertilized areas frequented by livestock; some *Culicoides*, living as larvae in the moist tissue in stems of cactus, are found even in deserts. Most species are crepuscular but *Leptoconops* Skuse and a few others fly in full sunshine.

Both sexes may visit flowers, especially those with easily accessible nectar. The females usually require a protein-rich meal, obtained by biting, for maturation of the eggs. *Culicoides, Leptoconops,* and some species of *Forcipomyia* are bloodsuckers of vertebrates, mainly mammals and birds. Other Forcipomyiinae feed on large insects such as moths or dragonflies, often piercing them through the veins of the wing (Wirth 1956, 1980), and on dead insects and pollen. Most Ceratopogoninae, except for *Culicoides,* feed on small Nematocera and Ephemeroptera, which are captured in flight from the mating swarms; in some genera the females also capture their own males and feed on them during mating (Downes 1978).

Certain species lay the first batch of eggs without taking a blood meal (autogeny) but need to feed to initiate the second ovarian cycle. Some species of *Culicoides* and *Forcipomyia,* and probably all species of *Dasyhelea,* have reduced mandibles and do not take a blood meal.

Many ceratopogonids assemble in swarms that maintain a to-and-fro dancing flight above a landmark such as a bush or the margin of a pond. The plumose antenna of the male is an auditory organ sensitive to the wingbeat tone of the incoming female, and mating takes place in flight. A few species mate on a substrate without a swarming flight, and in some of these the antennal plume is reduced.

The bite of bloodsucking ceratopogonids is irritating or painful, and wherever they occur in numbers these insects are substantial pests of man, livestock, and wildlife. Species of *Culicoides* are vectors of filarial worms, blood protozoa, and certain viruses, notably bluetongue in sheep and cattle.

Larvae of Ceratopogonidae are characteristic of damp habitats. Forcipomyiinae (Figs. 130, 131) are crawling forms, terrestrial or semiaquatic, often found in moist places such as under bark or among mosses. They feed on algae, plant debris, or fungi. Dasyheleinae (Fig. 132) are often found in restricted habitats such as rock pools, tree holes, and sap flows; they move by wriggling or clambering but do not swim freely. In Ceratopogoninae (Figs. 133, 134), larval habit varies from burrowing in moist soil to fully aquatic and free-swimming. Some genera live in benthos and plankton of large lakes or streams. Frequently, perhaps predominantly, they are carnivorous. Larvae of Leptoconopinae burrow in soil, chiefly in arid areas and on coastal and inland beaches; in some species they enter diapause as the soil dries out and resume development when seasonal rains reactivate them.

Pupae of Forcipomyiinae are sedentary; those of many Dasyheleinae and Ceratopogoninae can move slowly by twisting the abdomen, but only a few species are able to swim.

Classification and distribution. The division of Ceratopogonidae into four subfamilies and the division of Ceratopogoninae into six tribes was proposed by Wirth (1962*a*) and has been generally accepted. Krivosheina (1969), however, has given Leptoconopinae family rank. Wirth *et al.* (1974) have reviewed the family on a world basis, and their treatment of the genera has been followed closely here. Thirty-five of the 60 genera recognized have been found in the Nearctic region. Ten are represented by single species only, chiefly in southerly areas of the United States. Most others are widespread, and 10 extend to the tree line in northern Canada and Alaska. Single species of *Forcipomyia*, *Culicoides*, *Ceratopogon* Meigen, and *Isohelea* Kieffer range in the High Arctic to the northern limit of land.

The North American species of many groups have been reviewed in recent years by Wirth and his collaborators, but others, including several large genera, still await a modern treatment. Some 380 species were listed for North America by Stone *et al.* (1965), but a conservative estimate of the total would exceed twice that figure.

Fossils of the earliest known Ceratopogonidae are in amber of lower Cretaceous age from Lebanon. Upper

Cretaceous Canadian amber contains a rich fauna that includes *Leptoconops*, *Forcipomyia*, and several genera of Ceratopogoninae, including specialized insect predators.

Key to genera

Adult

1. Wing with crossvein r-m absent (Fig. 2), without macrotrichia. Female antenna with 11 or 12 flagellomeres (Figs. 2, 4) ................................LEPTOCONOPINAE....***Leptoconops*** **Skuse**....2
Wirth and Atchley 1973

   Wing with crossvein r-m present, usually with macrotrichia and microtrichia (Figs. 12, 13). Female antenna with 13 flagellomeres (Figs. 11, 13, 15)...5

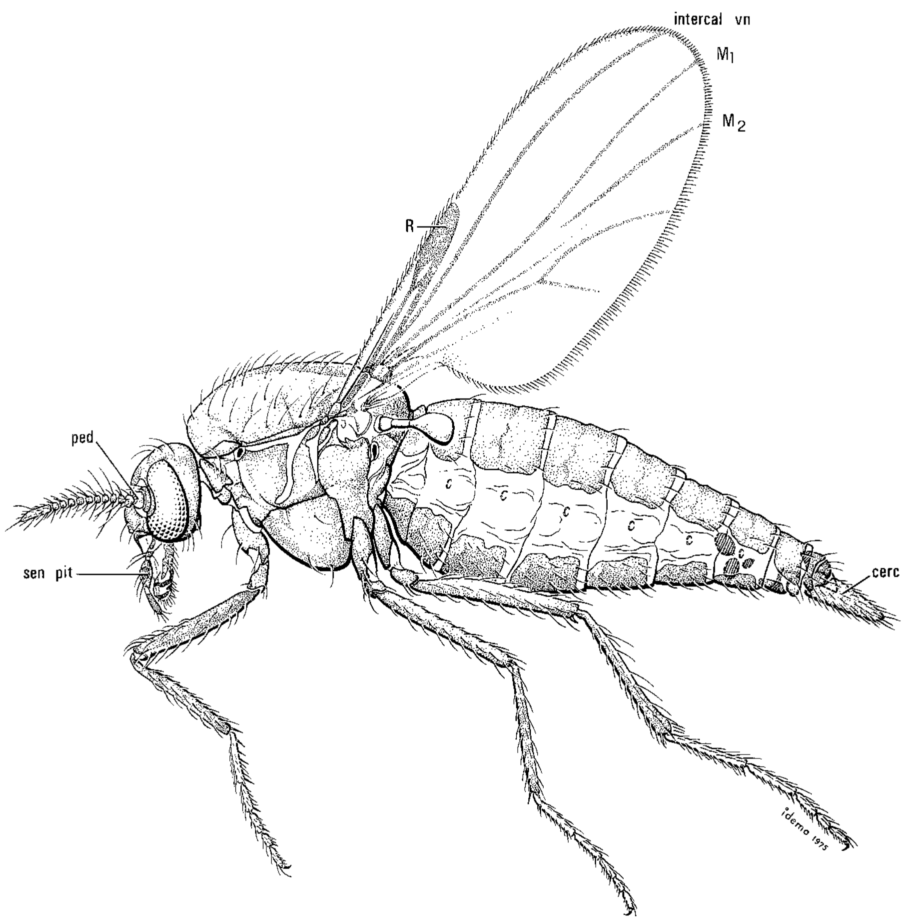
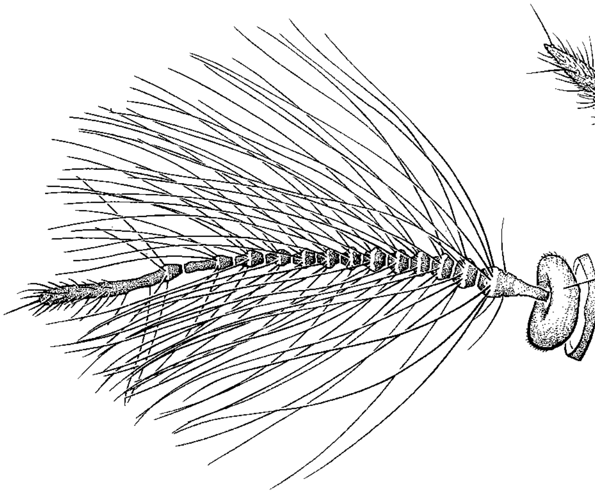


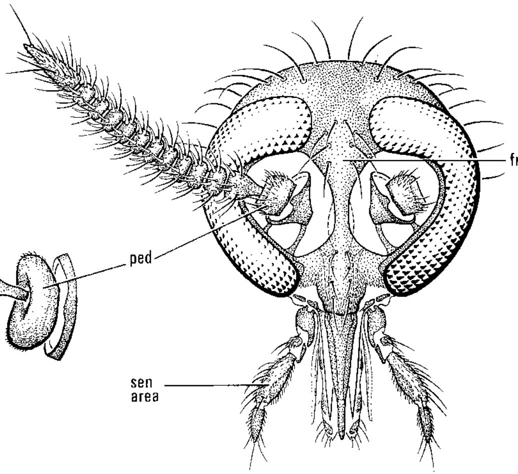
Fig. 28.2. Female of *Leptoconops* (*Holoconops*) sp.
Abbreviations: cerc, cercus; intercal vn, intercalary vein; ped, pedicel; sen pit, sensory pit.

Figs. 28.3–10. Species and structures of *Leptoconops*: (3) antenna of male of *L.* (*Holoconops*) sp.; (4) head of female of *L.* (*Megaconops*) *floridensis* Wirth; (5) claws and (6) foreleg of female of *L.* (*Brachyconops*) *californiensis* Wirth & Atchley; (7) spermathecae of female of *L.* (*Leptoconops*) *torrens* (Townsend); terminalia of (8) female of *L.* (*Brachyconops*) *californiensis*, (9) male of *L.* (*Leptoconops*) *torrens*, and (10) male of *L.* (*Megaconops*) *floridensis*.

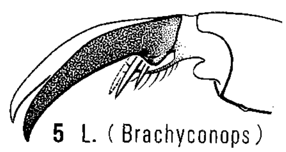
Abbreviations: apl proc, apicolateral process; cerc, cercus; fr, frons; goncx, gonocoxite; gonst, gonostylus; ped, pedicel; sen area, sensory area; tg, tergite.



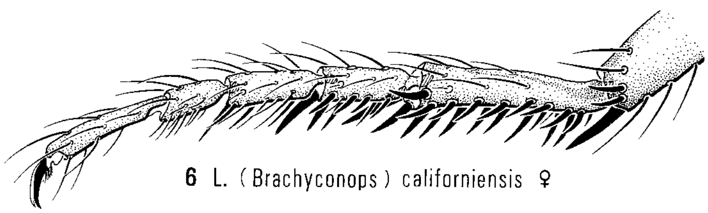
3 Leptoconops (Holoconops) sp. ♂



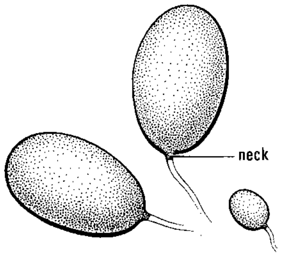
4 L. (Megaconops) floridensis ♀



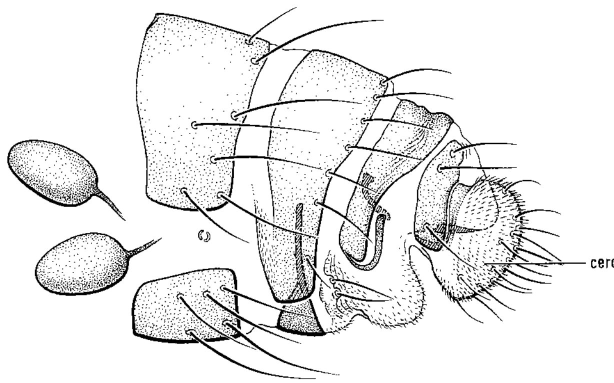
5 L. (Brachyconops) californiensis ♀



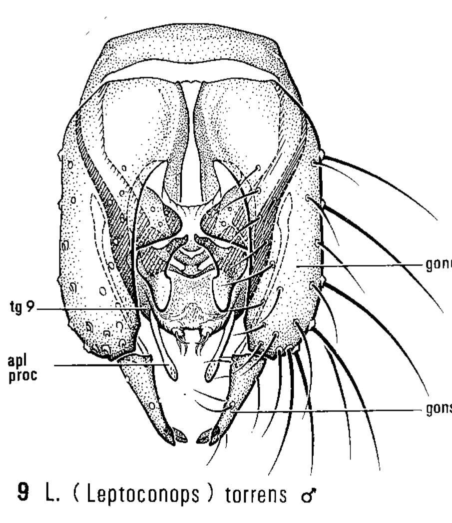
6 L. (Brachyconops) californiensis ♀



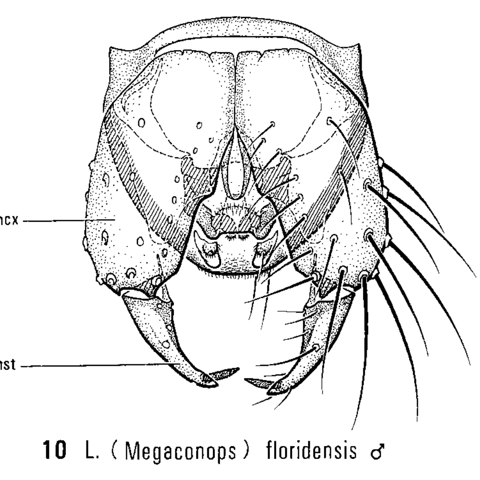
7 L. (Leptoconops) torrens ♀



8 L. (Brachyconops) californiensis ♀



9 L. (Leptoconops) torrens ♂



10 L. (Megaconops) floridensis ♂

2. Female abdomen with cerci broader than long (Fig. 8). Female antenna with 12 flagellomeres. Palpus with definite sensory pit. Tarsi with strong ventral spines (Fig. 6) .... ***Leptoconops*** (***Brachyconops*** Wirth & Atchley)
   1 sp., *californiensis* Wirth & Atchley; California; Wirth and Atchley 1973

   Female abdomen with cerci elongate (Fig. 2). Female antenna with 11 or 12 flagellomeres. Palpus with or without sensory pit. Tarsi with or without strong ventral spines 3

3. Female antenna with 11 flagellomeres (Fig. 2). Palpus with deep sensory pit (Fig. 2) .... ***Leptoconops*** (***Holoconops*** Kieffer)
   15 spp.; widespread; Clastrier and Wirth 1978

   Female antenna with 12 flagellomeres (Fig. 4). Palpus with sensory organ superficial (Fig. 4) ..4

4. Frons bare or at most with one or two small setae. Female claws with basal tooth or bristle (as in Fig. 5). Spermatheca with short neck (Fig. 7). Male tergite 9 with long slender apicolateral processes (Fig. 9) .... ***Leptoconops*** (***Leptoconops*** Skuse)
   6 spp.; western North America; Wirth and Atchley 1973

   Frons with four or five pairs of median setae (Fig. 4). Female claws without basal tooth or bristle. Spermatheca with filiform neck (as in Fig. 8). Male tergite 9 rounded without apicolateral processes (Fig. 10) .... ***Leptoconops*** (***Megaconops*** Wirth & Atchley)
   1 sp., *floridensis* Wirth; Florida; Wirth and Atchley 1973

5. Empodia well-developed, at least in female (Figs. 11, 65, 66); claws strongly curved (Figs. 65, 66). Wing usually with numerous macrotrichia (Fig. 11) ................FORCIPOMYIINAE....6

   Empodia small or vestigial (Figs. 67, 68); claws more gently curved (Figs. 67, 68). Wing usually with macrotrichia less numerous or absent 20

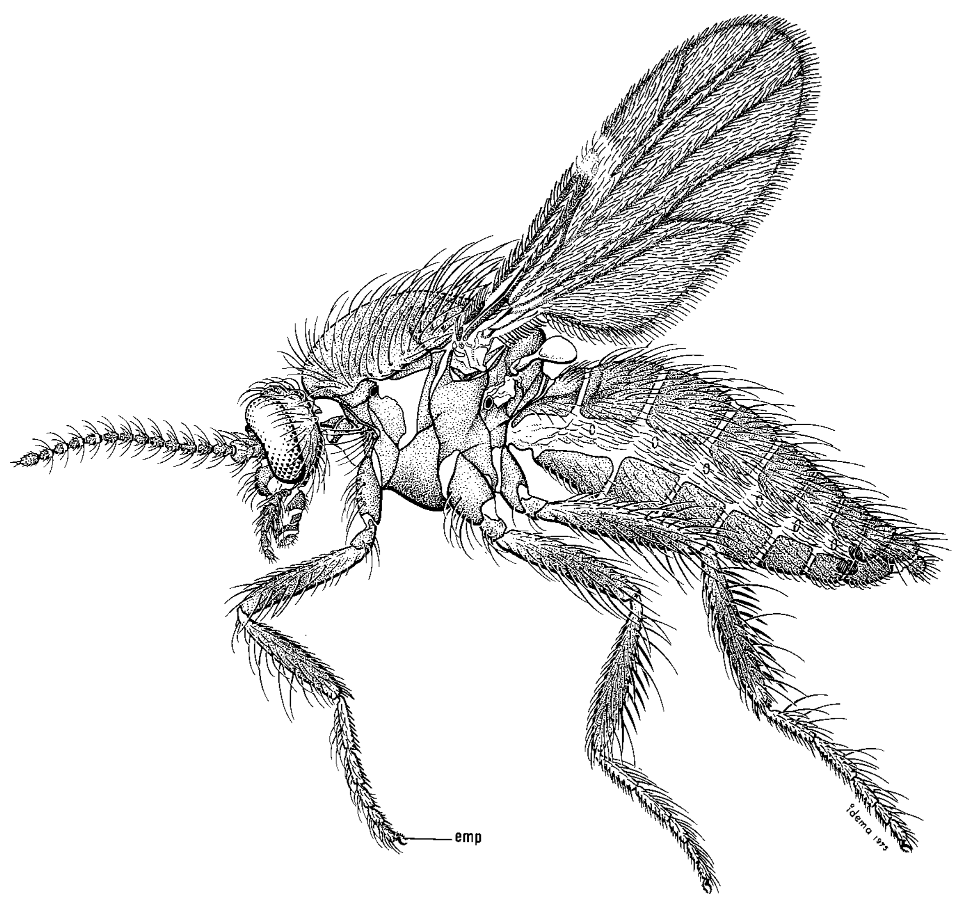


Fig. 28.11. Female of *Forcipomyia* (*Forcipomyia*) *bipunctata* (Linnaeus). Abbreviation: emp, empodium.

6. C reaching well beyond middle of wing (Fig. 16); cell r_{2+3} usually twice as long as cell r_1 (Fig. 16); microtrichia large and conspicuous; macrotrichia when present scattered, suberect, not scale-like; fringe of posterior border of wing simple, consisting of a single row of alternating longer and shorter hairs .... ***Atrichopogon*** Kieffer....7
   Wirth 1952*a*; Boesel 1973

   C short or long; cell r_{2+3} usually short, but if long distinctly narrow; microtrichia minute; macrotrichia moderately abundant, sloping, often scale-like, covering most of wing (Figs. 11, 17); fringe complex, not a single row of hairs .... ***Forcipomyia*** Meigen....9
   Wirth 1952*a*, Saunders 1956

7. Proboscis of female upcurved, making lateral profile of face concave (Fig. 57). Two spermathecae present. Wing with abundant macrotrichia. Eye bare .... ***Atrichopogon*** (***Meloehelea*** Wirth)
   3 spp.; widespread, feeding on Meloidae; Wirth 1980

   Proboscis of female straight in profile. One spermatheca present. Wing macrotrichia absent to moderately abundant. Eye bare or pubescent 8

8. Female abdomen with conspicuous armature on sternite 7 (Fig. 120). Wing macrotrichia few or absent (Fig. 18). Eye pubescent .... ***Atrichopogon*** (***Psilokempia*** Enderlein)
   3 spp.; northern North America

   Female abdomen without ventral armature. Wing macrotrichia more numerous (Fig. 16). Eye bare or pubescent .... ***Atrichopogon*** (***Atrichopogon*** Kieffer)
   18 spp.; widespread

9. Distal six flagellomeres of female elongated (Fig. 61). Female empodia large and broad, adapted for clinging to wings of insects (Fig. 66); hind tarsal ratio[1] 3.0 or more .... ***Forcipomyia*** (***Pterobosca*** Macfie)
   1 sp., *fusicornis* (Coquillett); Florida, Neotropical

   Distal five flagellomeres of female usually elongated, rarely all flagellomeres short. Empodia not greatly enlarged or modified; hind tarsal ratio 0.5–3.2 10

10. Palpus four-segmented, with only one segment distal to segment 3; sensory pit present on segment 3 (Fig. 53) 11

   Palpus five-segmented (Fig. 52), although segments 4 and 5 incompletely fused and unarticulated in *Euprojoannisia* (Fig. 54) and *Caloforcipomyia* 13

11. Female with one well-developed spermatheca. Female antenna with five distal flagellomeres greatly elongated. C long, with costal ratio[2] about 0.67. Hind tarsal ratio 1.3–1.75 .... ***Forcipomyia*** (***Warmkea*** Saunders)
   2 spp.; Florida, Neotropical

   Female with two well-developed spermathecae (Fig. 124). Antenna, venation, and hind tarsus various 12

12. Female antenna with five distal flagellomeres greatly elongated, and with proximal flagellomeres short and globular. Female hind tarsal ratio 2.66–3.00 .... ***Forcipomyia*** (***Blantonia*** Wirth & Dow)
   1 sp., *caribbea* Wirth & Dow; Florida, Neotropical; Wirth and Dow 1971

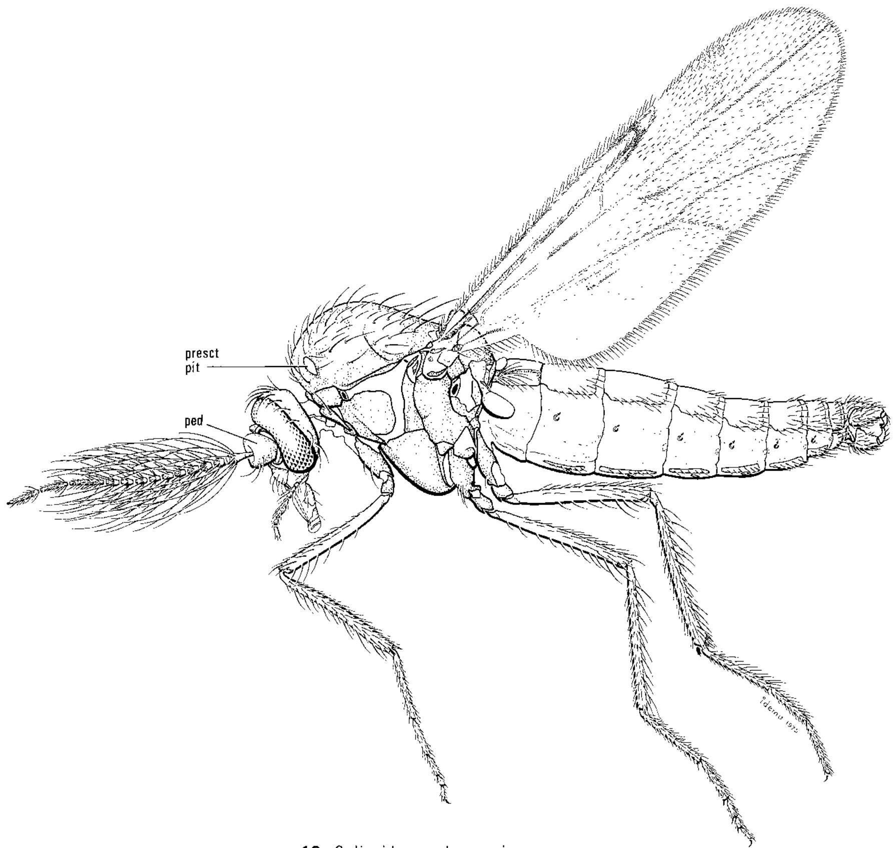
   Female antenna with distal flagellomeres not much longer than those in proximal series; all flagellomeres elongate and tapering. Female hind tarsal ratio about 2.0 .... ***Forcipomyia*** (***Metaforcipomyia*** Saunders)
   1 sp., *pluvialis* Malloch; widespread

13. Female antenna with flagellomeres of proximal series usually transverse, much shorter than five distal flagellomeres (Fig. 60) 14

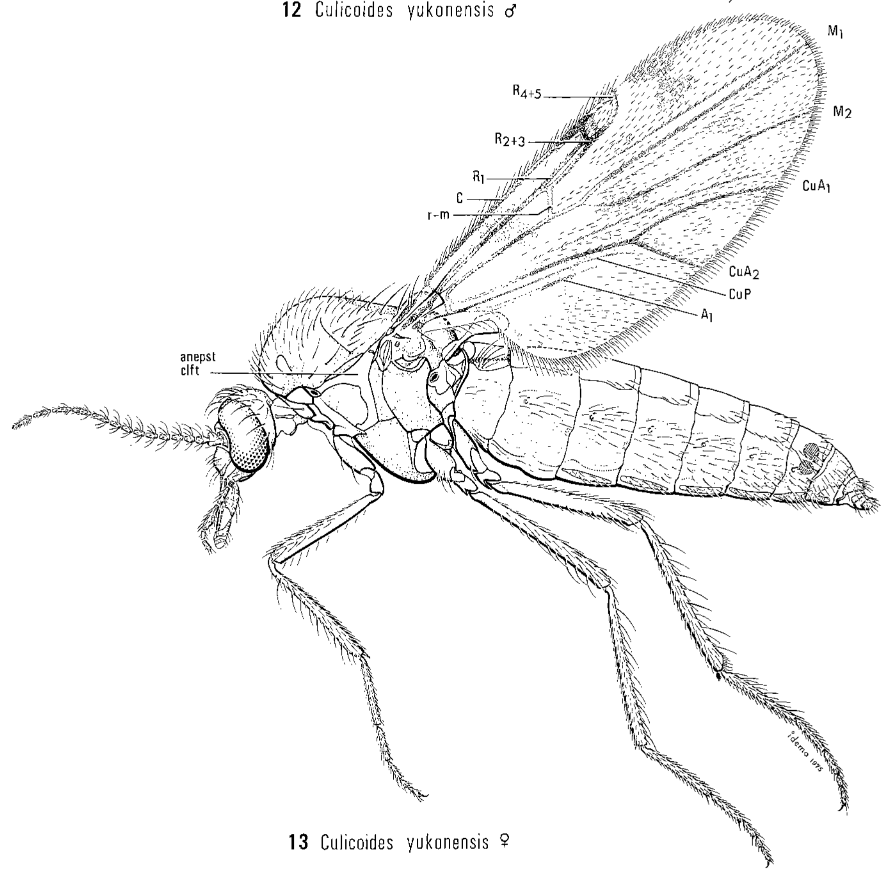
   Female antenna with flagellomeres of proximal series not much shorter than distal flagellomeres 15

14. C extending well beyond middle of wing; cell r_{2+3} much longer than cell r_1, very narrow (Fig. 17). One subspherical spermatheca present, without neck (Fig. 125). Female sucking

[1] Ratio of lengths of first and second tarsomeres of hindleg.
[2] Ratio of length of C to length of wing, both measured from MA (basal arculus).

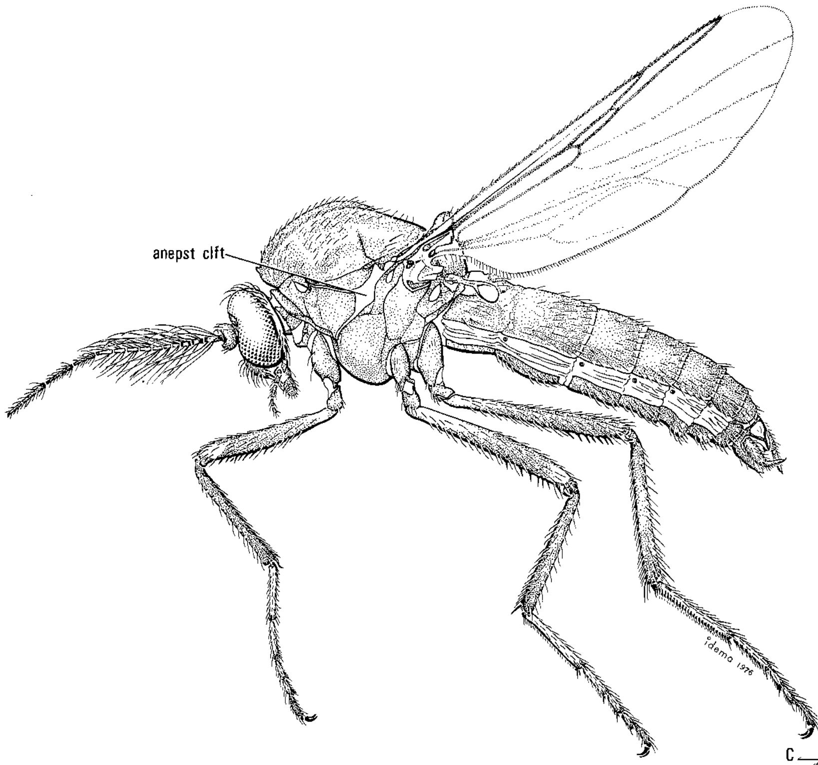


12 Culicoides yukonensis ♂

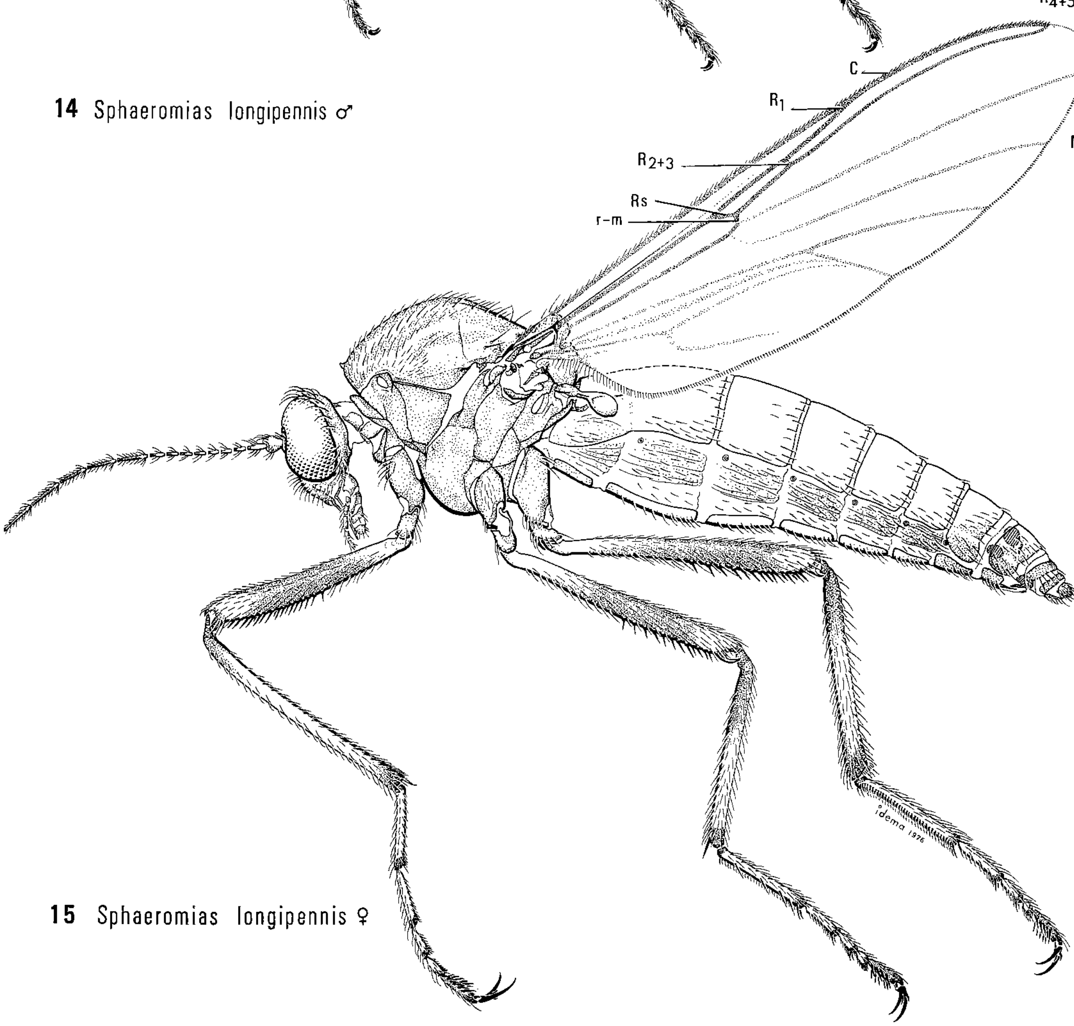


13 Culicoides yukonensis ♀

Figs. 28.12–13. *Culicoides yukonensis* Hoffman: (12) male; (13) female. Abbreviations: anepst clft, anepisternal cleft; ped, pedicel; presct pit, prescutal pit.

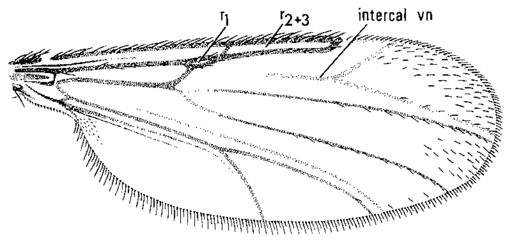


14 Sphaeromias longipennis ♂

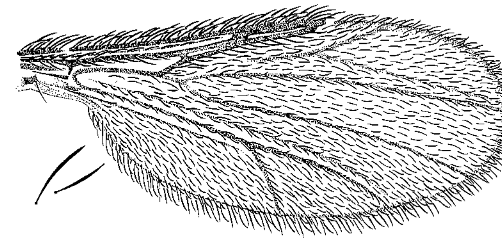


15 Sphaeromias longipennis ♀

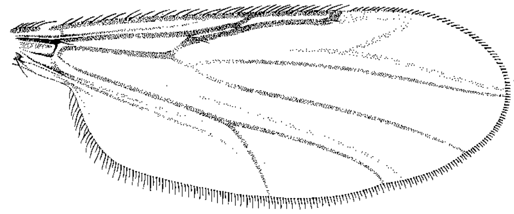
Figs. 28.14–15. *Sphaeromias longipennis* (Loew): (14) male; (15) female. Abbreviation: anepst clft, anepisternal cleft.



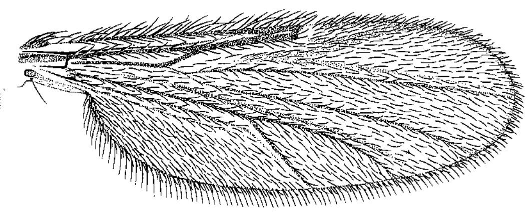
16 Atrichopogon (Atrichopogon) levis ♀



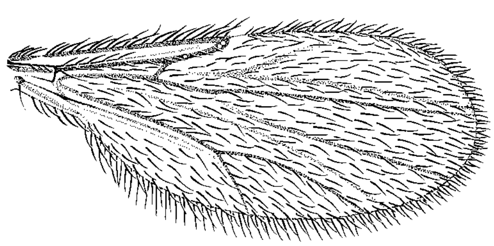
17 Forcipomyia (Lasiohelea) fairfaxensis ♀



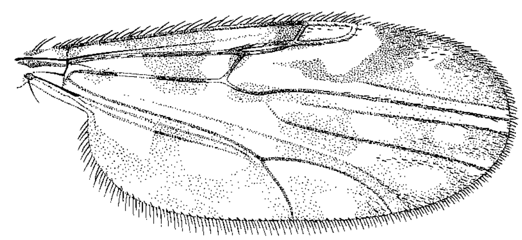
18 A. (Psilokempia) sp. ♀



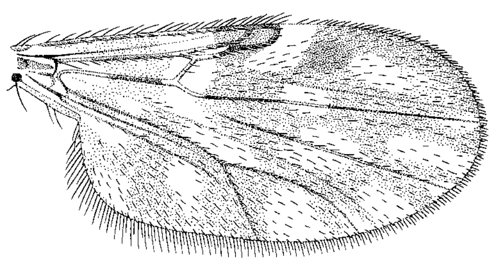
19 Dasyhelea pseudoincisurata ♀



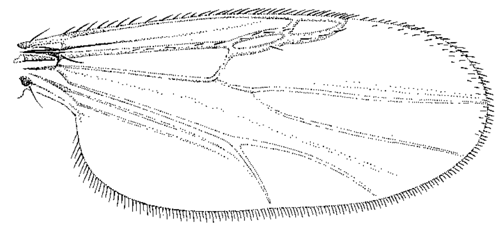
20 Paradasyhelea minuta ♀



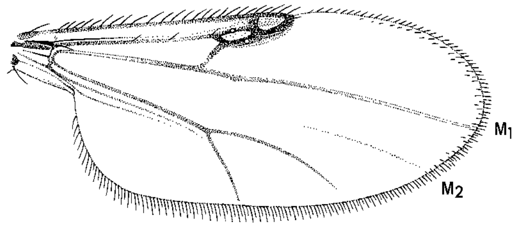
21 Culicoides insignis ♀



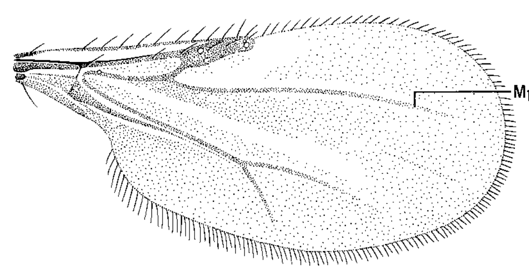
22 Culicoides copiosus ♀



23 Ceratopogon culicoidithorax ♀



24 Isohelea stigmalis ♀



25 Rhynchohelea monilicornis ♀

Figs. 28.16–25. Wings of female: (16) *Atrichopogon* (*Atrichopogon*) *levis* (Coquillett); (17) *Forcipomyia* (*Lasiohelea*) *fairfaxensis* Wirth; (18) *A.* (*Psilokempia*) sp.; (19) *Dasyhelea pseudoincisurata* Waugh & Wirth; (20) *Paradasyhelea minuta* Wirth & Lee (Australian); (21) *Culicoides insignis* Lutz; (22) *C. copiosus* Root & Hoffman; (23) *Ceratopogon culicoidithorax* Hoffman; (24) *Isohelea stigmalis* (Coquillett); (25) *Rhynchohelea monilicornis* Wirth & Blanton (*continued*).

Abbreviation: intercal vn, intercalary vein.

vertebrate blood .... ***Forcipomyia*** (***Lasiohelea*** Kieffer)
1 sp., *fairfaxensis* Wirth; eastern North America; Wirth 1951

C usually ending at or near middle of wing; cell r_{2+3} not unusually long and narrow. Two spermathecae present, with distinct necks (Fig. 124). Female sucking blood from insects .... ***Forcipomyia*** (***Trichohelea*** Goetghebuer)
9 spp.; widespread; Wirth and Messersmith 1971

15. Palpus with segments 4 and 5 incompletely fused, immovable (Fig. 54) 16
Palpus with segments 4 and 5 distinctly separated, articulated (Fig. 52) 17

16. Wing and body with color pattern and with green or blue subcutaneous pigmentation. Legs with hind tarsal ratio 1.36–1.75. Antenna usually elongate and slender (Fig. 58) .... ***Forcipomyia*** (***Caloforcipomyia*** Saunders)
1 sp., *glauca* Macfie; widespread; Utmar and Wirth 1976

Small unmarked grayish species. Legs with hind tarsal ratio greater than 1.0. Antenna less elongate .... ***Forcipomyia*** (***Euprojoannisia*** Brèthes)
14 spp.; widespread; Bystrak and Wirth 1978

17. Palpus with segment 3 broadly swollen on more than basal half, usually nearly to apex; sensory pit deep, extending nearly to base of segment; stout peg-like sensory spines on surface near sensory pit (Fig. 55). Hind tarsal ratio usually less than 0.5. Large species. Female sucking insect blood .... ***Forcipomyia*** (***Microhelea*** Kieffer)
2 spp.; widespread; Wirth 1972

Palpus variable, with segment 3 rarely swollen past mid length; no stout peg-like sensory spines on surface near sensory pit. Hind tarsal ratio usually more than 0.5. Size and habits various 18

18. Larger species often with conspicuous markings on body, legs, or wings (Fig. 11). Female antenna not always short. Tarsal ratio usually about 1.0 (0.5–1.5). Two spermathecae .... ***Forcipomyia*** (***Forcipomyia*** Meigen)
30 spp.; widespread

Small grayish or brownish unmarked species. Female antenna short; proximal flagellomeres subspherical (Fig. 59), gradually more elongated distally. Tarsal ratio usually greater than 2.0. One spermatheca 19

19. Male terminalia with club-shaped parameres extending backward from apodemes of gonocoxite (Fig. 98) .... ***Forcipomyia*** (***Synthyridomyia*** Saunders)
4 spp.; widespread; Dow and Wirth 1972

Male terminalia without backwardly directed parameres .... ***Forcipomyia*** (***Thyridomyia*** Saunders)
7 spp.; widespread; Dow and Wirth 1972

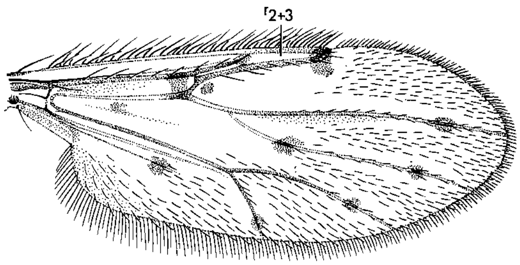
20. Flagellomeres sculptured (Figs. 63, 64). Cell r_1 nearly or completely closed; cell r_{2+3} square-ended, usually ending at or before middle of wing, sometimes closed (Fig. 19). Eye with short pubescence. Female claws small and equal (Fig. 67) .... DASYHELEINAE .... ***Dasyhelea*** Kieffer
37 spp.; widespread; Waugh and Wirth 1976

Flagellomeres not sculptured. Either cell r_1 or cell r_{2+3} or both well-developed (except in *Rhynchohelea* and *Brachypogon*); cell r_{2+3} not markedly square-ended, ending beyond middle of wing (except in *Paradasyhelea*). Eye usually bare. Female claws various .... CERATOPOGONINAE 21

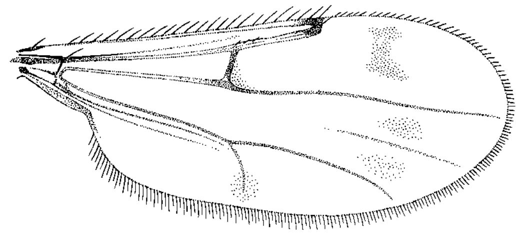
21. M usually forking beyond crossvein r-m, i.e. medial fork petiolate (Figs. 12, 13, 24), although in *Echinohelea*, with spinose legs, M forking just at crossvein (Fig. 28); M_2 sometimes obsolescent basally (Fig. 24) 22
M forking at or before crossvein r-m, i.e. medial fork sessile; M_2 nearly always complete (Figs. 14, 15, 37, 40) 43

22. Claws of both sexes small, equal, and simple (Figs. 12, 13). Wing with macrotrichia usually abundant; cell r_1 and cell r_{2+3} both usually well-developed, similar in size. Prescutal pits prominent (Figs. 12, 13). Empodia small .... CULICOIDINI 23

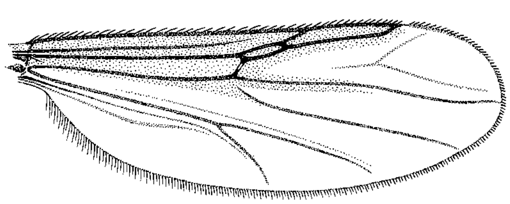
Claws of female usually larger, equal or unequal (Figs. 68–74); those of male smaller and equal. Wing with macrotrichia usually less numerous (Fig. 30), occasionally absent (Fig. 27); cell r_1, and more rarely cell r_{2+3} also, sometimes closed or lost; cell r_{2+3} usually distinctly larger



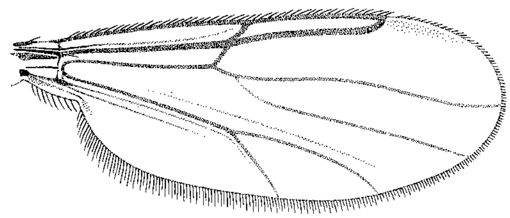
26 Alluaudomyia bella ♀



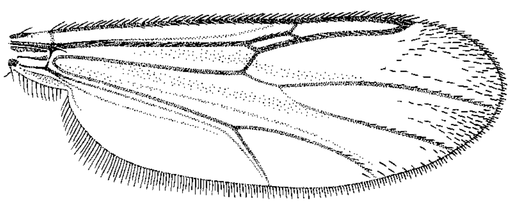
27 Brachypogon paraensis ♀



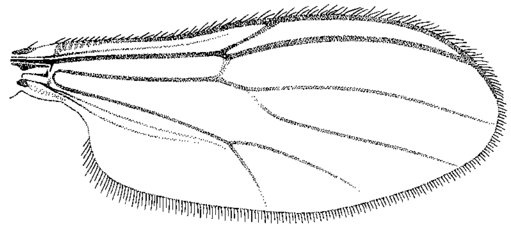
28 Echinohelea lanei ♀



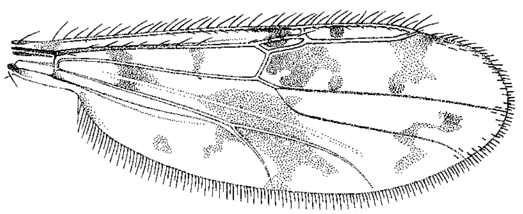
29 Stilobezzia (Eukraiohelea) elegantula ♀



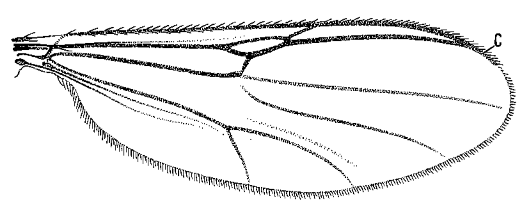
30 Stilobezzia (Neostilobezzia) lutea ♀



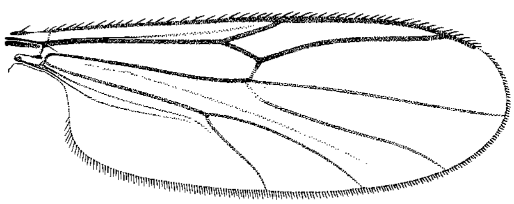
31 Parabezzia petiolata ♀



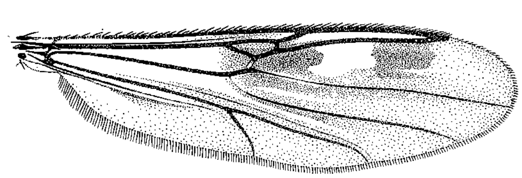
32 Monohelea hieroglyphica ♀



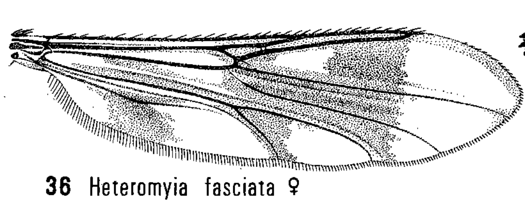
33 Neurohelea nigra ♀



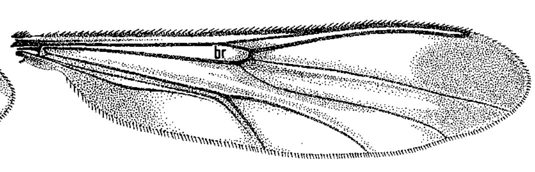
34 Neurobezzia granulosa ♀



35 Clinohelea bimaculata ♀



36 Heteromyia fasciata ♀



37 Paryphoconus angustipennis ♀

Figs. 28.26–37. Wings of female (*continued*): (26) ***Alluaudomyia bella*** (Coquillett); (27) ***Brachypogon paraensis*** Wirth & Blanton (Neotropical); (28) ***Echinohelea lanei*** Wirth; (29) ***Stilobezzia*** (***Eukraiohelea***) ***elegantula*** (Johannsen); (30) ***Stilobezzia*** (***Neostilobezzia***) ***lutea*** (Malloch); (31) ***Parabezzia petiolata*** Malloch; (32) ***Monohelea hieroglyphica*** Kieffer (Neotropical); (33) ***Neurohelea nigra*** Wirth; (34) ***Neurobezzia granulosa*** (Wirth); (35) ***Clinohelea bimaculata*** (Loew); (36) ***Heteromyia fasciata*** Say; (37) ***Paryphoconus angustipennis*** Enderlein (*continued*).

than cell r_1; crossvein r-m nearly perpendicular to R_{4+5}. Prescutal pits small or absent. Empodia small or absent 30

23. Cells r_1 and r_{2+3} usually well-formed; C usually extending past middle of wing; wing commonly adorned with pale or dark spots (Figs. 1, 12, 13). Palpus five-segmented; female mouthparts usually fitted for bloodsucking, with mandible toothed .... ***Culicoides*** Latreille...24
Jamnback 1965; Blanton and Wirth 1979

Cells r_1 and r_{2+3} obliterated; C short, not reaching to middle of wing; wing without pale or dark spots (Fig. 20). Palpus three- or four-segmented (Fig. 48); mouthparts reduced; female mandible not toothed .... ***Paradasyhelea*** Macfie
1 sp., *olympiae* Wirth & Blanton; Washington; Wirth and Blanton 1969*b*

24. Spermathecae unsclerotized (Fig. 128). Parameres broadly fused, small (Figs. 102, 103). Wing without pattern of light and dark spots .... ***Culicoides*** (***Selfia*** Khalaf)
7 spp.; western North America; Atchley 1970

Spermathecae sclerotized. Parameres fused basally or separate. Wing usually with conspicuous pattern of light and dark spots 25

25. One well-developed spermatheca. Parameres fused or separate 26
Two well-developed spermathecae (Fig. 127). Parameres separate 27

26. Spermatheca elongate to U-shaped with large opening to duct (Fig. 126). Female without sensoria on flagellomeres 9–13. Parameres fused basally .... ***Culicoides*** (***Monoculicoides*** Khalaf)
3 spp.; widespread; Wirth and Jones 1957

Spermatheca elliptical with narrow opening to duct. Female with sensoria present on some of flagellomeres 9–13. Parameres separate (Figs. 104, 105) .... ***Culicoides*** (***Beltranmyia*** Vargas)
8 spp.; widespread

27. Cell r_{2+3} dark to apex (Fig. 22), rarely pale at extreme apex. Wing frequently with pattern of light and dark spots; wing macrotrichia of female fairly numerous. Segment 3 of palpus with variously shaped sensory pit (as in Fig. 51). Paramere variously shaped, sometimes with fringing bristles apically (Figs. 106, 107) .... ***Culicoides*** (***Callotia*** Vargas & Kremer, ***Diphaomyia*** Vargas ***Drymodesmyia*** Vargas, ***Haematomyidium*** Goeldi, ***Oecacta*** Poey, and ***Wirthomyia*** Vargas)
93 spp.; widespread

Distal portion of cell r_{2+3} in a pale area (Fig. 21). Wing, palpus, and paramere various 28

28. Segment 3 of female palpus swollen to apex, with small round deep sensory pit (Fig. 50). Wing macrotrichia scanty; cell r_{2+3} short and broad .... ***Culicoides*** (***Avaritia*** Fox)
8 spp.; widespread; Jamnback and Wirth 1963

Segment 3 of female palpus tapering beyond sensory area; sensilla usually scattered, rarely in a definite pit (Fig. 49). Wing macrotrichia usually more numerous; cell r_{2+3} narrower (Figs. 12, 13, 21) 29

29. Wing with base of cell cua_1 and adjacent veins pale (Fig. 21) .... ***Culicoides*** (***Hoffmania*** Fox)
2 spp.; eastern North America

Wing with base of cell cua_1 and adjacent veins in a dark area (Figs. 12, 13) .... ***Culicoides*** (***Culicoides*** Latreille)
15 spp.; widespread; Wirth and Blanton 1969*a*

30. Cell r_{2+3} small, not or only a little longer than cell r_1 (Figs. 23, 24); one or both cells sometimes lost (Fig. 27). Wing often milky. Eye usually pubescent. [In *Alluaudomyia* (Fig. 26) cell r_1 closed; cell r_{2+3} long; macrotrichia usually numerous; wing usually with small black spots] .... CERATOPOGONINI....31

Cell r_{2+3} long, usually much longer than cell r_1 (Fig. 30); cell r_1 sometimes lost (Fig. 29); wing hyaline or with dark pattern, not milky. Eye usually bare .... STILOBEZZIINI....36

31. Cells r_1 and r_{2+3} complete (Figs. 23, 24) 32
One or both of cells r_1 and r_{2+3} obsolete (Figs. 25, 26) 33

32. C extending well past middle of wing; cells r_1 and r_{2+3} more elongate (Fig. 23). Three well-developed spermathecae present. Parameres separate .... ***Ceratopogon*** Meigen
4 spp.; northern North America

C extending to about middle of wing; cells r_1 and r_{2+3} short with adjacent veins thickened (Fig. 24). One or two well-developed spermathecae present. Parameres joined or broadly fused proximally .... ***Isohelea*** Kieffer
3 spp.; widespread

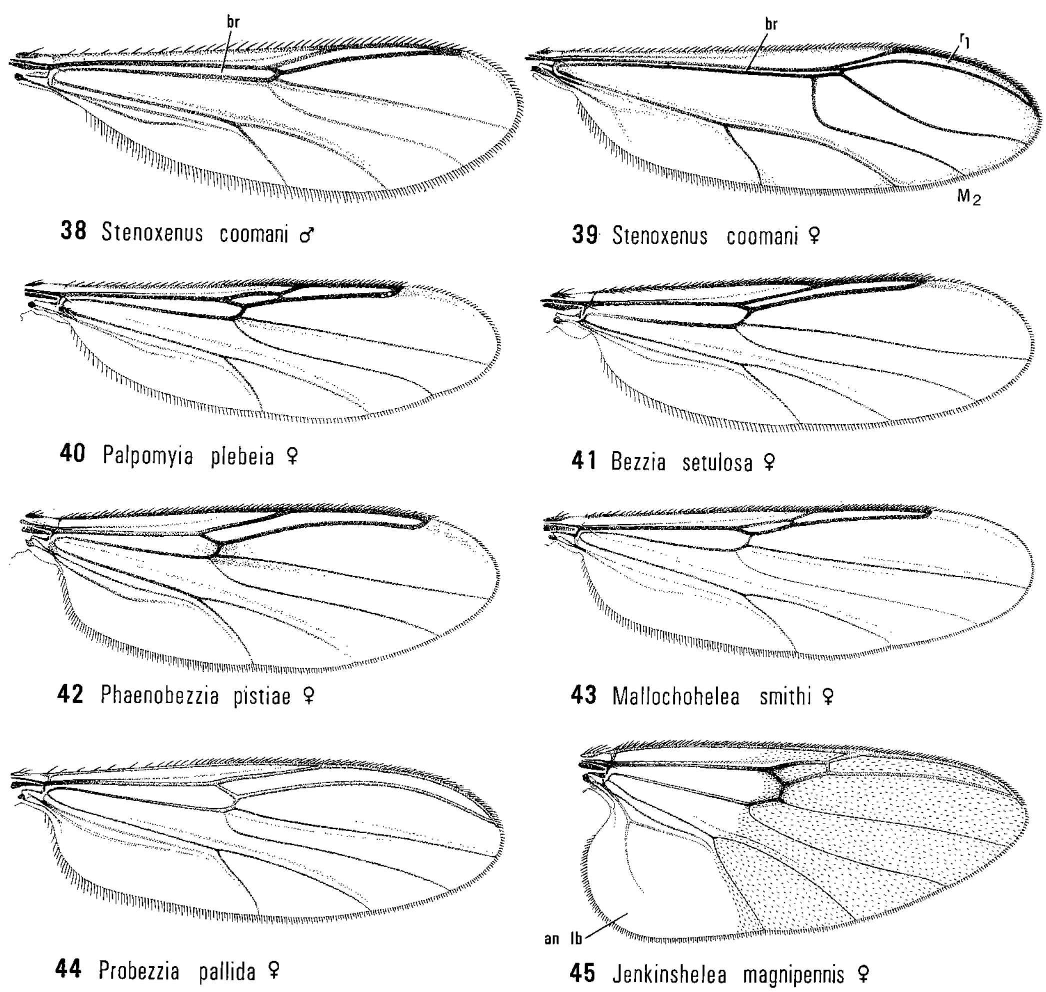
33\. Proboscis stout and truncate; palpus stout, with segment 3 greatly broadened (Fig. 56). Cells r_1 and r_{2+3} absent; M_1 obsolete distally; M_2 absent (Fig. 25). Female antenna very short, with 12 moniliform flagellomeres (Fig. 62) .... ***Rhynchohelea*** Wirth & Blanton
1 sp., *monilicornis* Wirth & Blanton; California and Florida, rare; Wirth and Blanton 1970

Proboscis normal; palpus slender. Cell r_1 obsolete; cell r_{2+3} obsolete or developed. Female flagellum 13-segmented, elongated, with slender segments 34

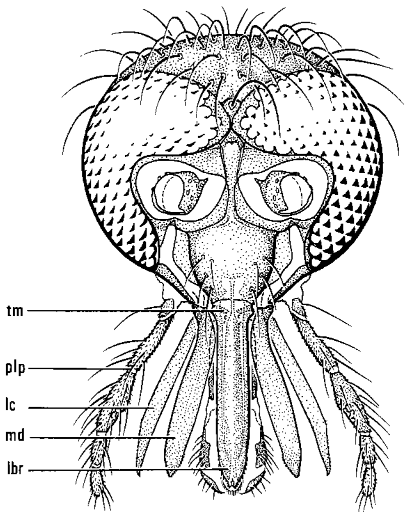
34\. Cell r_1 obsolete; cell r_{2+3} well-developed; wing usually with small isolated black spots or streaks (Fig. 26). Claws of female unequal on hindleg (Fig. 69) .... ***Alluaudomyia*** Kieffer
8 spp.; widespread; Wirth 1952*b*

Cell r_1 obsolete; cell r_{2+3} small or obsolete; wing pattern present or absent. Claws of female equal on all legs 35

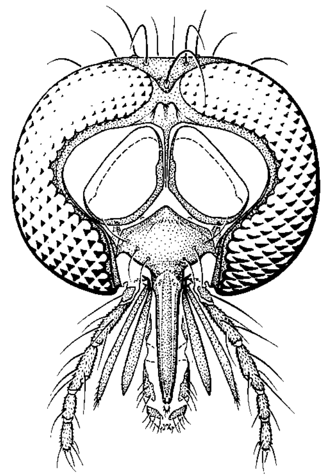
35\. Eyes contiguous. Cells r_1 and r_{2+3} obsolete (Fig. 27). Female claws slightly to moderately enlarged. Male tergite 9 without projecting apicolateral processes .... ***Brachypogon*** Kieffer
2 spp.; eastern North America; Wirth and Blanton 1970, Downes 1976



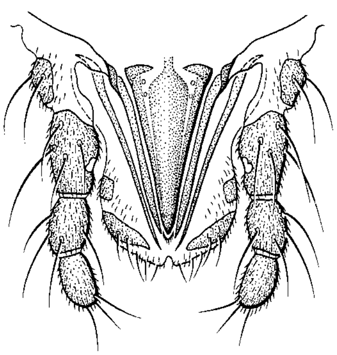
Figs. 28.38–45. Wings of female (*concluded*) and wings of male: (38) wing of female of *Stenoxenus coomani* Séguy (Oriental); wing of male of (39) *S. coomani*, (40) *Palpomyia plebeia* (Loew), (41) *Bezzia setulosa* (Loew), (42) *Phaenobezzia pistiae* Ingram & Macfie (African), (43) *Mallochohelea smithi* (Lewis), (44) *Probezzia pallida* Malloch, and (45) *Jenkinshelea magnipennis* (Johannsen).
Abbreviation: an lb, anal lobe.



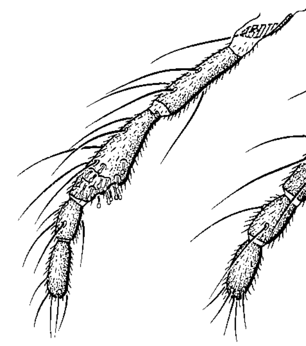
46 Culicoides (Culicoides) yukonensis ♀



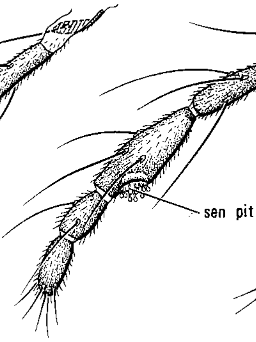
47 Culicoides (Culicoides) yukonensis ♂



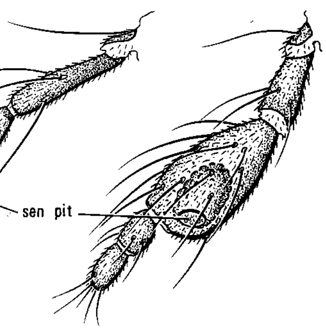
48 Paradasyhelea minuta ♀



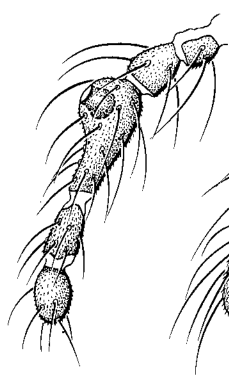
49 C. (Culicoides) yukonensis ♀



50 C. (Avaritia) obsoletus ♀

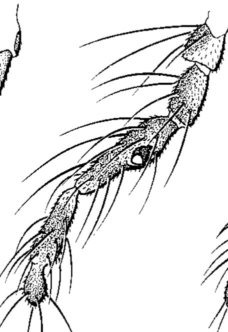


51 C. (Drymodesmyia) copiosus ♀



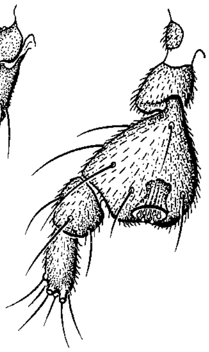
52 Forcipomyia (Forcipomyia) bipunctata ♀

53 F. (Warmkea) aeria ♀



54 F. (Euprojoannisia) wirthi ♀

55 F. (Microhelea) fuliginosa ♀



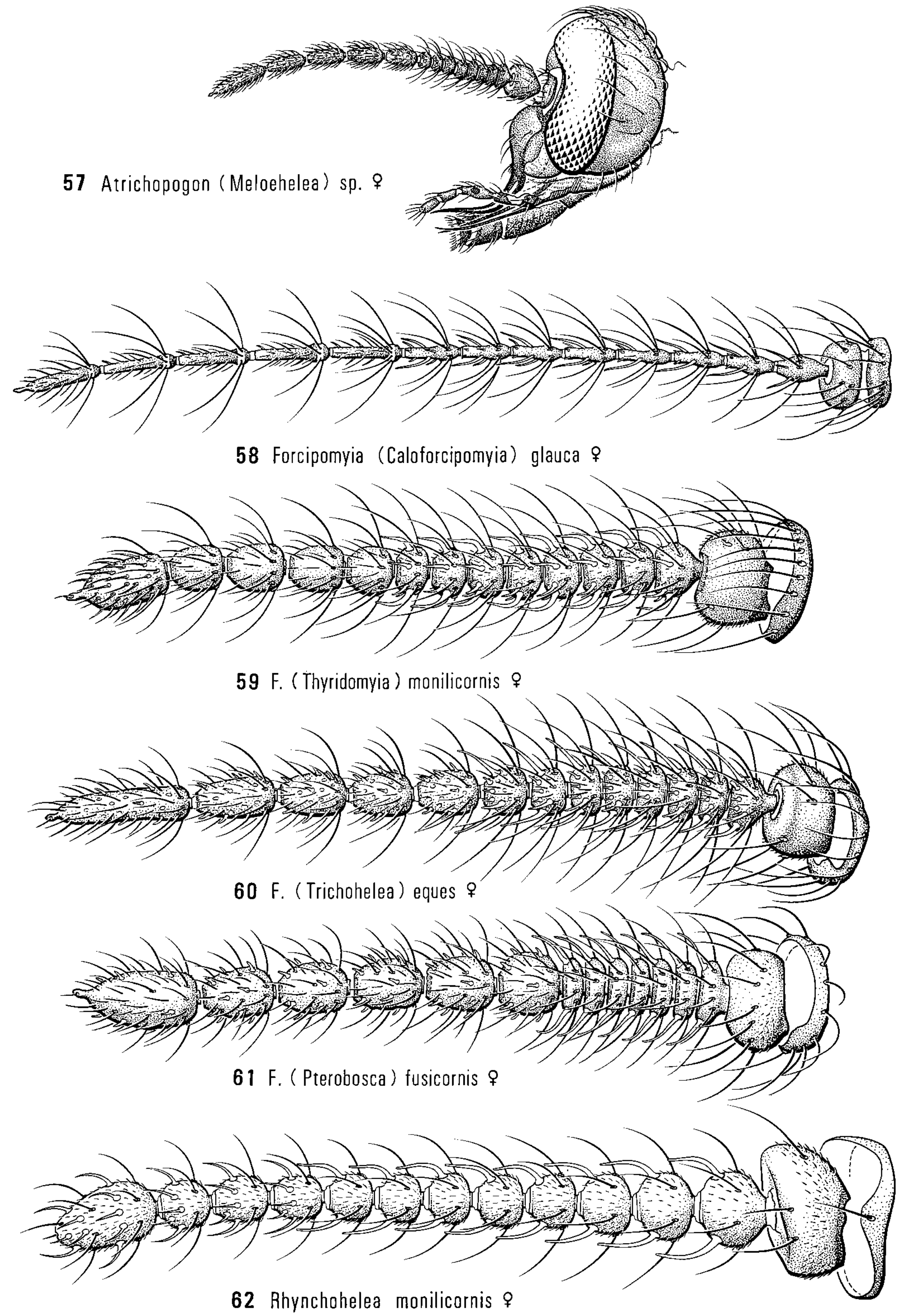
56 Rhynchohelea monilicornis ♀

Figs. 28.46–56. Details of head: (46) female and (47) male of *Culicoides yukonensis* Hoffman; (48) palpi and proboscis of female of *Paradasyhelea minuta* Wirth & Lee (Australian); female palpus of (49) C. (*Culicoides*) *yukonensis*, (50) *C.* (*Avaritia*) *obsoletus* (Meigen), (51) *C.* (*Drymodesmyia*) *copiosus* Root & Hoffman, (52) *Forcipomyia* (*Forcipomyia*) *bipunctata* (Linnaeus), (53) *F.* (*Warmkea*) *aeria* Saunders (Neotropical), (54) *F.* (*Euprojoannisia*) *wirthi* Saunders, (55) *F.* (*Microhelea*) *fuliginosa* (Meigen), and (56) *Rhynchohelea monilicornis* Wirth & Blanton.

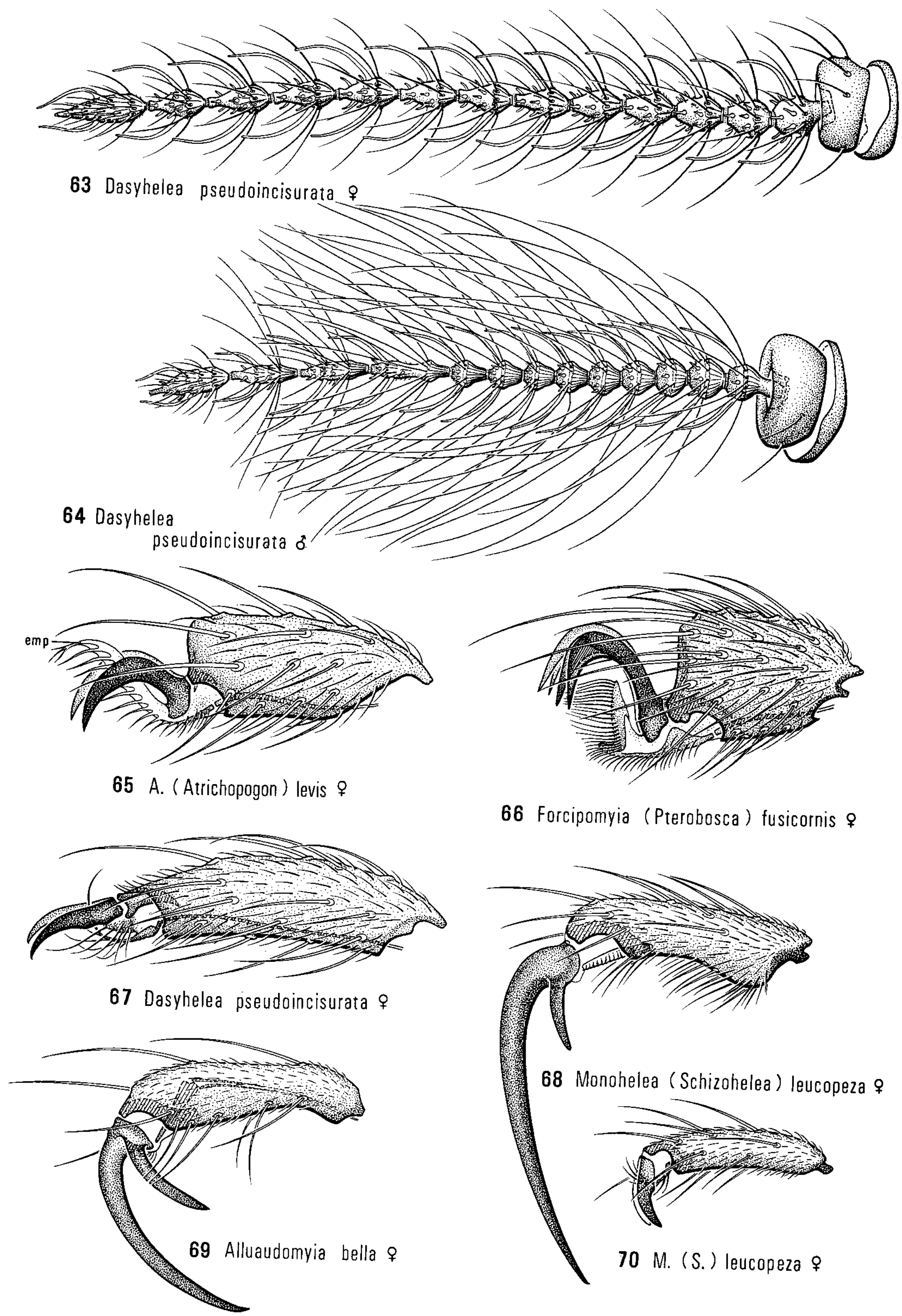
Abbreviations: lbr, labrum; lc, lacinia; md, mandible; plp, palpus; sen pit, sensory pit; tm, torma.

Eyes broadly separated. Cell r_1 obsolete; cell r_{2+3} present but small. Female claws small, at least on hindleg. Male tergite 9 with well-developed apicolateral processes .... ***Ceratoculicoides*** Wirth & Ratanaworabhan

3 spp.; widespread; Wirth and Ratanaworabhan 1971*b*



Figs. 28.57–62. Antennae of female: (57) antenna and head, side view, *Atrichopogon* (*Meloehelea*) sp.; (58) *Forcipomyia* (*Caloforcipomyia*) *glauca* Edwards; (59) *F.* (*Thyridomyia*) *monilicornis* (Coquillett); (60) *F.* (*Trichohelea*) *eques* (Johannsen); (61) *F.* (*Pterobosca*) *fusicornis* (Coquillett); (62) *Rhynchohelea monilicornis* Wirth & Blanton.



Figs. 28.63–70. Antennae and claws: antenna of (63) female and (64) male of *Dasyhelea pseudoincisurata* Waugh & Wirth; claws of hindleg of female of (65) *Atrichopogon* (*Atrichopogon*) *levis* (Coquillett), (66) *Forcipomyia* (*Pterobosca*) *fusicornis* (Coquillett), (67) *Dasyhelea pseudoincisurata*, (68) *Monohelea* (*Schizohelea*) *leucopeza* (Meigen), and (69) *Alluaudomyia bella* (Coquillett); (70) claws of foreleg of female of *M.* (*S.*) *leucopeza*.

Abbreviation: emp, empodium.

36. Femora armed with one or more ventral spines, at least on one pair of legs (Figs. 71, 72) 37
Femora not armed with ventral spines 39

37. All femora armed with numerous spines, at least in male; spines not confined to ventral surface (Fig. 71). Cells r_1 and r_{2+3} well-developed (Fig. 28). Male antenna not plumose; last five flagellomeres elongated. Reddish yellow pruinose species ....***Echinohelea*** Macfie
1 sp., *lanei* Wirth; eastern U.S.A., Neotropical; Wirth 1951
Only hind or fore femur armed with ventral spines. Cell r_1 or cell r_{2+3} sometimes lost. Male antenna plumose. Color various 38

38. Fore femur slender and unarmed; hind femur greatly swollen, arcuate, and armed with numerous ventral spines (Fig. 72). Cells r_1 and r_{2+3} well-developed. Shining black species ....***Serromyia*** Meigen
3 spp.; widespread
Fore femur with one or two ventral spines; hind femur slender and unarmed. Cell r_1 lost (Fig. 29). Pruinose yellow or brownish species ....***Stilobezzia*** (***Eukraiohelea*** Ingram & Macfie)
1 sp., *elegantula* (Johannsen); southeastern U.S.A., Neotropical

39. Cells r_1 and r_{2+3} confluent; in female C long, extending past end of R_{4+5} and ending nearly at wing tip (Fig. 31). Palpus four-segmented (segments 4 and 5 fused) ....***Parabezzia*** Malloch
14 spp.; widespread; Grogan and Wirth 1977*a*
Cells r_1 and r_{2+3} present, separate; in female C short, not extending beyond R_{4+5} and not ending nearly at wing tip (Fig. 30). Palpus five-segmented 40

40. Female claws large and unequal on all legs (Figs. 73, 74). Cell r_{2+3} two or three times longer than cell r_1 ....***Stilobezzia*** Kieffer, in part....41
Wirth 1953
Female claws equal on foreleg and midleg (Fig. 70); hindleg with one long talon, and with or without a short second claw (Fig. 68). Cell r_{2+3} less than twice as long as cell r_1 ....***Monohelea*** Kieffer....42
Wirth and Williams 1964

41. Wing with macrotrichia on membrane, at least near apex (Fig. 30) ....***Stilobezzia*** (***Neostilobezzia*** Goetghebuer)
3 spp.; widespread
Wing without macrotrichia on membrane ....***Stilobezzia*** (***Stilobezzia*** Kieffer)
14 spp.; widespread

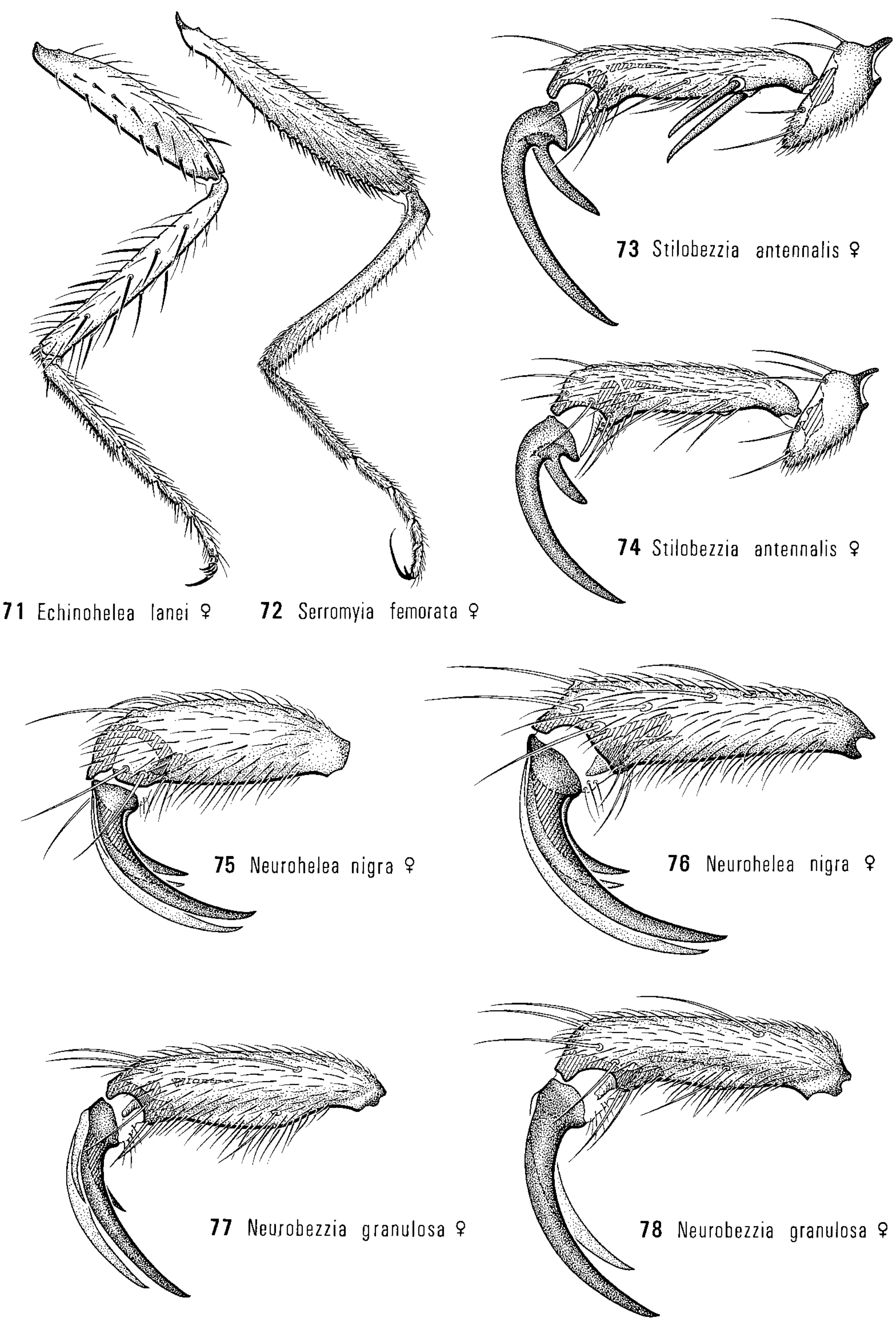
42. Wing with prominent color pattern (Fig. 32). Body usually pruinose.. ....***Monohelea*** (***Monohelea*** Kieffer)
15 spp.; widespread
Wing whitish hyaline without color pattern. Body shining black ....***Monohelea*** (***Schizohelea*** Kieffer)
1 sp., *leucopeza* (Meigen); Canada, northern U.S.A.

43. Tarsomere 5 of female armed ventrally with stout black blunt spines (batonnets) (Fig. 85). Female abdomen without internal sclerotized gland rods; sternite 8 of female often with pair of hair tufts (Fig. 121) ....SPHAEROMIINI....44
Tarsomere 5 of female unarmed or armed only with slender sharp-tipped spines; if tarsomere 5 armed, female abdomen usually with internal sclerotized gland rods (Figs. 122, 123); sternite 8 of female without hair tufts 50

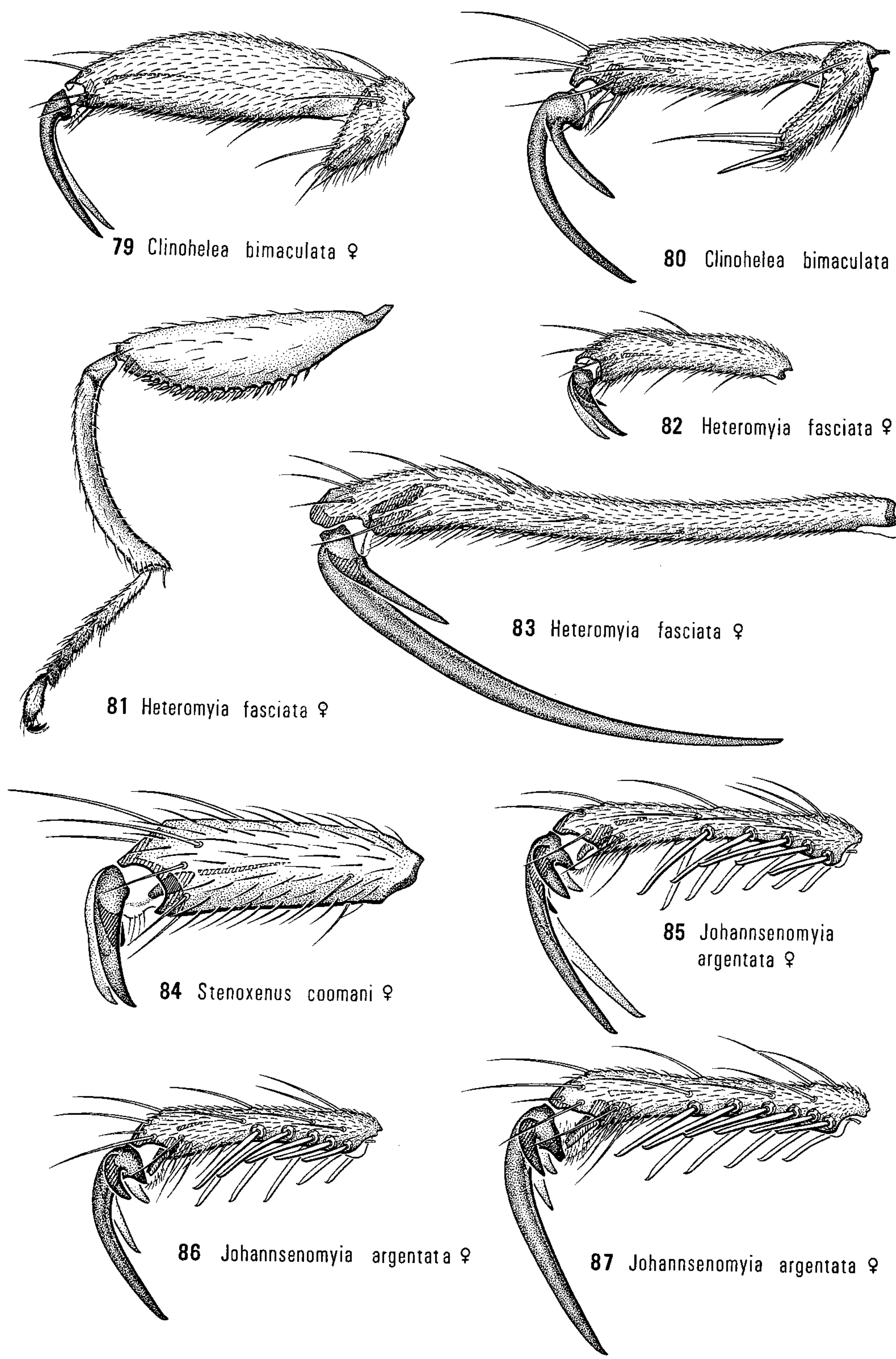
44. Female tarsal claws unequal on midleg and hindleg, equal on foreleg (Figs. 85–87); femora unarmed. Abdomen petiolate. C extending to about 0.8 of wing length; usually cells r_1 and r_{2+3} both present...***Johannsenomyia*** Malloch
2 spp.; eastern North America; Wirth 1962*a*
Female tarsal claws equal on all legs; femora armed or unarmed. Abdomen and venation various 45

45. Female claws with slender internal basal barb (Fig. 88), gently curved distally. C extending nearly to wing tip (Fig. 15) ....***Sphaeromias*** Kieffer
2 spp.; widespread; Wirth and Grogan 1978
Female claws with blunt external basal tooth (Fig. 89), usually straight or flattened distally. C various 46

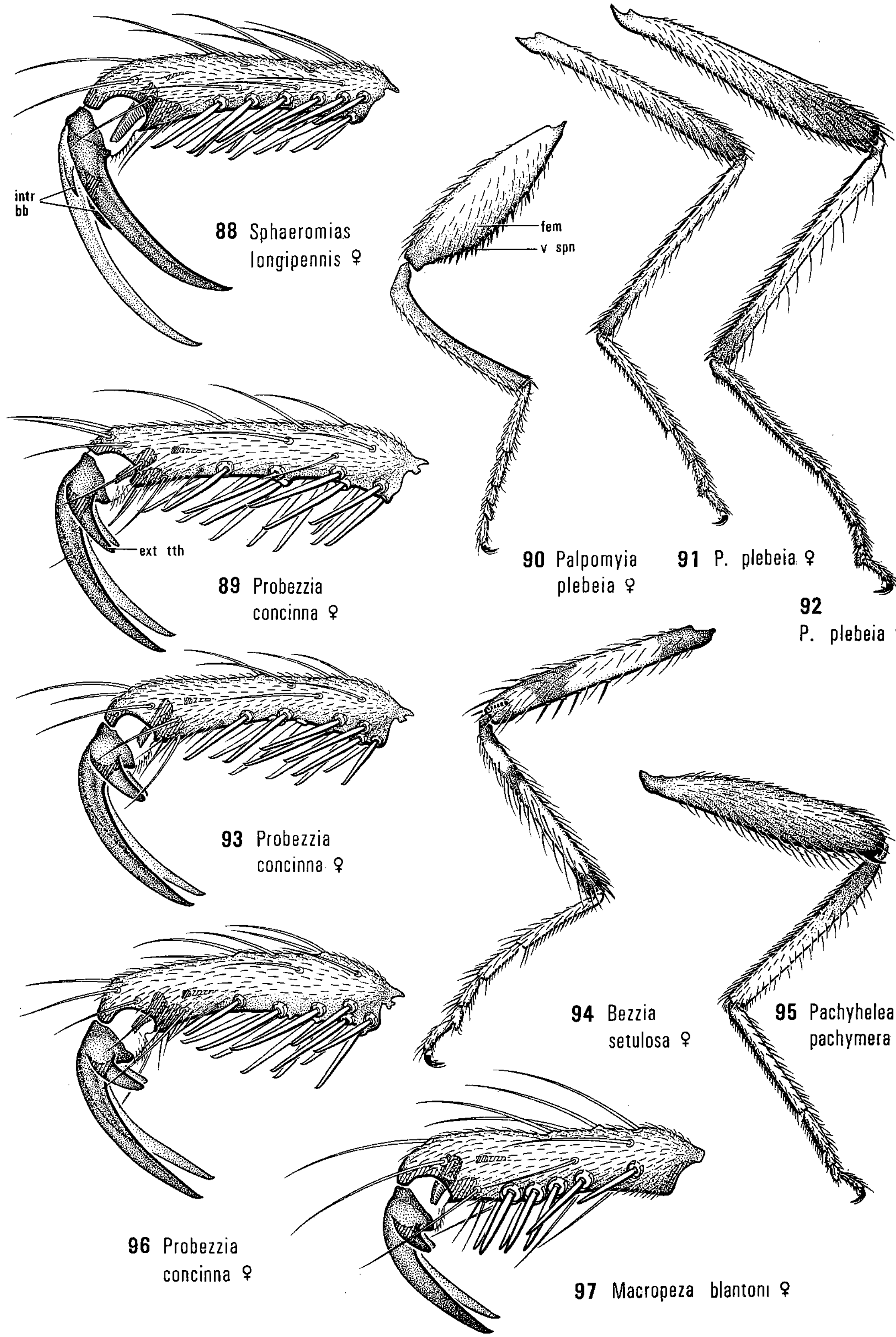
46. C short, extending to about 0.8 of wing length (Fig. 43) 47
C long in female, extending nearly to wing tip; costal ratio over 0.87 (Fig. 45) 48



Figs. 28.71–78. Legs and claws of female: (71) *Echinohelea lanei* Wirth, hindleg; (72) *Serromyia femorata* (Meigen), hindleg; (73) *Stilobezzia antennalis* (Coquillett), claws of foreleg; (74) *S. antennalis*, claws of hindleg; (75) *Neurohelea nigra* Wirth, claws of foreleg; (76) *N. nigra*, claws of hindleg; (77) *Neurobezzia granulosa* (Wirth), claws of foreleg; (78) *N. granulosa*, claws of hindleg (*continued*).



Figs. 28.79–87. Legs and claws of female (*continued*): (79) *Clinohelea bimaculata* (Loew), claws of foreleg; (80) *C. bimaculata*, claws of hindleg; (81) *Heteromyia fasciata* Say, foreleg; (82) *H. fasciata*, claws of midleg; (83) *H. fasciata*, claws of hindleg; (84) *Stenoxenus coomani* Séguy (Oriental), claws; (85) *Johannsenomyia argentata* (Loew), claws of foreleg; (86) *J. argentata*, claws of midleg; (87) *J. argentata*, claws of hindleg (*continued*).



Figs. 28.88–97. Legs and claws of female (*concluded*): (88) *Sphaeromias longipennis* (Loew), claws; (89) *Probezzia concinna* (Meigen), claws of foreleg; (90) *Palpomyia plebeia* (Loew), foreleg; (91) *P. plebeia*, midleg; (92) *P. plebeia*, hindleg; (93) *Probezzia concinna*, claws of midleg; (94) *Bezzia setulosa* (Loew), leg; (95) *Pachyhelea pachymera* (Williston), hindleg; (96) *Probezzia concinna*, claws of hindleg; (97) *Macropeza blantoni* Wirth & Ratanaworabhan, claws.

Abbreviations: ext tth, external tooth; fem, femur; intr bb, internal barb; v spn, ventral spine.

47. Body slender. Scutum shining yellow to black with little or no pollen. Femora armed or unarmed. Cells r_1 and r_{2+3} present and separate (Fig. 43). Male terminalia with well-developed gonocoxite and articulated gonostylus (Fig. 116) .... ***Mallochohelea*** Wirth
11 spp.; widespread; Wirth 1962*a*

Body stouter than above. Scutum dull, usually with dense whitish to grayish pollen. Femora ventrally and tibiae dorsally armed with numerous fine sharp spines. Cell r_{2+3} sometimes confluent with cell r_1. Male terminalia with short stout gonocoxite and immovable bud-like gonostylus (Fig. 119) .... ***Nilobezzia*** Kieffer
4 spp.; widespread; Wirth 1962*a*

48. Wing broad; anal lobe large, angular (Fig. 45) .... ***Jenkinshelea*** Macfie
4 spp.; eastern North America; Grogan and Wirth 1977*b*

Wing not unusually broad (Fig. 44); anal lobe not angularly developed 49

49. Female claws short, curved, and sharp-pointed, with a small external basal tooth on each (Fig. 97). Scutum without strong erect bristles .... ***Macropeza*** Meigen
1 sp., *blantoni* Wirth & Ratanaworabhan; Florida; Wirth and Ratanaworabhan 1972*a*

Female claws longer, straighter, and somewhat flattened distally, with a strong blunt external basal tooth on each (Figs. 89, 93, 96). Scutum of female with strong erect bristles .... ***Probezzia*** Kieffer
19 spp.; widespread; Wirth 1971

50. Claws of female usually unequal, at least on hindleg, or only a single claw present with a basal tooth. Female abdomen without internal sclerotized gland rods .... HETEROMYIINI 51
Claws of female equal on all legs. Female abdomen usually with internal sclerotized gland rods (Figs. 122, 123) 55

51. C extending well beyond tip of R_{4+5} (Fig. 33) 52
C not extending beyond tip of R_{4+5} (Fig. 35) 53

52. Cell r_1 and cell r_{2+3} present and separate (Figs. 33, 34). Claws equal on all legs; tarsomere 5 of foreleg somewhat inflated (Figs. 75, 76) .... ***Neurohelea*** Kieffer
2 spp.; western North America

Cells r_1 and r_{2+3} confluent (Fig. 34). Claws of female equal on foreleg and midleg, unequal on hindleg; tarsomere 5 of foreleg not inflated (Figs. 77, 78) .... ***Neurobezzia*** Wirth & Ratanaworabhan
1 sp., *granulosa* (Wirth); California, Oregon; Wirth and Ratanaworabhan 1972*b*

53. Tarsomere 4 cordiform on foreleg, and ending in two bifid lobes on midleg and hindleg (Figs. 79, 80); lobes armed with spines; tarsomere 5 of foreleg greatly swollen; claws equal on foreleg, unequal in female on midleg and hindleg .... ***Clinohelea*** Kieffer
7 spp.; widespread; Grogan and Wirth 1975

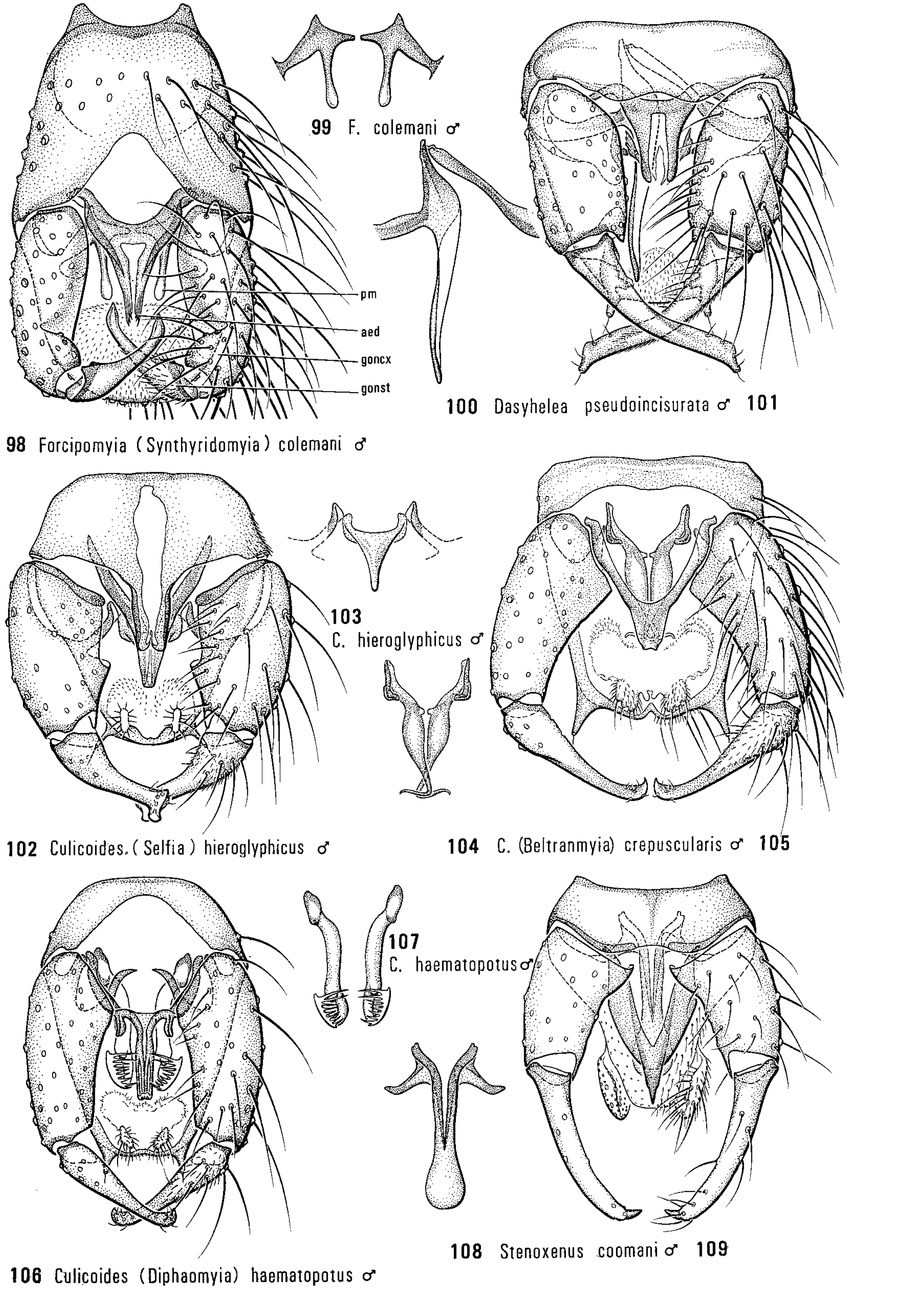
Tarsomere 4 cylindrical or cordiform, but not divided into spinose bifid lobes; tarsomere 5 of foreleg inflated and fusiform (Fig. 81); claws equal on foreleg and midleg; hindleg of female with one long talon and a much smaller second claw (Figs. 81–83) 54

54. Fore femur greatly swollen and armed ventrally, with tibia arcuate (Fig. 81); tarsomere 4 cordiform. Cells r_1 and r_{2+3} separate or confluent; wing fasciate (Fig. 36). Body somewhat shining .... ***Heteromyia*** Say
2 spp.; eastern North America; Wirth and Grogan 1977

Fore femur slender, unarmed, with tibia normal; tarsomere 4 not cordiform. Cell r_{2+3} not apparent, presumably confluent with cell r_1; wing milky white. Body densely pruinose .... ***Pellucidomyia*** Macfie
1 sp., *wirthi* (Lane); Texas; Wirth and Ratanaworabhan 1971*a*

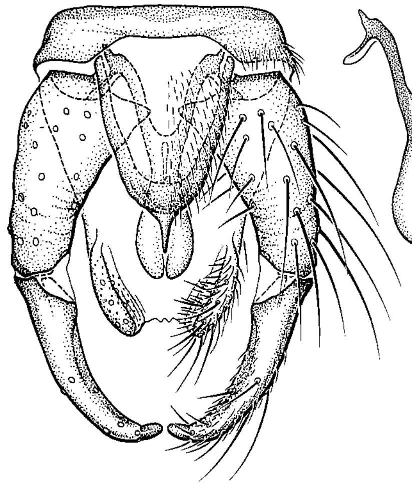
55. Body unusually slender and dorsoventrally flattened. R_{2+3} absent; cell r_1 very narrow in female, usually extending far toward wing tip, more normal in male (Figs. 37, 38, 39); crossvein r-m often very short; cell br very narrow or even obliterated. Eyes broadly separated. Legs long and slender, with fine hairs; femora unarmed; claws very short (Fig. 84) .... STENOXENINI 56
Wirth and Ratanaworabhan 1972*c*

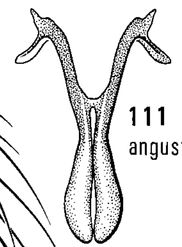
Body not unusually slender or dorsoventrally flattened. R_{2+3} present or absent, but if cells narrow C not extending nearly to wing tip; crossvein r-m longer; cell br well-formed and not very narrow (Figs. 40, 41). Eyes narrowly to moderately separated. Legs not unusually long; femora often armed; claws of female usually moderately long (Figs. 90–92) .... PALPOMYIINI 57



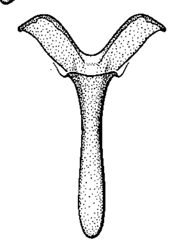
Figs. 28.98–109. Terminalia of male: (98) *Forcipomyia* (*Synthyridomyia*) *colemani* Wirth; (99) *F. colemani*, parameres; (100) *Dasyhelea pseudoincisurata* Waugh & Wirth, left paramere; (101) *D. pseudoincisurata*; (102) *Culicoides* (*Selfia*) *hieroglyphicus* Malloch; (103) *C.* (*S.*) *hieroglyphicus*, parameres; (104) *Culicoides* (*Beltranmyia*) *crepuscularis* Malloch, parameres; (105) *C.* (*B.*) *crepuscularis*; (106) *C.* (*Diphaomyia*) *haematopotus* Malloch; (107) *C.* (*D.*) *haematopotus*, parameres; (108) *Stenoxenus coomani* Séguy (Oriental), parameres; (109) *S. coomani* (*continued*).

Abbreviations: aed, aedeagus; goncx, gonocoxite; gonst, gonostylus; pm, paramere.

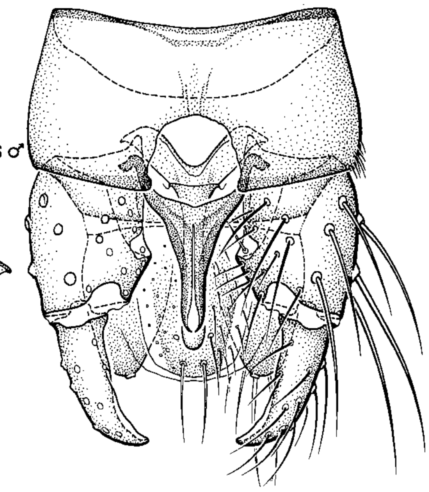




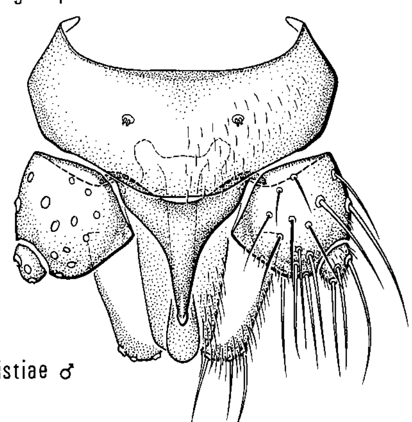
111 P. angustipennis ♂



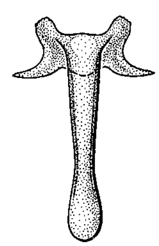
110 Paryphoconus angustipennis ♂



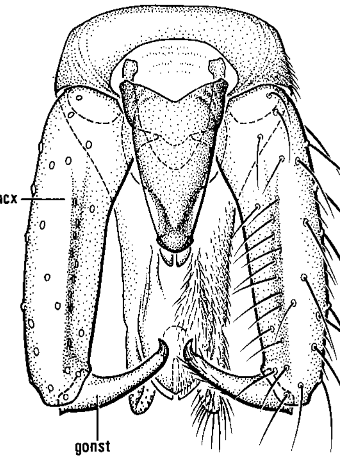
112 Bezzia setulosa ♂ 113

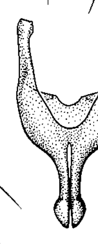


114 Phaenobezzia pistiae ♂

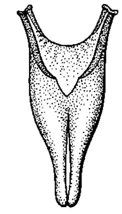


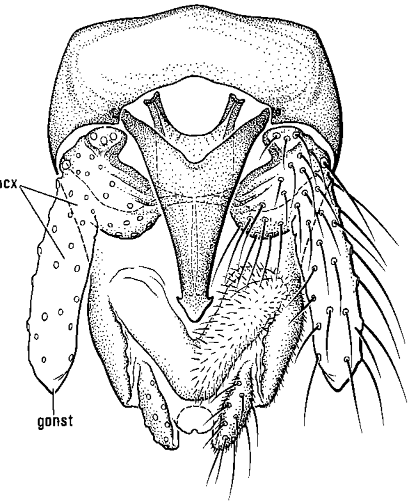
115 P. pistiae ♂





117 M. albibasis ♂

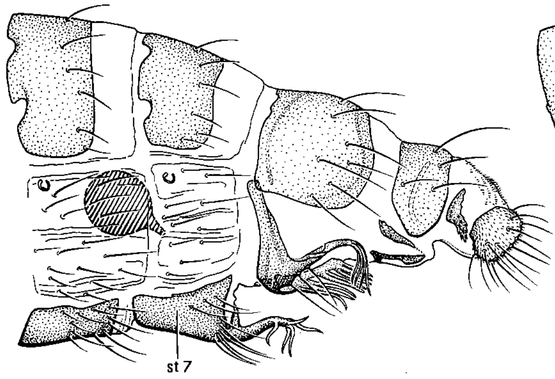




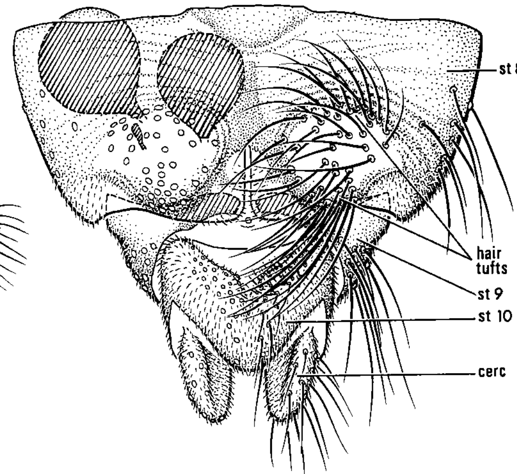
116 Mallochohelea albibasis ♂

118 Nilobezzia minor ♂ 119

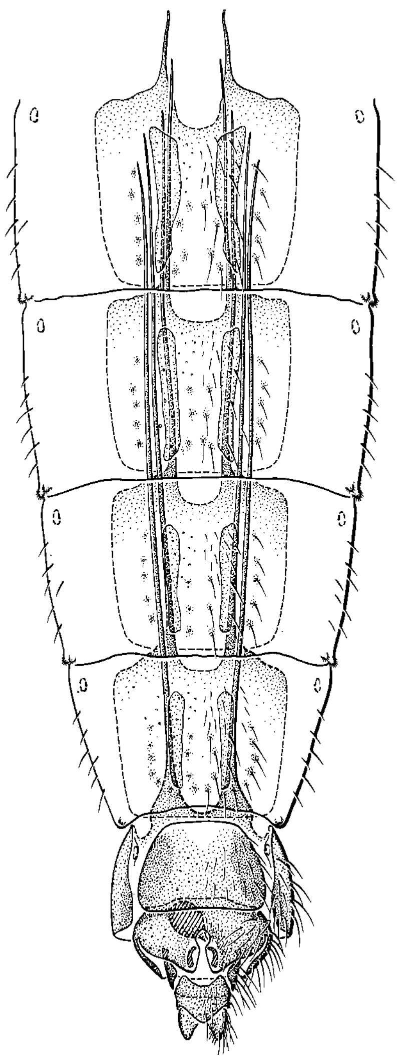
Figs. 28.110–119. Terminalia of male (*concluded*): (110) ***Paryphoconus angustipennis*** Enderlein; (111) ***P. angustipennis***, parameres; (112) ***Bezzia setulosa*** (Loew), parameres; (113) ***B. setulosa***; (114) ***Phaenobezzia pistiae*** Ingram & Macfie (African); (115) ***P. pistiae***, parameres; (116) ***Mallochohelea albibasis*** (Malloch); (117) ***M. albibasis***, parameres; (118) *Nilobezzia minor* (Wirth), parameres; (119) *N. minor*.
Abbreviations: goncx, gonocoxite; gonst, gonostylus.



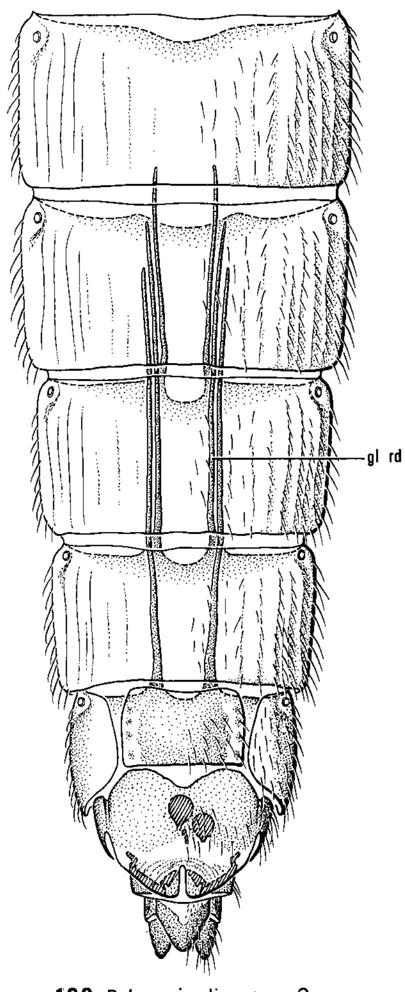
120 Atrichopogon (Psilokempia) sp. ♀



121 Probezzia concinna ♀



122 Paryphoconus angustipennis ♀



123 Palpomyia lineata ♀

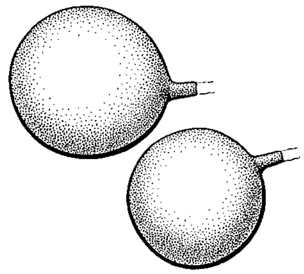
Figs. 28.120–123. Abdominal structures of female: (120) terminalia, lateral view, of *Atrichopogon* (*Psilokempia*) sp.; (121) terminalia, ventral view, of *Probezzia concinna* (Meigen); (122) abdomen, ventral view, of *Paryphoconus angustipennis* Enderlein; (123) abdomen, ventral view, of *Palpomyia lineata* (Meigen).
Abbreviations: cerc, cercus; gl rd, gland rod; st, sternite.

56. Thorax broadly rounded anteriorly, without median spine. Female wing with M_2 strikingly elbowed at base (Fig. 39). Palpus four-segmented. Parameres fused apically (Figs. 108, 109) .... ***Stenoxenus*** Coquillett
1 sp., *johnsoni* Coquillett; southeastern U.S.A.

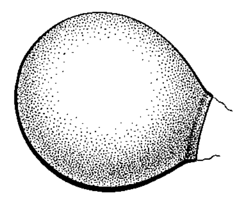
Thorax narrowed in front, more or less conical, with erect anteromedial spine (Fig. 129). Female wing with M_2 not elbowed at base (Fig. 37). Palpus five-segmented. Parameres separate apically (Figs. 110, 111) .... ***Paryphoconus*** Enderlein
1 sp., *sonorensis* Wirth & Ratanaworabhan; Oklahoma, Neotropical

57. Cells r_1 and r_{2+3} present, separate (Fig. 40) 58
Cells r_1 and r_{2+3} confluent (Fig. 41) 59

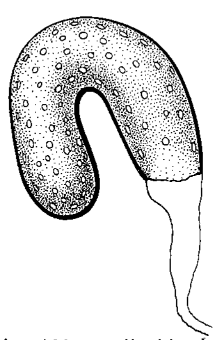
58. Hind femur greatly swollen; femora unarmed (Fig. 95); female with one to three pairs of stout pointed spines on tarsomere 5 .... ***Pachyhelea*** Wirth
1 sp., *pachymera* (Williston); Texas, Neotropical; Wirth 1959



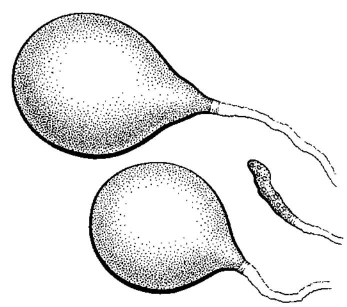
124 Forcipomyia (Trichohelea) eques ♀



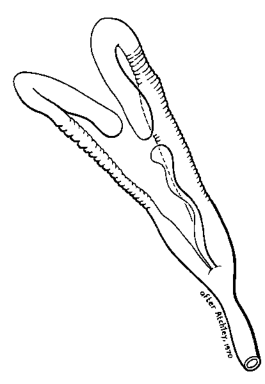
125 F. (Lasiohelea) fairfaxensis ♀



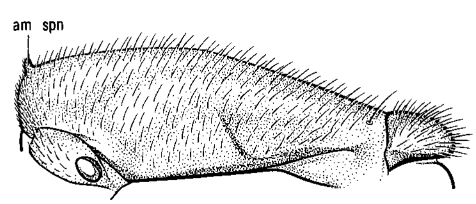
126 Culicoides (Monoculicoides) variipennis ♀



127 C. (Culicoides) yukonensis ♀



128 C. (Selfia) hieroglyphicus ♀



129 Paryphoconus angustipennis ♀

Figs. 28.124–129. Spermathecae and thorax: spermathecae of (124) *Forcipomyia* (*Trichohelea*) *eques* (Johannsen), (125) *F.* (*Lasiohelea*) *fairfaxensis* Wirth, (126) *Culicoides* (*Monoculicoides*) *variipennis* (Coquillett), (127) *C.* (*Culicoides*) *yukonensis* Hoffman, and (128) *C.* (*Selfia*) *hieroglyphicus* Malloch; (129) lateral view of thorax of *Paryphoconus angustipennis* Enderlein.

Abbreviation: am spn, anteromedial spine.

Hind femur not greatly swollen, but if moderately swollen, then at least one pair of femora armed with ventral spines (Figs. 90–92); fore femur often swollen (Fig. 90) .... **_Palpomyia_** Meigen

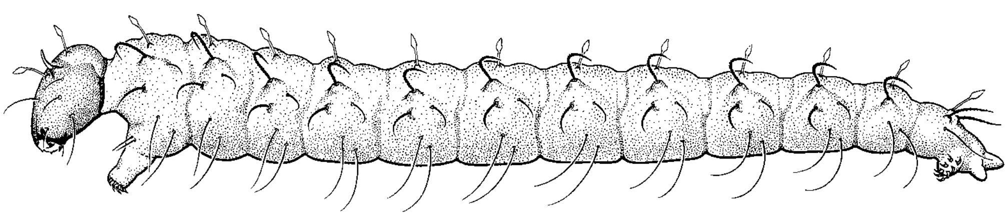
31 spp.; widespread; Grogan and Wirth 1979

59. Femora usually armed, at least on foreleg (Fig. 94); female tarsomere 5 without stout ventral spines. C short (Fig. 41); costal ratio 0.67–0.75. Gonostylus developed normally, articulated (Fig. 113) .... **_Bezzia_** Kieffer

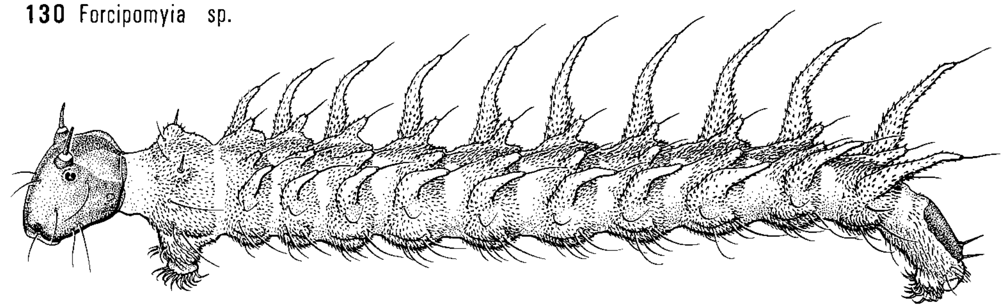
42 spp.; widespread; Dow and Turner 1976

Femora unarmed; female tarsomere 5 with stout ventral spines having sharp bent tips C longer than above (Fig. 42); costal ratio 0.87. Gonostylus short, not articulated (Fig. 114) .... **_Phaenobezzia_** Haeselbarth

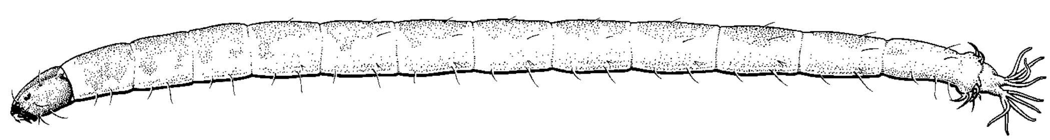
1 sp., *opaca* (Loew); widespread



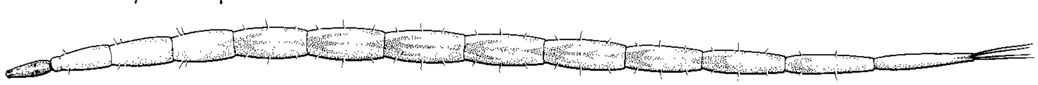
130 Forcipomyia sp.



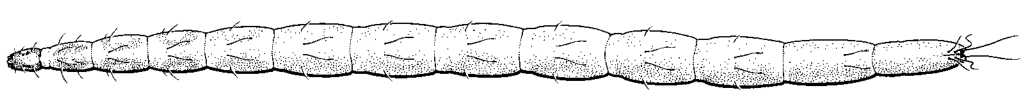
131 Atrichopogon polydactylus



132 Dasyhelea sp.



133 Bezzia sp.



134 Culicoides sp.

Figs. 28.130–134. Larvae: (130) *Forcipomyia* sp.; (131) *Atrichopogon polydactylus* Nielsen; (132) *Dasyhelea* sp.; (133) *Bezzia* sp.; (134) *Culicoides* sp.

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CHIRONOMIDAE 29

D. R. Oliver

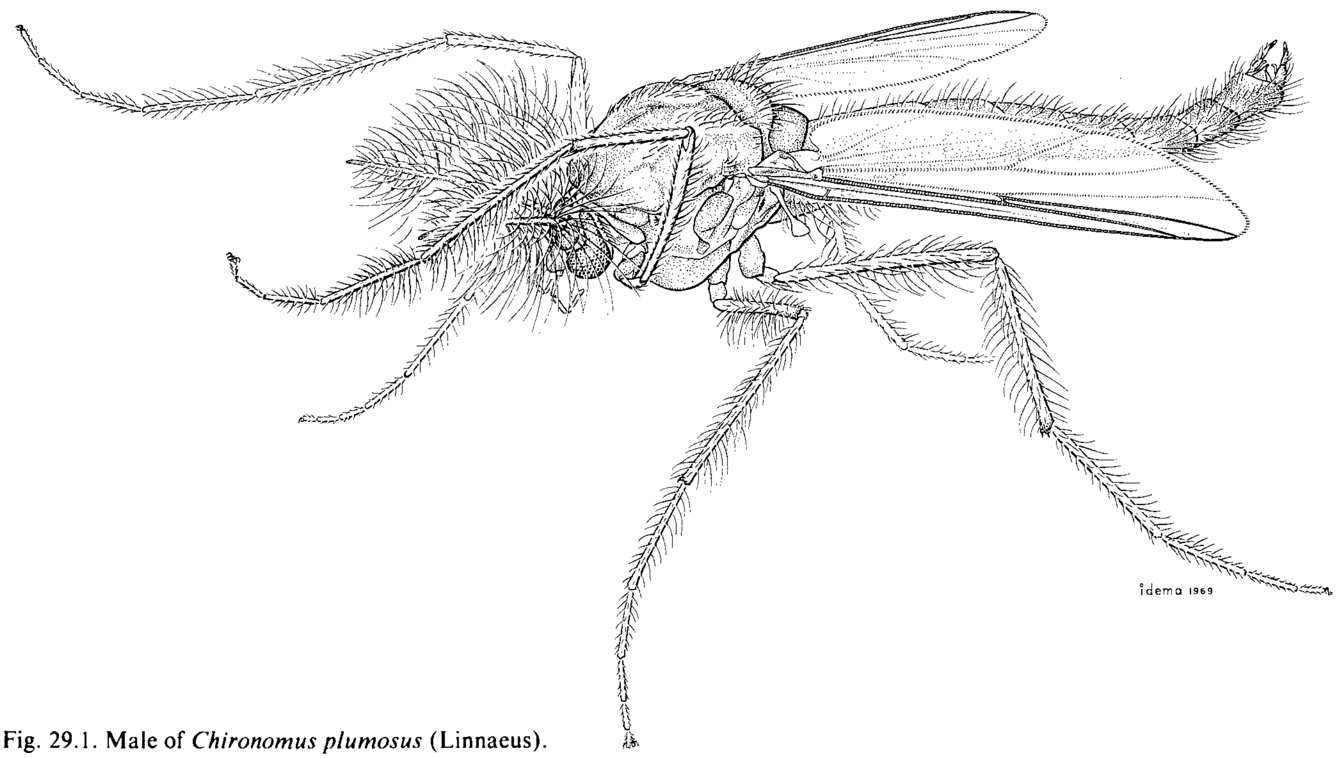


Fig. 29.1. Male of *Chironomus plumosus* (Linnaeus).

Small to medium-sized flies (Fig. 1), 1.0–10.0 mm long. Male antenna usually plumose. Wing narrow. Legs long and slender. Male abdomen usually long and slender; terminalia not inverted. Larva (Figs. 114–116) apneustic, long, narrow, cylindrical, with strongly sclerotized nonretractile head capsule, and usually with pairs of anterior and posterior prolegs bearing spines or claws. Pupa (Figs. 138–140) somewhat comma-shaped, with enlarged cephalothorax and with dorsoventrally flattened abdomen usually bearing apically a pair of flattened lobes; leg sheaths usually curved under wing pads but sometimes extending posteriorly.

Adult. Head: anteriorly flattened with reduced mouthparts (Figs. 20–22), although labrum elongate in some species. Eyes dichoptic, ovoid to reniform to elongate dorsally, bare or hairy. Ocelli vestigial; frontal tubercles on vertex in some species perhaps being modified ocelli. Antenna (Figs. 23–25) exhibiting strong sexual dimorphism, although antenna of male of some species resembles that of female; scape flattened; pedicel ovoid; flagellomeres numbering 1–15 with male usually having more flagellomeres than female, cylindrical and elongate with well-developed plume in male, without plume and cylindrical to flask-shaped with apical hyaline sensory setae (except on terminal segment) and usually with one whorl of a few strong setae in female. Labrum comprising a pair of fleshy lobes; mandible absent; palpus usually with five segments, rarely with four or less, with third palpal segment sometimes having a sensory vesicle.

Thorax: convex to flattened dorsally, sometimes with median scutal hump or tubercle (Figs. 26–48). Antepronotum collar-like; lobes usually joined medially, but sometimes separate; setation ranging from completely covered to present only ventrolaterally. Scutum with or without acrostichal setae; dorsolateral setae variable, sometimes extending anteriorly on to postpronotal area, usually erect, occasionally decumbent; supra-alar setae variable anteriorly, usually ending above medioanepisternum. Scutellum hemispherical; setation variable. Postnotum well-developed, usually with longitudinal median furrow, usually bare. Anapleural suture usually distinct. Anepisternum, medioanepisternum, postanepisternum, and katepisternum sometimes bearing short setae.

Legs (Figs. 49–76) long and slender; fore metatarsus longer than fore tibia only in Chironominae; fore tarsus of male sometimes bearded. Spurs and combs greatly variable, sometimes reduced, but rarely absent; fore tibia usually with one apical spur or scale; mid tibia usually with two combs of basally fused spines or two spurs; hind tibia usually with two combs of basally fused spines or two spurs and one comb of basally free spines. Claws pointed or toothed apically; pulvilli present or absent; empodia elongate, usually plumose.

Wing narrow, broader in female than in male, at rest lying flat or forming peak over abdomen (Figs. 1–19). Membrane hyaline, sometimes with dark markings; microtrichia usually present; macrotrichia present or absent. Calypter bare or with marginal fringe of setae. Wing venation of two basic types distinguished by presence or absence of crossvein m-cu; C usually fused with R_{4+5} near apex but coalesced with Rs in *Corynoneura* Winnertz (Fig. 11) and allied genera, rarely reaching wing apex; Sc free, usually evanescent apically; R three-branched; R_{2+3} often weak, sometimes absent, and in Tanypodinae forked into R_2 and R_3; crossvein r-m oblique to horizontal to plane of R_{4+5}; radial veins usually more strongly sclerotized than posterior veins; M straight, ending near wing tip; CuA forked, with furcation usually opposite or distal to crossvein r-m; CuA_2 straight to sinuous; A_1 rarely reaching wing margin.

Abdomen: seven or eight pregenital segments; segments stouter in female than in male. Tergal and sternal setae greatly variable in number, size, and extent.

Tergite 9 of male (Figs. 77–110) usually shortened and narrowed with poorly delimited anterior and posterior margins, and frequently bearing anal point posteriorly; sternite 9 much shortened medially and produced laterally up sides of abdomen; tergite 9 and sternite 9 completely fused in Podonominae and Tanypodinae. Gonocoxites rather large, cylindrical, joined to each other by gonocoxal apodemes (sternapodeme of Saether 1971*a*), and each usually bearing one to four basal or medial lobes; in Chironominae (Figs. 85–103), two to four lobes present, these being dorsal appendage 1, ventromedial appendage 2 anterior to appendage 1, appendage 1*a* ventral to appendage 1, and appendage 2*a* posterior to appendage 2 (Fig. 102); in other subfamilies, usually one or two lobes present on inner margin of gonocoxite [terminology for these lobes not standardized and debate about their homologies continuing (e.g. Schlee 1968; Saether 1971*a*, 1975*c*, 1977*a*; Hirvenoja 1973; Hansen and Cook 1976)]. Gonostylus hinged or fused to gonocoxite, when hinged folded dorsomedially; shape usually simple, but forked in some species, and with projections in others; strong tooth-like seta (gonostylar tooth) present apically in some groups. Paramere articulating with dorsobasal area of gonocoxite at base of gonocoxal apodeme, with parameral apodeme extending distally into gonocoxite (phallapodeme of Saether 1977*a*); medial portion of paramere forming a rod-like, sickle-shaped, or plate-like supporting sclerite in lateral wall of membranous aedeagus, detached from parameral apodeme in some Orthocladiinae. Aedeagus in some Orthocladiinae and Tanypodinae elaborated, with lobes, spines, or tufts of setae. Proctiger lying ventral to tergite 9.

Female terminalia (Figs. 111, 112) with segment 8 forming first genital segment. Tergite 8 generally unmodified, although strongly reduced in Telmatogetoninae; sternite 8 a large ventral plate bearing posteriorly several lobes and processes. Tergite 9 hood-shaped, often more or less divided into one or two pairs of lobes, and articulating with dorsal edge of sternite 9; sternite 9 somewhat Y-shaped, strongly sclerotized, with arms of fork loosely hinged to tergite 9. Segment 10 continuous around segment, not divided into tergite and sternite. A weakly developed plate, the hypoproct, usually present posterior and ventral to segment 10. Cercus free, lobe-like, closely associated with posterior and inner edges of segment 10. Two or three spermathecae present, weakly to strongly sclerotized, generally ovoid in shape; spermathecal ducts generally leading directly toward posterior, but sometimes coiling and fused near external opening. As with male terminalia, names for various parts of female terminalia not stabilized and some homologies uncertain (Wensler and Rempel 1962; Saether 1974, 1977*b*).

For further information on the morphology of the adult see Brundin (1966), Saether (1971*a*, 1977*b*), Hirvenoja (1973), and Hansen and Cook (1976).

Egg. Usually whitish or reddish but sometimes yellow or brownish, spherical to oblong, surrounded by a gelatinous matrix. Shape of egg mass either linear or compact; linear type characteristic of Orthocladiinae and Diamesinae, with eggs obliquely arranged along central axis of a ribbon-like matrix; compact type characteristic of Tanypodinae and Chironominae, with shape cylindrical, ovoid, tear-shaped, or fig-shaped, and with eggs peripheral, scattered, or coiled.

Larva. Elongate, cylindrical, usually slender with a sclerotized nonretractile head (Figs. 114–116). Respiratory system apneustic except in *Archaeochlus* Brundin, a genus from the southern hemisphere. Length 1–30 mm; color whitish, yellowish, brownish, greenish, purplish, pinkish, or very deep red.

Body composed of three thoracic segments and nine abdominal segments. Body setae usually simple and scattered, but sometimes plumose or bifid and sometimes arranged in rows along lateral margin of abdomen. First thoracic segment with pair of prolegs that are sometimes fused. Terminal abdominal segment usually with a pair of prolegs, two pairs of anal papillae but sometimes one or three pairs, and one pair of procerci with apical setae (Figs. 114, 136, 137); one or more of these structures sometimes lacking in many intertidal or terrestrial species; penultimate segment sometimes with one or two pairs of tubuli arising from ventrolateral surface.

Head (Figs. 117–122) prognathous, with one to three pairs of lateral eyespots. Head capsule chiefly composed of two lateral sclerites fused ventrally and separated dorsomedially by a narrow sclerite; surface usually smooth, occasionally rugose or patterned and with a few simple setae, sometimes with plumose setae or covered with thick vestiture.

In Tanypodinae, antenna usually four-segmented, retractile within socket on cranium. Hypostoma (mentum) a median membranous area sometimes flanked by toothed plates. Hypopharynx consisting of median ligula bearing four to seven teeth, paired paraglossae, and arched hypopharyngeal pecten. Mandible hooked or sickle-shaped, usually with one or two inner teeth, but sometimes without inner teeth, only rarely having a row of inner teeth, and without an inner brush. Lacinia bearing numerous flat hyaline sensillae. Maxillary palpus one- to six-segmented with complex arrangement of apical sensillae. Premandible (messor) rudimentary or vesicular in shape. Labrum weakly sclerotized, vesicular in shape, bearing only simple setae or sensillae.

In other subfamilies, antenna nonretractile, generally five-segmented but occasionally four-, six-, or seven-segmented, sometimes reduced so that terminal three segments difficult to discern; Lauterborn's organs usually present on apex of second antennal segment or alternating on apices of second and third segments, and frequently borne on long stalks in Tanytarsini; basal segment generally longer than combined length of remaining segments, with one to three ring organs, and bearing apically a blade and other sensory structures. Hypostoma in form of a broad ventral toothed plate, flanked in some groups by distinct paralabial plates; hypostoma greatly variable in general coloration, shape, and number and arrangement of teeth; hypostomal teeth occasionally absent; paralabial plate ranging in shape from broad and strap-like to small and ovoid to absent (sometimes adjacent plates present), striated or bearded in some groups but generally bare. Hypopharynx not clearly differentiated into parts, but broadly triangular bearing long setae or modified setae or scales. Mandible generally gently curved with inner row of teeth and setal brush; inner brush occasionally absent; a tooth dorsosubapically and a row of setae usually present in Chironominae; inner margin usually smooth but sometimes serrated. Maxilla in two lobes, palpifer and galea, both with diverse and variable setae, sensillae, or scales. Maxillary palpus generally short, but elongate in some groups. Premandible present in all except Podonominae, with one to eleven teeth, usually with less than five. Labrum with numerous modified setae, usually with four pairs of central setae flanked by groups or rows of other setae; SI (seta I) simple, forked, plumose, or palmate; anteroventrally toothed epipharyngeal pecten and U-shaped arch present; in some Chironominae epipharyngeal comb present between SI and epipharyngeal pecten.

For further information on the morphology of the larvae see Mozley (1971), Saether (1971*a*), and Hirvenoja (1973).

Pupa. Cephalothorax usually with pair of prothoracic horns; horns tubular with or without sieve plate, or filamentous; frontal tubercle bearing a seta sometimes present; leg sheaths rarely reaching tips of wing sheaths and at least hindleg sheath curved under wing sheath, but all sheaths sometimes directed straight backward reaching beyond posterior tip of wing sheaths. Chaetotaxies and spine patterns of abdominal segments very diverse. Anal segment usually composed of a pair of flattened anal lobes flanking genital sheath, but disc-like in Telmatogetoninae; anal lobe with or without lateral and apical setae, and sometimes bearing spines or produced apically (as in Figs. 138–140).

The pupae of the Chironomidae have not been extensively studied, but for additional information see Zavřel (1942), Fittkau (1962), Brundin (1966), Saether (1971*a*), and Hirvenoja (1973).

Biology and behavior. Literature published before 1950 was thoroughly reviewed by Thienemann (1954), and recently several publications with extensive bibliographies have appeared: on life history (Oliver 1971); on overwintering (Danks 1971); and on larval dispersal (Davies 1976). Useful lists of habitats and ecological requirements for the larvae of a number of Nearctic species are given by Curry (1965), Roback (1974), and Beck (1977). Only a little information, summarized by Thienemann, is available concerning the biology and behavior of terrestrial chironomids. The following summary is therefore mainly restricted to aquatic chironomids.

The immature stages of this family occur in nearly every habitat that is aquatic or wet, including the peripheral areas of the oceans. Many species also inhabit soil and other terrestrial environments that are rich in organic matter. Most of the life cycle is spent in the larval stage, sometimes up to 3 yr; the adult stage is relatively ephemeral, lasting at most several weeks.

Oviposition generally occurs on the water surface. Sometimes the egg mass is attached to emergent vegetation. In other cases where oviposition occurs while the female is at rest, the egg mass is carried by the legs and dropped into the water. It is protected by a gelatinous matrix that expands in water and is very adhesive. There is little information on the duration of the egg stage, but hatching probably occurs within several weeks, and most frequently after only a few days.

There are four larval instars. Very few species have been investigated, but some degree of hypermetamorphosis is usually exhibited, with change occurring between the first and second instars. Kalugina (1959) noted that the first instars of related groups are more alike morphologically than are the later instars. Apparently, first-instar larvae of lentic species are photopositive (Lellák 1968) and search for a suitable habitat for future development.

Except for the larvae of the Tanypodinae, the Podonominae, and a few carnivorous species in other groups that are free living, most chironomid larvae construct cases composed of fine particles of substrate cemented together with salivary secretion. Generally, the cases are tube-like or loosely constructed, but some genera (*Abiskomyia* Edwards and *Heterotanytarsus* Spärck) build cases similar to those of Trichoptera larvae. Some rheophilic species adhere to surfaces by fastening the claws of their posterior prolegs to globs of salivary secretion placed onto the substrate; other species are encased in a gelatinous envelope that adheres readily to surfaces.

The broad environmental requirements of the larvae of the various subfamilies are fairly well known and are outlined in the section on Classification and Distribution. Certain groups or species are characteristic of a lotic or lentic environment, deep or shallow water, oxygen-poor or oxygen-rich water, or cold or warm water. The composition of chironomid communities has been frequently used as an indicator of various trophic levels (Brundin 1949, Saether 1975*b*) and is increasingly being used to indicate the level of pollution.

Chironomid larvae are generally microphagous, feeding on detritus and on small plants and animals; Tanypodinae and some chironomine and orthoclad species are carnivorous. Most species probably ingest food directly from or with substrate, but a few filter feeders use salivary threads to capture drifting food particles.

Pupae of the Tanypodinae and some Podonominae are free-living active swimmers, but most of the pupae of the rest of the family are sedentary, protected by a case. Adult eclosion occurs at the water surface. The adult emerges fully formed, except for crinkled wings, through a dorsal slit in the cephalothorax of the pupal exuvia. Eclosion occurs very rapidly, usually in less than 30 s, and at most in several minutes. The pupal exuvium is used as a platform by the adult as the wings are expanded and stiffened.

In warm habitats emergence can occur throughout the season. At higher latitudes or their climatic equivalents, the emergence period becomes shorter. Each species has a more or less restricted period of emergence; many species are multivoltine in warm habitats, whereas emergence in cool habitats tends to be univoltine and highly synchronized. Lunar emergence rhythms have been demonstrated in several marine species (Neumann 1966). Many species exhibit a diel periodicity of emergence; the peak generally occurs around sunset but it may occur during other parts of the diel.

After eclosion and wing expansion the adult flies to shore. The direction of flight is frequently determined by wind direction. A period of rest often occurs before mating. One of the most commonly noted features of the adult chironomid is its ability to form swarms. Swarming generally occurs around sunset but can occur during other parts of the diel. The swarm is usually composed only of males and is positioned relative to a marker, which is probably the main factor in determining the composition of the swarm (Downes 1969). Females are attracted to the swarm and copulation ensues. Mating is frequently completed in a few seconds, but in some Orthocladiinae the mated pair drifts to the ground and sometimes remains *in copula* up to several hours. Mating on the ground without swarming occurs in several species. In these species the structure of the male is frequently modified, i.e. reduced antenna, enlarged terminalia, and reduced wings.

It is frequently repeated in the literature that chironomid adults do not feed except for several terrestrial species that imbibe nectar (Oliver 1971). However, Downes (1974) reported a number of species feeding on honeydew, and this food habit may be more common than is now known.

Classification and distribution. There has been considerable confusion in the classification of the Chironomidae at the familial and subfamilial levels. However, several rulings by the International Commission on Zoological Nomenclature have established the status of several key names. The name *Tendipes* Meigen 1800 has been suppressed in favor of *Chironomus* Meigen 1803, and *Pelopia* Meigen in favor of *Tanypus* Meigen (see Fittkau 1966). This action established Chironomidae, not Tendipedidae, as the correct name for the family. *Tanytarsus* Wulp has been used for a genus name in the tribe Chironomini, but another ruling by the International Commission on Zoological Nomenclature (Bull. zool. Nom. 18, Opinion 616) established it instead as a genus name in the tribe Tanytarsini. Although not covered by a ruling, Orthocladiinae is generally accepted in place of Hydrobaeninae.

In this work six subfamilies are recognized: Tanypodinae, Podonominae, Telmatogetoninae, Diamesinae, Orthocladiinae, and Chironominae. A seventh small subfamily from the southern hemisphere, the Aphroteniinae, is not included in the keys in this book. This subfamilial classification follows that of Brundin (1966).

In developing a classification of a family of holometabolous insects, the characteristics of all life stages should be considered. However, in the Chironomidae, the ecological requirements of each stage has often resulted in greater diversity, both ecologically and morphologically, in one stage than in another. The imagines of the Chironomidae are generally more uniform in structure than are the larvae (Fittkau 1962). In certain groups adults appear to have close taxonomic affinities whereas the larvae may be quite diverse. The opposite also occurs. This ecological and morphological diversity among the life stages is reflected in the two systems of classification that have evolved: the larval–pupal system of Thienemann and his colleagues and the imago system of Edwards and Goetghebuer (Brundin 1956). Fortunately, many of the recent studies (e.g. Brundin 1956, 1966; Fittkau 1962; Hirvenoja 1973; Saether 1969, 1975*a*) are based on all stages although Roback (1971) based his revision of the Nearctic Tanypodinae mainly on imaginal characteristics.

The distribution of the Chironomidae is world wide. The two species found in Antarctica are the southernmost free-living holometabolous insects (Wirth and Gressitt 1967), and in the northern hemisphere chironomids extend to the northern limits of land. The distribution of each of the subfamilies within their geographical range is governed mainly by the availability of water ecologically suited to the requirements of the larvae. The Aphroteniinae, the smallest subfamily, is rheophilic and restricted in distribution to the southern hemisphere. The Podonominae, which is mainly cold adapted and rheophilic, is much more common in the southern than in the northern hemisphere. The Diamesinae, also mainly cold adapted and rheophilic, inhabits the cooler parts of circumpolar land and mountain ranges throughout the world. Most species of chironomids belong to one of the three subfamilies Tanypodinae, Chironominae, or Orthocladiinae. The Tanypodinae and Chironominae are mainly thermophilous and adapted to living in lotic environments; however, both groups occur in cold and running water. They are very abundant in the warmer parts of the Nearctic and decrease in relative numbers of species with increasing latitude or its climatic equivalent. By contrast the Orthocladiinae is the dominant subfamily in the Arctic (Oliver 1968) and decreases proportionally in number of species in warmer areas. The larvae of this cool-adapted subfamily live in all types of lentic and lotic environments. It is the only subfamily with terrestrial species, and along with the Telmatogetoninae and a few species of Chironominae it occurs in intertidal regions.

Fossils of adults of *Protendipes* and pupae of *Eopodonomus* and *Pachyneuronympha*, recorded by Rohdendorf (1964) from middle Jurassic deposits in Kazakhstan, are chironomid-like in form (Wootton 1972). Hennig (Brundin 1972) suggests that *Protobibio jurassicus* Rohdendorf belongs to the Podonominae or a related branch of the family. The earliest known fossils that can definitely be assigned to the Chironomidae are in amber of lower Cretaceous age from Lebanon (Schlee and Dietrich 1970) and belong to the subfamily Podonominae (Brundin 1972). Upper Cretaceous Canadian amber contains a rich fauna (Boesel 1937, McAlpine and Martin 1969), including terrestrial genera such as *Smittia* Holmgren.

In the keys that follow the number of named species known to occur in the Nearctic is the number usually given for each genus. Unnamed species are known in most genera, and occasionally an estimate of the total number of species is given. The distribution given for each genus includes the distribution of all species known to me, not just that of the named species.

Unless stated otherwise the most useful reference for the Tanypodinae is Roback (1971) and for the Chironomini it is Townes (1945).

Key to genera

Adult

1. Wing absent or strongly reduced, not extending posterior to first abdominal segment .... ORTHOCLADIINAE, in part....89

   Wing present, extending posterior to first abdominal segment 2

2. Crossvein m-cu present (Figs. 2–9) 3

   Crossvein m-cu absent (Figs. 10–19) 5

3. R_{2+3} absent, and R_1 and R_{4+5} widely separated (Figs. 6, 7). Postnotum smooth and lacking median fissure .... PODONOMINAE....8

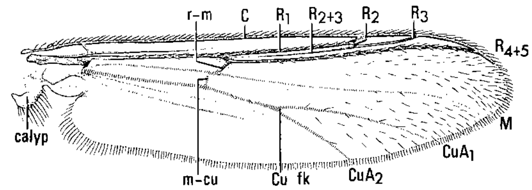
   R_{2+3} present or absent; if absent, then space between R_1 and R_{4+5} very narrow, at most scarcely wider than thickness of one vein. Postnotum rarely lacking longitudinal median fissure (Figs. 26–29) 4

4. R_{2+3} usually forked (Figs. 2–4); if R_{2+3} simple or absent, then R_1 and R_{4+5} closely approximated and wing always densely covered with macrotrichia (Fig. 5) .... TANYPODINAE....11

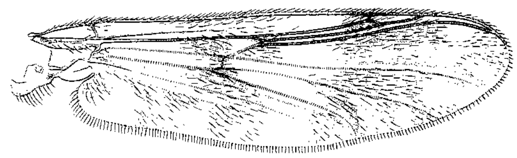
   R_{2+3} present and simple (Figs. 8, 9); wing usually bare, at most with only a few macrotrichia on distal third .... DIAMESINAE....38

5. First tarsomere of foreleg longer than fore tibia (Fig. 52), rarely equal to or slightly shorter;[1] hind tibia with two combs composed of basally fused spines (Figs. 67–71). Gonostylus fused to gonocoxite and directed backward (Figs. 85–103), rarely folded inward[1] .... CHIRONOMINAE....48

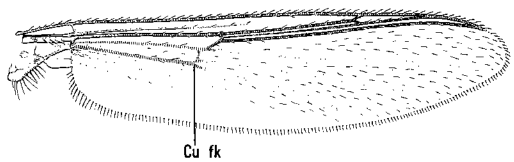
[1] One genus of Chironominae, *Stictochironomus* Kieffer, has hinged gonostyli and in some species the first tarsomere of the foreleg is shorter than the fore tibia; however, the tibial comb of the hindleg is composed of basally fused spines. Also, some species of *Phaenopsectra* Kieffer have the first tarsomere of the foreleg shorter than the fore tibia.



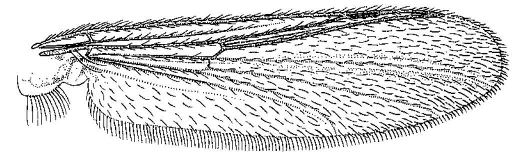
2 Procladius freemani ♂



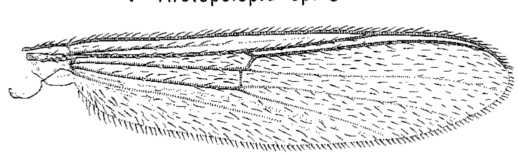
3 Psectrotanypus dyari ♂



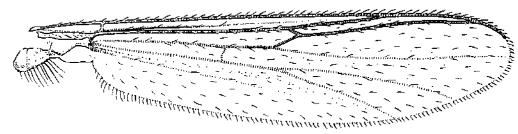
4 Arctopelopia sp. ♂



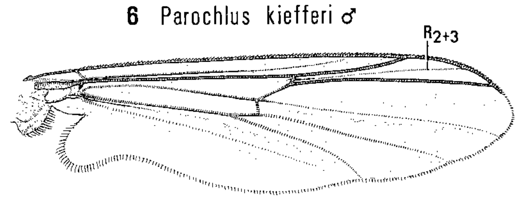
5 Monopelopia boliekae ♂



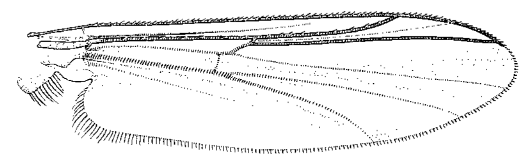
6 Parochlus kiefferi ♂



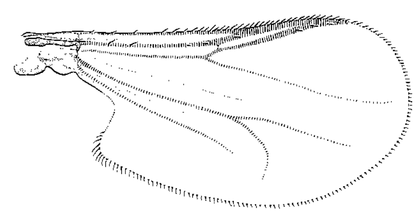
7 Trichotanypus posticalis ♂



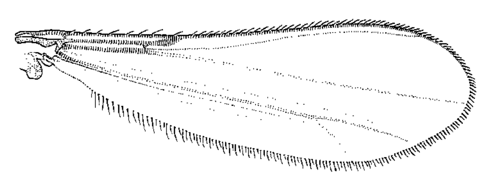
8 Pseudodiamesa arctica ♂



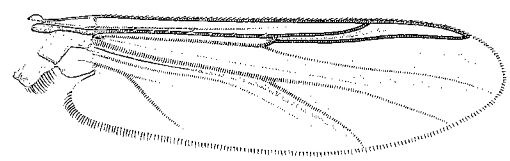
9 Prodiamesa olivacea ♂



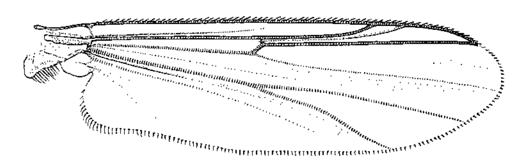
10 Clunio sp. ♂



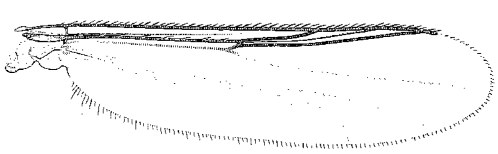
11 Corynoneura sp. ♂



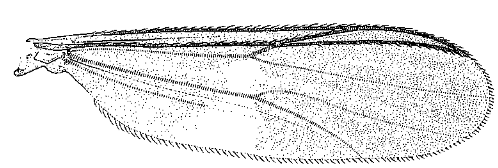
12 Cardiocladius obscurus ♂



13 Orthocladius decoratus ♂

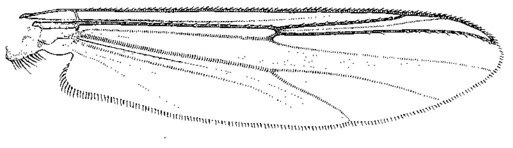


14 Smittia sp. ♂

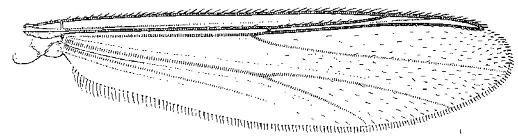


15 Chasmatonotus unimaculatus ♂

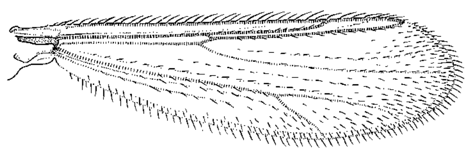
Figs. 29.2–15. Wings of male: (2) *Procladius freemani* Sublette; (3) *Psectrotanypus dyari* (Coquillett); (4) *Arctopelopia* sp.; (5) *Monopelopia boliekae* Beck & Beck; (6) *Parochlus kiefferi* (Garrett); (7) *Trichotanypus posticalis* (Lundbeck); (8) *Pseudodiamesa arctica* (Malloch); (9) *Prodiamesa olivacea* (Meigen); (10) *Clunio* sp.; (11) *Corynoneura* sp.; (12) *Cardiocladius obscurus* (Johannsen); (13) *Orthocladius decoratus* (Holmgren); (14) *Smittia* sp.; (15) *Chasmatonotus unimaculatus* Loew.
Abbreviations: calyp, calypter; Cu fk, cubital fork.



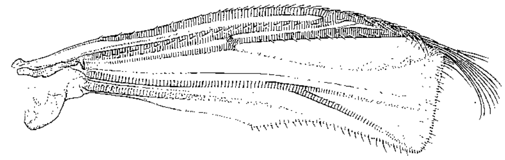
16 Chironomus riparius ♂



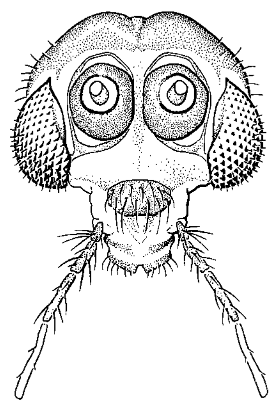
17 Micropsectra sp. ♂



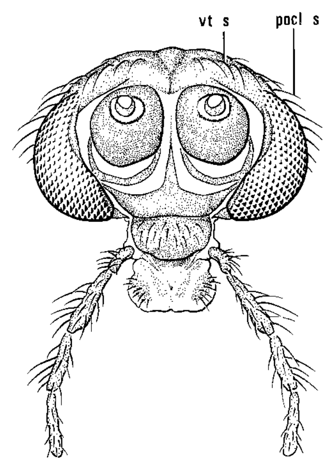
18 Stempellina sp. ♂



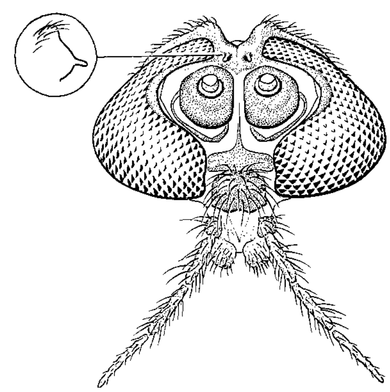
19 Corynocera sp. ♂



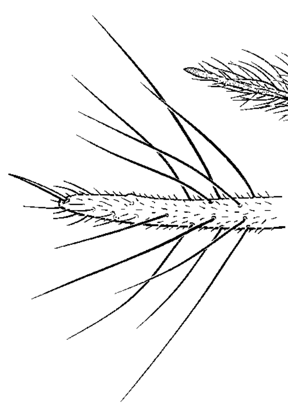
20 Nanocladius sp. ♂



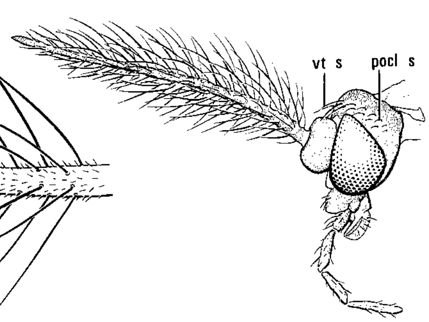
21 Orthocladius consobrinus ♂



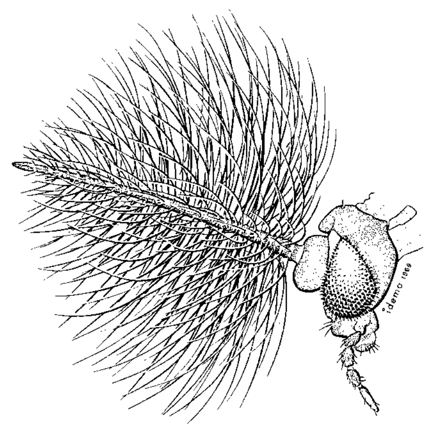
22 Glyptotendipes barbipes ♂



23 Smittia sp. ♂



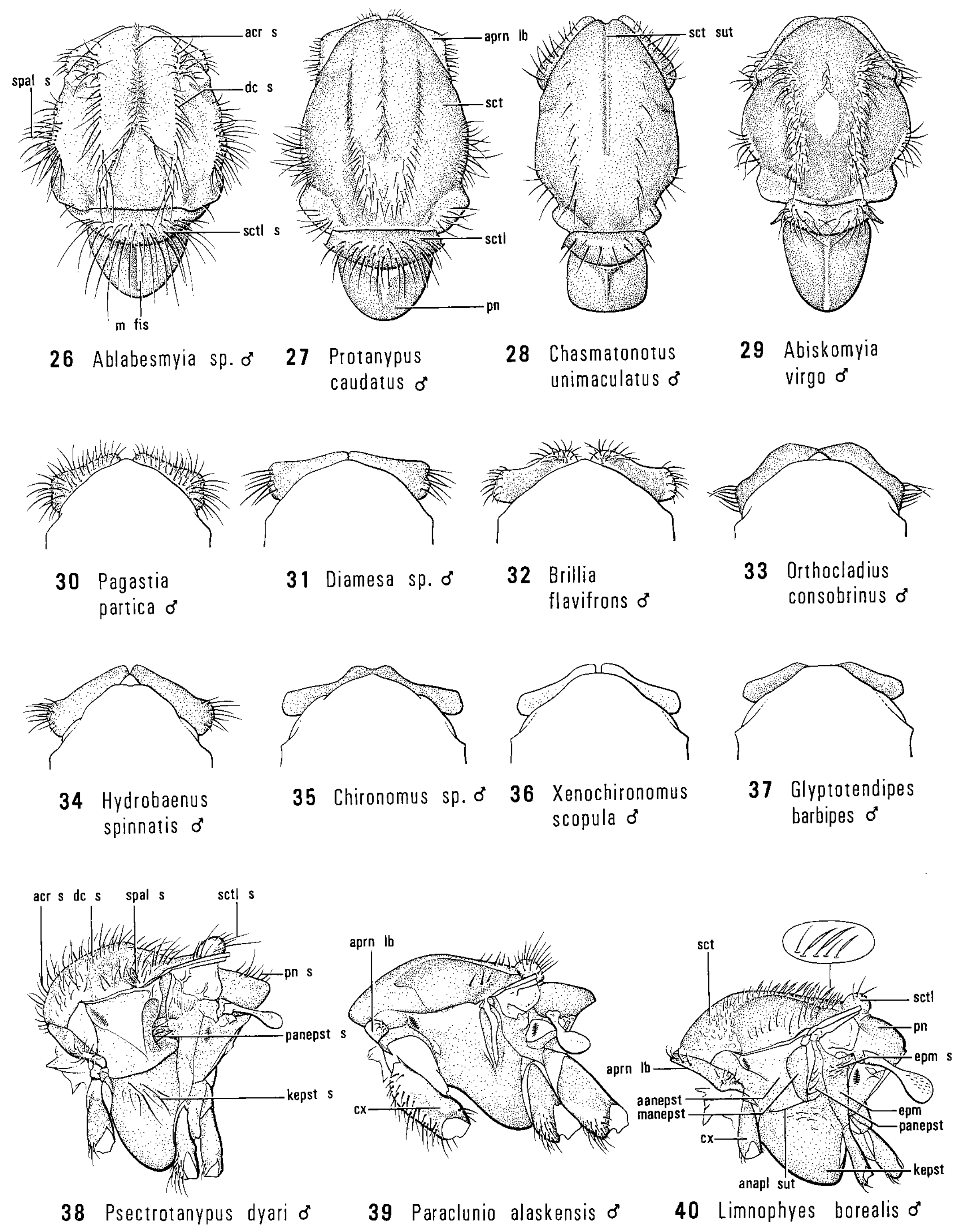
24 Chaetocladius sp. ♂



25 Acricotopus nitidellus ♂

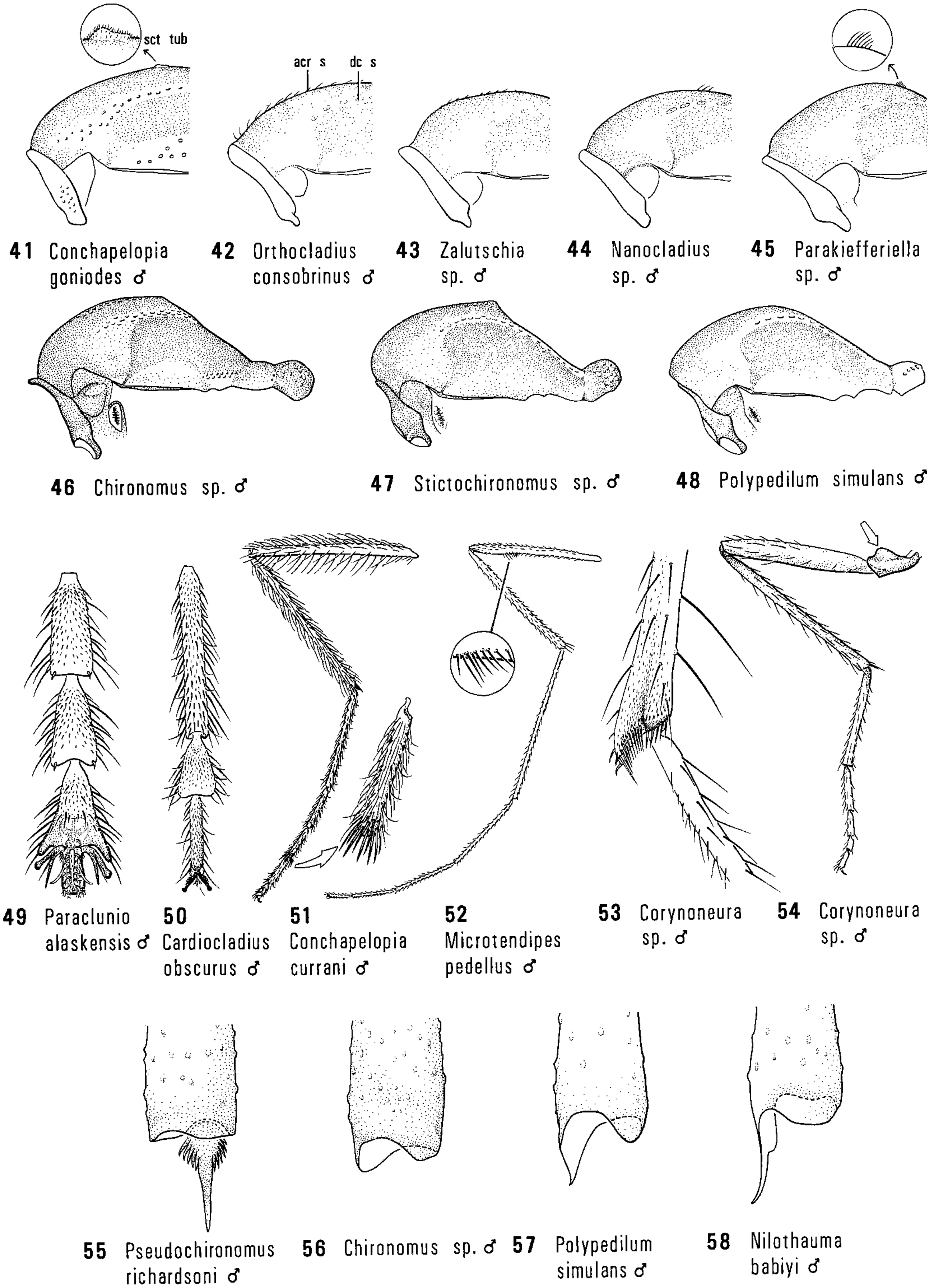
Figs. 29.16–25. Wings and details of head of male: wing of (16) *Chironomus riparius* Meigen, (17) *Micropsectra* sp., (18) *Stempellina* sp., and (19) *Corynocera* sp.; anterior view of head, with flagellum removed, of (20) *Nanocladius* sp., (21) *Orthocladius consobrinus* (Holmgren), and (22) *Glyptotendipes barbipes* (Staeger); (23) apex of flagellum of *Smittia* sp.; lateral view of left side of head of (24) *Chaetocladius* sp. and (25) *Acricotopus nitidellus* (Malloch).

Abbreviations: pocl s, postocular seta; vt s, vertical seta.



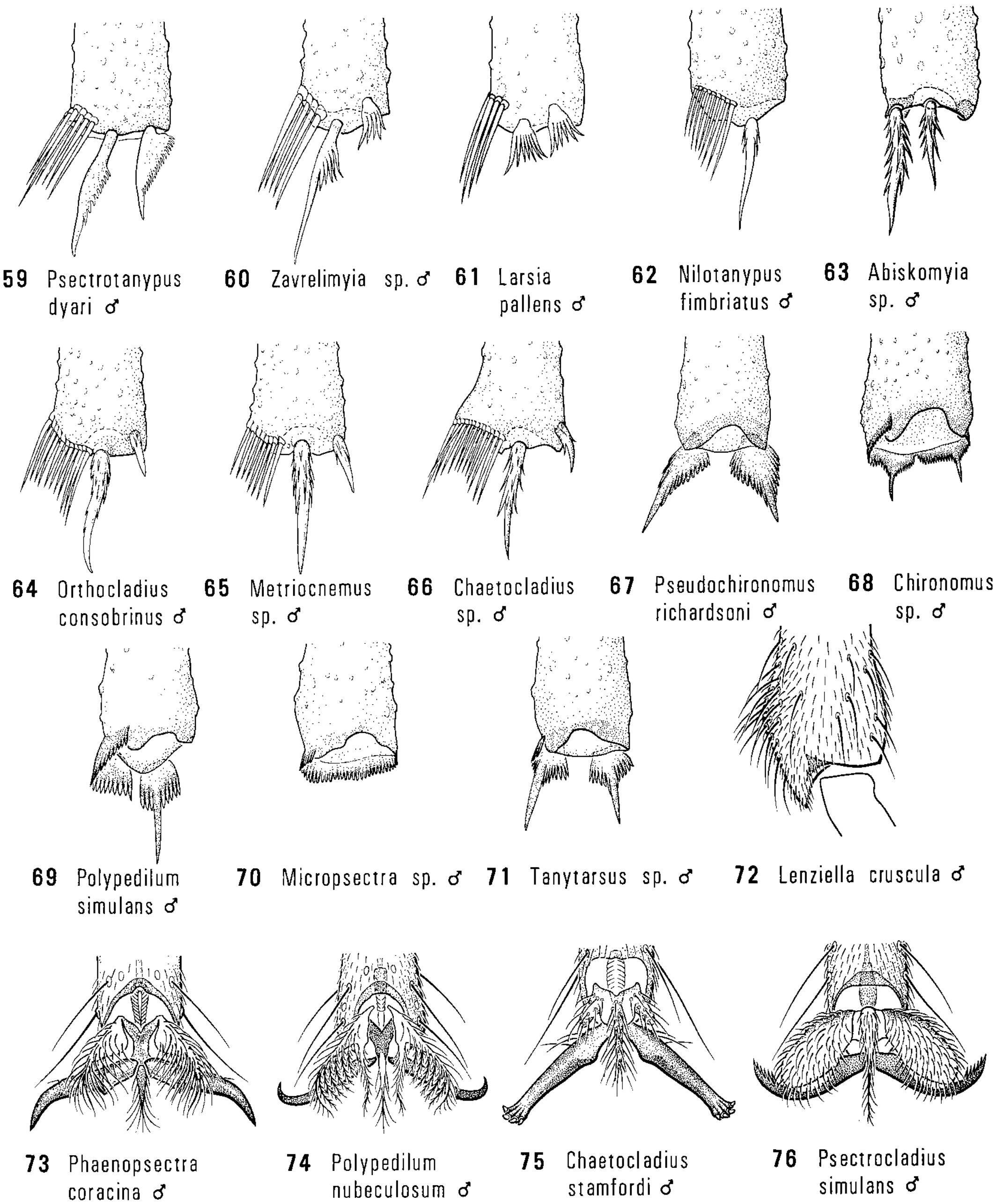
Figs. 29.26–40. Thoraces of male: dorsal view of thorax of (26) *Ablabesmyia* sp., (27) *Protanypus caudatus* Edwards, (28) *Chasmatonotus unimaculatus* Loew, and (29) *Abiskomyia virgo* Edwards; dorsal view of pronotum and anterior part of scutum of (30) *Pagastia partica* (Roback), (31) *Diamesa* sp., (32) *Brillia flavifrons* (Johannsen), (33) *Orthocladius consobrinus* (Holmgren), (34) *Hydrobaenus spinnatis* Saether, (35) *Chironomus* sp., (36) *Xenochironomus scopula* Townes, and (37) *Glyptotendipes barbipes* (Staeger); lateral view of left side of thorax of (38) *Psectrotanypus dyari* (Coquillett), (39) *Paraclunio alaskensis* (Coquillett), and (40) *Limnophyes borealis* Goetghebuer (*continued*).

Abbreviations: aanepst, anteanepisternum; acr s, acrostichal seta; anapl sut, anapleural suture; aprn lb, antepronotal lobe; cx, coxa; dc s, dorsocentral seta; epm, epimeron; epm s, epimeral setae; kepst, katepisternum; kepst s, katepisternal seta; manepst, medioanepisternum; m fis, median fissure; panepst, postanepisternum; panepst s, postanepisternal seta; pn, postnotum; pn s, postnotal seta; sct, scutum; sctl, scutellum; sctl s, scutellar seta; sct sut, scutal suture; spal s, supra-alar seta.



Figs. 29.41–58. Thoraces (*concluded*) and details of legs of male: lateral view of left side of pronotum and anterior part of scutum of (41) *Conchapelopia goniodes* (Sublette), (42) *Orthocladius consobrinus* (Holmgren), (43) *Zalutschia* sp., (44) *Nanocladius* sp., and (45) *Parakiefferiella* sp.; lateral view of left side of pronotum, scutum, and scutellum of (46) *Chironomus* sp., (47) *Stictochironomus* sp., and (48) *Polypedilum simulans* Townes; ventral view of terminal three tarsomeres of left hindleg of (49) *Paraclunio alaskensis* (Coquillett) and (50) *Cardiocladius obscurus* (Johannsen); (51) lateral view of right midleg of *Conchapelopia currani* (Walley); (52) lateral view of right foreleg of *Microtendipes pedellus* (De Geer); (53) lateral view of apex of tibia of left hindleg of *Corynoneura* sp.; (54) lateral view of right foreleg of *Corynoneura* sp.; dorsal view of apex of tibia of left foreleg of (55) *Pseudochironomus richardsoni* Malloch, (56) *Chironomus* sp., (57) *Polypedilum simulans* Townes, and (58) *Nilothauma babiyi* (Rempel) (*continued*).

Abbreviations: acr s, acrostichal seta; dc s, dorsocentral seta; sct tub, scutal tubercle.



Figs. 29.59–76. Details of legs of male (*concluded*): ventral view of apex of tibia of left hindleg of (59) *Psectrotanypus dyari* (Coquillett), (60) *Zavrelimyia* sp., (61) *Larsia pallens* (Coquillett), (62) *Nilotanypus fimbriatus* (Walker), (63) *Abiskomyia* sp., (64) *Orthocladius consobrinus* (Holmgren), (65) *Metriocnemus* sp., and (66) *Chaetocladius* sp.; dorsal view of apex of tibia of right hindleg of (67) *Pseudochironomus richardsoni* Malloch, (68) *Chironomus* sp., (69) *Polypedilum simulans* Townes, (70) *Micropsectra* sp., and (71) *Tanytarsus* sp.; (72) lateral view of apex of tibia of right hindleg of *Lenziella cruscula* Saether; ventral view of acropod of right hindleg of (73) *Phaenopsectra coracina* (Zetterstedt), (74) *Polypedilum nubeculosum* (Meigen), and (75) *Chaetocladius stamfordi* (Johannsen); (76) ventral view of acropod of left hindleg of *Psectrocladius simulans* (Johannsen).

First tarsomere of foreleg shorter than fore tibia; hind tibia usually with one or two spurs and a comb composed of basally separate spines (Figs. 64–67); comb or spurs rarely absent. Gonostylus hinged to gonocoxite and folded inward (Figs. 104–110) 6

6. Antepronotal lobes in contact medially or narrowly separated (Figs. 32–34, 40). Fore coxa rarely enlarged; hind tibial comb usually present. Anapleural suture distinct (Fig. 40) ....ORTHOCLADIINAE, in part....90

Antepronotal lobes widely separated (Fig. 39). Fore coxa enlarged (Fig. 39); hind tibial comb usually absent. Anapleural suture often indistinct or lacking (Fig. 39) 7

7. Second tarsomere of hindleg longer than third tarsomere; all legs with fourth tarsomere cordiform (Fig. 49) and with fifth tarsomere simple or trilobate (Fig. 49). Eye bare ....TELMATOGETONINAE....148

Second tarsomere of hindleg shorter than or equal to length of third tarsomere; all legs with fourth tarsomere cylindrical and with fifth tarsomere simple and never trilobate. Eye usually hairy ....ORTHOCLADIINAE, in part....90

PODONOMINAE

8. Gonostylus bifurcate (Fig. 82) ....PODONOMINI....***Parochlus*** Enderlein
   1 sp., *kiefferi* (Garrett); Alaska south to California and New Mexico, Minnesota, Oklahoma, Arkansas, Greenland, Ontario to New Brunswick south to New York; Wirth and Sublette 1970

   Gonostylus simple, sometimes lobate (Fig. 84) ....BOREOCHLINI....9

9. Crossvein m-cu opposite or slightly proximal to crossvein r-m (as in Fig. 6). Anal point bearing lamelliform setae (Fig. 83) ....***Lasiodiamesa*** Kieffer
   4 spp.; Alaska and British Columbia to Northwest Territories and Saskatchewan, Minnesota to New Brunswick and New York, Wyoming; Wirth and Sublette 1970

   Crossvein m-cu far proximal to crossvein r-m (Fig. 7). Anal point absent; tergite 9, at most, triangularly produced (Fig. 84) 10

10. Pulvilli well-developed. Eye hairy ....***Trichotanypus*** Kieffer
   5 spp.; Alaska to Greenland, Wyoming; Wirth and Sublette 1970

   Pulvilli absent. Eye bare ....***Boreochlus*** Edwards
   3 spp.; Alaska south to Wyoming and California, New Brunswick to Virginia; Wirth and Sublette 1970

TANYPODINAE

11. Fourth tarsomere cordiform (as in Fig. 50), shorter than fifth tarsomere. Wing membrane without macrotrichia ....COELOTANYPODINI....12

   Fourth tarsomere cylindrical or laterally flattened, never cordiform, as long as or longer than fifth tarsomere. Wing membrane usually with macrotrichia 13

12. Stem of cubital fork one-quarter or more longer than length of CuA_2. Scutal tubercle absent; postnotal setae present ....***Clinotanypus*** Kieffer
   5 spp.; Quebec and Ontario south to eastern half of U.S.A.

   Stem of cubital fork one-sixth or less longer than length of CuA_2, or absent. Small scutal tubercle present (as in Fig. 41); postnotal setae absent ....***Coelotanypus*** Kieffer
   6 spp.; Quebec and Ontario south to eastern half of U.S.A., British Columbia

13. Cubital fork distal to crossvein m-cu (Fig. 2) 14

   Cubital fork proximal to or opposite crossvein m-cu (Figs. 3–5)...15

14. Stem of cubital fork one-third or less longer than length of CuA_2. Scutal tubercle present. Gonostylus elongate, tapering to apex; heel nearly always absent ....TANYPODINI....***Tanypus*** Meigen
   11 spp.; widespread in United States extending into southern areas of Canada, Northwest Territories

   Stem of cubital fork one-half or more longer than length of CuA_2 (Fig. 2). Scutal tubercle absent. Gonostylus shorter, usually subtriangular with heel (Fig. 77) ....MACROPELOPIINI, in part....***Procladius*** Skuse[2]
   42 spp.; widespread

[2] Roback and Moss (1978) placed *Procladius* in the tribe Procladiini.

15. C distinctly produced past R_{4+5}, usually by at least length of crossvein r-m (Fig. 3). Postanepisternal setae present (Fig. 38); usually a few katepisternal and postnotal setae present (Fig. 38). Tibial spurs of hindleg usually flattened (Fig. 59) ...... MACROPELOPIINI, in part 16

C not produced or produced by less than length of crossvein r-m (Fig. 4). Postanepisternal and katepisternal setae usually absent; postnotal setae always absent. Tibial spurs of hindleg cylindrical to comb-like (Figs. 60–62) .... PENTANEURINI 21

16. Scutal tubercle present (as in Fig. 41) 17

Scutal tubercle absent 18

17. Tergite 9 of male without dorsal setae. Vertical setae uniserial .... ***Parapelopia*** Roback

1 sp., *serta* Roback; Florida

Tergite 9 of male with a few scattered dorsal setae. Vertical setae multiserial .... ***Macropelopia*** Thienemann

1 sp., *decedens* (Walker); Ontario to New Brunswick, south to Massachusetts

18. Postnotal setae absent 19

Postnotal setae present (Fig. 38) 20

19. Foreleg and hindleg each with a tibial comb .... ***Alotanypus*** Roback

2 spp.; western United States, North Carolina, New Hampshire

Foreleg without, and hindleg without or with, a reduced tibial comb .... ***Derotanypus*** Roback[3]

2 spp.; western Canada, Ontario, Alaska, southwestern U.S.A.

20. Vertical setae uniserial. Wing with only fork of Cu and crossvein r-m darkened, or completely unmarked .... ***Natarsia*** Fittkau[3]

2 spp.; eastern U.S.A., Newfoundland, southeastern Canada, California, Northwest Territories

Vertical setae multiserial; part of row occasionally uniserial. Wing with bands or maculation (Fig. 3), rarely unmarked .... ***Psectrotanypus*** Kieffer

7 spp.; widespread in U.S.A. and extending north into southern tier of Canada, Alaska, Greenland

21. Tibiae each with three or more distinct dark rings. Rows of acrostichal bristles divergent around prescutellar area (Fig. 26). Gonostylar tooth subapical, spoon-shaped (Fig. 78); dorsomedial lobe elaborated into several chitinized rods and setiferous lobes (Fig. 78) .... ***Ablabesmyia*** Johannsen

18 spp.; widespread south of treeline

Tibiae uniform in color, or rings present only on ends of tibiae, not on shaft. Rows of acrostichal bristles ending in or before prescutellar area, and if divergent then only around anterior part of prescutellar area. Gonostylar tooth apical, peg-like (Figs. 79–81); dorsomedial lobe membranous, or only setiferous lobes present (Figs. 79, 80) 22

22. Dorsomedial setiferous lobes present on gonocoxite (Figs. 79, 80) 23

Dorsomedial setiferous lobes absent on gonocoxite (Fig. 81) 28

23. Scutal tubercle present (Fig. 41) 24

Scutal tubercle absent 26

24. Apex of third tarsomere of midleg with setal tuft (Fig. 51) .... ***Conchapelopia*** Fittkau

11 spp.; widespread

Apex of third tarsomere of midleg without setal tuft 25

25. Gonocoxite with dorsal knob-like projection bearing apical setae .... ***Telopelopia*** Roback

1 sp., *okoboji* (Walley); Iowa, Minnesota

Gonocoxite without dorsal knob-like projection bearing apical setae .... ***Thienemannimyia*** Fittkau, in part

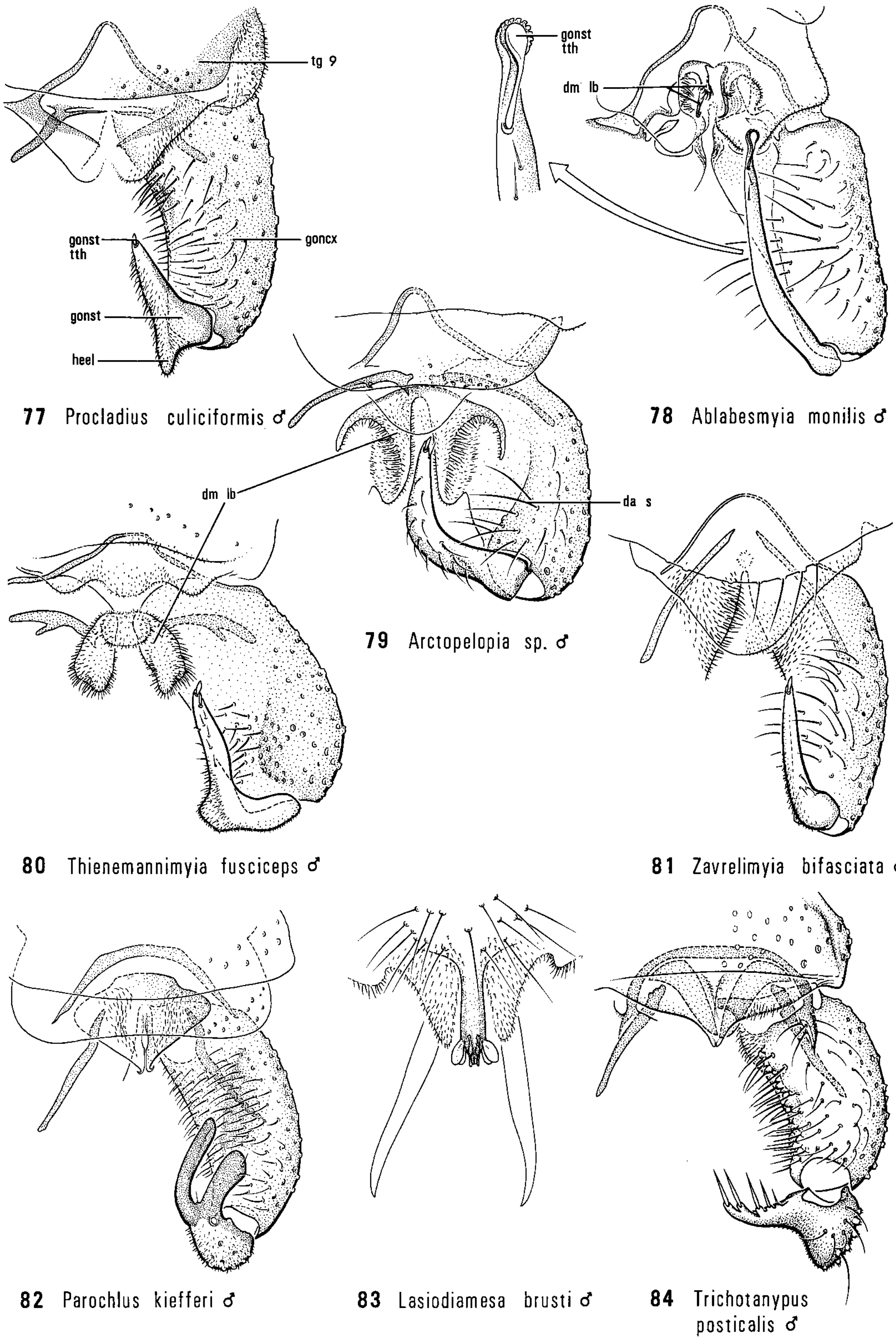
7 spp.; Alaska to New Brunswick south to California, Kansas, and Virginia

26. Tergite 8 of male broadened around base of terminalia and covering tergite 9; tergite 9 bare .... ***Xenopelopia*** Fittkau

1 sp., *tincta* Roback; California

Tergite 8 of male not broadened around base of terminalia nor covering tergite 9; tergite 9 with dorsal setae 27

[3] Roback and Moss (1978) placed *Natarsia* in the tribe Natarsiini and placed *Derotanypus* as a subgenus of *Psectrotanypus*.



Figs. 29.77–84. Terminalia of male: (77) *Procladius culiciformis* (Linnaeus); (78) *Ablabesmyia monilis* (Linnaeus); (79) *Arctopelopia* sp.; (80) *Thienemannimyia fusciceps* (Edwards); (81) *Zavrelimyia bifasciata* (Coquillett); (82) *Parochlus kiefferi* (Garrett); (83) anal point of *Lasiodiamesa brusti* Saether; (84) *Trichotanypus posticalis* (Lundbeck) (*continued*).

Abbreviations: da s, dorsoapical seta; dm lb, dorsomedial lobe; goncx, gonocoxite; gonst, gonostylus; gonst tth, gonostylar tooth; tg, tergite.

27. Gonocoxite with less than 15 dorsoapical setae (Fig. 79). Wing unmarked. Third tarsomere of midleg without setal tuft .... ***Arctopelopia*** Fittkau
4 spp.; Alaska to Greenland, Washington, Alberta, South Dakota, Indiana, Ontario to New Brunswick south to Florida

Gonocoxite with more than 20 dorsoapical setae (Fig. 80). Wing with bands or spots. Third tarsomere of midleg with or without setal tuft .... ***Thienemannimyia*** Fittkau, in part
see couplet 25

28. Gonostylus broad, not tapering to apex .... ***Cantopelopia*** Roback
1 sp., *gesta* Roback; Illinois, New York, Quebec

Gonostylus narrower, tapering to apex (Fig. 81) 29

29. Eye haired .... ***Nilotanypus*** Kieffer
2 spp.; Northwest Territories and Alberta to Newfoundland south to New York, California, Arizona, Florida

Eye bare 30

30. Wing intensively patterned with light spots on grayish background. Femoral apex as well as tibial base and apex with brown rings; apex of male claw spatulate .... ***Guttipelopia*** Fittkau
2 spp.; Northwest Territories, Manitoba to Ontario south to South Dakota, Kansas, and Florida

Wing usually unmarked, but if patterned, having spots or bands on light background. Femur and tibia not ringed; apex of male claw pointed 31

31. Hind and mid tibiae each with two spurs (Figs. 60, 61). C ending distal to level of apex of CuA_1 32

Hind tibia with one spur (Fig. 62) or no spurs; mid tibia with one spur. C ending proximal to or above level of CuA_1 (Fig. 5) 37

32. All tibial spurs comb-like (Fig. 61); tibial comb of hindleg absent or indistinct 33

At least one spur of mid or hind tibia elongate (Fig. 60); tibial comb of hindleg present, occasionally indistinct 35

33. Scutal tubercle present. R_2 absent; R_3 present, fading out toward apex .... ***Larsia*** Fittkau
6 spp.; widespread

Scutal tubercle absent. R_2 present; R_3 present, sometimes fading out toward apex 34

34. Pulvilli present. C ending near level of apex of M .... ***Trissopelopia*** Kieffer
1 sp., *ogemawi* Roback; Northwest Territories and Washington to Newfoundland and New Jersey

Pulvilli absent. C ending far proximal to level of apex of M, only shortly distal to level of apex of CuA_1 .... ***Pentaneura*** Philippi
2 spp.; Washington and California to Florida, Ontario

35. Spur of fore tibia comb-like; one spur of mid and hind tibiae elongate, other comb-like (Fig. 60). Wing generally banded .... ***Zavrelimyia*** Fittkau
3 spp.; widespread

All tibial spurs elongate. Wing usually unmarked 36

36. C produced past apex of R_{4+5}. Tergite 9 of male with few dorsal setae .... ***Krenopelopia*** Fittkau
1 sp., *narda* Roback; Alaska

C not produced past apex of R_{4+5}. Tergite 9 of male usually bare .... ***Paramerina*** Fittkau
5 spp.; Northwest Territories, British Columbia to Ontario south to California, South Dakota, and Virginia

37. Hind tibia with one narrow elongate spur (as in Fig. 60). Distal margin of tergite 9 of male straight to weakly concave, with only a few setae .... ***Monopelopia*** Fittkau
2 spp.; British Columbia, Alberta, Ontario, Newfoundland, Florida

Hind tibia without spurs. Distal margin of tergite 9 of male strongly convex, with transverse row of setae .... ***Labrundinia*** Fittkau
6 spp.; Alaska to Quebec south to New Mexico and Florida

DIAMESINAE

38. Cubital fork proximal to (Fig. 8) or opposite crossvein m-cu 39

Cubital fork distal to crossvein m-cu (Fig. 9) 46

39. Rows of dorsocentral setae convergent in prescutellar area (Fig. 27); anepisternal and katepisternal setae present .... ***Protanypus*** Kieffer
3 spp.; Yukon, Northwest Territories, British Columbia, Manitoba to Quebec; Saether 1975*c*

Rows of dorsocentral setae not convergent (as in Figs. 28, 29), sometimes diverging slightly posteriorly; anepisternal setae absent; rarely a few short katepisternal setae present 40

40. Scutum with numerous fine setae besides acrostichal, dorsocentral, and supra-alar setae; dorsolateral surface sometimes rugose .... ***Boreoheptagyia*** Brundin
1 sp., *lurida* (Garrett); British Columbia, Alaska, Wyoming, New York; Brundin 1966

Scutum without fine setae; dorsolateral surface never rugose 41

41. Eye produced dorsally (as in Fig. 22). Antepronotal lobes separated medially by a wide notch (Fig. 30). Fourth tarsomere cylindrical 42

Eye not produced dorsally (as in Fig. 21) or only slightly produced. Antepronotal lobes fused medially (Fig. 31) or very narrowly separated. Fourth tarsomere variable, frequently cordiform 44

42. Antepronotum with ventrolateral setae only .... ***Pseudodiamesa*** Goetghebuer
3 spp.; Northwest Territories, Alaska, Greenland, British Columbia, Alberta, Wyoming, Utah; Oliver 1959

Antepronotum with dorsomedial and ventrolateral setae, or entirely covered with setae (Fig. 30) 43

43. Eye bare .... ***Pagastia*** Oliver
2 spp.; Alaska, Yukon, Alberta, Ontario to Newfoundland south to Utah and Illinois; Oliver 1959

Eye hairy .... ***Hesperodiamesa*** Sublette
1 sp., *sequax* (Garrett); British Columbia; Sublette 1967*a*

44. Vertical setae present. R_{4+5} with setae. Fourth tarsomere usually cordiform .... ***Diamesa*** Meigen
30 spp.; widespread in Alaska, Canada, and Greenland south to California, Nebraska, and Virginia; Hansen and Cook 1976

Vertical setae absent. R_{4+5} without setae. Fourth tarsomere variable 45

45. Fourth tarsomere somewhat cordiform, shorter than fifth tarsomere. Dorsocentral setae uniserial .... ***Potthastia*** Kieffer
2 spp.; Yukon, Northwest Territories, Ontario to Newfoundland

Fourth tarsomere cylindrical or with slightly enlarged apex, about equal in length to fifth tarsomere. Dorsocentral setae multiserial .... ***Sympotthastia*** Pagast
1 sp., *fulva* (Johannsen); Quebec, New York

46. Third palpal segment with distomedial tooth .... ***Odontomesa*** Pagast[4]
1 sp., *lutosopra* (Garrett); British Columbia, Alberta, Colorado, Wisconsin, Ontario, Quebec

Third palpal segment without distomedial tooth 47

47. Gonostylus bifurcate; anal point absent .... ***Prodiamesa*** Kieffer[4]
2 spp.; British Columbia, Alberta, Northwest Territories, Greenland, Ontario, Quebec, Michigan, Massachusetts, New Jersey, Pennsylvania

Gonostylus simple; anal point present .... ***Monodiamesa*** Kieffer[4]
4 spp.; British Columbia, Northwest Territories, Manitoba to Quebec, Michigan, Wisconsin, California; Saether 1973*a*

CHIRONOMINAE

48. Wing membrane without or with macrotrichia; if with macrotrichia, then calypter with fringe; crossvein r-m definitely oblique to R_{4+5} (Fig. 16) .... CHIRONOMINI.... 49
unless stated otherwise, the main reference for this tribe is Townes (1945)

Wing membrane usually with macrotrichia; calypter always without fringe; crossvein r-m nearly parallel to R_{4+5} and continuous with it (Figs. 17, 18), or if oblique, then wing apex truncated (Fig. 19) .... TANYTARSINI[5].... 80

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[4] Saether (1977*b*) placed *Odontomesa*, *Prodiamesa*, and *Monodiamesa* in the subfamily Prodiamesinae.

[5] Current knowledge of this relatively large tribe in the Nearctic is poor. Dr. J. E. Sublette is preparing a revision at this time.

49. Male antenna with 11 flagellomeres. Apex of fore tibia with inner low rounded scale that projects slightly beyond similar outer scale (Fig. 56) 50

Male antenna with 13 flagellomeres. Apex of fore tibia truncated or with distinctly projecting scale or subtriangular spine (Figs. 55, 57, 58); scale frequently armed with spine; scale on outer margin usually absent 64

50. Antepronotal lobes separated medially (Figs. 36, 37) 51

Antepronotal lobes not separated medially though usually distinctly notched (Fig. 35) 52

51. Median separation of pronotal lobes narrow, not as broad as deep (Fig. 36). Appendage 1 of terminalia broad with numerous short setae; anal point broad (Fig. 99) .... ***Xenochironomus*** Kieffer

6 spp.; widespread

Median separation of pronotal lobes V-shaped, broader than deep (Fig. 37). Appendage 1 of terminalia horn-shaped, at most with one seta beyond base; anal point narrow .... ***Glyptotendipes*** Kieffer

13 spp.; widespread

52. Gonocoxite and gonostylus fused (Figs. 85–91); appendage 2 equal to or shorter than appendage 1 with no or few apical setae, or absent .... ***Harnischia*** complex[6] 53

Gonocoxite and gonostylus not fused (Figs. 92–98); appendage 2 always present and longer than appendage 1, with many apical setae 60

53. Appendage 2 with one or more apical setae (Fig. 85) .... ***Cryptochironomus*** Kieffer

6 spp.; widespread

Appendage 2 absent, or if present, without apical setae although covered with fine pubescence 54

54. Appendage 1 rod-shaped, usually more than three times as long as wide and with one to four apical setae (Figs. 86–88). Frontal tubercles (as in Fig. 22) present or absent 55

Appendage 1 lobe-shaped (Fig. 90), apically expanded (Fig. 89), or rod-shaped; if rod-shaped, then appendage 1 less than three times as long as wide and having not more than two apical setae (Fig. 91). Frontal tubercles present 58

55. Frontal tubercles present. Basal half or more of anal point wedge-shaped and grading into tergite 9 (Fig. 86) .... ***Demicryptochironomus*** Lenz

1 sp., *cuneata* (Townes); widespread

Frontal tubercles absent or vestigial. Lateral margins of basal part of anal point straight to weakly wedge-shaped, forming angle with tergite 9 (Figs. 87, 88) 56

56. Tergite 9 of male with small lobe bearing setae on either side of anal point .... ***Microchironomus*** Kieffer

1 sp., *nigrovittatus* (Malloch); Iowa, Illinois, Michigan, New York, Ontario

Tergite 9 of male without small lobe bearing setae on either side of anal point 57

57. Inner margin of apical half of gonostylus distinctly notched (Fig. 88); apex of appendage 1 rounded or truncated .... ***Cryptotendipes*** Lenz

3 spp.; British Columbia to Quebec, Iowa, Ohio, Michigan, New York, Pennsylvania, Northwest Territories

Inner margin of apical half of gonostylus curved or swollen, not notched (Fig. 87); apex of appendage 1 excavated (Fig. 87) .... ***Parachironomus*** Lenz

16 spp.; widespread

58. Appendage 1 distinct, usually apically expanded, with more than three setae (Fig. 89) .... ***Paracladopelma*** Harnisch[7]

11 spp.; California, Florida north to South Dakota and Ontario, Northwest Territories

Appendage 1 reduced, either a small lobe or unsclerotized flap (Fig. 90) or short and rod-like (Fig. 91), with not more than two apical setae 59

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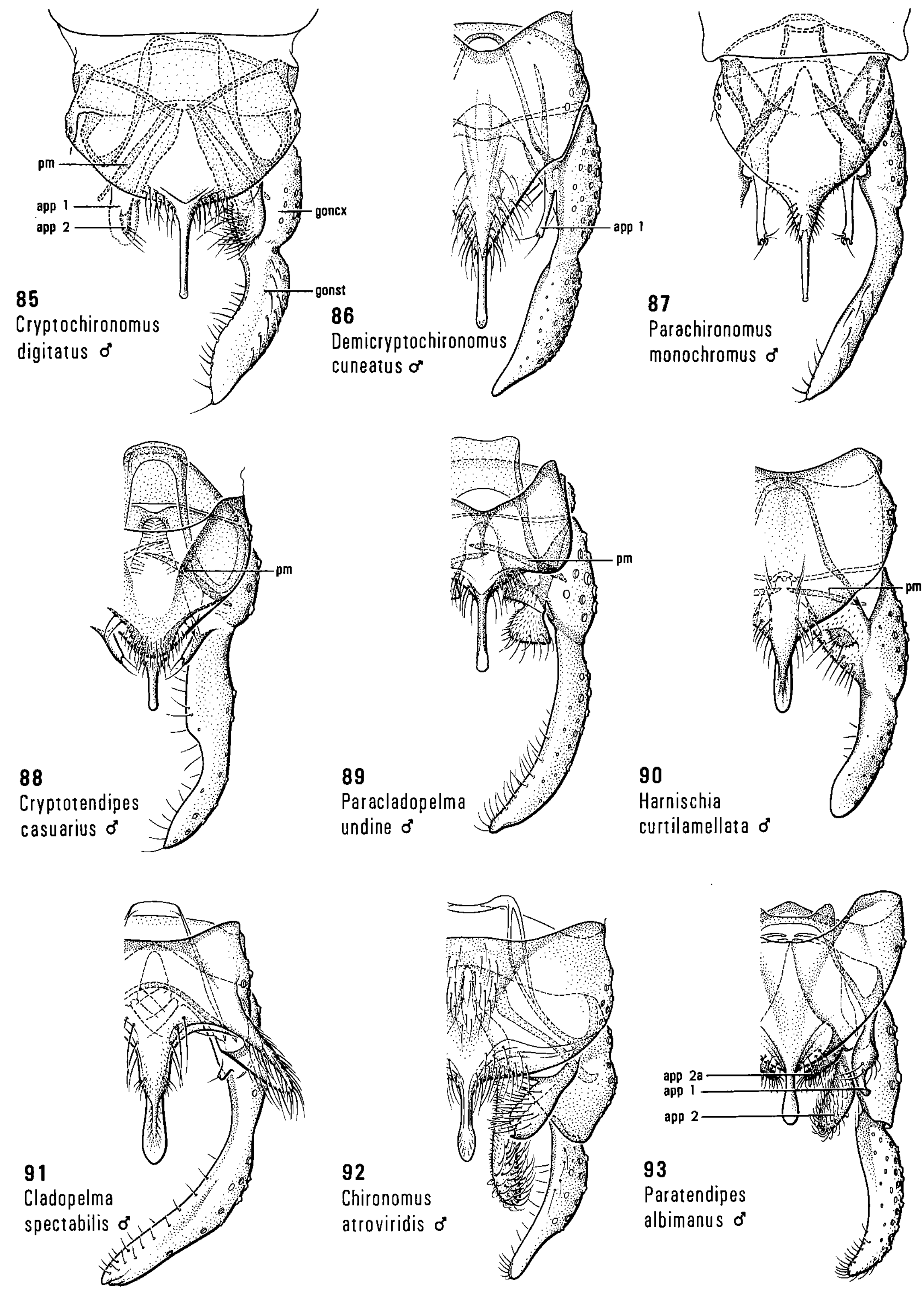
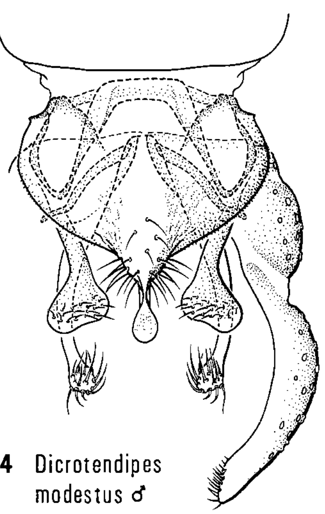
[6] The generic classification of the *Harnischia* complex follows that of Saether (1971*b*), except in accordance with Saether (1977*a*) *Microchironomus* is used for *Leptochironomus* and *Cladopelma* for *Cryptocladopelma*. However, Saether (1977*a*) recognized six genera (four new), namely *Cyphomella* Saether, *Acalcarella* Shilova, *Beckidia* Saether, *Chernovskiia* Saether, *Robackia* Saether, and *Gillotia* Kieffer, that are not keyed here.

[7] *Saetheria* Jackson also keys here. According to Jackson (1977) *Saetheria* is distinguished by the presence of two ridges converging posteriorly on tergite 9 of the male, whereas *Paracladopelma* has a single median ridge or no distinct ridge.

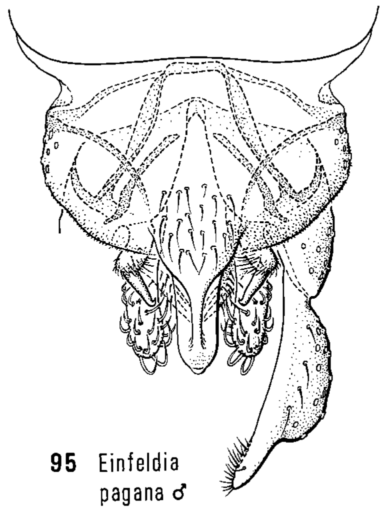


Figs. 29.85–93. Terminalia of male (*continued*): (85) ***Cryptochironomus digitatus*** (Malloch); (86) ***Demicryptochironomus cuneatus*** (Townes); (87) ***Parachironomus monochromus*** (Wulp); (88) ***Cryptotendipes casuarius*** (Townes); (89) ***Paracladopelma undine*** (Townes); (90) ***Harnischia curtilamellata*** (Malloch); (91) ***Cladopelma spectabilis*** (Townes); (92) ***Chironomus atroviridis*** (Townes); (93) ***Paratendipes albimanus*** (Meigen) (*continued*).

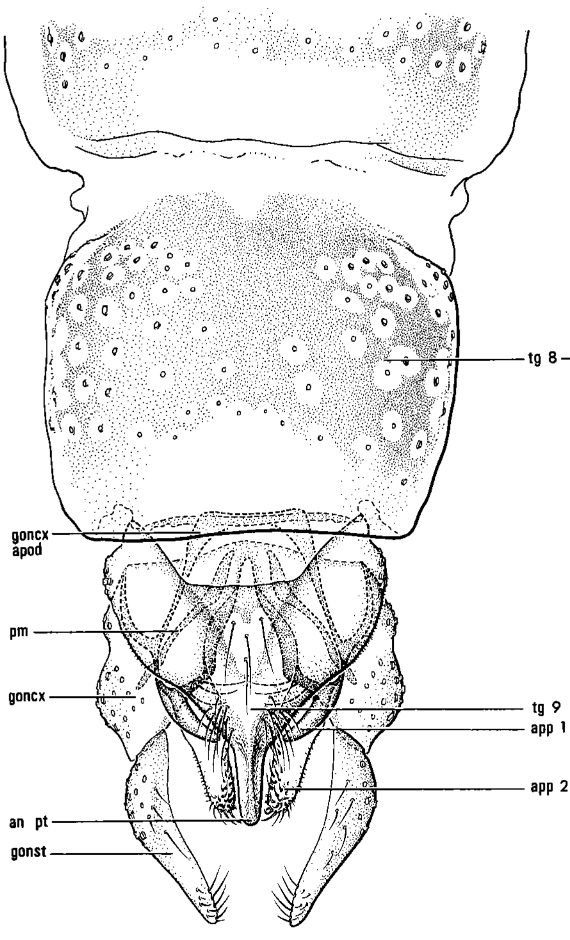
Abbreviations: app, appendage; goncx, gonocoxite; gonst, gonostylus; pm, paramere.



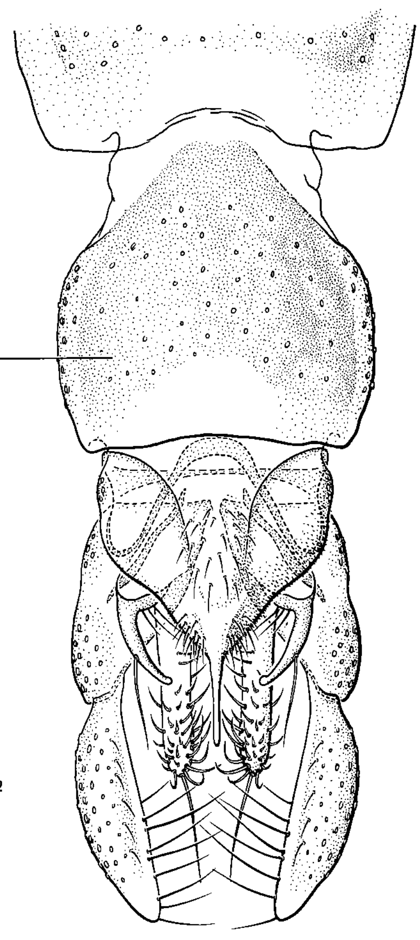
94 Dicrotendipes modestus ♂



95 Einfeldia pagana ♂



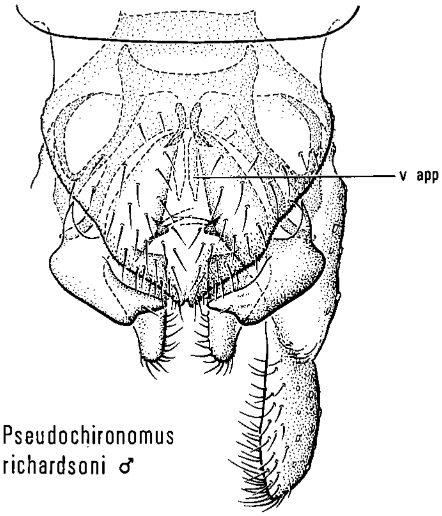
96 Chironomus staegeri ♂



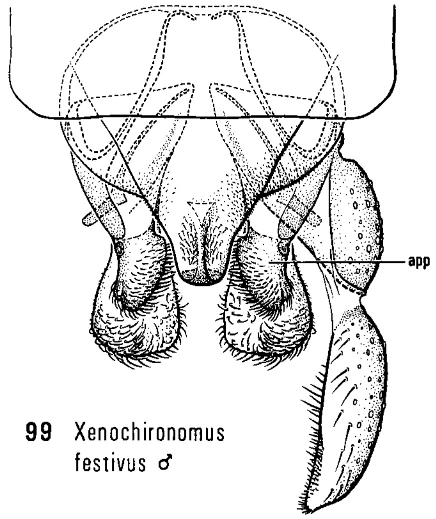
97 Polypedilum walleyi ♂

Figs. 29.94–97. Terminalia of male (*continued*): (94) *Dicrotendipes modestus* (Say); (95) *Einfeldia pagana* (Meigen); (96) *Chironomus staegeri* Lundbeck; (97) *Polypedilum walleyi* Townes (*continued*).

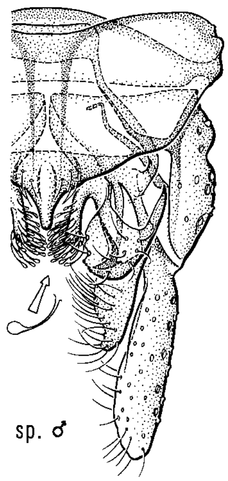
Abbreviations: an pt, anal point; app, appendage; goncx, gonocoxite; goncx apod, gonocoxal apodeme; gonst, gonostylus; pm, paramere; tg, tergite.



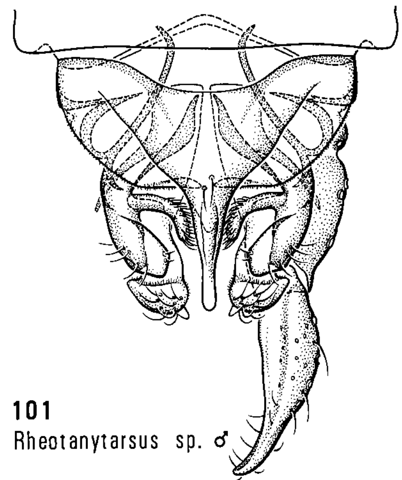
98 Pseudochironomus richardsoni ♂



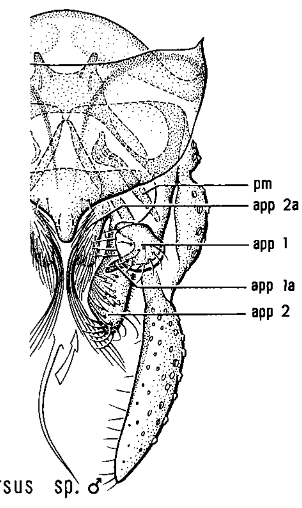
99 Xenochironomus festivus ♂



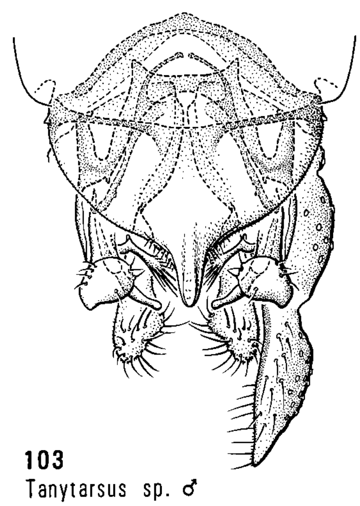
100 Lauterbornia sp. ♂



101 Rheotanytarsus sp. ♂



102 Paratanytarsus sp. ♂



103 Tanytarsus sp. ♂

Figs. 29.98–103. Terminalia of male (*continued*): (98) *Pseudochironomus richardsoni* Malloch; (99) *Xenochironomus festivus* (Say); (100) *Lauterbornia* sp.; (101) *Rheotanytarsus* sp.; (102) *Paratanytarsus* sp.; (103) *Tanytarsus* sp. (*continued*).
Abbreviations: app, appendage; pm, paramere; v app, ventral appendage.

59. Appendage 1 a small lobe or unsclerotized flap (Fig. 90) .... ***Harnischia*** Kieffer
2 spp.; Oklahoma, Illinois, New York, Virginia, Ontario, Manitoba
Appendage 1 more rod-like (Fig. 91) .... ***Cladopelma*** Kieffer
7 spp.; widespread

60. Appendage 2 oval, much broader than maximum width of gonostylus .. ***Kiefferulus*** Goetghebuer
1 sp., *dux* (Johannsen); British Columbia to Quebec, south to Florida
Appendage 2 subcylindrical, narrower, at most slightly wider than maximum width of gonostylus 61

61. Appendage 2 long, slender, strongly curved dorsally, with enlarged setiferous apex (Fig. 94)........ .... ***Dicrotendipes*** Kieffer
9 spp.; widespread
Appendage 2 not unusually long, slender, and curved dorsally, and without enlarged setiferous apex (Figs. 93, 96, 97) 62

62. Appendage 1 with enlarged setiferous base beyond which appendage abruptly narrowed (Fig. 95) .... ***Einfeldia*** Kieffer
7 spp.; widespread
Appendage 1 without enlarged setiferous base and without abruptly narrowed apical part (Figs. 96, 97) 63

63. Appendage 1 with basal long setae (Fig. 96), or rarely with long setae only on apical two-thirds (Fig. 92) .... ***Chironomus*** Meigen
more than 25 spp.; widespread
Appendage 1 without long setae .... ***Goeldichironomus*** Fittkau
1 sp., *holoprasinus* (Goeldi); Florida, Alabama, Louisiana, California; Reiss 1974

64. Apex of fore tibia truncated, without spur or scale 65
Apex of fore tibia with spur or scale (Figs. 55, 57, 58) 66

65. Calypter with fringe. Fore femur with patch of backward-directed setae medially on apical half (Fig. 52) .... ***Microtendipes*** Kieffer
4 spp.; widespread
Calypter without fringe. Fore femur without patch of backward-directed setae .... ***Paralauterborniella*** Lenz
3 spp.; Yukon and Alberta to New Brunswick and New York, California, Florida

66. Fore tibia with black crenulate spur (Fig. 55); both combs of mid and hind tibiae (Fig. 67) triangular in shape and widely separated at base. Pair of ventral appendages present between gonocoxal bases (Fig. 98) .... ***Pseudochironomus*** Malloch[8]
11 spp.; widespread; Saether 1977*a*
Fore tibia without spur, but with smooth scale or spine (Figs. 57, 58); combs of mid and hind tibiae not triangular in shape or not usually widely separate; if combs widely separate, then only one comb present on each leg with spine (Fig. 69). Ventral appendages between gonocoxal bases absent; appendage 2*a* sometimes present (Fig. 93) 67

67. Antepronotum projecting anteriorly from most anterior point on scutum; lobes slightly broader medially than laterally .... ***Omisus*** Townes
1 sp., *pica* Townes; Ontario, Connecticut, New Hampshire, Massachusetts, Florida
Antepronotum not reaching or scarcely reaching most anterior point of scutum; lobes usually narrower medially than laterally (Figs. 47, 48) 68

68. Appendage 2*a* present (Fig. 93) .... ***Paratendipes*** Kieffer
6 spp.; Idaho to Newfoundland south to California and Alaska, Northwest Territories
Appendage 2*a* absent 69

69. Calypter without fringe 70
Calypter with at least two setae on margin, usually fully fringed 71

70. Flagellomere 13 shorter than combined length of flagellomeres 1–12. Pulvilli small, less than half length of claws. Appendage 1 bifid .... ***Nilothauma*** Kieffer
3 spp.; British Columbia, Ontario to Newfoundland south to Florida

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[8] *Pseudochironomus* is the only Nearctic representative of the tribe Pseudochironomini erected by Saether (1977*b*).

Flagellomere 13 longer than combined length of flagellomeres 1–12. Pulvilli longer than half length of claws. Appendage 1 not bifid .... ***Lauterborniella*** Bause
3 spp.; Northwest Territories, South Dakota to Quebec south to Florida

71. Tibial combs of midleg with two spines, one on each comb 72
Tibial combs of midleg usually with one spine on inner comb and none on outer comb, or both combs without spines 73

72. Scutum projecting far anteriorly above most anterior point of antepronotum .... ***Stenochironomus*** Kieffer
11 spp.; widespread
Scutum about even with anterior point of antepronotum .... ***Endochironomus*** Kieffer
2 spp.; widespread

73. Combs of mid and hind tibiae without spines. Palpus short, less than width of head .... ***Graceus*** Goetghebuer
1 undescr. sp.; southeastern Ontario
At least one comb on mid and hind tibiae with spine (Fig. 69). Palpus longer, at least equal to width of head 74

74. Wing membrane with macrotrichia 75
Wing membrane without macrotrichia 76

75. Base of sternite 8 and tergite 8 of male triangularly produced (Fig. 97). Pulvilli bilobate or branched (Fig. 74) .... ***Polypedilum*** Kieffer, in part
more than 40 spp.; widespread
Base of sternite 8 and tergite 8 of male subtruncate (as in Fig. 96). Pulvilli entire (Fig. 73) .... ***Phaenopsectra*** Kieffer
8 spp.; widespread

76. Gonostylus movable, not fused with gonocoxite. Scutum with distinct median tubercle (Fig. 47) .... ***Stictochironomus*** Kieffer
13 spp.; widespread
Gonostylus fused to gonocoxite. Scutum without distinct median tubercle 77

77. Base of sternite 8 and tergite 8 of male triangularly produced (Fig. 97). Pulvilli bilobate or branched (Fig. 74) .... ***Polypedilum*** Kieffer, in part
see couplet 75
Base of sternite 8 and tergite 8 of male subtruncate. Pulvilli usually entire 78

78. Calypter with two to six setae .... ***Pagastiella*** Brundin
1 sp., *ostansa* (Webb); British Columbia, Manitoba to Quebec, Michigan, Northwest Territories
Calypter with more than six setae, usually fully fringed 79

79. Both combs of hind tibia each with a spine although one spine is frequently very small. Apex of gonostylus with inner row of setae (as in Fig. 97) .... ***Tribelos*** Townes
6 spp.; Alberta to Newfoundland, south to Texas and Florida, California
Only one comb of hind tibia with a spine. Apex of gonostylus without inner row of setae .... ***Pedionomus*** Sublette
1 sp., *beckae* Sublette; Florida to Texas; Sublette 1964

80. Mid and hind tibiae without combs 81
Mid and hind tibiae with combs, though combs sometimes composed of free spinules 82

81. Apex of wing truncated, with setal tuft (Fig. 19). Apex of hind tibia with dark strongly sclerotized spurs .... ***Corynocera*** Zetterstedt
2 spp.; Alberta, Northwest Territories
Apex of wing rounded, without setal tuft. Apex of hind tibia without spurs but enlarged into a broad hook-shaped process (Fig. 72) .... ***Lenziella*** Kieffer
1 sp., *cruscula* Saether; South Dakota; Saether 1971*b*

82. Eye haired .... ***Zavrelia*** Kieffer
1 undescr. sp.; Pennsylvania, New Brunswick
Eye bare 83

83. Combs of mid and hind tibiae without spines and contiguous or overlapping, occupying more than half apical circumference of tibia (Fig. 70) .... ***Micropsectra*** Kieffer
more than 15 spp.; widespread

Combs of mid and hind tibiae with or without spines and usually separate (Fig. 71), but if contiguous, occupying at most half of circumference of tibia 84

84. R_{4+5} ending proximal to CuA_1 (Fig. 18) .... ***Stempellina*** Bause
several undescribed species; New York, Ontario, Northwest Territories

R_{4+5} ending opposite or distal to CuA_1 (Fig. 17) 85

85. R_{2+3} apically evanescent to absent. Appendage 1*a* vestigial (Fig. 101) .... ***Rheotanytarsus*** Bause
3 spp.; Wisconsin to Ontario south to Iowa and Kentucky, Idaho, Yukon, Northwest Territories

R_{2+3} distinct or faint. If R_{2+3} faint, then appendage 1*a* (Figs. 102, 103) always well-developed 86

86. Appendage 2*a* with apically expanded (spoon-shaped) setae (Fig. 100). Inner margin of appendage 1 serrated .... ***Lauterbornia*** Kieffer
2 spp.; Northwest Territories, Greenland

Appendage 2*a* with simple, lamellate (Fig. 102), or branched setae. Inner margin of appendage 1 not serrated 87

87. Combs of mid and hind tibiae without spines or with spines; if with spines, then combs contiguous and occupying about half of circumference of tibia. Appendage 2*a* usually with lamellate setae, rarely with simple setae (Fig. 102) .... ***Paratanytarsus*** Bause
more than 5 spp.; widespread in Canada

One or both combs of mid and hind tibiae with spines; combs always separate (Fig. 71). Setae on appendage 2*a* variable 88

88. Appendage 2*a* with branched setae .... ***Cladotanytarsus*** Kieffer
1 sp., *viridiventris* Malloch; widespread in Canada, Michigan, New York, Alabama, Louisiana

Appendage 2*a* with unbranched setae, either simple or lamellate .... ***Tanytarsus*** Wulp
more than 20 spp.; widespread

ORTHOCLADIINAE

89. Antenna with one clavate flagellomere. Halter absent (Fig. 113) .... ***Oreadomyia*** Kevan & Cutten-Ali-Khan
1 sp., *albertae* Kevan & Cutten-Ali-Khan; Alberta; Kevan and Cutten-Ali-Khan 1975

Antenna with four or more flagellomeres. Halter normal 90

90. Antepronotal lobes widely separate (as in Fig. 39). Fore coxa enlarged (as in Fig. 39). Male flagellum not plumose 91

Antepronotal lobes meeting medially (Figs. 33, 34, 40) or narrowly separate (Figs. 28, 32). Fore coxa rarely enlarged (Fig. 40). Male flagellum usually plumose (Figs. 24, 25) 94

91. Tibial comb of hindleg present. Anapleural suture distinct, straight, usually extending from base of midleg to base of foreleg .... ***Thalassosmittia*** Strenzke & Remmert
3 spp.; coastal British Columbia; Sublette 1967*a* (as *Saunderia* Sublette)

Tibial comb of hindleg absent. Anapleural suture weaker, curved, not extending to base of foreleg 92

92. Second tarsomere of hindleg much shorter than third; fifth tarsomere slightly bilobate. Wing fully developed in male (Fig. 10), absent in female .... ***Clunio*** Haliday
1 sp., *marshalli* Stone & Wirth; coastal Florida; Wirth 1949

Second tarsomere of hindleg subequal in length to third; fifth tarsomere simple. Wing strap-like or absent 93

93. Palpus short, two-segmented. Wing present, reaching abdominal segment 4. Tergite 9 of male produced distally into broadly pointed pubescent anal point .... ***Eretmoptera*** Kellogg
1 sp., *browni* Kellogg; coastal California; Wirth 1949

Palpus longer, four- or five-segmented. Wing absent. Tergite 9 of male truncate distally, without an anal point .... ***Tethymyia*** Wirth
1 sp., *aptena* Wirth; coastal California; Wirth 1949

94. R_{4+5} completely fused with C (Fig. 11) 95

R_{4+5} only fused with C at apex (Figs. 12–15) 96

95. Fore trochanter with dorsal keel (Fig. 54); apex of hind tibia enlarged (Fig. 53) .... ***Corynoneura*** Winnertz
more than 20 spp.; widespread; Schlee 1968 (European species)
Fore trochanter without dorsal keel; apex of hind tibia usually not enlarged .... ***Thienemanniella*** Kieffer
4 spp.; British Columbia, Ontario, Northwest Territories, Utah, Texas, Illinois, Pennsylvania; Sublette 1970

96. Eye hairy (Fig. 20) 97
Eye bare 111

97. Palpus four-segmented .... ***Symbiocladius*** Kieffer
1 sp., *equitans* Claassen; California, New Mexico, Utah, Colorado, Vermont, Northwest Territories
Palpus five-segmented 98

98. Dorsocentral setae erect; sockets usually light-colored 99
Dorsocentral setae decumbent; sockets not contrasting in color with rest of scutum 109

99. Antepronotal lobe entirely covered with setae; medioanepisternal and katepisternal setae present .... ***Heleniella*** Gowin
1 sp., *curtistila* Saether; British Columbia, Alberta, Quebec, Ontario; Saether 1969
Antepronotal lobe only with ventrolateral setae (Figs. 33, 34); medioanepisternal and katepisternal setae absent, or rarely, one or two medioanepisternal setae present 100

100. Postocular setae absent (Fig. 25). Fourth palpal segment short, about twice as long as broad .... ***Acricotopus*** Kieffer
2 spp.; Alberta, Manitoba to Quebec, New York, Pennsylvania, Iowa, Northwest Territories, Alaska
Postocular setae present (Fig. 24). Fourth palpal segment longer, at least three times as long as broad 101

101. Supra-alar setae absent .... ***Plecopteracoluthus*** Steffan[9]
1 sp., *downsi* Steffan; Quebec, Wisconsin; Steffan 1965
Supra-alar setae present 102

102. Outer spur of hind tibia more than half length of inner spur (as in Fig. 63). Gonostylus bifurcate .... ***Diplocladius*** Kieffer
1 sp., *cultriger* Kieffer; Ontario to New Brunswick, Northwest Territories, Yukon, Greenland
Outer spur of hind tibia less than half length of inner spur (Figs. 64–66). Gonostylus simple .. 103

103. Calyptral fringe absent. R_{4+5} ending proximal to apex of CuA_1 (Fig. 14) 104
Calyptral fringe present. R_{4+5} usually ending distal to or opposite apex of CuA_1 (Figs. 12, 13) 105

104. Apex of antenna with a strong straight seta (Fig. 23). CuA_2 strongly curved (Fig. 14) .... ***Smittia*** Holmgren, in part
more than 20 spp.; widespread
Apex of antenna without a strong straight seta. CuA_2 straight (as in Figs. 12, 13) .... ***Eukiefferiella*** Thienemann, in part
more than 9 spp.; widespread

105. Eye strongly produced dorsomedially (as in Fig. 22). Pulvilli absent 106
Eye not produced dorsomedially (Figs. 20, 21). Pulvilli present 107

106. R_{2+3} midway between R_1 and R_{4+5}. Tergite 9 of male distally straight to weakly concave, without an anal point .... ***Paratrichocladius*** Santos Abreu
2 spp.; Manitoba to New Brunswick, Illinois, Alaska; Hirvenoja 1973
R_{2+3} close to and parallel with R_{4+5}. Tergite 9 of male distally with setiferous broadly rounded anal point .... ***Mesocricotopus*** Brundin
1 sp., *thienemanni* (Goetghebuer); Alberta; Saether 1969

107. Two or three acrostichal setae present only on median area of scutum (Fig. 44). Area behind eye deeply excavated (Fig. 20) .... ***Nanocladius*** Kieffer
13 spp.; widespread in Canada, Montana, and Colorado to Maryland and North Carolina; Saether 1977*a*

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[9] Saether (1977*a*) placed *Plecopteracoluthus* as a subgenus of *Nanocladius*.

Acrostichal setae more numerous, beginning near antepronotum and extending to median area of scutum (Fig. 42). Area behind eye not deeply excavated (Fig. 21) 108

108. R_{4+5} ending distal to apex of CuA_1. Setae on tergites scattered over most of surface, although sparse .... ***Rheocricotopus*** Thienemann & Harnisch
9 spp.; British Columbia and Yukon to New Brunswick, Illinois, Pennsylvania

R_{4+5} ending opposite or proximal to apex of CuA_1. Setae on tergites arranged in two transverse rows, one medial or anterior and one posterior .... ***Paracricotopus*** Thienemann & Harnisch
1 undescr. sp.; Ontario, Quebec, Northwest Territories

109. Longitudinal median area of tergites 2–5 bare; lateral area thickly setose. Anal point present .... ***Paracladius*** Hirvenoja
2 spp.; Northwest Territories, Quebec, Greenland; Oliver 1976

Longitudinal median area of tergites 2–5 with setae; chaetotaxy of lateral area variable. Anal point usually absent; if present, then chaetotaxy of lateral area of tergites reduced 110

110. Supra-alar setae extending anterior to level of medioanepisternum; dorsocentral setae not meeting at midline of scutum .... ***Halocladius*** Hirvenoja
1 sp., *variabilis* (Staeger); Manitoba, Greenland; Hirvenoja 1973

Supra-alar setae usually not extending anterior to level of medioanepisternum; if extending, then dorsocentral setae meeting at midline of scutum .... ***Cricotopus*** Wulp
more than 50 spp.; widespread; Hirvenoja 1973 (European species)

111. Wing membrane usually with macrotrichia at least on wing tip; if absent, then clypeus enlarged and apical junction of C and R_{4+5} rounded (as in Fig. 17) 112

Wing membrane bare 120

112. Antepronotal lobes with dorsomedial and ventrolateral setae (Fig. 32). Gonostylus bifurcate 113

Antepronotal lobes with only ventrolateral setae (as in Figs. 33, 34). Gonostylus simple 114

113. Ventral lobe of gonostylus with several long well-developed setae .... ***Eurycnemus*** Wulp
1 sp., *annuliventris* (Malloch); California, Northwest Territories; Sublette 1970

Ventral lobe of gonostylus without long well-developed setae, only with small short setae .... ***Brillia*** Kieffer
6 spp.; British Columbia to Newfoundland, northeastern United States, Northwest Territories; Sublette 1967*b*

114. R_{4+5} and C ending proximal to apex of CuA_1 .... ***Paraphaenocladius*** Thienemann
5 spp.; widespread in Canada, New York, Illinois, Greenland

R_{4+5} usually and C always ending distal to or opposite apex of CuA_1 115

115. C not produced past apex of R_{4+5}; apex of junction of C and R_{4+5} rounded .... ***Heterotrissocladius*** Spärck
6 spp.; widespread; Saether 1975*a*

C produced past apex of R_{4+5}; when produced only slightly, then apex of junction of C and R_{4+5} angular 116

116. Acrostichal setae beginning near antepronotum and extending to median area of scutum (as in Fig. 42) 117

Acrostichal setae present only on median area of scutum (as in Fig. 43) 119

117. CuA_2 straight (as in Figs. 12, 13). Calyptral fringe composed of very long setae .... ***Metriocnemus*** Wulp
14 spp.; widespread

CuA_2 strongly curved (as in Fig. 14). Calyptral fringe normal, composed of shorter setae 118

118. Apex of eye parallel-sided, strongly produced dorsally. Anal point long, without apical setae .... ***Parametriocnemus*** Goetghebuer
5 spp.; Northwest Territories, Greenland, Alberta, Ontario to New Brunswick, South Dakota, Quebec south to Florida, Yukon

Apex of eye wedge-shaped, moderately produced dorsally. Anal point short, broadly triangular with strong apical setae .... ***Pseudorthocladius*** Goetghebuer, in part
3 spp.; British Columbia, Ontario, New Brunswick

119. Calyptral fringe present. Scutum with two acrostichal setae on median area .... ***Heterotanytarsus*** Spärck
2 spp.; British Columbia, Ontario; Saether 1975*d*

Calyptral fringe absent. Scutum with more than two acrostichal setae .... ***Gymnometriocnemus*** Goetghebuer
2 spp.; British Columbia, Ontario, New Brunswick, Yukon, Northwest Territories; Saether 1969

120. Calypter with at least one marginal seta, usually with a fringe of setae 121
Calypter without marginal setae 140

121. Fourth tarsomere cordiform (Fig. 50) .... ***Cardiocladius*** Kieffer
3 spp.; Washington, Ontario to Newfoundland, New York, Pennsylvania, Florida, Arizona, Yukon

Fourth tarsomere cylindrical 122

122. Outer spur of hind tibia at least half length of inner spur (Fig. 63) 123
Outer spur of hind tibia less than half length of inner spur (Figs. 64, 65); outer spur rarely absent 124

123. Scutum with weakly sclerotized dorsomedial field (Fig. 29). Pulvilli absent .... ***Abiskomyia*** Edwards
1 undescr. sp.; Greenland, Northwest Territories, Alaska

Scutum evenly sclerotized. Pulvilli present (Fig. 76) .... ***Psectrocladius*** Kieffer, in part
more than 19 spp.; widespread

124. Anepisternal and katepisternal setae present (Fig. 40) 125
Anepisternal and katepisternal setae absent or very rarely, one or two katepisternal setae present 126

125. Postanepisternal and epimeral setae present; medioanepisternal setae absent; antepronotal lobes with dorsomedial and ventrolateral setae; lancet-shaped dorsocentral setae usually present (Fig. 40) .... ***Limnophyes*** Eaton
more than 20 spp.; widespread; Saether 1975*e*

Postanepisternal and epimeral setae absent; medioanepisternal setae present; antepronotal lobes with only ventrolateral setae; dorsocentral setae simple .... ***Parachaetocladius*** Wülker
2 spp.; Quebec, British Columbia

126. R_{4+5} ending proximal to apex of CuA_1 127
R_{4+5} ending distal to or opposite apex of CuA_1 128

127. Antepronotal lobes joined medially. Anal point short, triangular, without setae .... ***Synorthocladius*** Thienemann
1 sp., *semivirens* (Kieffer); British Columbia, Alberta, Manitoba, Northwest Territories, Yukon

Antepronotal lobes narrowly separated medially. Anal point absent or present; if present, then longer and with setae on basal half .... ***Eukiefferiella*** Thienemann, in part[10]
see couplet 104

128. Crossvein r-m elongate and almost parallel to M .... ***Clinocladius*** Sublette
1 sp., *subparallelus* (Malloch); Illinois; Sublette 1970

Crossvein r-m at an angle to M 129

129. Pulvilli distinct, usually longer than half length of claw (Figs. 75, 76) 130
Pulvilli absent or present; if present, then indistinct and never longer than half length of claw 133

130. Spines on spurs of mid and hind tibiae divergent from shaft of spur (Fig. 66). Wing membrane with large microtrichia, clearly visible at 60× magnification .... ***Chaetocladius*** Kieffer
6 spp.; Quebec, Ontario, New York, Connecticut, Yukon, Northwest Territories, Greenland

Spines on spurs of mid and hind tibiae appressed to shaft of spur (as in Figs. 64, 65). Wing membrane with small microtrichia, not visible or barely visible at 60× magnification 131

131. Acrostichal setae absent. Anal point narrow and with tergite 9 usually forming equitriangular outline; inner gonocoxal lobe usually rectangular (Fig. 106) .... ***Psectrocladius*** Kieffer, in part
see couplet 123

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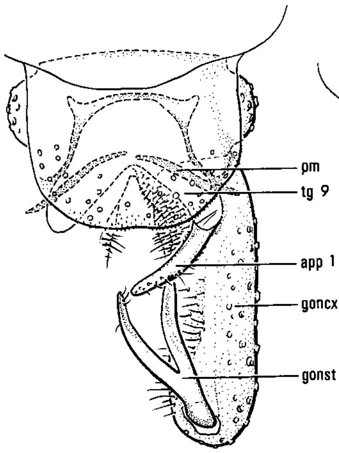
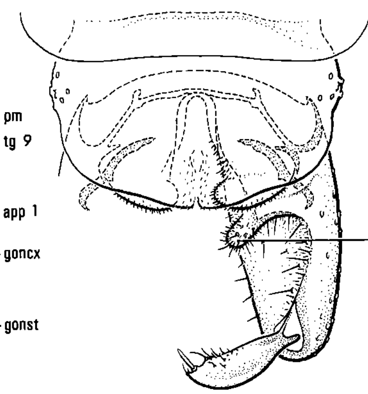
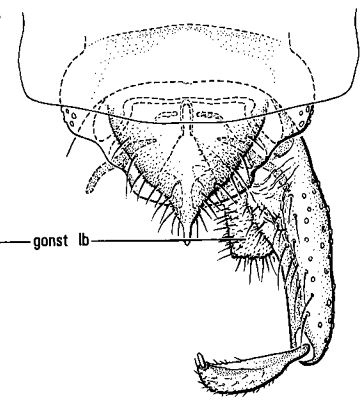
[10] *Tokunagaia* Saether also keys here; however, according to Saether (1973*b*) the adult cannot be separated from *Eukiefferiella*.



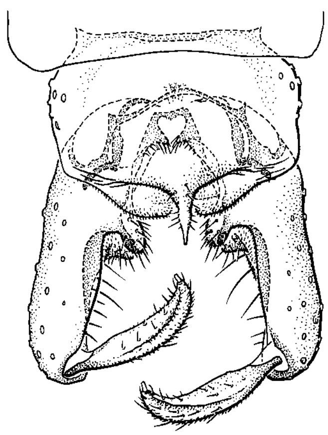
104 Brillia retifinis ♂



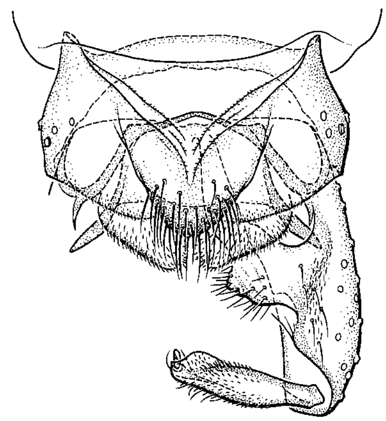
105 Cricotopus laricomalis ♂



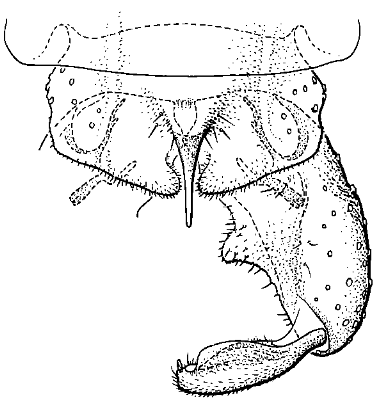
106 Psectrocladius sp. ♂



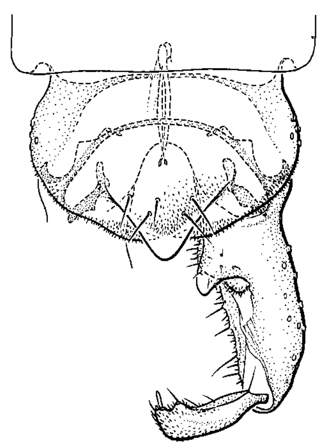
107 Orthocladius decoratus ♂



108 Pseudorthocladius dumicaudus ♂



109 Smittia sp. ♂



110 Parakiefferiella sp. ♂

Figs. 29.104–110. Terminalia of male (*concluded*): (104) ***Brillia retifinis*** Saether; (105) ***Cricotopus laricomalis*** Edwards; (106) ***Psectrocladius*** sp.; (107) ***Orthocladius decoratus*** (Holmgren); (108) ***Pseudorthocladius dumicaudus*** Saether; (109) ***Smittia*** sp.; (110) ***Parakiefferiella*** sp.

Abbreviations: app, appendage; goncx, gonocoxite; gonst, gonostylus; gonst lb, gonostylar lobe; pm, paramere; tg, tergite.

Acrostichal setae present. Anal point broad, semicircular, and with tergite 9 not forming such an outline (Figs. 107–110); inner lobe of gonocoxite variable, rarely rectangular (Figs. 107–110) 132

132. Apex of antenna of male with several curved setae. Anal point with short setae .... ***Platycladius*** Sublette

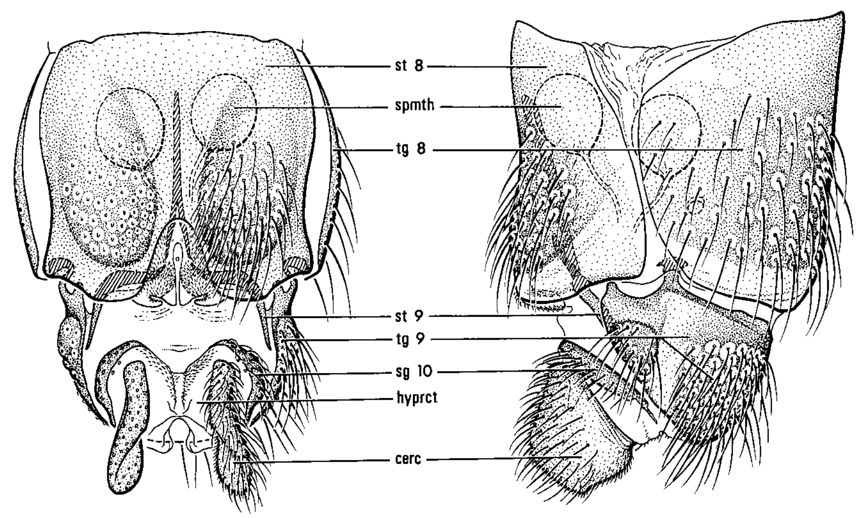
1 sp., *pleuralis* (Malloch); Illinois; Sublette 1970

Apex of antenna of male with a single long straight seta (as in Fig. 23). Anal point with long strong setae (Fig. 108) .... ***Pseudorthocladius*** Goetghebuer, in part

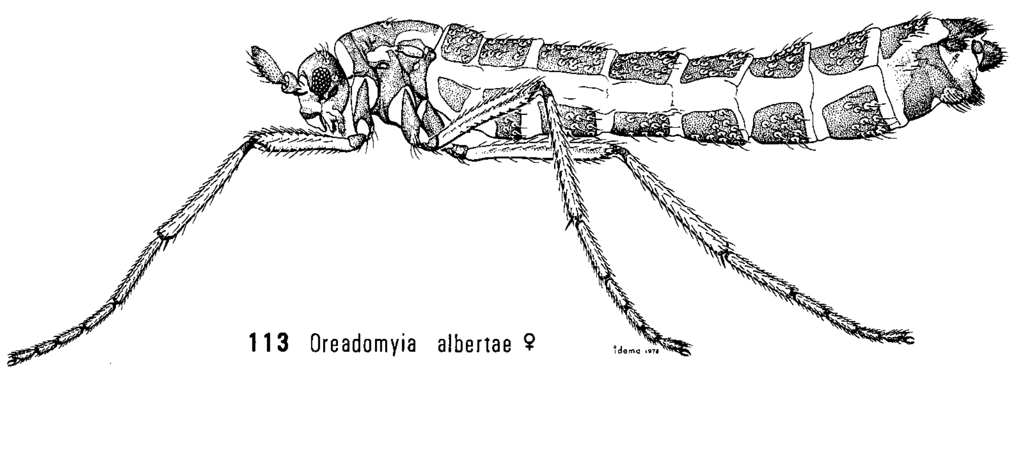
see couplet 118

133. Acrostichal setae absent 134

Acrostichal setae present 136



111 Chironomus plumosus ♀ **112** Chironomus plumosus ♀



113 Oreadomyia albertae ♀

Figs. 29.111–113. Chironomidae: terminalia of female of *Chironomus plumosus* (Linnaeus) in (111) ventral aspect and (112) lateral aspect; (113) left lateral view of female of *Oreadomyia albertae* Kevan & Cutten-Ali-Khan.

Abbreviations: cerc, cercus; hyprct, hypoproct; sg, segment; spmth, spermatheca; st, sternite; tg, tergite.

134. Tibial comb of hindleg reduced to one stout seta. Anal point broadly triangular, not set off from tergite 9 .... ***Baeoctenus*** Saether
1 sp., *bicolor* Saether; Manitoba; Saether 1976

Tibial comb of hindleg normal. Anal point narrower, extending from tergite 9 135

135. Mediobasal margin of gonocoxite with hook-like lobes (Fig. 107). Calypter with eight or more setae on margin .... ***Orthocladius*** Wulp, in part
29 spp.; widespread; Soponis 1977

Mediobasal margin of gonocoxite with broadly rounded lobes. Calypter with two setae on margin .... ***Psilometriocnemus*** Saether
1 sp., *triannulatus* Saether; New Hampshire; Saether 1969

136. Acrostichal setae beginning far from antepronotum (Fig. 43). Antepronotal lobes usually separated medially by V-shaped notch (Fig. 34) 137

Acrostichal setae beginning near antepronotum (Fig. 42). Antepronotal lobes joined or separated medially; if separated, then wing membrane with distinct microtrichia 139

137. Tergite 9 of male with two black strongly sclerotized pointed projections anterolateral to anal point .... ***Oliveria*** Saether
1 sp., *tricornis* (Oliver); Northwest Territories; Saether 1976

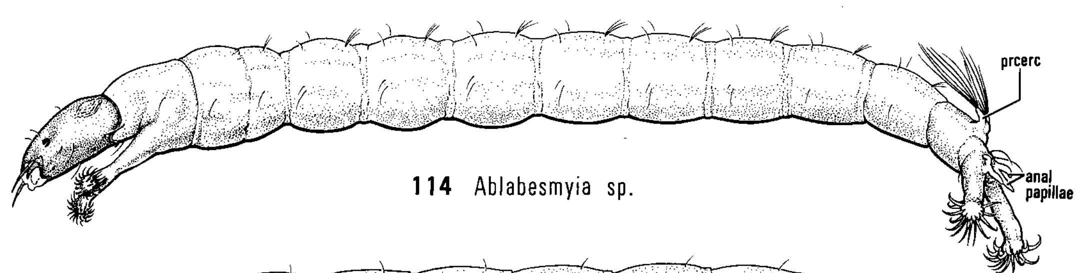
Tergite 9 of male without projections 138

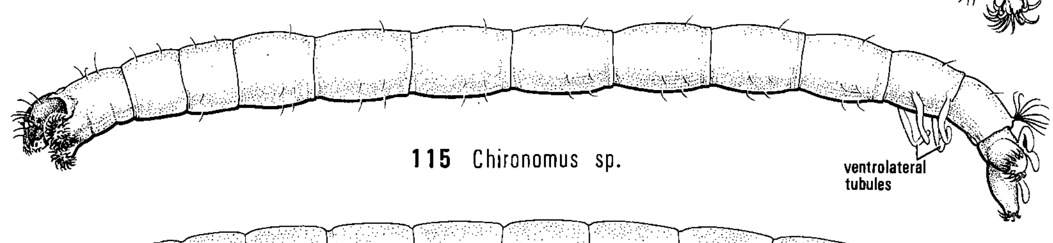
138. Anal point with setae .... ***Zalutschia*** Lipina
7 spp.; Alaska, widespread in Canada, South Dakota, Indiana, Florida; Saether 1976

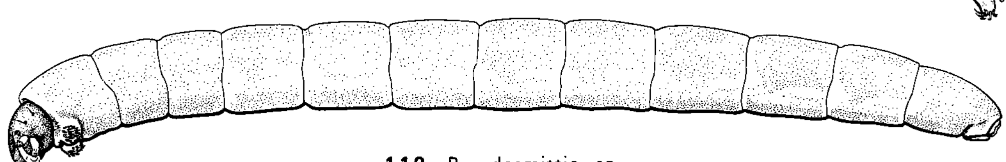
Anal point nearly always without setae; if setae present, then antenna, palpus, and legs reduced .... ***Hydrobaenus*** Fries[11]
13 spp.; widespread; Saether 1976

139. Anal point with setae (Fig. 107). Antepronotal lobes jointed medially (Fig. 33) .... ***Orthocladius*** Wulp, in part
see couplet 135

Anal point bare. Antepronotal lobes separated medially .... ***Bryophaenocladius*** Thienemann
5 spp.; Yukon, British Columbia, Ontario, Quebec, South Dakota, Illinois, South Carolina, New York; Saether 1973*b*



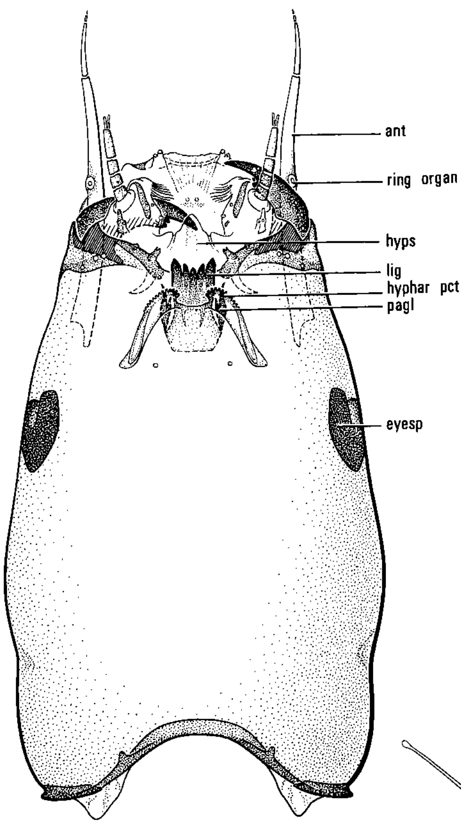




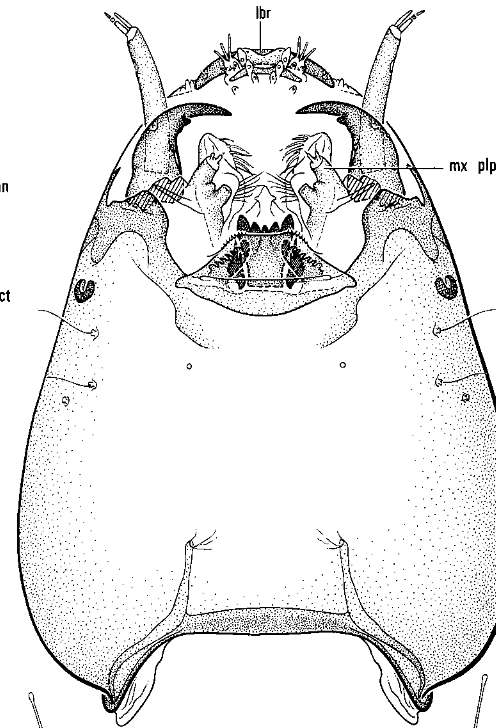
Figs. 29.114–116. Fourth instar larvae: (114) *Ablabesmyia* sp.; (115) *Chironomus* sp.; (116) *Pseudosmittia* sp.

Abbreviation: prcerc, procercus.

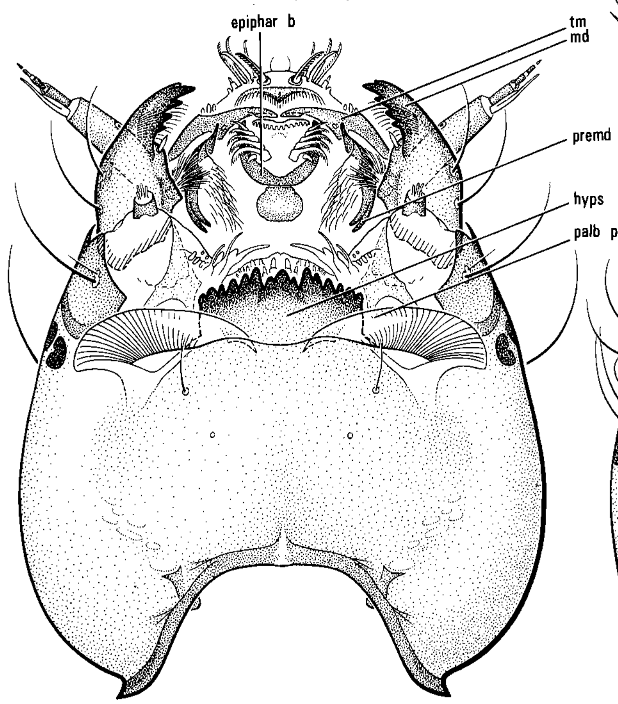
[11] Species with reduced antenna, palpus, and legs (the *lugubris* Fries group) (Saether 1976) are not known to occur in the Nearctic.



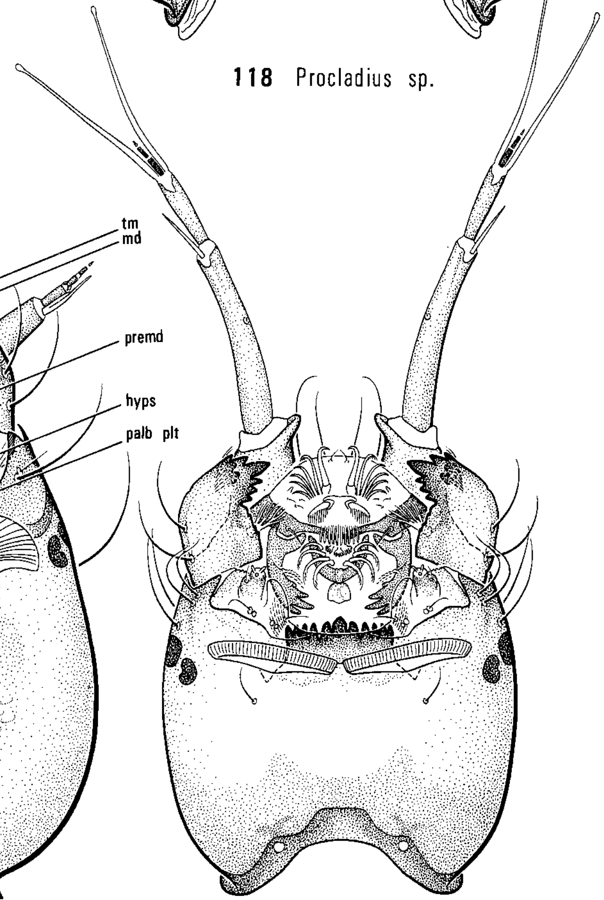
117 Ablabesmyia sp.



118 Procladius sp.



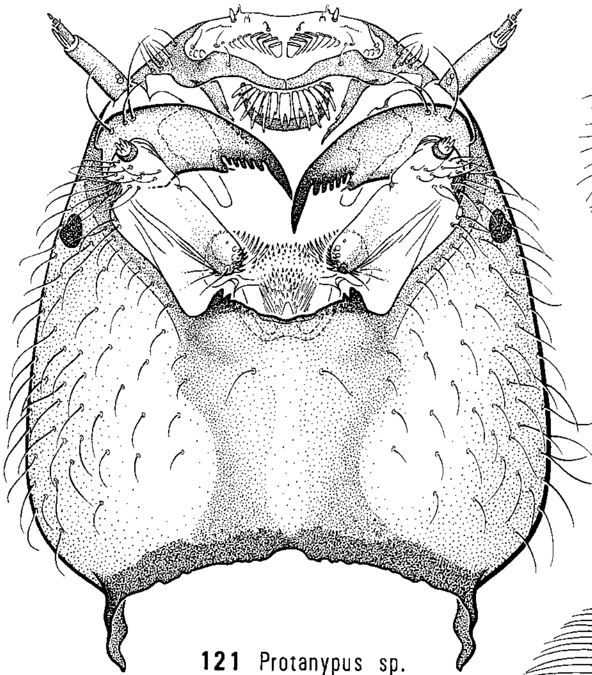
119 Chironomus sp.



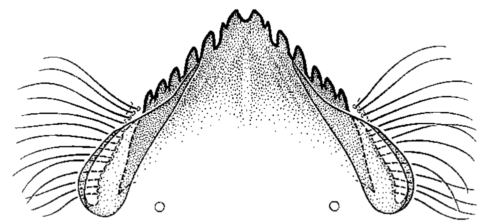
120 Micropsectra sp.

Figs. 29.117–120. Ventral aspects of fourth instar larval head capsule: (117) *Ablabesmyia* sp.; (118) *Procladius* sp.; (119) *Chironomus* sp.; (120) *Micropsectra* sp. (*continued*).

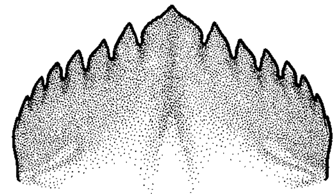
Abbreviations: ant, antenna; epiphar b, epipharyngeal bar; eyesp, eyespot; hyphar pct, hypopharyngeal pecten; hyps, hypostoma; lbr, labrum; lig, ligula; md, mandible; mx plp, maxillary palpus; pagl, paraglossa; palb plt, paralabial plate; premd, premandible; tm, torma.



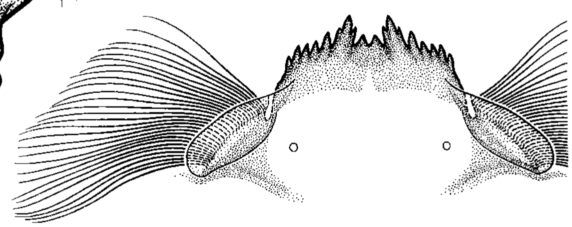
121 Protanypus sp.



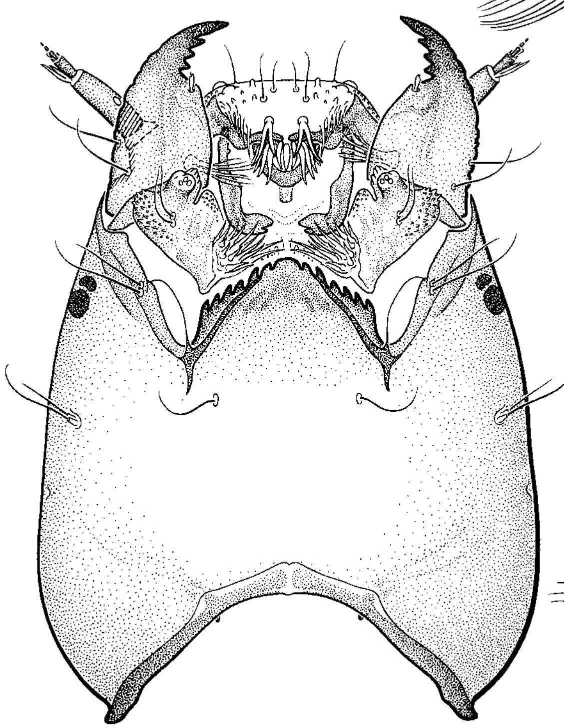
123 Rheocricotopus sp.



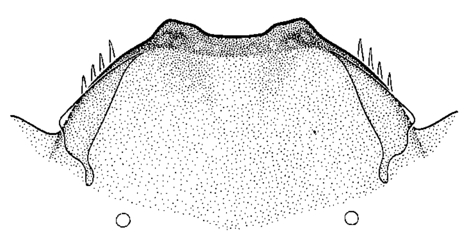
124 Paraclunio alaskensis



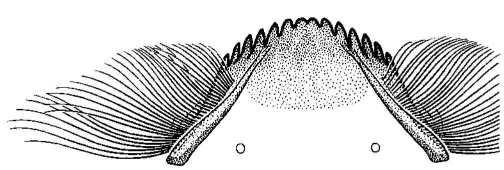
125 Prodiamesa olivacea



122 Cricotopus sp.

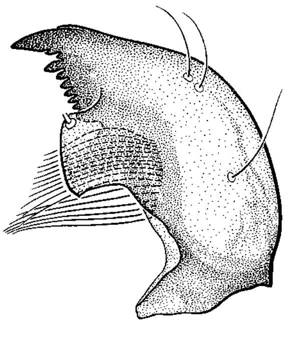


126 Symbiocladius equitans

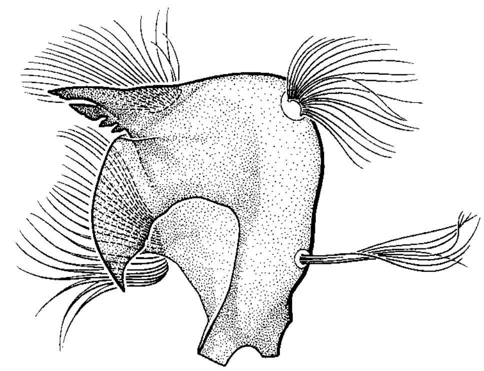


127 Diplocladius cultriger

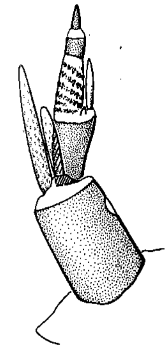
Figs. 29.121–127. Details of fourth instar larval head capsule: ventral aspects of head capsule (*concluded*) of (121) ***Protanypus*** sp. and (122) *Cricotopus* sp.; hypostoma of (123) *Rheocricotopus* sp., (124) *Paraclunio alaskensis* (Coquillett), (125) *Prodiamesa olivacea* (Meigen), (126) *Symbiocladius equitans* (Claassen), and (127) *Diplocladius cultriger* Kieffer (*continued*).



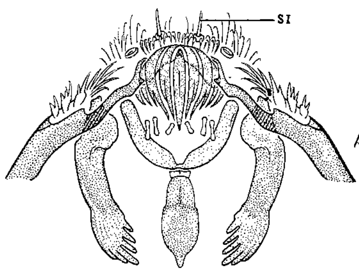
128 Lasiodiamesa sp.



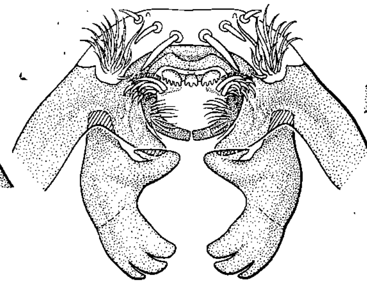
129 Odontomesa sp.



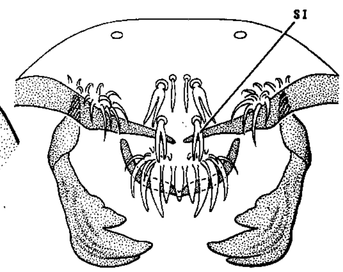
130 Diamesa sp.



131 Diamesa sp.

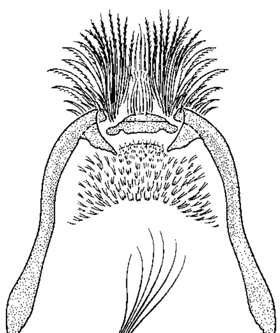


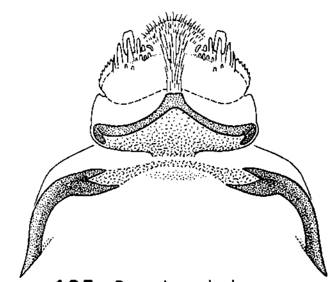
132 Paraclunio alaskensis



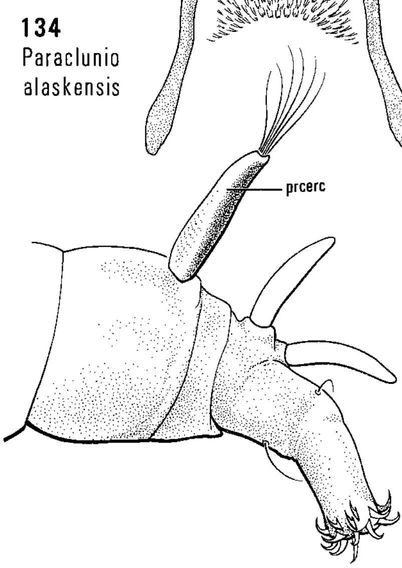
133 Pseudosmittia sp.

134 Paraclunio alaskensis

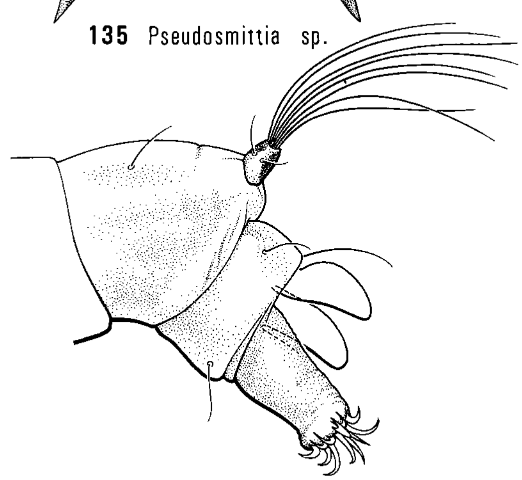




135 Pseudosmittia sp.



136 Trichotanypus posticalis



137 Hydrobaenus johannseni

Figs. 29.128–137. Details of head capsule (*concluded*) and terminalia of fourth instar larva: mandible of (128) *Lasiodiamesa* sp. and (129) *Odontomesa* sp.; (130) antenna of *Diamesa* sp.; labral setae and premandibles of (131) *Diamesa* sp., (132) *Paraclunio alaskensis* (Coquillett), and (133) *Pseudosmittia* sp.; hypopharynx of (134) *Paraclunio alaskensis* and (135) *Pseudosmittia* sp.; terminalia of (136) *Trichotanypus posticalis* (Lundbeck) and (137) *Hydrobaenus johannseni* (Sublette).

Abbreviations: prcerc, procercus; SI, seta 1.

140. Scutum with scutal suture depressed (Fig. 28). Wing dark, usually with light markings (Fig. 15) .... ***Chasmatonotus*** Loew
   12 spp.; Alaska to California, Ontario to Newfoundland south to North Carolina; Rempel 1937, Arntfield 1977

   Scutum smooth; scutal suture not depressed. Wing unmarked 141

141. Apex of antenna with a single straight strong seta (Fig. 23). Anal point long and narrow (Fig. 109) .... ***Smittia*** Holmgren, in part
   see couplet 104

   Apex of antenna without a single straight seta, but sometimes with several curved weak setae. Anal point short or absent 142

142. Scutum without medial tuft of acrostichal setae or scutal tubercle .... ***Krenosmittia*** Thienemann
   2 spp.; British Columbia, Alberta, Yukon, Northwest Territories

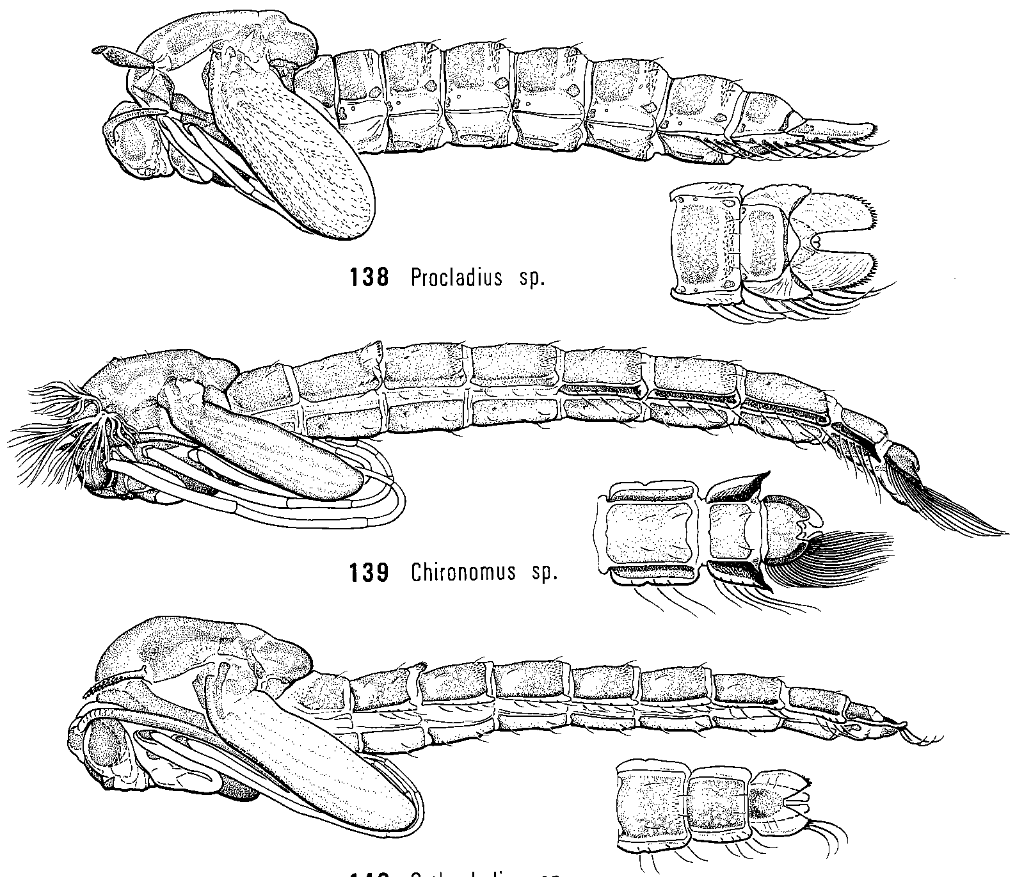
   Scutum with medial tuft of acrostichal setae (Fig. 45) or scutal tubercle (as in Fig. 41) 143

143. Anal point on dorsal surface of tergite 9 not extending distal to posterior margin of tergite .... ***Pseudosmittia*** Goetghebuer
   1 sp., *setavena* Saether; British Columbia, Ontario, New Brunswick; Saether 1969

   Anal point extending distally beyond posterior margin of tergite 9 144

144. Apex of antenna truncated. Anal point short, narrow, and parallel-sided with blunt apex .... ***Phycoidella*** Saether
   1 sp., *dentolatens* Saether; Ontario; Saether 1971*b*

   Apex of antenna pointed or angular. Anal point longer and broader, usually broadly rounded (Fig. 110), occasionally pointed 145



138 Procladius sp.

139 Chironomus sp.

140 Orthocladius sp.

Figs. 29.138–140. General views of pupae, with enlargements of terminalia: (138) *Procladius* sp.; (139) *Chironomus* sp.; (140) *Orthocladius* sp.

145. R_{2+3} running close to or partly fused with R_{4+5} .... ***Parakiefferiella*** Thienemann
2 spp.; widespread in Canada

R_{2+3} running about midway between R_1 and R_{4+5} 146

146. Anal point apically broadly rounded. R_{4+5} ending distal to apex of CuA_1 .... ***Epoicocladius*** Zavřel
1 sp., *flavens* (Malloch); Saskatchewan to Quebec, Illinois, Michigan, Northwest Territories; Saether 1969

Anal point apically pointed. R_{4+5} ending proximal to apex of CuA_1 .... ***Mariocladius*** Sublette
1 sp., *subaterrimus* (Malloch); Illinois; Sublette 1970

TELOMATOGETONINAE

147. Palpus five-segmented. Fifth tarsomere simple or weakly bilobate at tip .... ***Thalassomyia*** Schiner
1 sp., *bureni* Wirth; coastal Florida; Wirth 1949

Palpus two- or three-segmented. Fifth tarsomere deeply trilobate at tip (Fig. 49) 148

148. Fore femur swollen with angular projection that interlocks with basal projection of fore tibia; leg setae strong, sometimes flattened as appressed scales .... ***Paraclunio*** Kieffer
3 spp.; coastal California, Oregon, British Columbia, Alaska; Wirth 1949

Fore femur unmodified; leg setae weaker, never flattened as appressed scales .... ***Telmatogeton*** Schiner
2 spp.; coastal New York, Florida, California; Wirth 1949

Key to subfamilies

Larva

1. Antenna retractile into head capsule socket (Figs. 114, 117, 118). Separate four- to eight-toothed ligula and paired paraglossae present (Figs. 117, 118). Hypostoma membranous, sometimes flanked by toothed plates (Fig. 118) or rows of teeth.......................... **Tanypodinae**

Antenna nonretractile. Separate ligula and paired paraglossae absent (Figs. 119–122). Hypostoma sclerotized, almost always toothed (Figs. 119–122) 2

2. Procercus at least five times as long as wide (Fig. 136). Premandible absent; mandible with at least six inner teeth (Fig. 128) .... **Podonominae**

Procercus, if present, less than five times as long as wide, usually less than three times (Fig. 137). Premandible almost always present; mandible generally with less than six inner teeth 3

3. Paralabial plates distinct, almost always striated, never with setae (Figs. 118, 119). Eyespots usually separate and in vertical plane (Figs. 118, 119), but sometimes dorsal eyespot situated anterior to ventral eyespot .... **Chironominae**

Paralabial plates, if present, usually reduced, never striated, with or without setae (Figs. 122, 123, 126, 127). Eyespots single or separate; if separate, dorsal eyespot always posterior to ventral eyespot 4

4. Preanal abdominal segment with a pair of procerci each bearing apical setae longer than length of procercus (Fig. 137) 5

Preanal abdominal segment without procerci (Fig. 116); setae, if present, usually shorter and arising directly from dorsolateral area of segment 8

5. Third antennal segment annulate (Fig. 130). Premandible frequently distally palmate (Fig. 131) .... **Diamesinae**, in part

Third antennal segment nonannulate. Premandible simple or bifid, or with more than two teeth; if with more than two teeth, then premandible not palmate but having subapical teeth on median margin (Fig. 133) 6

6. Occipital margin of head with distinct posteriorly directed projection on each side (Fig. 121); head capsule with numerous setae (Fig. 121); hypostoma without central teeth (Fig. 121) .... **Diamesinae**, in part

Occipital margin of head without or with small posteriorly directed projection on each side (Fig. 122); setae less numerous or numerous, but if numerous, then hypostoma having central teeth; hypostoma variable, usually with central teeth 7

7. Paralabial plates large, bearing setae that usually form a dense patch (Fig. 125); central part of hypostoma emarginate (Fig. 125), or if not centrally emarginate, then mandible circular (Fig. 129) .... **Diamesinae**, in part

Paralabial plates, if present, smaller, with[12] or without setae (Figs. 123, 126, 127); hypostoma variable, but usually convex (Figs. 123, 126, 127); mandible never circular .... **Orthocladiinae**, in part

8. Hypostoma with single median tooth, usually subtriangular (Fig. 124), occasionally rounded and with five or more pairs of lateral teeth; SI simple (Fig. 132). Hypopharynx with continuous beard of long setae (Fig. 134) .... **Telmatogetoninae**[13]

Hypostoma with paired median teeth, one median tooth, or none at all (Fig. 126), and usually with four pairs of lateral teeth; if hypostoma with a single median tooth and five pairs of lateral teeth, then SI bifurcate (as in Fig. 133). Hypopharnyx with scales and without a beard of long setae (Fig. 135) .... **Orthocladiinae**, in part

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[12] *Diplocladius*, a genus in Orthocladiinae, has fairly large paralabial plates bearing a long, dense patch of setae (Fig. 127); however, the hypostoma is convex, with a pair of median teeth.

[13] Most of the larvae that key to couplet 8 live in coastal, brackish water or in semiterrestrial to terrestrial habitats.

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PELECORHYNCHIDAE 30

H. J. TESKEY

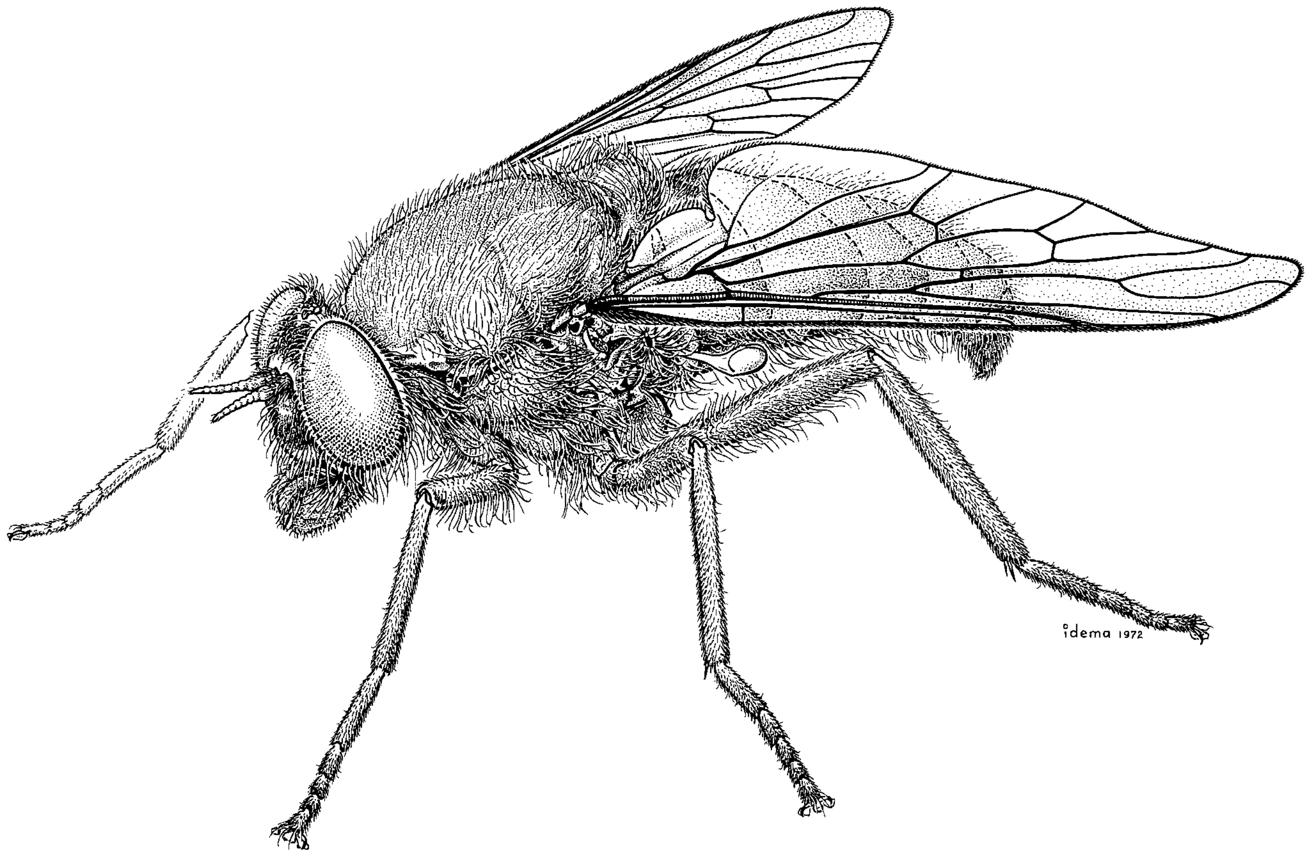


Fig. 30.1. Female of *Bequaertomyia jonesi* (Cresson).

Flies moderate to large in size, 4–18 mm long, usually with brown to black opaque unmarked bodies (Fig. 1). Clypeus and parafacial usually strongly swollen and convex. Antenna porrect with stylate flagellum. Wing clear to moderately infuscated; calypter large. Empodia pulvilliform.

Adult. Head: large, as wide as or wider than thorax, and flattened ellipsoidal in shape viewed from above. Eyes holoptic in male, well-separated in female (Figs. 1, 4); each one large and uniformly colored, hairy only in *Bequaertomyia* Brennan; facets subequal. Three well-developed ocelli on vertex. Antenna porrect and subulate, three-segmented; scape and pedicel simple; flagellum stout, stylate, primitively with eight flagellomeres, although in *Glutops* Burgess these may be variously fused; first flagellomere largest, sometimes lengthened and constricted medially (Figs. 1, 4). Face broad; median clypeus or parafacial sclerites, or both, prominent and strongly convex, separated from each other by deep clefts (Fig. 4). Proboscis shorter than length of head, with large labella; mandible variously reduced or absent. Palpus similar in both sexes, two-segmented; both segments cylindrical and subequal in length, or second segment slightly longer and usually wider than first. Head hairs prominent especially in males, longer and denser on facial regions and on palpi.

Thorax: scutum nearly as broad as long; postpronotum small; transverse suture shallow, incomplete, ending at dorsocentral line; prescutal declivity absent or very weakly indicated; notopleuron and prealar callus not distinctly defined; small prescutellum and postscutellum developed. Scutum, scutellum, proepisternum, and mesepisternum more or less prominently hairy, with hairs sometimes very colorful (*Pelecorhynchus* Macquart); anepimeron, meron, metapleuron (except for a small clump of hairs on metepisternum), and laterotergite bare of hairs, except in *Bequaertomyia* where laterotergite, especially, is densely hairy. Legs strong; diameter of all three legs subequal; tibia and femur of hindleg longer than those of midleg and foreleg; tibial spur formulae 0–2–2, 1–2–2, and 0–2–1 in *Pelecorhynchus*, *Bequaertomyia*, and *Glutops*, respectively; empodia pulvilliform. Wing with typical tabaniform venation (Figs. 2, 3), but with cell cu*p* narrowly open at wing margin and A_1 more or less sinuate; calypter large, with fringe of long hairs.

Abdomen: convex dorsally, about as broad as thorax, suboval although more or less strongly tapered behind. Five to seven segments usually exposed, first four exposed in female and first five in male; most prominent of remaining segments telescoped within one another. Seven pairs of spiracles.

Female terminalia with two-segmented cerci; first segment of cercus with a ventrally attenuated lobe. Three spermathecae present.

Male terminalia differing in *Pelecorhynchus* from those in *Glutops* and *Bequaertomyia*. In *Glutops* and *Bequaertomyia*, sternite 8 small, thereby leaving gonopods exposed ventrally; sternite 9 triangular, closely attached to base of gonocoxites; gonostylus simple; aedeagus with a simple intromittent organ enclosed in a simple unarmed sheath. In *Pelecorhynchus*, sternite 8 large, covering gonopods ventrally, and deeply notched apically; sternite 9 slender, strap-shaped; gonostylus bifurcate; aedeagal sheath with two stout dorsally curved apical spines.

Larva. Translucent white, elongate cylindrical, pointed at both ends, with 11 similar segments that are incapable of telescoping (Fig. 5).

Head capsule capable of complete invagination within thorax, and rather similar in structure to Tabanidae and Rhagionidae but differing most notably from them in having stout spines located laterally on labrum and apically on maxilla (Mackerras and Fuller 1942, Teskey 1970*a*).

Integument thick, with a glossy sheen, waxy and firm to touch, and perfectly smooth; striations, projections, or other surface irregularities lacking except for moderately swollen lobes laterally flanking an anal slit that is located ventrally on terminal segment. Respiratory system propneustic or apneustic (*Glutops*), or amphipneustic (*Pelecorhynchus*); anterior spiracles present in *Glutops*, but probably not functional; posterior spiracles when present located on upper surface of a transverse cleft in apex of terminal segment.

Biology and behavior. Larvae have been found in saturated soil of swamps or stream banks and apparently prey on other invertebrates. Mature larvae move to dryer soil to pupate. Adults of a few species are known to feed on flowers.

Classification and distribution. The family was erected by Mackerras and Fuller (1942) for *Pelecorhynchus*, a genus of 34 Australian and Chilean species that was originally placed in the Tabanidae. Philip (1965) transferred the monotypic western North American genus *Bequaertomyia* (as *Pseudoerinna* Shiraki in Nagatomi 1975) from the Coenomyiidae. *Glutops*, with seven Nearctic and four eastern Palaearctic species, has been at different times placed in the Rhagionidae, the Coenomyiidae, and the Xylophagidae, and in a monotypic family of its own; it was transferred to the Pelecorhynchidae by Teskey (1970*a*) mainly because of similarities shown to exist in the larvae. The systematics of this family and other primitive Brachycera that have pulvilliform empodia and unspecialized antennae and wing venation is still unsettled and will probably not be stabilized until more is known of the immature stages.

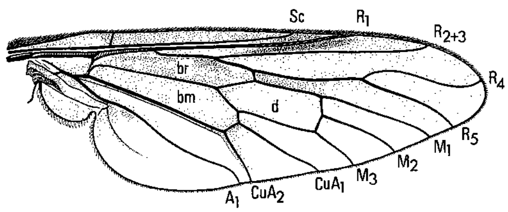
Key to genera

1. R_{2+3} or R_4, or both, curving strongly to anterior; A_1 sinuous (Fig. 2). Apical palpal segment usually less than twice as long as diameter, or if slightly longer than this, differing in color and wider than basal segment. Flies medium to large, longer than 10 mm 2

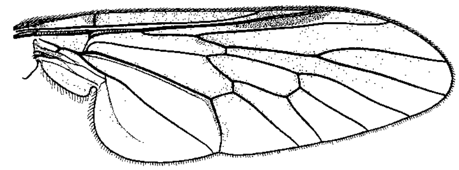
   R_{2+3} and R_4 proceeding straight to margin; A_1 rather straight (Fig. 3). Apical palpal segment more than twice as long as diameter, concolorous with and same diameter as basal segment. Flies smaller, less than 10 mm long .... ***Glutops*** Burgess
   11 spp., 7 Nearctic; Teskey 1970*b*

2. Scutum and abdomen usually with attractive and prominent markings. Portions of thorax and head, not including meropleurite and laterotergite, with distinctly colored tufts of silky hair. Eye bare .... ***Pelecorhynchus*** Macquart
   34 spp.; Australia and Chile, none Nearctic; Mackerras and Fuller 1942

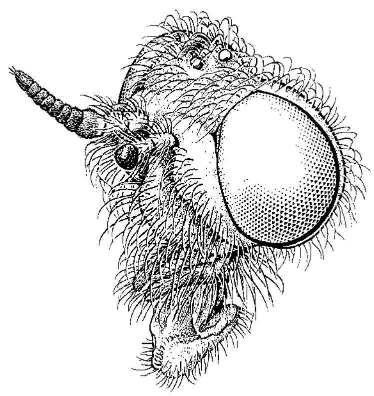
   Scutum and abdomen dark and lacking distinctive markings. Hairs of thorax and head, including tufts on meropleurite and laterotergite, concolorous with integument. Eye hairy...... .... ***Bequaertomyia*** Brennan
   1 sp., *jonesi* (Cresson); west Nearctic



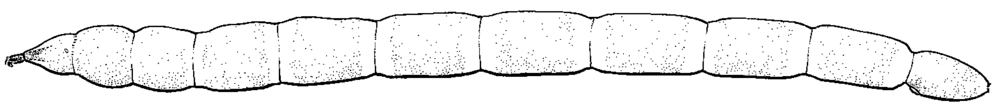
2 Bequaertomyia jonesi ♀



3 Glutops rossi ♀



4 Glutops bandus ♀



5 Glutops rossi

Figs. 30.2–5. Pelecorhynchidae: wing of (2) *Bequaertomyia jonesi* (Cresson) and (3) *Glutops rossi* Pechuman; (4) head of *Glutops bandus* Teskey; (5) lateral view of larva of *Glutops rossi*.

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TABANIDAE 31

L. L. Pechuman and H. J. Teskey

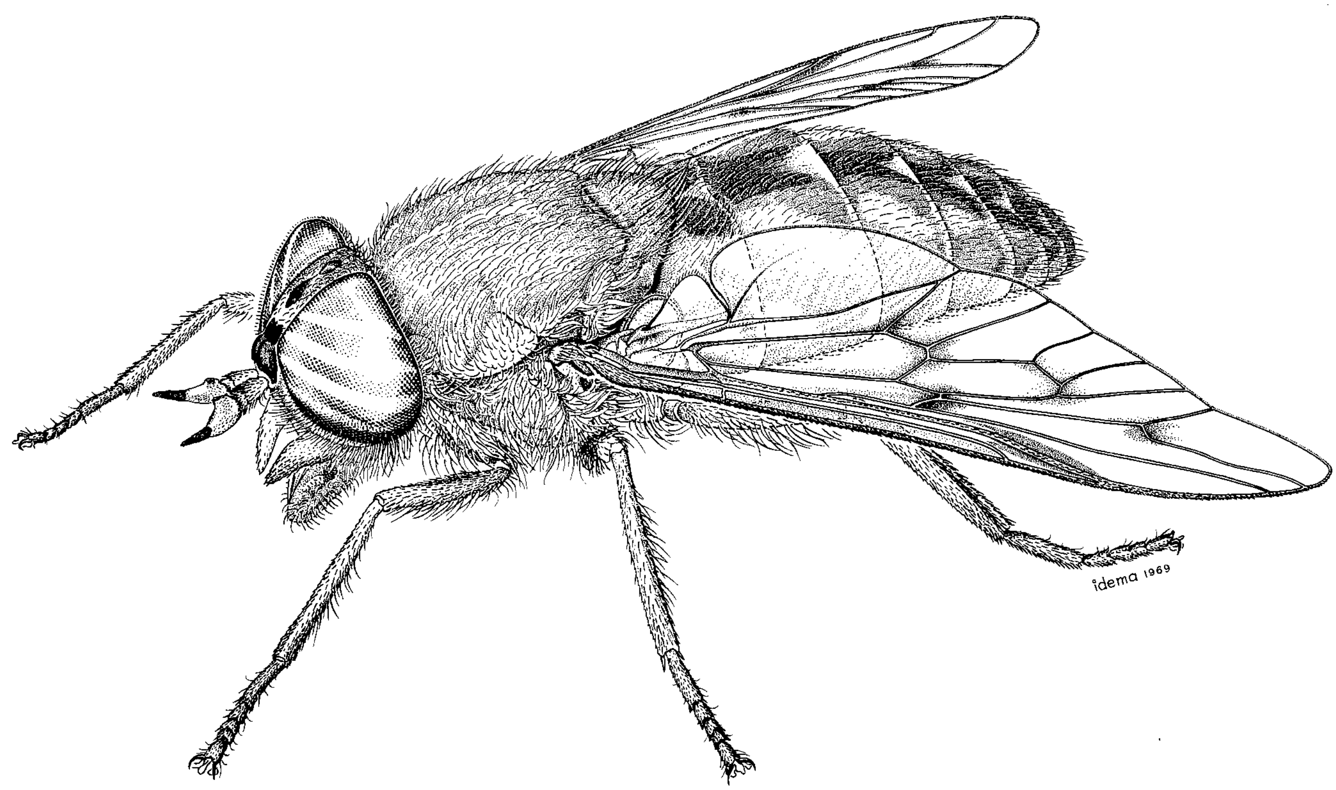


Fig. 31.1. Female of *Hybomitra lasiophthalma* (Macquart).

Moderate to large flies, 6–30 mm long, without bristles (Fig. 1). Flagellum with annuli. Empodia pulvilliform. Calypter large.

Adult. Head: large. Eyes large, often brightly patterned, holoptic in male, separated by frons in female. Frons sometimes bearing one or more shining areas designated as frontal calli (Figs. 9–11). Antenna (Figs. 12–27) porrect and composed of scape, pedicel, and flagellum; flagellum usually consisting of a larger basal portion and terminal annulations usually numbering four to eight but sometimes as few as two; subcallus (Figs. 7–9), from which antenna arises, usually inconspicuous, but sometimes bare and shining, rarely inflated. Palpus composed of two segments; basal palpal segment usually rather small; other palpal segment usually rather long and curved downward in female, often inflated near base. Proboscis stout and rigid; mandible and maxilla of female often styliform and adapted for piercing, but sometimes absent in species that are not bloodsuckers.

Thorax: large; notopleural lobe prominent; scutellum without spines or macrotrichia. Legs rather stout; apical spurs present on mid tibia, absent on fore tibia, and present or absent on hind tibia; tarsi each with three pads formed by a pulvilliform empodium located between two pulvilli. Wing venation (Fig. 30) rather primitive and very consistent throughout family (Figs. 28–38) with as many as 11 veins reaching margin (Sc, four branches of R, three branches of M, CuA_1, CuA_2, A_1), C extending around wing, cells br, bm, and d conspicuous, and cell cu*p* usually closed near wing margin. Wing membrane often darkened to various extent and intensity, and with a variety of distinctive patterns.

Abdomen: broad, often with a distinct pattern, with seven segments usually visible. Terminalia of both sexes (Figs. 41–50) usually inconspicuous. Male with gonocoxites fused with sternite 9, and with gonostylus single or partially divided; aedeagus and associated pair of slender filamentous recurved aedeagal tines enclosed in a sheath apparently derived from the parameres (as in Fig. 32.6); tergite 9 entire or divided; tergite 10 absent; cercus flattened, round to oval or somewhat pointed. Female usually with tergite 10 divided, with sternite 8 shield-shaped, and with cercus one-segmented.

Egg. Fusiform, 1.5–2.5 mm long, all cemented side by side at an angle of less than 90° to substrate by end opposite micropyle; arrangement often very symmetric, in one to two or three tiers. Egg masses neat, compact, containing up to several hundred eggs, and deposited on vegetation overhanging water or wet soil; characteristics somewhat species-specific, but differences not yet properly systematized.

Larva. Fusiform (Chrysopsinae, Tabaninae) (Figs. 51, 52) or more or less expanded posteriorly or anteriorly (Pangoniinae) (Figs. 53, 54), comprising 11 body segments and a completely retractile head capsule.

Head capsule (Figs. 56, 57) elongate, subcylindrical, tapering anteriorly. Features including semitubular cranium; paired tentorial arms attached anteriorly to inner dorsal surfaces of cranium and appearing to be free posteriorly; three-segmented antennae; median down-curved labrum; mandibular–maxillary sclerites, including maxillary palpi; and labium closing head capsule ventrally. Mandibles each with central canal for excretion of a paralytic enzyme, and linked with subdorsal brushes of spines that are erected to anchor head within host when mandibles strike downward.

Body without projecting appendages on thoracic segments, but with annular rings of small tubercles and crenulate frills or with prolegs on abdominal segments. Prolegs usually with apical spicules, or in those few species inhabiting swiftly flowing streams, with one or more concentric rows of hook-like spines or crochets; three or four pairs of prolegs present on each segment, arranged dorsally, laterally, ventrally, and, when fourth pair present, ventrolaterally. Integument with prominent longitudinal striations, or with areas of dense micropubescence or a scale-like reticulate pattern (Pangoniinae) on one or more body segments, usually confined to anterior or posterior border of segments or bordering prolegs posteriorly, but sometimes with pubescence covering entire body. Respiratory system functionally metapneustic; remnants of anterior spiracles sometimes evident dorsolaterally between prothorax and metathorax; visible elements of posterior spiracles either in form of closely appressed vertically linear bars or a blade-like spine (Figs. 55, 58, 59) at apex of a distinctly projecting respiratory siphon (Chrysopsinae, Tabaninae), or a circularly delineated area at apex of terminal segment (Pangoniinae).

Pupa. Obtect, with head, thoracic, and abdominal divisions and appendage sheaths distinct (Fig. 61). Head (Figs. 61, 63) usually with a distinct medially divided antennal ridge, but sometimes in form of paired tubercles between antennal sheaths; paired calli and vertical tubercles bearing setae anteriorly on head; paired anterior and posterior orbital setae and two pairs of lateral orbital setae sometimes arising from small tubercles on face. Anterior spiracle simply curved or shaped like a question mark, mounted on a spiracular mound of variable size. Mesothorax with two or three pairs of notal setae and one or two pairs of basal alar setae. Wing sheath extending to second abdominal segment and equal in length to leg sheaths. Metanotum with three to five pairs of setae, one or two pairs always behind posterior basal angle of wing sheath. Abdominal segment 1 usually with two pairs of tergal and three pairs of pleural hairs or spines or occasionally with a complete or abbreviated fringe of spines (Figs. 61, 62, 64). Abdominal segments 2–7 with encircling fringe of spines arranged in one or two series; anterior spines in fringe of each segment usually distinctly shorter, though sometimes much stouter than adjacent posterior spines. Terminal abdominal segment terminating in an aster of one to three pairs of stout pointed spine-like tubercles.

Biology and behavior. Most adult female Tabanidae feed on the blood of warm-blooded animals, but a few species are known to attack cold-blooded vertebrates. Several species in all three subfamilies are not hematophagous. These, as well as the females that are blood feeders and males that are not hematophagous, are known to visit flowers. The annoyance and loss of blood suffered by domestic and wild animals and man from attacks of Tabanidae make these flies serious economic pests. Besides the problems resulting from direct attacks, the Tabanidae are also vectors for several disease-producing organisms that affect man and animals. Bacteria, viruses, rickettsiae, Protozoa, and filarial worms can be transmitted by them, causing such diseases as anthrax, tularemia, anaplasmosis, various forms of trypanosomiasis, Q fever, and filariasis. Transmission is usually mechanical, but *Loa loa* (Cobbold), for example, the causative agent of an important filarial disease in Africa, undergoes development within the insect vector. Most of these diseases except tularemia and anaplasmosis are absent or unimportant in North America. Although arboviruses have been isolated from Tabanidae in North America, the role of Tabanidae in their transmission is not well known at present.

Larvae of most species inhabit wetland soil such as is found in freshwater and saline marshes and bogs, and at margins of streams and ponds. A few species are restricted to sand and gravel in the beds of swiftly flowing streams. Others, including some of the most common species, have invaded drier but still marginally arable land. Larvae of most species apparently prey on other invertebrates and annelids. The feeding habits of many species, including most *Chrysops*, are unknown. Larvae grow through up to nine instars and usually require almost a year to do so; some species, however, complete two generations a year and others, particularly in northern regions, require two or more years to complete their development. The pupal period requires 1 or 2 wk.

Mating of adults usually occurs shortly after emergence. Individuals or small groups of males establish a station where they hover in flight. Females come to the station and are pursued by the males.

Oviposition of some species depends on the female taking a blood meal as nourishment for egg maturation. Many species, however, are autogenous for the first ovarian cycle; enough food reserves are passed on through the pupa for the first batch of eggs. However, blood must be taken for any subsequent egg development.

The larval and pupal keys given here are based on descriptions of immature stages by Burger (1977), Goodwin (1972, 1973*a*, 1973*b*, 1973*c*, 1974), Lane (1975), Teskey (1969), Teskey and Burger (1976), Tidwell (1973), and Tidwell and Tidwell (1973).

Classification and distribution. Two subfamilies of Tabanidae, the Pangoniinae and Tabaninae, were recognized by Loew (1860). Much more complex classifications were proposed by Lutz (1909, 1913) and Enderlein (1922, 1925). These classifications often did not show true relationships and had other contradicting features. Attempts to adapt these classifications for various areas, including the Nearctic (Philip 1941, 1947, 1950), were made by several workers.

Mackerras (1954) believed that a false impression of relationships resulted from classifications then in use and proposed a new classification of four subfamilies. One of these, the Scepsidinae with no Nearctic forms, is now considered invalid. He removed *Chrysops* Meigen and related genera from the Pangoniinae and formed the subfamily Chrysopsinae,[1] which he regarded as more closely related to the Tabaninae than to the Pangoniinae. Mackerras used genitalic characters to separate his subfamilies and tribes and was generally able to correlate these with differences in external morphology. Subsequent papers by Mackerras (1955) presented additional details on the classification of the Pangoniinae and Chrysopsinae. His classification currently has general acceptance by workers throughout the world (Fairchild 1969; Leclercq 1960, 1966; Oldroyd 1954, 1957; Philip 1957; Travassos Dias 1966).

[1] Mackerras used Chrysopinae, but because this name has earlier usage in the Neuroptera, Chrysopsinae is preferable.

Two of the three tribes of Pangoniinae have Nearctic representatives: the Pangoniini, which includes *Apatolestes* Williston, *Asaphomyia* Stone, *Brennania* Philip, *Esenbeckia* Rondani, *Pilimas* Brennan, and *Stonemyia* Brennan; and the Scionini, which is represented by *Goniops* Aldrich with a single species. Two of the three tribes placed in the Chrysopsinae are found in the Nearctic: the Bouvieromyiini, with the one genus *Merycomyia* Hine; and the Chrysopsini, with the genera *Chrysops* Meigen, *Neochrysops* Walton, and *Silvius* Meigen. All three tribes assigned to the Tabaninae have Nearctic genera: the Diachlorini, with *Anacimas* Enderlein, *Bolbodimyia* Bigot, *Chlorotabanus* Lutz, *Diachlorus* Osten Sacken, *Leucotabanus* Lutz, *Microtabanus* Fairchild, *Stenotabanus* Lutz, and possibly *Holcopsis* Enderlein; the Haematopotini, with *Haematopota* Meigen; and the Tabanini, with *Agkistrocerus* Philip, *Atylotus* Osten Sacken, *Hamatabanus* Philip, *Hybomitra* Enderlein, *Tabanus* Linnaeus, and *Whitneyomyia* Bequaert.

The Tabanidae are found in most parts of the world, sometimes in great numbers. They are found on all continents except Antarctica and are unreported from Hawaii, Greenland, and Iceland. Their range extends from the Arctic Ocean to the Straits of Magellan, the southern tip of Africa, and New Zealand. Many common names have been applied to them; those in most general use in North America include horse fly, mule fly, deer fly, and greenheads; in the far north they are called bulldogs.

The species of Tabanidae found in the Nearctic are restricted to the area below the tree line. A few are Holarctic and some are closely related to Palaearctic species. Some genera such as *Bolbodimyia*, *Chlorotabanus*, *Diachlorus*, *Esenbeckia*, *Leucotabanus*, and *Stenotabanus* reach their greatest development in the Neotropical region, but are represented in southern or southwestern United States by a few species found only there or by species in common with Mexico or the Antilles. *Diachlorus ferrugatus* (Fabricius), a species found in Mexico and portions of Central America, ranges north in the eastern Nearctic to New Jersey.

Three species of fossil Tabanidae, apparently representing recent genera, have been described from the Miocene deposits of Colorado.

Keys to genera

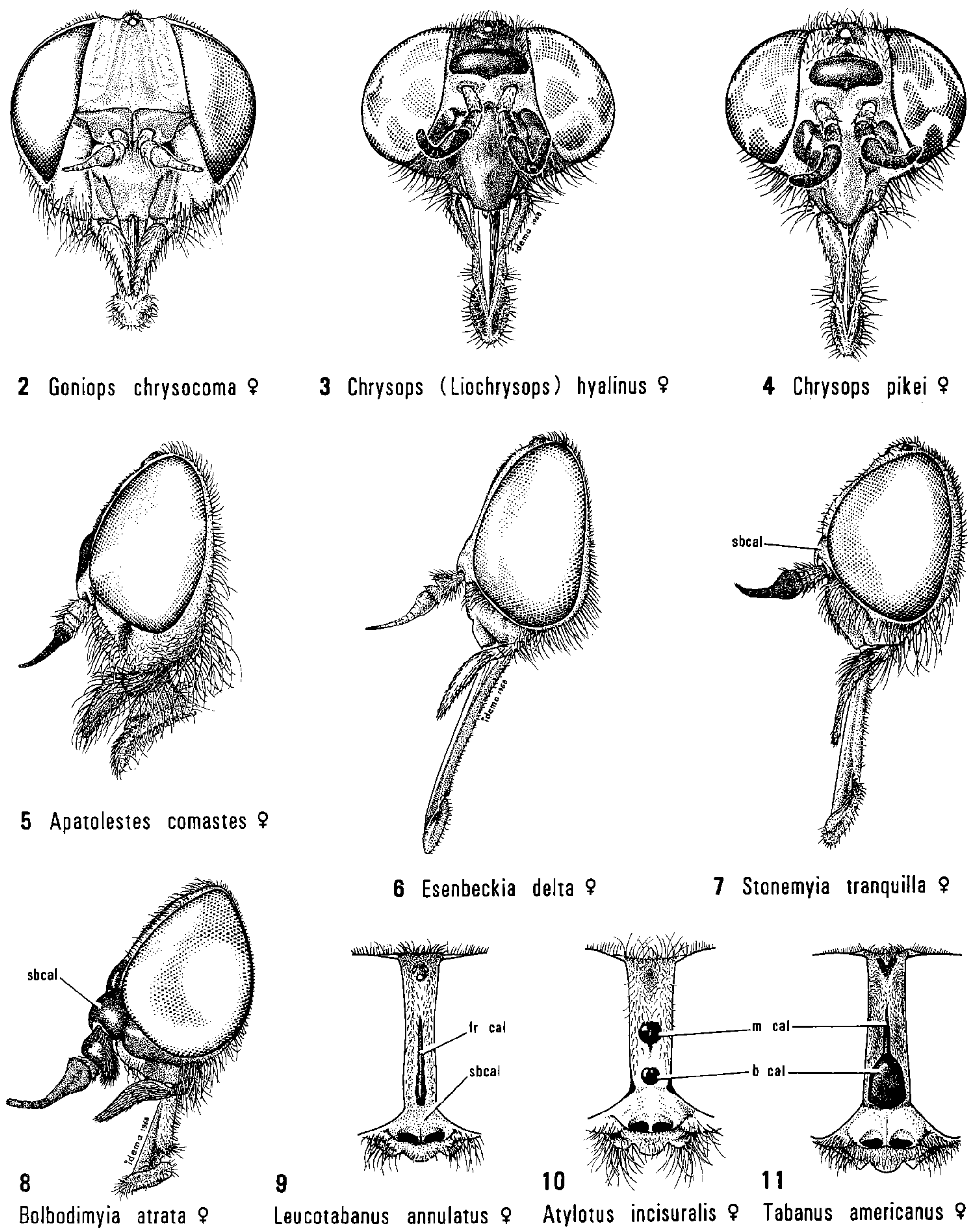
Adult

1. Hind tibia with apical spurs; these spurs quite small in some *Merycomyia* spp. Apex of gonostylus of male terminalia rather pointed, simple or bifid, never truncate. Ends of spermathecal ducts in female not expanded 2

   Hind tibia without apical spurs. Male gonostylus truncate. Ends of spermathecal ducts in female with mushroom-like expansions .... TABANINAE.... 16
   Stone 1938

2. Flagellum composed of a basal segment plus four or fewer flagellomeres (Fig. 12) that never form a stylus. Tergite 9 divided in both sexes (Figs. 41, 45). Gonostylus of male terminalia simple and pointed (Fig. 47) .... CHRYSOPSINAE....9
Philip 1954, 1955

Flagellum usually divided into seven or eight apparent flagellomeres (Fig. 13), or rarely bearing a rod-like stylus with indistinct annulations (Fig. 14). Tergite 9 undivided in both sexes (Figs. 42–44, 46). Gonostylus ot male terminalia simple (Fig. 50) or bifid (Figs. 48, 49) .... PANGONIINAE....3
Philip 1954



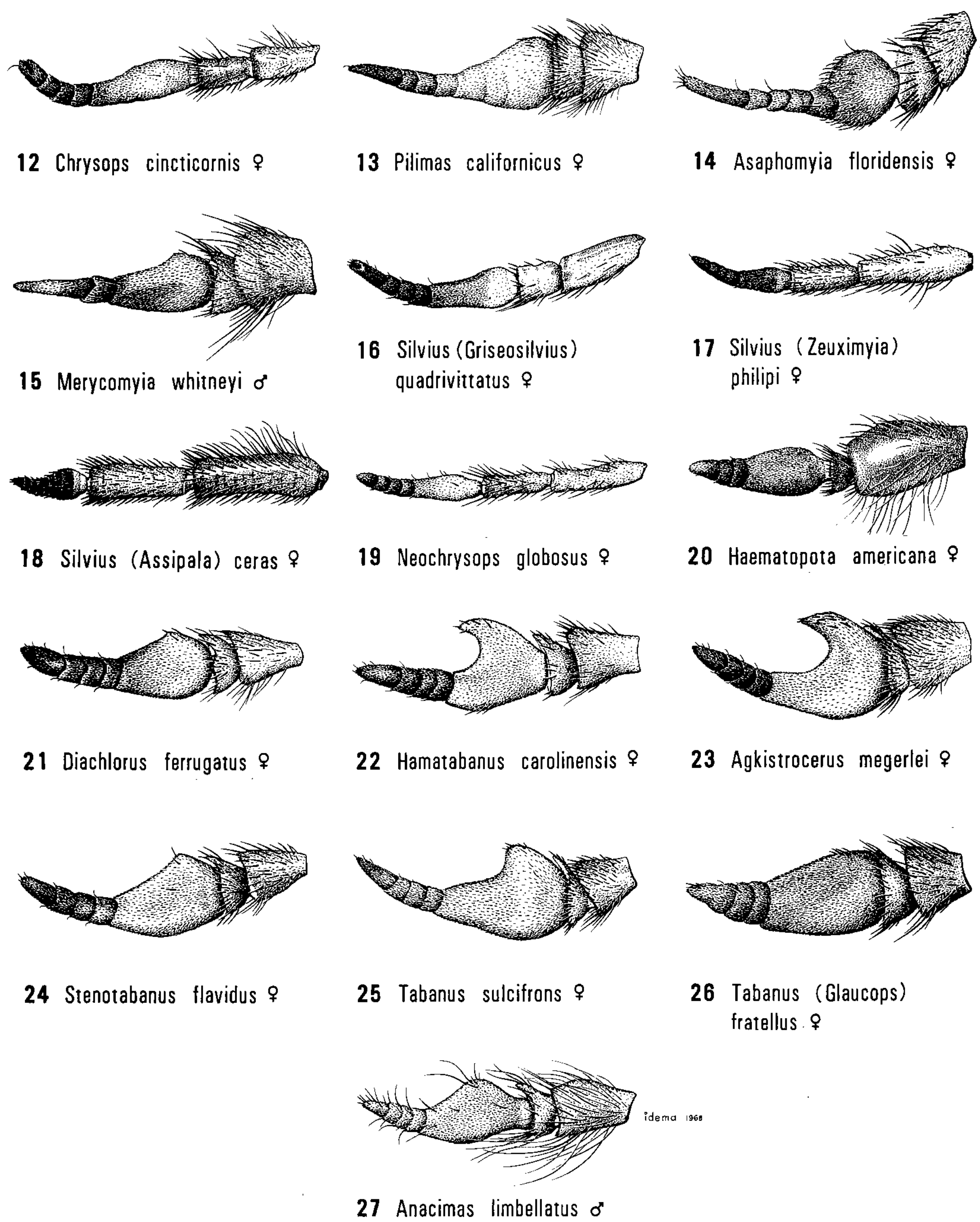
Figs. 31.2–11. Heads: frontal view of (2) *Goniops chrysocoma* (Osten Sacken), (3) *Chrysops* (*Liochrysops*) *hyalinus* Shannon, and (4) *Chrysops pikei* Whitney; lateral view of (5) *Apatolestes comastes* Williston, (6) *Esenbeckia delta* (Hine), (7) *Stonemyia tranquilla* (Osten Sacken), and (8) *Bolbodimyia atrata* (Hine); frons of (9) *Leucotabanus annulatus* (Say), (10) *Atylotus incisuralis* (Macquart), and (11) *Tabanus americanus* Forster.

Abbreviations: b cal, basal callus; fr cal, frontal callus; m cal, median callus; sbcal, subcallus.

3. Eye of female with upper inner angle acute and with width narrower than frons (Fig. 2). Wing in both sexes with dark picture anteriorly (Fig. 28). Gonostylus of male terminalia simple (Fig. 50) .... SCIONINI....*Goniops* Aldrich

1 sp., *chrysocoma* (Osten Sacken); eastern

Wing and eye not with above combination of characters. Stylus of male terminalia bifid (Figs. 48, 49) .... PANGONIINI....4



Figs. 31.12–27. Antennae: (12) *Chrysops cincticornis* Walker; (13) *Pilimas californicus* (Bigot); (14) *Asaphomyia floridensis* Pechuman; (15) *Merycomyia whitneyi* (Johnson); (16) *Silvius* (*Griseosilvius*) *quadrivittatus* (Say); (17) *Silvius* (*Zeuximyia*) *philipi* Pechuman; (18) *Silvius* (*Assipala*) *ceras* (Townsend); (19) *Neochrysops globosus* Walton; (20) *Haematopota americana* Osten Sacken; (21) *Diachlorus ferrugatus* (Fabricius); (22) *Hamatabanus carolinensis* (Macquart); (23) *Agkistrocerus megerlei* (Wiedemann); (24) *Stenotabanus flavidus* (Hine); (25) *Tabanus sulcifrons* Macquart; (26) *Tabanus* (*Glaucops*) *fratellus* Williston; (27) *Anacimas limbellatus* Enderlein.

4. Basal flagellomere short and stout; terminal flagellomeres long and style-like, sometimes with indistinct sutures (Fig. 14). Palpus stout and densely haired; proboscis very short. R_4 with an appendix (as in Figs. 29, 31, 36) .... ***Asaphomyia*** Stone
   2 spp.; Texas, Florida; Pechuman 1974
   Not with above combination of characters 5

5. Proboscis stout and about half height of head, with large fleshy labella; palpus nearly same length as proboscis (Fig. 5) 6
   Proboscis often slender, nearly equal to or considerably longer than height of head; palpus conspicuously shorter than proboscis (Figs. 6, 7) 7

6. Eye hairy. Body very pilose .... ***Brennania*** Philip
   2 spp.; California
   Eye bare. Body moderately or not pilose .... ***Apatolestes*** Williston
   13 spp.; western; Philip 1954

7. Cell r_5 closed and often petiolate (Fig. 29) .... ***Esenbeckia*** Rondani
   4 spp.; southwest; Philip 1954
   Cell r_5 wide open to margin (Figs. 30, 31) 8

8. R_4 usually with an appendix (Fig. 31). Eye bare in female, with short hairs in male. Female cercus with an apical lobe (Fig. 42) or rather pointed (Fig. 43). Gonostylus of male terminalia without an outwardly projecting basal process (Fig. 48) .... ***Pilimas*** Brennan
   3 spp.; western
   R_4 usually without an appendix (Fig. 30). Eye bare in both sexes. Female cercus rounded (Fig. 44). Male gonostylus with an outwardly projecting basal process (Fig. 49) .... ***Stonemyia*** Brennan
   5 spp.; eastern and western; Philip 1954

9. Flagellum composed of a rather broad basal plate and two or three more flagellomeres (Fig. 15); scape only slightly longer than wide; total length of antenna equal to or shorter than head. Larger species with very small hind tibial spurs .... BOUVIEROMYIINI.... ***Merycomyia*** Hine
   2 spp.; eastern; Pechuman 1964
   Flagellum with a rather narrow basal portion and four more flagellomeres; scape usually at least twice as long as wide; total length of antenna longer than head (Figs. 12, 16–19). Hind tibial spurs pronounced .... CHRYSOPSINI....10

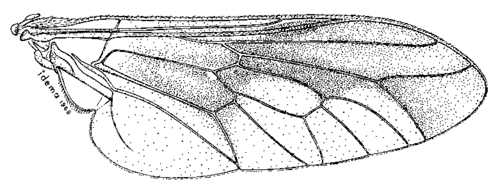
10. Abdomen globose, much wider than thorax, with two rows of dark spots. Wing rather evenly fumose (Fig. 32) .... ***Neochrysops*** Walton
   1 sp., *globosus* Walton; eastern
   Abdomen slender and variously marked or unpatterned. Wing only rarely evenly fumose 11

11. Wing hyaline or with isolated clouds (Fig. 33), rarely rather evenly fumose. Pedicel usually only about half length of scape; if subequal, flagellum shorter than scape (Figs. 16–18) .... ***Silvius*** Meigen....12
   Philip 1954
   Wing usually with at least a dark crossband (Figs. 34, 35); if wing unpatterned, gena without pollen (Fig. 3). Scape and pedicel subequal (Fig. 12) .... ***Chrysops*** Meigen....15
   Philip 1955

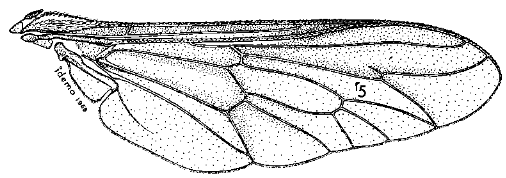
12. Flagellum longer than scape and pedicel combined (Fig. 16) 13
   Flagellum shorter than scape and pedicel combined, usually shorter than scape (Figs. 17, 18)..14

13. Stout yellowish species, with unspotted wing .... ***Silvius*** (***Silvius*** Meigen)
   2 spp.; western, eastern
   Slender grayish species, with spotted wing (Fig. 33) .... ***Silvius*** (***Griseosilvius*** Philip)
   9 spp.; western to midwestern

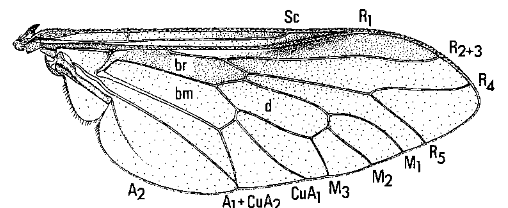
14. Antenna longer than width of head and as long as or longer than notum; flagellum usually shorter than pedicel but subequal in one extralimital species, and from one-half to two-thirds length of scape (Fig. 18) .... ***Silvius*** (***Assipala*** Philip)
   1 sp., *ceras* (Townsend); southwestern



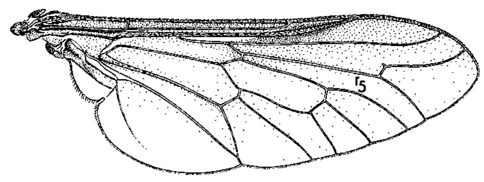
28 Goniops chrysocoma ♀



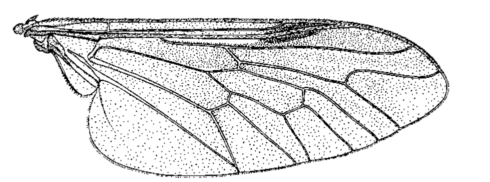
29 Esenbeckia delta ♂



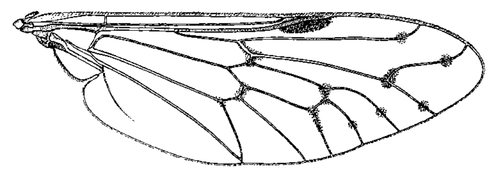
30 Stonemyia tranquilla ♀



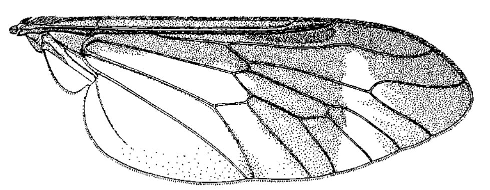
31 Pilimas californicus ♀



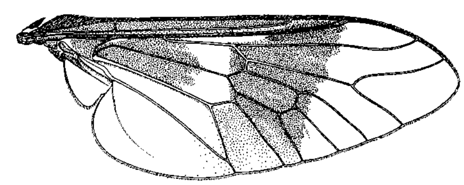
32 Neochrysops globosus ♀



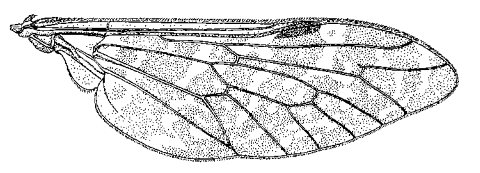
33 Silvius quadrivittatus ♀



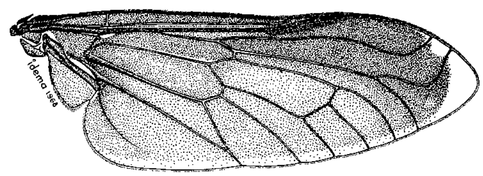
34 Chrysops pikei ♀



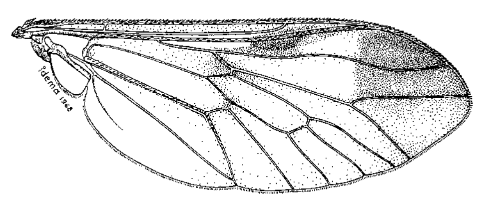
35 Chrysops cincticornis ♀



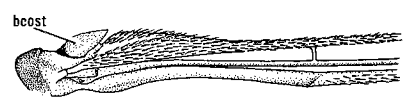
36 Haematopota americana ♀



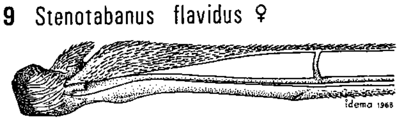
37 Bolbodimyia atrata ♀



38 Diachlorus ferrugatus ♀



39 Stenotabanus flavidus ♀



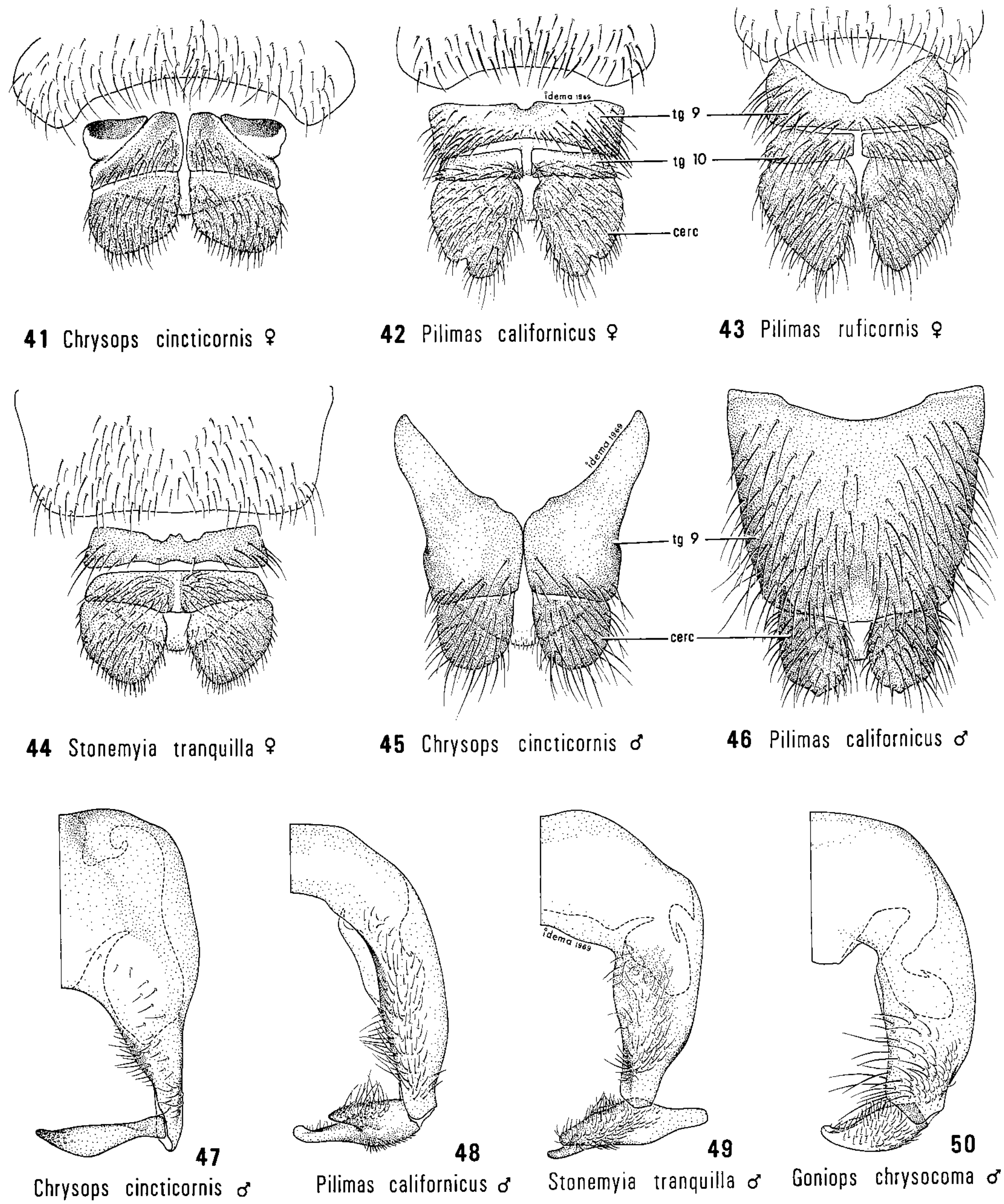
40 Tabanus americanus ♀

Figs. 31.28–40. Wings: (28) *Goniops chrysocoma* (Osten Sacken); (29) *Esenbeckia delta* (Hine); (30) *Stonemyia tranquilla* (Osten Sacken); (31) *Pilimas californicus* (Bigot); (32) *Neochrysops globosus* Walton; (33) *Silvius quadrivittatus* (Say); (34) *Chrysops pikei* Whitney; (35) *Chrysops cincticornis* Walker; (36) *Haematopota americana* Osten Sacken; (37) *Bolbodimyia atrata* (Hine); (38) *Diachlorus ferrugatus* (Fabricius); (39) wing base of *Stenotabanus flavidus* (Hine) and (40) *Tabanus americanus* Forster.

Abbreviation: bcost, basicosta.

Antenna subequal to width of head and shorter than notum; flagellum longer than pedicel and three-quarters length of to nearly same length as scape (Fig. 17)..***Silvius*** **(*Zeuximyia*** Philip)
1 sp., *philipi* Pechuman; Pacific coast

15. Wing with a dark crossband or traces of one (Figs. 34, 35). Gena at least partly pruinose (Fig. 4) ....***Chrysops*** **(*Chrysops*** Meigen)
100 spp.; widespread



Figs. 31.41–50. Terminalia: configuration of tergites and cerci on female and male terminalia of (41) *Chrysops cincticornis* Walker, (42) *Pilimas californicus* (Bigot), (43) *Pilimas ruficornis* (Bigot), (44) *Stonemyia tranquilla* (Osten Sacken), (45) *Chrysops cincticornis*, and (46) *Pilimas californicus*; gonopod of (47) *Chrysops cincticornis*, (48) *Pilimas californicus*, (49) *Stonemyia tranquilla*, and (50) *Goniops chrysocoma* (Osten Sacken).
Abbreviations: cerc, cercus; tg, tergite.

Wing hyaline except for yellowish costal cell. Face and gena completely shining (Fig. 3) .... ***Chrysops*** **(*Liochrysops*** **Philip)**
1 sp., *hyalinus* Shannon; southeastern

16. Scape considerably longer than wide (Fig. 20). Wing pattern composed of gray and white maculations (Fig. 36) .... HAEMATOPOTINI.... ***Haematopota*** Meigen
5 spp.; much of North America; Philip 1953 (as *Chrysozona*)

Scape barely longer than wide (Figs. 21–26). Wing markings, if present, other than above 17

17. Basicosta (subepaulet) bare or nearly so (Fig. 39) .... DIACHLORINI[1]....18

Basicosta with macrotrichia similar in appearance and density to those on C (Fig. 40) .... TABANINI....26

18. Subcallus denuded and inflated (Fig. 8). Wing with a pattern, or almost uniformly darkened. Scape often enlarged (Fig. 8) 19

Subcallus pruinose and flat. Wing with a pattern, or hyaline. Scape never enlarged 20

19. Scape greatly enlarged, shining black in single Nearctic species (Fig. 8). R_4 sharply angled in direction of costal margin (Fig. 37). All tibiae somewhat enlarged .... ***Bolbodimyia*** Bigot
1 sp., *atrata* (Hine); Arizona; Stone 1954

Scape slightly enlarged, subshining yellow. R_4 not sharply angled. Tibiae normal .... ***Holcopsis*** Enderlein
4 spp.; Mexico at high altitudes, possibly southwestern U.S.A.; Pechuman 1969

20. Frontal callus absent or vestigial in female. Flagellum of both sexes either with a basal plate plus two or three more flagellomeres or with labella sclerotized 21

Frontal callus present in female (Fig. 9). Flagellum in both sexes with a basal plate plus four more flagellomeres (Figs. 24, 27) and with labella never sclerotized 22

21. Flagellum with a basal plate plus two or three more flagellomeres. Small dark species under 10 mm. Labella fleshy .... ***Microtabanus*** Fairchild, in part
1 sp., *pygmaeus* (Williston); eastern

Flagellum with a basal plate plus four more flagellomeres. Green or yellowish species over 11 mm. Labella sclerotized .... ***Chlorotabanus*** Lutz
1 sp., *crepuscularis* (Bequaert); eastern; Philip and Fairchild 1956

22. Fore tibia somewhat inflated. Mesopleuron pearly pruinose. Wing usually with a dark pattern (Fig. 38). Eye in life with a characteristic pattern of spots .... ***Diachlorus*** Osten Sacken
1 sp., *ferrugatus* (Fabricius); eastern

Fore tibia slender. Mesopleuron not pearly pruinose. Wing hyaline or with spots. Eye in life unicolorous or banded 23

23. Frons parallel-sided, narrow (length–width ratio 5:1); frontal callus narrow and ridge-like, well-removed from eyes (Fig. 9). Eye in life unicolorous. At least scutellum and sometimes mesonotum pale pruinose, contrasting with abdomen. R_4 without an appendix .... ***Leucotabanus*** Lutz, in part
2 spp.; southern, southwestern; Stone 1938

Frons usually broader; if narrow, widened above and frontal callus usually touching eyes. Eye in life banded. Scutellum usually not contrasting with abdomen. R_4 sometimes with an appendix 24

24. Terminal flagellomeres hairy (Fig. 27). R_4 without an appendix. Species 13 mm or more in length .... ***Anacimas*** Enderlein, in part
2 spp.; southeastern, midwestern; Stone 1938

Terminal flagellomeres without conspicuous hairs (Fig. 24) or R_4 with an appendix, or both. Species under 13 mm .... ***Stenotabanus*** Lutz....25

25. Abdomen with a definite pattern. Frons of female three or more times as high as basal width, or widest below. Occipital tubercle of male at least as high as adjacent eye margin .... ***Stenotabanus*** **(*Stenotabanus*** **Lutz), in part**
3 spp.; southern, southwestern; Stone 1938

[1] Because *Anacimas*, *Stenotabanus*, and *Microtabanus* occasionally and *Leucotabanus* frequently have macrotrichia on the basicosta, these genera of Diachlorini are also keyed under Tabanini.

Grayish species with no distinct abdominal pattern. Frons of female less than three times basal width and not widest below. Occipital tubercle of male rudimentary .... ***Stenotabanus*** (***Aegialomyia*** Philip)
4 spp.; south coastal, Bermuda; Philip 1958

26. Flagellum with a hook-like projection from basal plate (Figs. 22, 23); eye sparsely hairy 27
Flagellum rarely with such a projection, but if present eye bare 28

27. Subcallus with erect black hairs .... ***Agkistrocerus*** Philip
2 spp.; southern
Subcallus without such hairs .... ***Hamatabanus*** Philip
3 spp.; southern, midwestern

28. Small but distinct ocelli present. Frons narrow; frontal callus narrow and ridge-like, well removed from eyes (Fig. 9) .... ***Leucotabanus*** Lutz, in part
see couplet 23
Ocelli absent, but an ocellar tubercle sometimes present. Frons and calli variable 29

29. Vertex with a distinct denuded ocellar tubercle in female and with an elevated anteriorly shining tubercle in male. Eye usually hairy .... ***Hybomitra*** Enderlein
60 spp.; all North America but mostly northern; Stone 1938 (as *Tabanus*, in part)
Vertex without an ocellar tubercle; if an elevated tubercle present in male, it is completely pruinose 30

30. Frons of female with calli reduced to one or two small oval spots well-separated from eyes (Fig. 10) or completely absent. Eye hairy, often yellow or pale brown in dried specimens 31
Frons with at least a broad basal callus (Fig. 11). Eye blackish in dried specimens, hairy or bare 32

31. Flagellum with a basal plate plus two or three flagellomeres........ ***Microtabanus*** Fairchild, in part
see couplet 21
Flagellum with four distinct flagellomeres beyond basal plate .... ***Atylotus*** Osten Sacken
12 spp.; northern, western; Stone 1938

32. Annulate portion of flagellum hairy. Palpus blunt and stout with erect hairs; proboscis small .... ***Anacimas*** Enderlein, in part
see couplet 24
Annuli without conspicuous hairs and differing in at least one other character from above 33

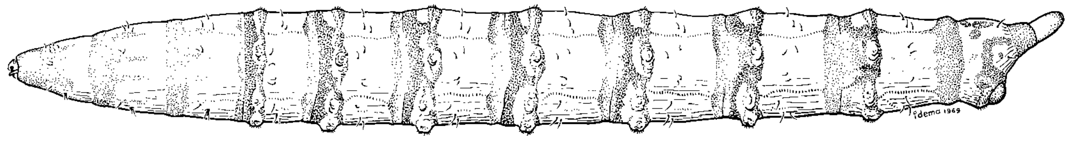
33. Body and wings deep brown to black. Facial and frontal calli protuberant and shining .... ***Whitneyomyia*** Bequaert
1 sp., *beatifica* (Whitney); southern
Body and wings variable, but if as above, body length over 15 mm 34

34. Rather small species. Almost no angle and no dorsal excision on basal plate of flagellum (Fig. 24). R_4 often with an appendix .... ***Stenotabanus*** (***Stenotabanus*** Lutz), in part
see couplet 25
Size small to large. If R_4 with an appendix, either dorsal angle of basal plate of flagellum distinct (Fig. 25) or eye pilose, or both .... ***Tabanus*** Linnaeus.... 35

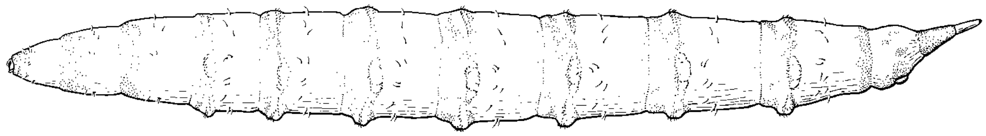
35. Flagellum with a basal plate plus three more flagellomeres (Fig. 26). Small species, under 12 mm .... ***Tabanus*** (***Glaucops*** Szilady)
1 sp., *fratellus* Williston; northwestern
Flagellum with four terminal flagellomeres (Fig. 25). Small to very large species .... ***Tabanus*** (***Tabanus*** Linnaeus)
100 spp.; widespread; Stone 1938

Larva

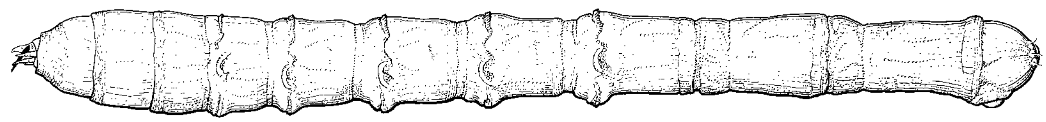
1. Body pear-shaped. Integument opaque and roughened. All segments with an annular ring of small tubercles or crenulate frills (Fig. 54) .... ***Goniops***
Body elongate, more or less cylindrical. Integument membranous and transparent, usually with longitudinal striations on some aspect of most segments, or integument entirely covered by short dense pubescence. Some abdominal segments with prolegs (Figs. 51–53) 2



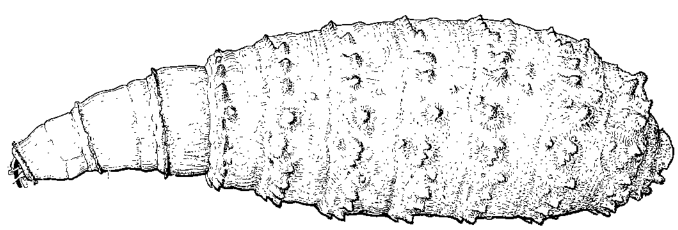
51 Tabanus reinwardtii



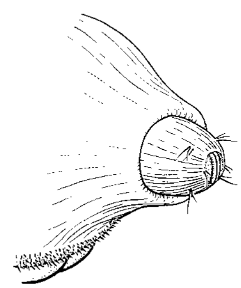
52 Chrysops furcatus



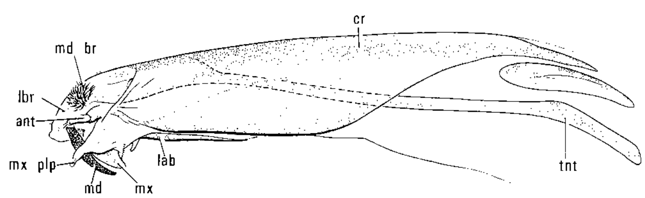
53 Esenbeckia delta



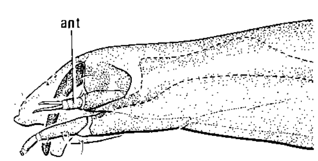
54 Goniops chrysocoma



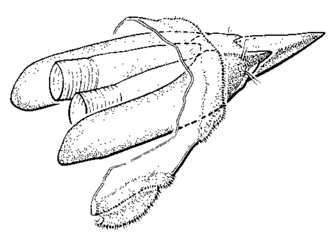
55 Tabanus marginalis



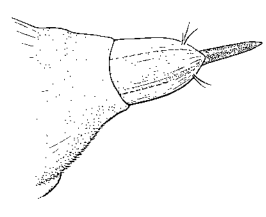
56 Tabanus reinwardtii



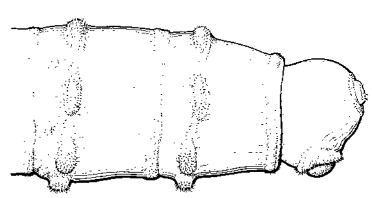
57 Chrysops excitans



58 Merycomyia whitneyi



59 Chrysops cincticornis



60 Leucotabanus annulatus

Figs. 31.51–60. Larvae: lateral view of (51) *Tabanus reinwardtii* Wiedemann, (52) *Chrysops furcatus* Walker, (53) *Esenbeckia delta* (Hine), and (54) *Goniops chrysocoma* (Osten Sacken); (55) respiratory siphon of *Tabanus marginalis* Fabricius; lateral view of head capsule of (56) *Tabanus reinwardtii* and (57) *Chrysops excitans* Walker; respiratory siphon and spine of (58) *Merycomyia whitneyi* (Johnson) and (59) *Chrysops cincticornis* Walker; (60) terminal segments of *Leucotabanus annulatus* (Say).

Abbreviations: ant, antenna; cr, cranium; lab, labium; lbr, labrum; md, mandible; md br, mandibular brush; mx, maxilla; mx plp, maxillary palpus; tnt, tentorium.

2. Prolegs present only on first five abdominal segments (Fig. 53). Body widest in region of mesothoracic and metathoracic segments. Integument of intersegmental regions and posterior borders of prolegs with a reticulate fishscale-like pattern. Terminal segment hemispherical; posterior spiracle sessile, or nearly sessile, on surface of terminal segment. Mandible straight and blade-like 3

Prolegs present on each of first seven abdominal segments (Figs. 51, 52). Body normally widest near middle. Integument lacking reticulate fishscale-like patterned areas, instead often with microtrichial pubescence intersegmentally and bordering prolegs. Posterior spiracle at least slightly elevated. Mandible curved 4

3. Posterior spiracle surrounded by four short bluntly rounded fleshy lobes; a fifth sharply pointed lobe immediately dorsal to spiracle .... ***Apatolestes***

Posterior spiracle surrounded by six pale slender setae, each arising from a pale spherical plate .... ***Esenbeckia***

4. Three pairs of prolegs dorsally, laterally, and ventrally on each of first seven abdominal segments (Fig. 52) 5

Four pairs of prolegs, including an additional ventrolateral pair, on first seven abdominal segments (Fig. 51) 8

5. Body surface, except respiratory siphon, completely clothed with a dense covering of short pubescence 6

Pubescence restricted to anterior or posterior margin or posterior border of prolegs of one or more segments 7

6. Pubescent integumental covering conspicuously mottled with dark and paler areas. Third antennal segment shorter than second. Respiratory siphon equal to or only slightly longer than its basal diameter .... ***Chlorotabanus***

Pubescence not conspicuously mottled. Third antennal segment longer than second segment. Respiratory siphon length about twice its basal diameter .... ***Diachlorus***

7. Third antennal segment about half the length of the second segment. Respiratory siphon shorter than its basal diameter, lacking a respiratory spine. Prolegs with prominent hook-like crochets .... ***Silvius* (*Zeuximyia*)**

Third antennal segment longer than second segment (Fig. 57). Respiratory siphon either longer than its basal diameter or with a respiratory spine (Fig. 59). Prolegs lacking crochets .... ***Chrysops***

8. Body surface, except respiratory siphon, completely clothed with a dense velvety mottled covering of short pubescence. Respiratory siphon length about equal to basal diameter .... ***Bolbodimyia***

Pubescence usually restricted to anterior or posterior margin or posterior border of prolegs of one or more segments, but if completely covering body, not conspicuously mottled and respiratory siphon longer than basal diameter 9

9. Respiratory siphon comprising distal ends of two opposed sclerotized plates between which tracheal trunks terminate in an exsertile spiracular spine (Fig. 58). Inconspicuous and incomplete striations present only laterally on segments .... ***Merycomyia***

Although tracheal trunks sometimes terminating in a spiracular spine, respiratory siphon always membranous and lacking sclerotized plates. Striations present or absent on abdominal segments 10

10. Respiratory siphon shorter than its basal diameter. Integumental striations extremely fine on all aspects of body, and usually visible only under high magnification; striations spaced at approximately 5 μm .... ***Haematopota***

If respiratory siphon shorter than its basal diameter, striations more coarsely spaced at usually more than 20 μm 11

11. Respiratory siphon very short, projecting no more than half its diameter. Terminal abdominal segment usually shorter than greatest diameter, hemispherical (Fig. 60). Striations uniformly spaced on all aspects of body 12

Respiratory siphon length ranging from slightly shorter (Fig. 55) to about four times longer than its basal diameter. Terminal abdominal segment usually somewhat attenuated posteriorly toward respiratory siphon (Fig. 51). Striations normally absent from dorsal and ventral surfaces of at least the prothorax, and more widely spaced dorsally and ventrally than laterally on other segments 14

12. Pubescence encircling anterior three-quarters of prothorax and broadly encircling posterior half of terminal abdominal segment so that anal lobes and base of respiratory siphon are covered by enlarged pubescent area .... ***Silvius (Griseosilvius)***

Pubescence encircling little more than anterior quarter of prothorax, and on terminal abdominal segment restricted to narrow annulus around base of respiratory siphon and investiture of anal lobes so that pubescence on anal lobes separated from that encircling base of respiratory siphon 13

13. Terminal abdominal segment two-thirds length of penultimate segment (Fig. 60). Larva inhabiting decaying wood and treeholes .... ***Leucotabanus***

Terminal abdominal segment less than half length of penultimate segment. Larva inhabiting damp sand on coastal beaches .... ***Stenotabanus (Aegialomyia)***

14. Median lateral surfaces of terminal segment lacking pubescent markings. Striations present on dorsal and ventral surfaces of all abdominal segments or, if absent, pubescence restricted, at most, to a prothoracic annulus and vestiture on anal ridges .... ***Hybomitra***

Either median lateral surfaces of anal segment with pubescent markings (Fig. 51), or striations absent or poorly developed on dorsal or ventral surface or both surfaces of abdominal segments .... ***Tabanus***
Whitneyomyia
Atylotus

Pupa

1. Three pairs of notal setae dorsally on mesothorax exclusive of basal alar setae (Fig. 64) 2

Only two pairs of notal setae dorsally on mesothorax (Fig. 61) 5

2. Terminal aster with a single pair of large acutely pointed tubercles. Abdominal fringes with stout spines of widely variable length; largest ones (three pairs on tergites, one on each pleurite, and a pair on sternites) uniformly positioned in fringes of each segment. Spiracular prominences on thorax and abdominal segments globular .... ***Goniops***

Aster with two or three pairs of tubercles. Abdominal fringes and spiracular prominences otherwise 3

3. Base of each wing sheath with two setae arising from a common base. Five pairs of metanotal setae, with one pair in each anterolateral angle of sclerite. A fringe of spines present dorsally on second abdominal segment (Fig. 64). Terminal aster with three pairs of tubercles 4

Basal alar seta single. Three pairs of metanotal setae; only one seta in each anterolateral angle of sclerite (as in Fig. 61). Second abdominal tergite lacking a fringe of spines. Terminal aster with two pairs of tubercles .... ***Esenbeckia***

4. Bristles on abdominal tergite 1 hair-like, much smaller than those on metanotum and in fringe of abdominal tergite 2 .... ***Apatolestes***

Bristles on abdominal tergite 1 of approximately same size as bristles on metanotum and in fringe of abdominal tergite 2 (Fig. 64) .... ***Brennania***

5. Callus tubercles each with two setae 6

Callus tubercles each with one seta (Fig. 63) 7

6. Antennal sheath rather long, exceeding eclosion line and curved anterodorsally. Abdominal fringes uniseriate. Only a ventral or ventrolateral pair of preanal combs present .... ***Chrysops***

Antennal sheath straight and not exceeding eclosion line. Abdominal fringes biseriate. Dorsolateral, lateral, and ventral or ventrolateral pairs of preanal combs present .... ***Stenotabanus (Aegialomyia)***

7. Abdominal tergite 1 with row of small tubercles between paired setiferous sublateral tubercles (Fig. 62) .... ***Chlorotabanus***

Abdominal tergite 1 lacking a row of small tubercles dorsomedially; paired sublateral setae usually not arising from tubercles 8

8. Only lateral and ventral tubercles of aster acutely pointed; dorsal pair of tubercles represented by small knobs arising from dorsomedial surface of lateral tubercles. Abdominal fringes uniseriate, greatly reduced on pleura and sternites, and almost absent from pleura and sternite of segment 2 .... ***Diachlorus***

   All three pairs of aster tubercles acutely pointed. Abdominal fringes biseriate or, if uniseriate, not conspicuously more reduced on pleura and sternites than on respective tergites 9

9. Tubercles of aster long and slender; lengths of dorsal, lateral, and ventral pairs at least 0.35, 1.0, and 0.5 mm, respectively. Ventral or ventrolateral, lateral, and dorsolateral preanal combs well-developed. Tergal and pleural setae of abdominal segment 1 arising from small tubercles. Antennal ridges divided sublaterally; submedian portions elevated at least 0.3 mm and falcate. Callus tubercles large and globose, elevated at least 0.3 mm. Pupal length 18–24 mm .... ***Leucotabanus***

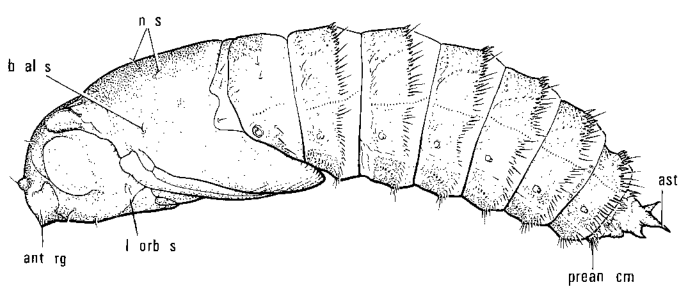
   Lateral tubercles of aster and usually dorsal and ventral tubercles shorter. Disagreeing with one or more of other features 10

10. Paired setae in each basal alar region. All tubercles of head rather large and very prominent; antennal ridges tuberculate; frontal and callus tubercles subequal and elevated 0.15–0.2 mm. Pupal length 13 mm .... ***Silvius***

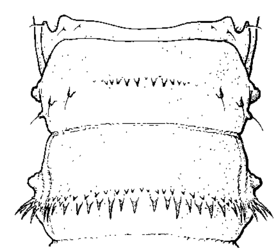
   One seta in each basal alar region. If antennal ridges or callus tubercles large, frontal tubercles rarely more than half their size 11

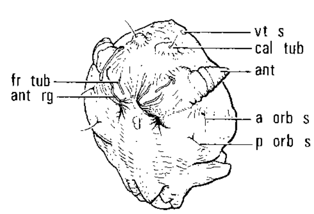
11. Callus tubercles large and globular in shape, elevated about 0.4 mm. Frons with prominent ridge between upper basal angle of each antennal sheath and callus tubercle. Anterior spiracle 1.5–2 mm long. Pupal length 30–35 mm .... ***Merycomyia***

   Not as above 12

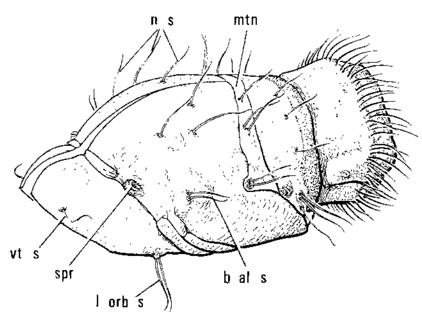


61 Hybomitra epistates


62 Chlorotabanus crepuscularis



63 Bolbodimyia atrata



64 Brennania hera

Figs. 31.61–64. Pupae: (61) lateral view of *Hybomitra epistates* (Osten Sacken); (62) dorsal view of tergites 1 and 2 of *Chlorotabanus crepuscularis* (Bequaert); (63) oblique view of frontal plate of *Bolbodimyia atrata* (Hine); (64) dorsolateral view of thorax and anterior two abdominal segments of *Brennania hera* (Osten Sacken).

Abbreviations: ant, antenna; ant rg, antennal ridge; ant sh, antennal sheath; a orb s, anterior orbital seta; ast, aster; b al s, basal alar seta; cal tub, callus tubercle; fr tub, frontal tubercle; l orb s, lateral orbital seta; mtn, metanotum; n s, notal seta; p orb s, posterior orbital seta; prean cm, preanal comb; spr, spiracle; vt s, vertical seta.

12. Dorsolateral pair of preanal combs each with about six spines; lateral pair of combs absent. Abdominal fringes uniseriate. Pupal length about 13 mm .... ***Haematopota***

    Dorsolateral and lateral preanal combs present or, if lateral pair absent, dorsolateral combs vestigial or absent. Abdominal fringes usually biseriate. Pupal length usually more than 13 mm 13

13. Abdominal fringes biseriate and spines of anterior series on at least tergite 7 stouter than those on adjacent posterior spines (Fig. 61) or, in few cases where fringes uniseriate or spines of two series equal in basal diameter, length more than 16 mm, integument very darkly colored, and fewer than 50 spines in fringe of tergite 7 .... ***Hybomitra***

    Basal diameter of spines of anterior fringe series same as or smaller than that of adjacent posterior spines. Disagreeing with at least one of last three statements above 14

14. Ventral or ventrolateral, lateral, and dorsolateral preanal combs well-developed, distinguished from each other merely by integumental folds. Antennal sheath with a prominent basal annulus marked off from distal portion by a prominent sulcus (Fig. 63) .... ***Bolbodimyia***

    Lateral and dorsolateral combs either markedly reduced or with quite noticeable spatial separation from each other and from ventral or ventrolateral comb. Antennal sheaths lacking such a prominent basal annulus. (Species of *Atylotus*, together with *T. lineola* Fabricius, *T. similis* Macquart, and *T. subsimilis* Bellardi, distinguished from others by dorsal and lateral tubercles of aster being inclined dorsoposteriorly on same plane) ..***Tabanus***
    Whitneyomyia
    Atylotus

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ATHERICIDAE 32

DONALD W. WEBB

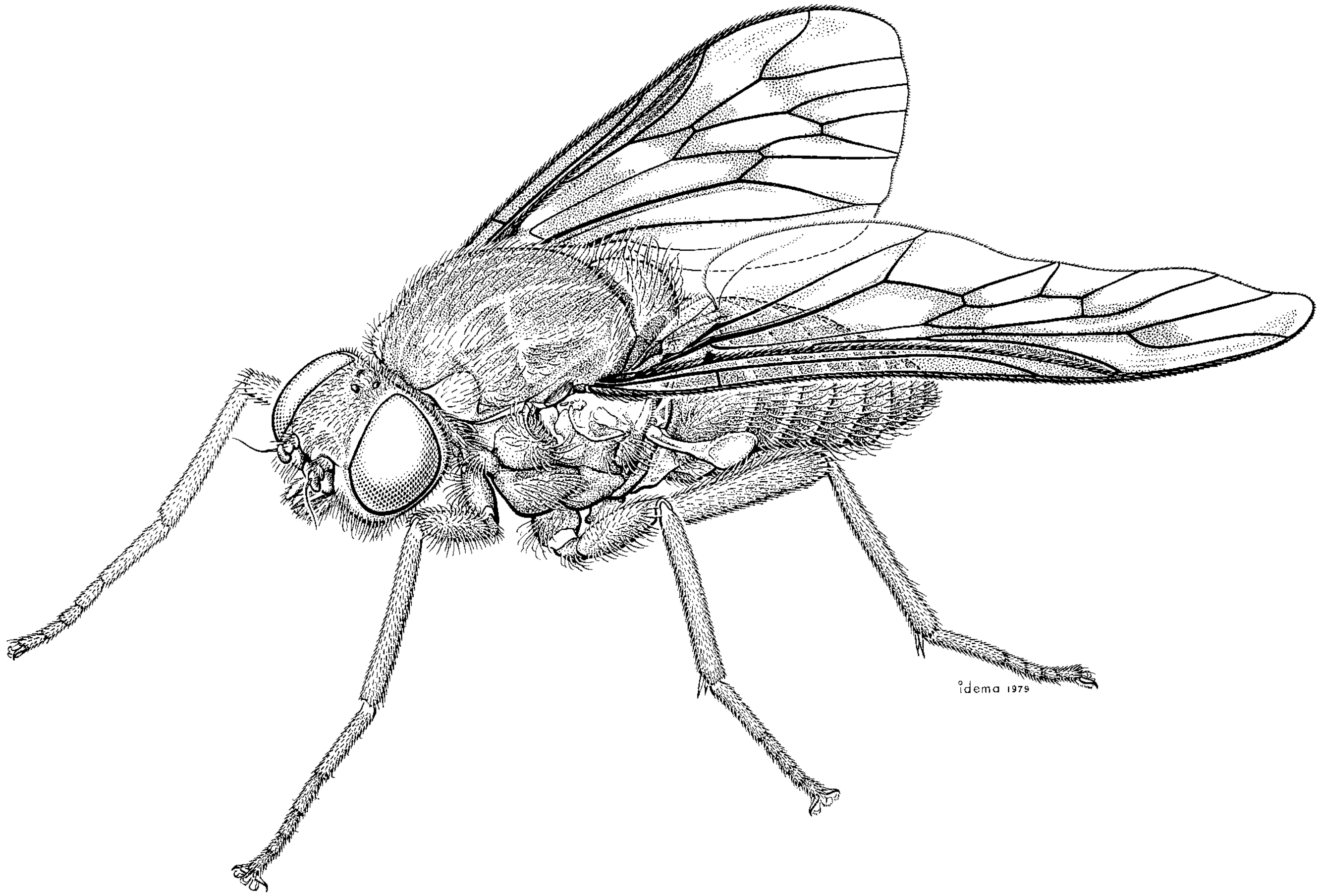


Fig. 32.1. Female of *Atherix variegata* Walker.

Medium sized flies, 7–8 mm long, fuscous to black with fasciate abdomens (Fig. 1).

Adult. Head: dark brown to black. Eyes nearly contiguous medially in male, widely separated in female (Figs. 2, 3); facets of equal size, with or without short erect setae; ocelli hyaline to fuscous on large raised subtriangular tubercle, with numerous erect elongate brown to fuscous setae. Antenna with scape and pedicel globose; basal flagellomere reniform, extending ventrally beyond pedicel; erect brown setae present on dorsal surface of scape and on dorsal and ventral or entire surface of pedicel, absent on basal flagellomere; arista on basal flagellomere subapical, narrow, elongate, bare. Frons with numerous erect elongate brown to fuscous setae, and in female of *Suragina* Walker (Fig. 2) with a distinct median longitudinal groove. Gena with numerous erect elongate white to black setae. Palpus two-segmented; basal palpal segment short, globular; apical palpal segment elongate, sinuate; setae numerous, erect, elongate, black. Labrum fuscous, glossy, narrow, tapering to apex. Labium membranous, with numerous elongate erect black setae. Occiput occasionally with dense gray pile consisting of numerous erect elongate white setae that become short and blackish brown near vertex.

Thorax: fuscous to black, with numerous short erect fuscous setae arranged in no distinct pattern. Postpronotal lobe pale or concolorous with mesothorax, bearing several elongate erect straw-colored to fuscous setae. Vitta generally indistinct, although occasionally present as a narrow or broad gray stripe. Pleuron glabrous except for propleural and mesopleural setae. Stem of halter yellow to fuscous, concolorous or darker than knob. Scutellum smoothly rounded apically, glossy, with numerous elongate erect straw-colored to fuscous setae.

Wing (Fig. 4) large and broad, with straw-colored faintly banded membrane covered with microtrichia. C circumambient, broader along anterior margin; Sc ending in C distal to crossveins r-m and m-cu; R_1 and R_{2+3} ending together in C above or distal to fork of R_{4+5}; R_{4+5} forked, enclosing apex of wing; cell d distinct, large, giving rise separately to three branches of M; cubital fork prominent; cell cu*p* closed. Anal lobe and alula broadly rounded. Calypter large, fringed with white setae. Pterostigma occasionally darker than wing membrane.

Legs straw-colored to fuscous, concolorous or with tarsomeres darker. No tibial spurs on foreleg, two on midleg and hindleg; hind coxa with (Fig. 5) or without anteroapical tubercle. Empodia distinct, pulvilliform; claws on each tarsomere simple; pulvilli distinct.

Abdomen: fuscous to black, with segments fasciate. Male terminalia (Fig. 6) with tergites 9 and 10 fused, convex, completely covering more ventral parts of terminalia; sternite 9 indistinguishable; cerci separated medially; gonocoxites broad, united dorsally by a narrow bridge from which slender gonocoxal apodemes project anteriorly; gonostyli simple, short, subcylindrical. Aedeagus foreshortened at apex of a strong aedeagal apodeme, articulating with a pair of long recurved filamentous aedeagal tines (endophallic tines) projecting caudally that are typical of Tabanidae and close relatives; aedeagus and aedeagal tines enclosed within a membranous sack, itself lying within an outer largely sclerotized aedeagal sheath derived from parameres. Aedeagal sheath articulated with inner margin of gonocoxites, with a short parameral apodeme projecting within base of each gonocoxite; ventrolateral subapical margin of sheath spiculate or spinous.

Female terminalia tapered caudally. Tergite 9 wider than long, with caudal margin truncate to sinuate; tergite 10 reduced to two small lateral medially separated sclerites; cerci paired, conical, each about 1.5 times longer than basal width. Sternite 8 as long as wide, with caudal margin broadly rounded; sternite 9 greatly modified, invaginated dorsally to sternite 8 forming an internal genital fork. Hypoproct wider than long, with caudal margin broadly rounded.

Larva. Larva of Nearctic species of *Suragina* unknown. Larva of *Atherix* Meigen aquatic, collected in riffles and among aquatic vegetation, and when fully extended (Fig. 7) elongate and tapered anteriorly. Head small, tabanid-like, retractable into first two thoracic segments. Thoracic segments increasing in length and width caudally, bearing no spiracles, spines, or tubercles. Abdomen with eight distinct segments; segments 1–7 with paired acute tubercles subdorsally and laterally and paired prolegs ventrally; each proleg with apical and subapical semicircle of curved simple claws (crochets); abdominal segment 8 with a single proleg ventromedially, a single posterior spiracle dorsomedially, and two elongate projections caudally each bearing fine filamentous setae.

Pupa. Pupa of Nearctic species of *Suragina* unknown. Pupa of *Atherix* 6.6–8.8 mm long, 1.8–1.9 mm wide, obtect, dark brown with posterior half of abdominal tergites pale. Head separated from thorax by cephalothoracic suture extending ventrally from in front of anterior spiracle to beneath sheath of mouthparts. Antennal sheath small, posterolaterally divergent, slightly longer than basal width. Callar setae (as in Fig. 31.63) placed anteriorly on head, each arising singly from a short tubercle; posterior orbital setae short, situated anteromedial to antennal sheath. Frontal suture situated anteromedial to posterior orbital setae. Sheath of maxillary palpus diverging laterally from base of sheath of mouthparts.

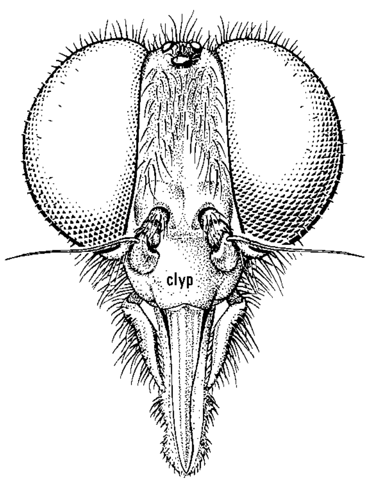
Anterior spiracle situated anteriorly on mesothorax; anterior opening convoluted; posterior opening small; oval slit near posterior base. Dorsolateral setae short, situated along with anterior and posterior mesonotal setae posterior to anterior spiracle. Wing and leg sheaths ventrally extending posteriorly over anterior half of abdominal sternite 1. Metanotum visible as narrow segment dorsal to wing sheath, bearing no setae.

Abdomen with eight distinct segments. Tergites 1–7 each bearing four barbed spines along caudal border. Pleurites 1–7 each bearing a single spiracle on each side; pleurites 2–7 each with two pairs of barbed spines; pleurite 1 with a single pair of barbed spines. Sternites 2–7 bearing six short bare spines along caudal margin; sternite 1 spineless. Abdominal segment 8 in dorsal view with four pairs of large acute projections, and bearing posterior spiracles between anteromedial projections.

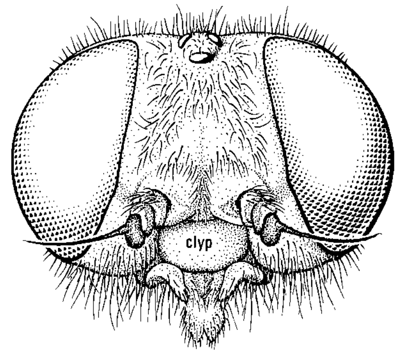
Biology and behavior. Adults of both *Atherix* and *Suragina* have been collected from the vegetation bordering streams (Nagatomi 1962) from May through August. Adults apparently imbibe honeydew or water, although the female of *Suragina* is bloodsucking, feeding on man and cattle. Females of *Atherix* are often collected in large numbers as they aggregate on top of one another to oviposit. Eggs (Nagatomi 1960) are laid on foliage above a stream or on the underside of bridges, from which the larvae drop into the water upon hatching. Larvae are aquatic, living in riffles or on aquatic vegetation, and feeding on the larvae of Chironomidae and nymphs of Ephemeroptera. Pupation occurs in the soil along the stream edge. Although the larvae and pupae of Nearctic species of *Suragina* are unknown, Nagatomi (1961*a*, 1961*b*) has described the immature stages of some Japanese species.

Classification and distribution. The family Athericidae was erected by Stuckenberg (1973) for several genera that had previously been associated with the family Rhagionidae. In the Nearctic region two genera, *Atherix* and *Suragina*, are included in this family, each containing three species (Webb 1977). Stuckenberg (1973) associated the family Athericidae with the Tabanidae, combining them in the Tabanoidea. Nagatomi (1977) considered this a natural arrangement.

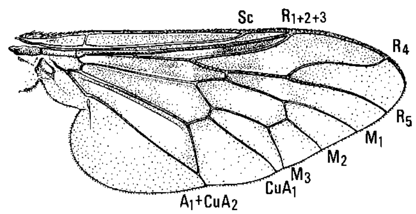
The genus *Atherix* is widely distributed throughout Canada and the United States (Webb 1977), with *Suragina* limited to southwestern Texas and Mexico.



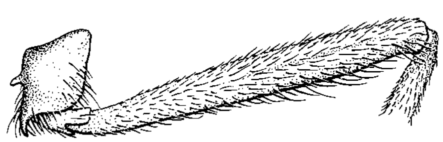
2 Suragina concinna ♀



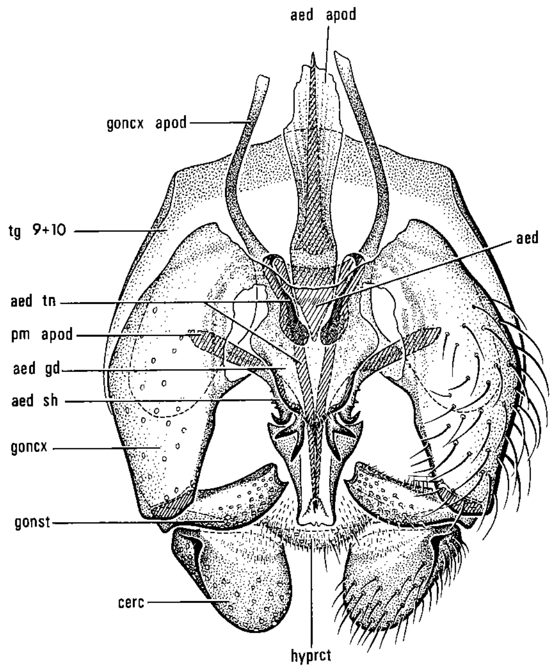
3 Atherix variegata ♀



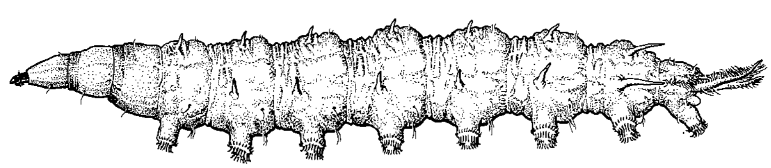
4 Atherix variegata ♀



5 Suragina concinna ♀



6 Atherix lantha ♂



7 Atherix sp.

Figs. 32.2–7. *Suragina* and *Atherix* spp.: anterior view of head of (2) *S. concinna* (Williston) and (3) *A. variegata* Walker; (4) wing of *A. variegata*; (5) coxa of *S. concinna*; (6) ventral view of male terminalia of *A. lantha* Webb; (7) larva of *Atherix* sp.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; aed sh, aedeagal sheath; aed tn, aedeagal tine; cerc, cercus; clyp, clypeus; goncx, gonocoxite; goncx apod, gonocoxal apodeme; gonst, gonostylus; hyprct, hypoproct; pm apod, parameral apodeme; tg, tergite.

Key to genera

1. Clypeus much wider than parafacial and projecting below ventral margin of eye. Frons, at antenna, narrower than eye in female (Fig. 2). Hind coxa with anteroapical spine-like tubercle (Fig. 4) .... ***Suragina*** Walker
   1 sp., *concinna* (Williston); southwestern Texas and Mexico

   Clypeus about as wide as parafacial and not, or only slightly, projecting below lower margin of eye. Frons wider than eye in female (Fig. 3). Hind coxa not produced into an anteroapical spine-like tubercle .... ***Atherix*** Meigen
   3 spp.; southern United States to Yukon Territory

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RHAGIONIDAE 33

MAURICE T. JAMES AND WILLIAM J. TURNER

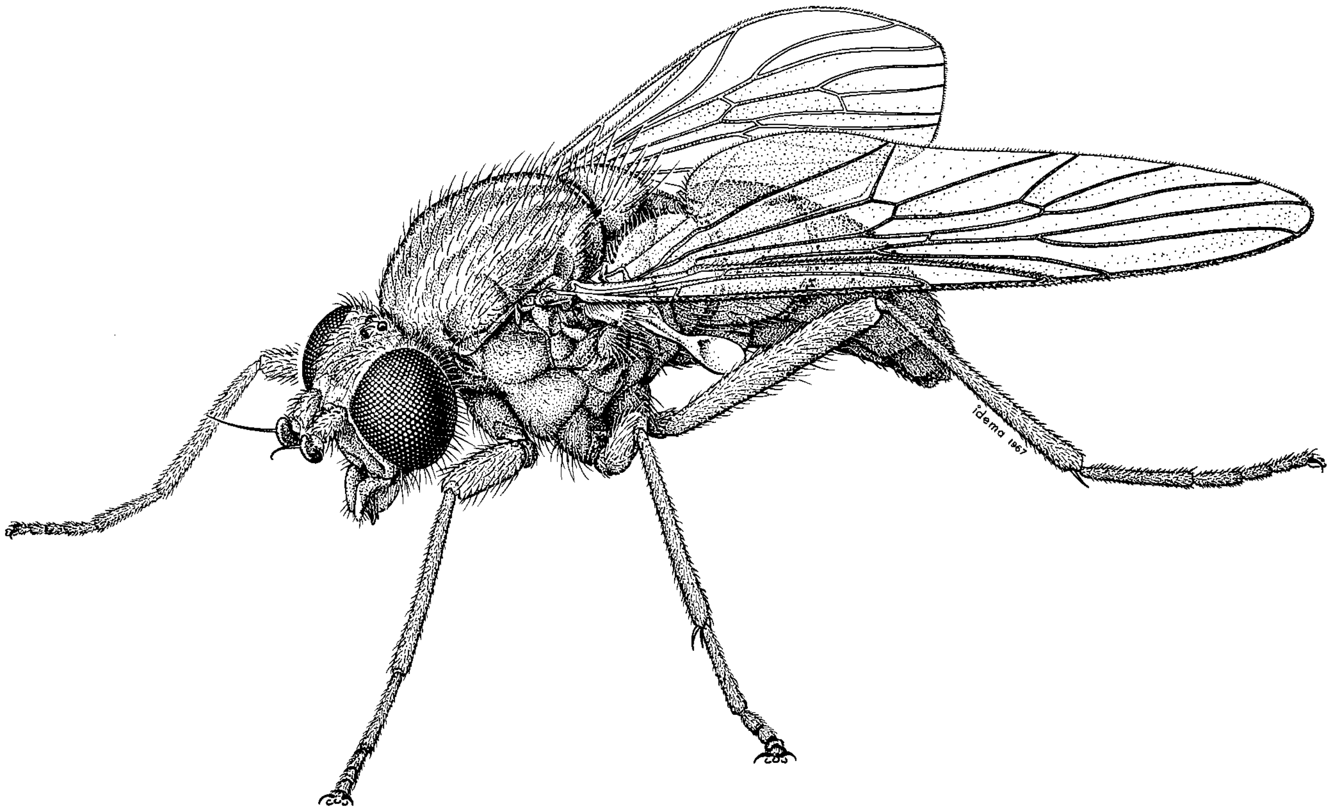


Fig. 33.1. Female of *Symphoromyia hirta* Johnson.

Slender flies, 4–15 mm long (Fig. 1). Legs usually elongated. Abdomen elongated and conical. Body usually thinly clothed with stiff pile, but rarely with bristles. Color basically drab, but frequently with yellow or orange markings, rarely predominantly so.

Adult. Head: hemispherical, sometimes narrower than thorax. Vertex nearly flush with eyes. Facial area with prominent strongly convex clypeus extending almost to base of antennae and separated from parafacials by deep grooves (Fig. 3). Eyes bare, holoptic or narrowly separated in male, widely separated in female; upper ommatidia in male usually enlarged (Fig. 2). Antenna variable in form (Figs. 4–8); scape and pedicel usually small, but scape sometimes lengthened, expanded, or densely haired; flagellum with eight tapering flagellomeres, or with an enlarged sometimes pendulous basal flagellomere bearing an apical usually unsegmented stylus or arista. Proboscis usually fleshy, sometimes equipped for sucking blood; palpus well-developed, two-segmented.

Thorax: of ordinary form; scutellum fairly large, unarmed. Legs simple, never dilated, at most with hind femur somewhat clubbed; hind coxa usually with small tubercle anteriorly; spurs present at apex of at least mid tibia though these are sometimes small, and one or two usually present on hind tibia; fore tarsus frequently with erect tactile hairs below; empodia pulvilliform. Calypter small. Wing always present, elongated; venation strong (Figs. 9–12); C continued around wing as an ambient vein; cell d or dm situated near center of wing, rarely absent (Fig. 12); M two- or three-branched; Rs arising far before base of cell d or dm; crossvein r-m usually well before, rarely at, middle of cell d or dm.

Abdomen: usually with seven segments and portions of terminalia visible, tapered posteriorly; seven pairs of spiracles present. Female terminalia (Fig. 13) with ovipositor telescopic; cercus two-segmented, with first segment usually expanded ventrolaterally; three round spermathecae. Male terminalia (Fig. 14) with hypandrium partially or completely distinguishable from bases of gonocoxi (except in *Chrysopilus* Macquart and *Litoleptis* Chillcott); gonostylus simple; parameres forming conical aedeagal sheath; epandrium together with a narrow tergite 10 and cerci not completely covering gonopods.

Larva. Elongated, cylindrical, somewhat maggot-like, tapering anteriorly, more or less truncate and variously lobed posteriorly, consisting of a head and 11 distinct body segments that are never secondarily divided (Fig. 18).

Head capsule slender, widely open posteroventrally, mostly retracted within thorax; tentorial phragmata and tentorial arms present; no metacephalic rods; mandible slender, curved, blade-like, not provided with a poison canal, articulated to mandibular brush of posteriorly curved spines and to maxilla lying laterally (Figs. 15, 22).

Body smooth or with hairs and bristles. Creeping welts present ventrally on abdominal segments 1–6 or 1–7. Respiratory system amphipneustic or apneustic; anterior spiracles probably not functional; posterior ones usually functional, located flush with body wall on posterior face of terminal segment. Terminal segment with lobes or tubercles of various form surrounding spiracles; no respiratory tube.

Biology and behavior. Adult females of *Symphoromyia* Frauenfeld suck blood of warm-blooded vertebrates and sometimes become major pests. Food habits of most other adult rhagionids are not well known.

Larvae of *Symphoromyia, Rhagio* Fabricius, and *Chrysopilus* have been found in damp soils rich in decaying organic matter. They are presumed to survive, at least partially, as predators on other insects.

Classification and distribution. Historically, the Rhagionidae has included a rather heterogeneous mixture of genera, some of which are seemingly related to other families of lower Brachycera, especially the Stratiomyidae, the Xylophagidae, and the Tabanidae. Therefore, the precise limits of the family have remained unclear and are much debated. As defined here, the family is represented in the Nearctic region by 108 species in nine genera: *Arthroceras* Williston, *Symphoromyia* Frauenfeld, *Rhagio* Fabricius, *Chrysopilus* Macquart, *Litoleptis* Chillcott, *Bolbomyia* Loew, *Spania* Meigen, and *Ptiolina* Zetterstedt. *Symphoromyia* contains several additional undescribed species, and undoubtedly some species of *Chrysopilus* and perhaps other genera as well still remain to be described. The North American larvae are badly in need of comprehensive study.

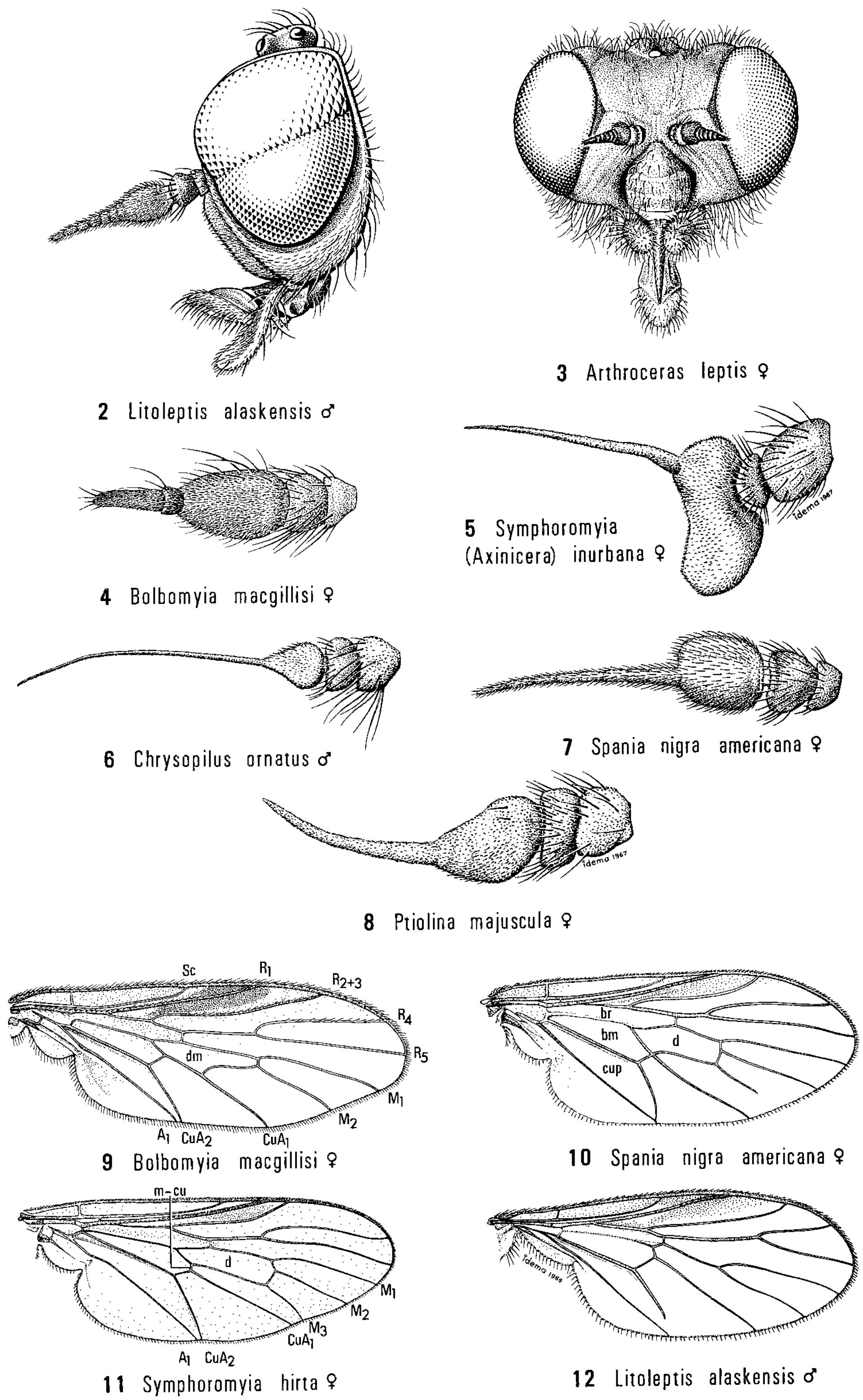
Atherix Meigen, *Bequaertomyia* Brennan (as *Pseudoerinna* Nagatomi in Nagatomi 1975), *Glutops* Burgess, *Hilarimorpha* Schiner, and *Suragina* Walker have, at times, been considered rhagionids. However, Stuckenberg (1973) provides convincing evidence that both *Atherix* and *Suragina* are sufficiently distinct to justify placing them in the newly erected Athericidae. Similarly, the anomalous *Hilarimorpha* probably belongs to the Hilarimorphidae (James 1965*c*, Webb 1974) rather than to the Rhagionidae as suggested by Chillcott (1961, 1963) and Cole (1969). *Glutops*, variously placed in the Xylophagidae (James 1965*b*), in the Glutopidae (Krivosheina 1971), with *Bequaertomyia* in the Coenomyiidae (Steyskal 1953, Wirth 1954, Nagatomi and Saigusa 1970), and most recently in the Rhagionidae (Nagatomi 1975), is recognized here and by Philip (1965) and Teskey (1970) as belonging to the Pelecorhynchidae. *Bolbomyia* is considered here to belong with the stylus-bearing rhagionids *Litoleptis*, *Ptiolina*, and *Spania* (Chillcott 1961, 1963; Hennig 1967; Webb 1974; Nagatomi 1975), instead of with the Xylophagidae (James 1965*b*). Other genera commonly grouped with rhagionids, namely *Dialysis* Walker and *Vermileo* Macquart, are relegated to the Xylophagidae and to the Vermileonidae, respectively, as proposed by Nagatomi (1975, 1977). *Dialysis*, in most features of the head, thorax, and abdomen, including the terminalia, shows a close relationship to *Coenomyia* and *Arthropeas*. Its retention in the Rhagionidae can only be justified on the basis of its aristate antenna. *Vermileo* Macquart and related exotic genera have apparently been included as a subfamily of the Rhagionidae for want of a better place to put them. This presumed relationship is not justified on the basis of morphology and behavior. The group has several unique features, and its recognition by Nagatomi (1977) as a separate family seems appropriate.

Fossil Rhagionidae date back to the Upper Jurassic, from which three genera are known (Rohdendorf 1974). The family, and especially *Symphoromyia* spp., is evidently well represented in the Oligocene deposits of Baltic amber (Stuckenberg 1974). Melander (1949) lists six species from the Oligocene-age Florissant shales.

Keys to genera

Adult

1. Laterotergite haired 2
   Laterotergite bare 5
2. Cell d or dm lacking (Fig. 12). Tibiae without apical spurs .... ***Litoleptis*** Chillcott
   1 sp., *alaskensis* Chillcott; Chillcott 1963
   Cell d or dm present (Figs. 9–11). At least mid tibia with apical spurs 3
3. Crossvein m-cu absent; CuA_1 broadly confluent with underside of cell dm; M_3 absent (Fig. 9). Antenna with two-segmented pseudostylus no longer than enlarged basal flagellomere (Fig. 4) .... ***Bolbomyia*** Loew
   4 spp.; widespread; Chillcott 1961 and 1963, Webb 1969



Figs. 33.2–12. Heads, antennae, and wings: head of (2) *Litoleptis alaskensis* Chillcott in lateral view and (3) *Arthroceras leptis* (Osten Sacken) in anterior view; antenna of (4) *Bolbomyia macgillisi* Chillcott, (5) *Symphoromyia* (*Axinicera*) *inurbana* Aldrich, (6) *Chrysopilus ornatus* (Say), (7) *Spania nigra americana* Johnson, and (8) *Ptiolina majuscula* Loew; wing of (9) *Bolbomyia macgillisi*, (10) *Spania nigra americana*, (11) *Symphoromyia hirta* Johnson, and (12) *Litoleptis alaskensis*.

Crossvein m-cu present (Fig. 11) or, if absent (Fig. 10), CuA_1 confluent with cell d at only a point; M_3 present. Antennal flagellum with a stylus; stylus usually without apparent segmentation, and longer than basal enlargement (Figs. 7, 8) 4

4. Upper margin of anepisternum haired. Hind tibia usually with one apical spur. Antennal stylus no longer than remainder of antenna (Fig. 8) ....***Ptiolina*** Zetterstedt
12 spp.; widespread; Hardy and McGuire 1974

Upper margin of anepisternum bare. Hind tibia lacking an apical spur. Antennal stylus usually distinctly longer than remainder of antenna (Fig. 7) ....***Spania*** Meigen
1 sp., *nigra americana* Johnson; New England

5. Antennal flagellum with eight tapered flagellomeres (Fig. 3)......................***Arthroceras*** Williston
4 spp.; widespread; Nagatomi 1966

Antenna aristate (Figs. 5, 6) 6

6. Basal flagellomere kidney-shaped; arista distinctly dorsal (Fig. 5). Hind tibia with one terminal spur ....***Symphoromyia*** Frauenfeld....7
29 spp.; widespread; Aldrich 1915, Leonard 1930, Turner and Chillcott 1973, Turner 1974

Basal flagellomere round, oval, or conical; arista apical (Fig. 6). Hind tibia with one or two terminal spurs 10

7. Basal flagellomere concave (rarely straight) along anterior margin beneath arista; outline hatchet-shaped (Fig. 5). Parafacial sclerite usually haired laterally on upper half, infrequently bare ....***Symphoromyia*** (***Axinicera*** Turner)

Basal flagellomere convex beneath arista; outline nearly round or kidney-shaped. Parafacial sclerite without hair or, if hair present, it is arranged otherwise 8

8. Hind coxa usually haired behind on posterior margin, but if bare, then scape of female pale, or male terminalia transverse along posterior margin and not or scarcely produced apically ....***Symphoromyia*** (***Paraphoromyia*** Becker)

Hind coxa bare behind 9

9. Parafacial sclerite densely haired. Basal flagellomere subequally rounded above and below. Male eyes distinctly separated above. Female abdomen typically densely gray pruinose ....***Symphoromyia*** (***Pogonaria*** Turner)

Parafacial sclerite usually bare, or at most with only a few hairs. Basal flagellomere less rounded above than below. Male eyes broadly contiguous above. Female abdomen usually glossy, rarely pruinose ....***Symphoromyia*** (***Ochleromyia*** Turner)

10. Hind tibia with two apical spurs ....***Rhagio*** Fabricius
25 spp.; widespread; James 1964 and 1965*a*, Chillcott 1965, Thompson 1969

Hind tibia with one apical spur...***Chrysopilus*** Macquart
32 spp.; widespread; Hardy 1949, Leonard 1930

Larva

(modified from Hennig 1952)

1. Spiracular disc shallowly concave; a pair of sclerotized horn-like processes present above disc and a pair of rounded lobes below it (Fig. 20) ....***Ptiolina***

Spiracular disc deeply cleft, resulting in formation posteriorly on terminal abdominal segment of an upper lip and a lower lip (Figs. 18, 19), each of which are sometimes also divided (Figs. 16, 18, 19, 21); no sclerotized horn-like processes dorsal to spiracular disc 2

2. Upper and lower lips of spiracular cleft undivided, but with a broadly dentate margin (Fig. 16) ....***Symphoromyia***

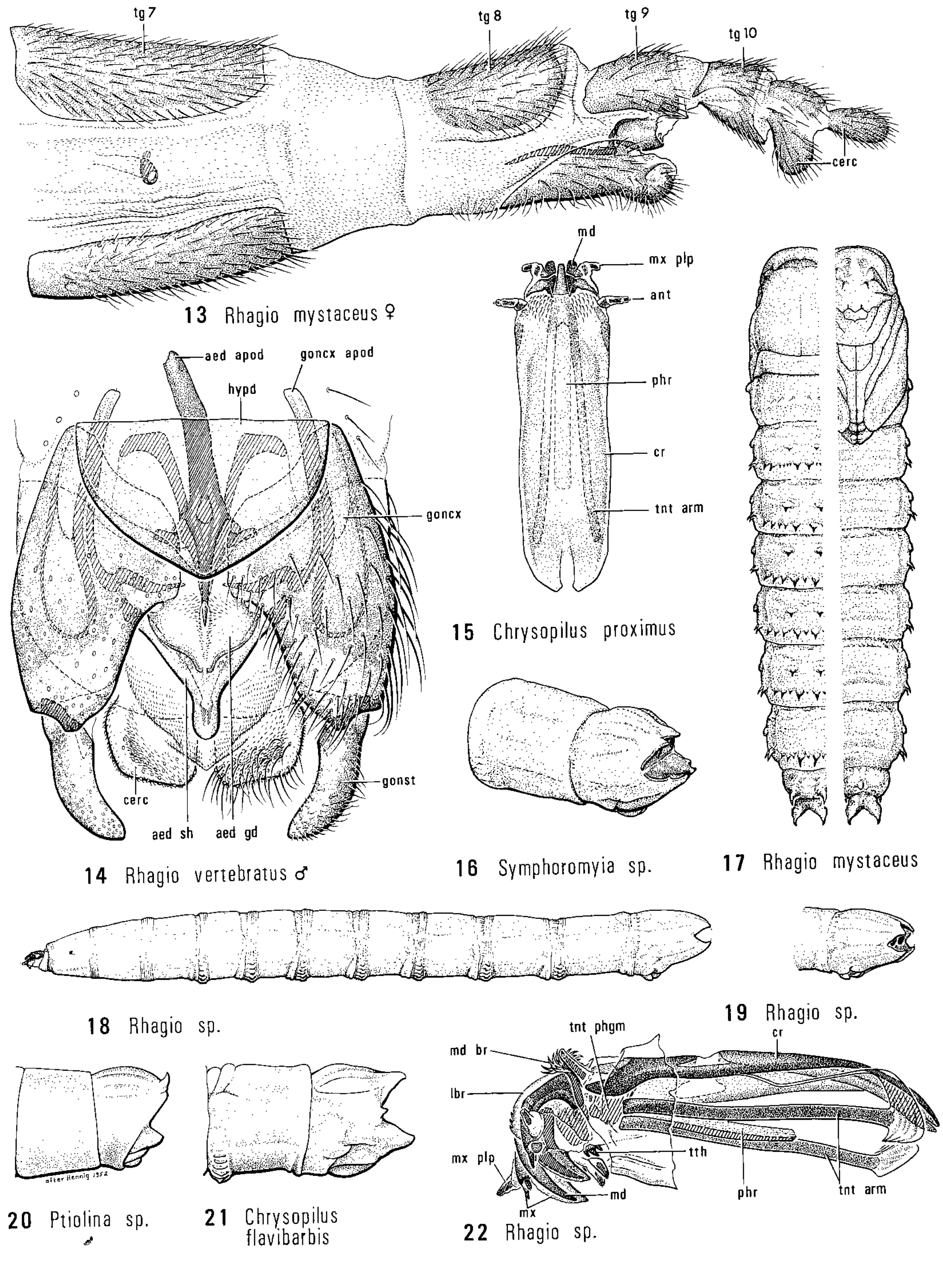
Upper and lower lips of spiracular cleft each divided, forming four lobes in all 3

3. A small lateral process on each side located between dorsal and ventral lips of spiracular cleft (Fig. 21)..***Chrysopilus,*** in part

No such process located between dorsal and ventral lips of spiracular cleft (Figs. 18, 19)............4

4. Basal sclerite of mandible toothed (Fig. 22) ....***Rhagio***

Basal sclerite of mandible not toothed ....***Chrysopilus***, in part



Figs. 33.13–22. Terminalia and immature stages: (13) female terminalia of *Rhagio mystaceus* (Macquart); (14) male terminalia of *Rhagio vertebratus* (Say); (15) larval head capsule of *Chrysopilus proximus* (Walker) in dorsal view; (16) terminal segments of larva of *Symphoromyia* sp.; (17) half dorsal and half ventral views of pupa of *Rhagio mystaceus*; (18) lateral view and (19) posterolateral view of terminal segment of larva of *Rhagio* sp.; lateral view of larval terminal segments of (20) *Ptiolina* sp. and (21) *Chrysopilus flavibarbis* Adams; (22) lateral view of larval head capsule of *Rhagio* sp.

Abbreviations: aed apod, aedeagal apodeme; aed gd, aedeagal guide; aed sh, aedeagal sheath; ant, antenna; cerc, cercus; cr, cranium; goncx, gonocoxite; goncx apod, gonocoxal apodeme; gonst, gonostylus; hypd, hypandrium; lbr, labrum; md, mandible; md br, mandibular brush; mx, maxilla; mx plp, maxillary palpus; phr, pharynx; tg, tergite; tnt arm, tentorial arm; tnt phgm, tentorial phragma; tth, tooth.

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XYLOPHAGIDAE 34

MAURICE T. JAMES

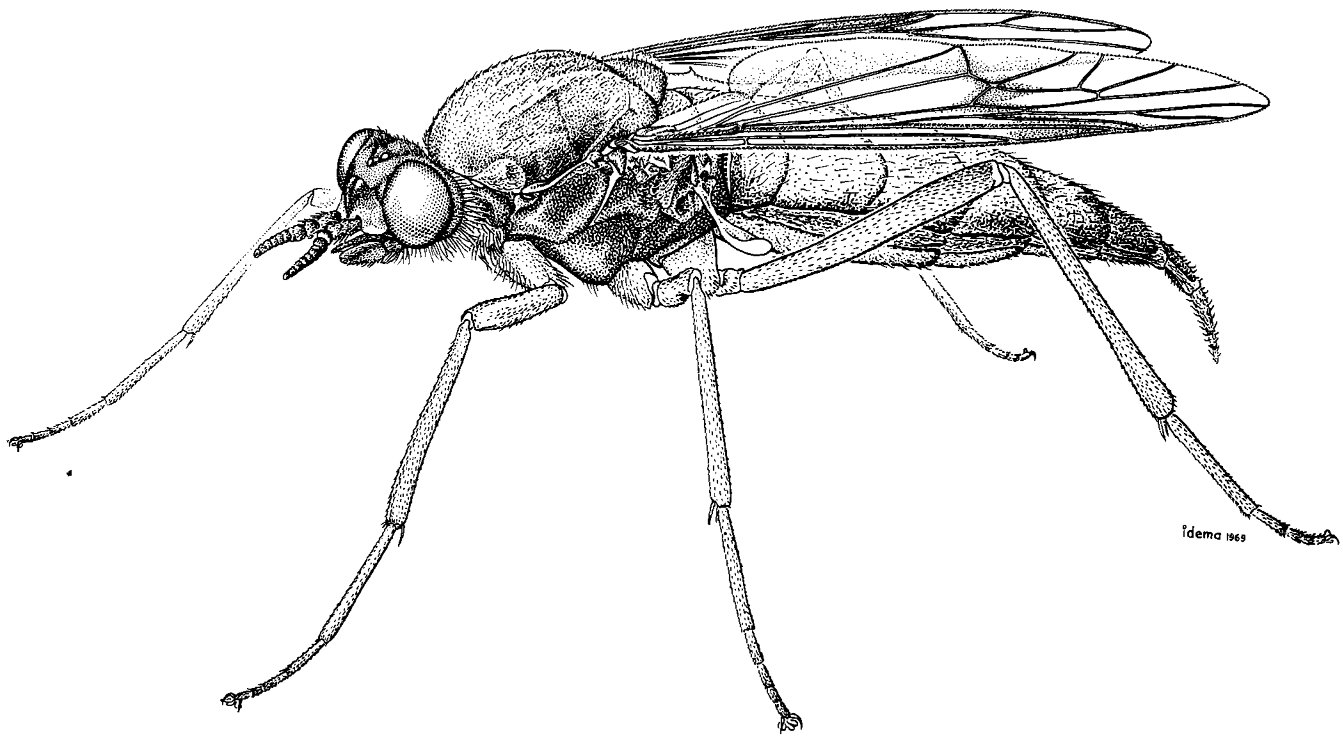


Fig. 34.1. Female of *Xylophagus abdominalis* Loew.

Robust and rhagionid-like to slender and wasp-like flies (Fig. 1), 2–25 mm long. Body not conspicuously hairy and without bristles; color blackish sometimes marked with yellow, or completely yellow.

Adult. Head: hemispherical to almost spherical (Figs. 4–7, 10). Vertex flush with eyes or slightly depressed. Facial area either nearly flush or sunken deeply below level of eyes; clypeus with surface moderately flat, sometimes prominently outlined by deep grooves (Figs. 7, 10). Eyes broadly separated in female, more narrowly separated or contiguous in male. Antennal flagellum with an apical arista (*Dialysis* Walker, Fig. 10), or with 8 or 20–36 flagellomeres; larger number of flagellomeres partly pectinate, subpectinate, or serrate (Fig. 5). Proboscis fleshy; palpus two-segmented, prominent.

Thorax: robust or slender; scutellum unarmed except in *Coenomyia* Latreille. Legs slender; tibiae each with one or two spurs; empodia pulvilliform. Calypter small. Wing (Figs. 2, 3) always present; C continued around wing as an ambient vein except in *Rachicerus* Walker; cell d large, at least as close to posterior margin as to anterior margin of wing; M usually three-branched; Rs arising well before base of cell d; crossvein r-m close to base of cell d.

Abdomen: swollen or slender, tapered posteriorly, with seven to nine segments visible. Ovipositor telescopic; cercus slender, two-segmented. Male terminalia with little or no evidence of hypandrium separated from gonocoxites; epandrium in Xylophaginae enlarged, with cerci small or absent.

Larva. Only those of *Xylophagus* Meigen, *Rachicerus*, and *Coenomyia* known (Figs. 11–13). Shape elongated, cylindrical, orthosomatic. Head conical, well-sclerotized, not retractile; two metacephalic rods and two tentorial arms present; tentorial phragmata absent or poorly developed; mandible and maxilla nearly completely fused. Respiratory system amphipneustic, although nonfunctional vestiges of posterior thoracic and first seven abdominal spiracles often present; terminal segment with a sclerotized more or less flattened dorsal plate bearing posterior spiracles and terminating in a pair of finger-like processes (Figs. 11, 12). Prolegs absent, but roughened setose areas usually present on anterior margin of most abdominal segments.

Biology and behavior. Adults usually occur in wooded and forested areas, particularly near water. The larvae, so far as known, live under bark and in decaying wood, or in the earthy debris of fallen trees; they are generally considered to be predacious.

Classification and distribution. Twenty-seven Nearctic species in five genera are known. In the *Catalog of the Diptera of America north of Mexico, Coenomyia* was placed with *Xylophagus* and *Rachicerus* in the Xylophaginae (James 1965). The strong similarities in the larvae of these three genera warranted this grouping, but because of the divergence of the adults, *Coenomyia* is being placed here in a separate subfamily together with *Arthropeas* Loew and *Dialysis*. *Dialysis* has been transferred from a rather traditional placement in the Rhagionidae. Adults of these three genera show many similarities, particularly in the structure of the facial region, the clypeus, and the male and female terminalia (Nagatomi 1975). *Arthroceras* Williston, *Bolbomyia* Loew, and *Glutops* Burgess, which were grouped in the Xylophagidae in the Catalog (James 1965), are now considered to have closer affinities with other families, the first two with the Rhagionidae (Nagatomi 1977) and the latter with the Pelecorhynchidae (Teskey 1970).

Fossil representatives of this family date back as early as the Baltic amber (Paleocene).

Keys to genera

Adult

1. Clypeus recessed in a deep facial groove well below eye level, and bounded laterally and above by a prominent sulcus (Figs. 7, 10). Facial area narrowed toward antennae. Alula with strongly convex margin .... COENOMYIINAE....2

   Clypeus only slightly recessed below anterior margin of eyes, and not outlined dorsally by a sulcus. Facial area nearly parallel-sided. Alula with nearly straight margin (Figs. 2, 3) .... XYLOPHAGINAE....4

2. Antenna with seven or eight flagellomeres (Figs. 6–8). Robust flies 3

   Antenna with an apical arista (Fig. 10). Relatively slender flies .... ***Dialysis*** Walker
   9 spp.; widespread; Webb 1978

3. Eye densely haired (Fig. 6). Scutellum with a pair of strong spines .... ***Coenomyia*** Latreille
   1 sp., *ferruginea* Scopoli; Holarctic

   Eye bare. Scutellum without spines .... ***Arthropeas*** Loew
   2 spp.; western; Leonard 1930

4. Flagellum consisting of 20–35 flagellomeres; flagellomeres pectinate, subpectinate, or serrate (Figs. 4, 5). Cell m_3 closed (Fig. 2). Eye with a distinct emargination above or opposite antenna (Fig. 4) .... ***Rachicerus*** Walker
   5 spp.; eastern and western; Leonard 1930

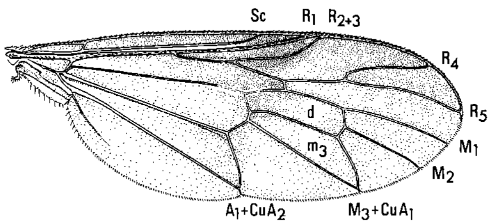
   Flagellum consisting of eight simple flagellomeres. Cell m_3 open (Fig. 3). Eye not emarginate .... ***Xylophagus*** Meigen....5
   Malloch *et al.* 1931, Curran 1933

5. Hind coxa (Fig. 9) with a short blunt process on inner side near middle. Entire frons gray pruinose .... ***Xylophagus*** (***Anaxylophagus*** Malloch)
   1 sp., *nitidus* Adams; New England

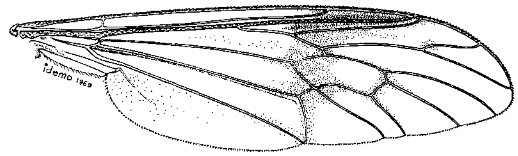
   Hind coxa without a process on inner side near middle. Frons at least partly glossy, except in *X. gracilis* Williston 6

6. Antennal scape less than three times length of pedicel, and shorter than distance from antennal base to anterior ocellus .... ***Xylophagus*** (***Xylophagus*** Meigen)
   4 spp.; widespread, boreal

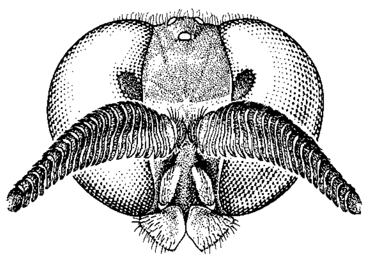
   Antennal scape fully three times length of pedicel and as long as distance from antennal base to anterior ocellus .... ***Xylophagus*** (***Archimyia*** Enderlein)
   5 spp.; widespread, boreal



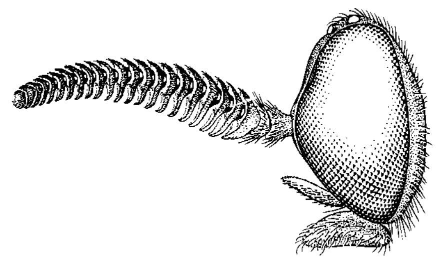
2 Rachicerus obscuripennis ♀



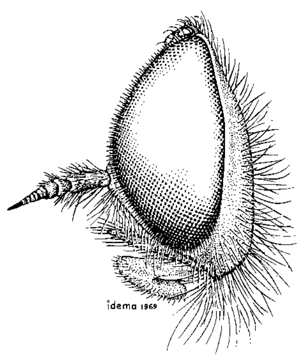
3 Xylophagus abdominalis ♀



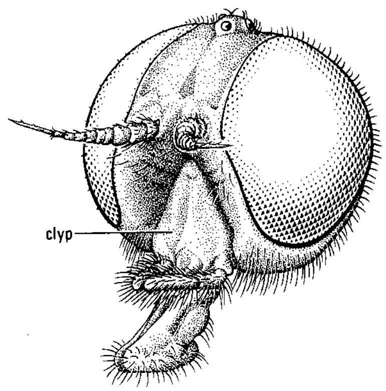
4 Rachicerus obscuripennis ♀



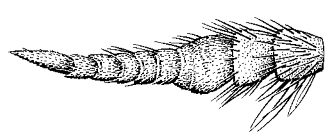
5 Rachicerus obscuripennis ♀



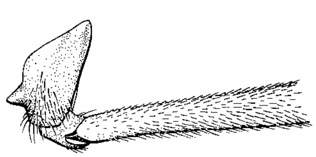
6 Coenomyia ferruginea ♂



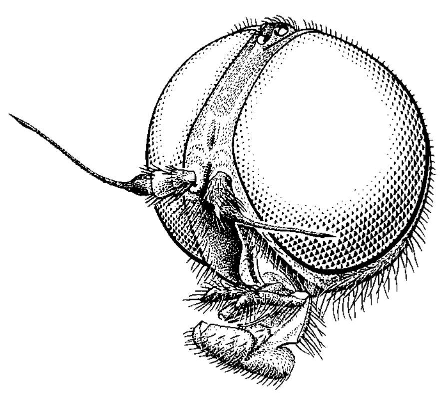
7 Arthropeas americana ♀



8 Arthropeas magna ♀



9 Xylophagus nitidus ♀



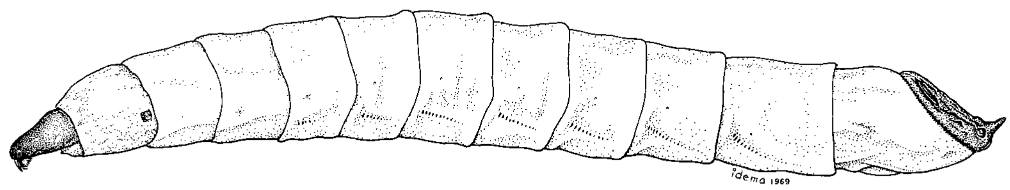
10 Dialysis lauta ♀

Figs. 34.2–10. Wings, heads, and legs: wing of (2) *Rachicerus obscuripennis* Loew and (3) *Xylophagus abdominalis* Loew; head of *Rachicerus obscuripennis* (4) in frontal view and (5) in lateral view; (6) lateral view of head of *Coenomyia ferruginea* (Scopoli); (7) oblique anterior view of head of *Arthropeas americana* Loew; (8) antenna of *Arthropeas magna* Johnson; (9) hind coxa and femur of *Xylophagus nitidus* Adams; (10) oblique anterior view of head of *Dialysis lauta* (Loew).

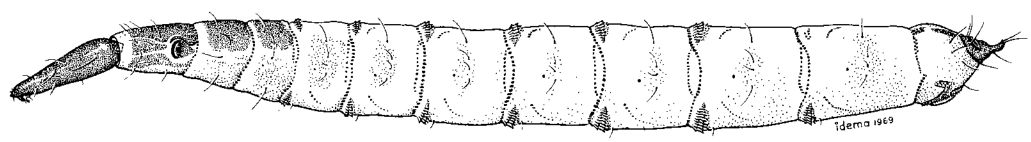
Abbreviation: clyp, clypeus.

Larva

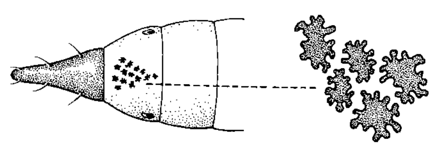
1. Head capsule at least three times as long as broad. Thoracic segments with sclerotized plates dorsally (Figs. 12, 13) 2
   Head capsule not more than twice as long as broad. Thoracic segments not sclerotized dorsally (Fig. 11) .... ***Coenomyia***
2. Sclerotization of prothorax in form of amoeba-shaped plates (Figs. 13, 14) .... ***Rachicerus***
   Sclerotized area of prothorax (Fig. 12) not divided into amoeba-shaped plates .... ***Xylophagus***



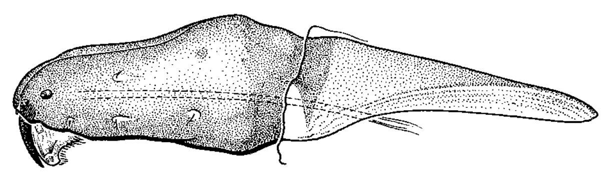
11 Coenomyia ferruginea



12 Xylophagus sp.



13 Rachicerus nitidus **14**



15 Coenomyia ferruginea

Figs. 34.11–15. Larvae: lateral view of (11) *Coenomyia ferruginea* (Scopoli) and (12) *Xylophagus* sp.; (13) dorsal view of head and thoracic segments of *Rachicerus nitidus* Johnson, with (14) enlargement of amoeboid sclerotic patches; (15) head capsule of *Coenomyia ferruginea.*

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XYLOMYIDAE 35

MAURICE T. JAMES

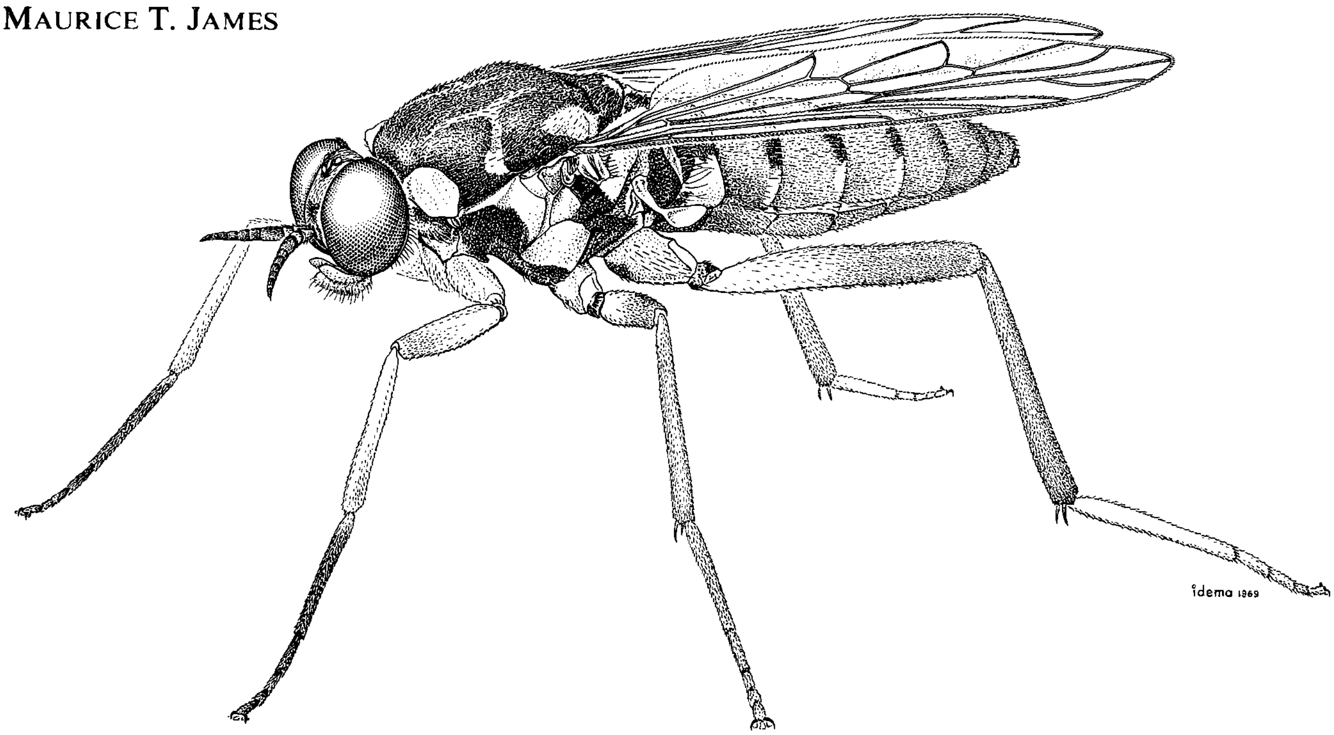


Fig. 35.1. Female of *Xylomya americana* (Wiedemann).

Rather slender wasp-like flies, 5–15 mm long, more or less brightly colored or with distinct pale markings against a black or blackish background, clothed with only inconspicuous hairs and never with bristles (Fig. 1). Abdomen fairly slender, oval or parallel-sided.

Adult. Head: hemispherical. Vertex flush with eyes; facial area and frons flush with eyes or a little depressed. Eyes bare, well-separated in both sexes, more narrowly separated in male. Antenna as long as or longer than head; flagellum consisting of eight flagellomeres, tapering, but without a stylus. Proboscis large, fleshy; palpus prominent, two-segmented.

Thorax: short, oval, not noticeably arched; scutellum without spines. Hindleg with femur elongated and slender or thickened; fore tibia without apical spurs; mid and hind tibiae with one or two apical spurs; empodia pulvilliform. Wing (Figs. 2, 3) always present, lying parallel to abdomen when at rest (Fig. 1), always hyaline; C extending no farther than apex of M_2; cell d rather large, at least as close to posterior margin of wing as to anterior margin; Rs arising well before base of cell d; crossvein r-m near base of cell d; three branches of M present; cells m_3 and cu*p* closed.

Abdomen: seven or eight distinct segments. Terminalia of male large (Figs. 2.121–123); gonostylus well-developed; aedeagus simple; paramere prominent, rod-like or hooked. Ovipositor of female short, barely protruding from abdomen.

Larva. Very similar to that of Stratiomyidae (compare Figs. 7 and 8 with Figs. 36.71–73 of Stratiomyidae), amphipneustic. Integument shagreened from deposit of calcium carbonate plates. Prothoracic and mesothoracic segments each with a transverse more or less smooth field on dorsum.

Head relatively broad, partially retracted within thorax, incapable of much independent movement, incomplete posteriorly. Mandible operating vertically. No free pharyngeal skeleton within head capsule. Tentorial arms present.

Prothorax broader than head. Body oval in outline, flattened, with eight abdominal segments. Posterior spiracles located in a transverse cleft at apex of terminal abdominal segment; hydrofuge hairs lacking. Prolegs lacking. Terminal abdominal segment ventrally with a row of posteriorly directed denticles just in front of anus (Fig. 8). Pupation occurring within last larval integument.

Biology and behavior. Adults characteristically occur in forested or wooded areas. Larvae are predacious or saprophagous and occur under bark.

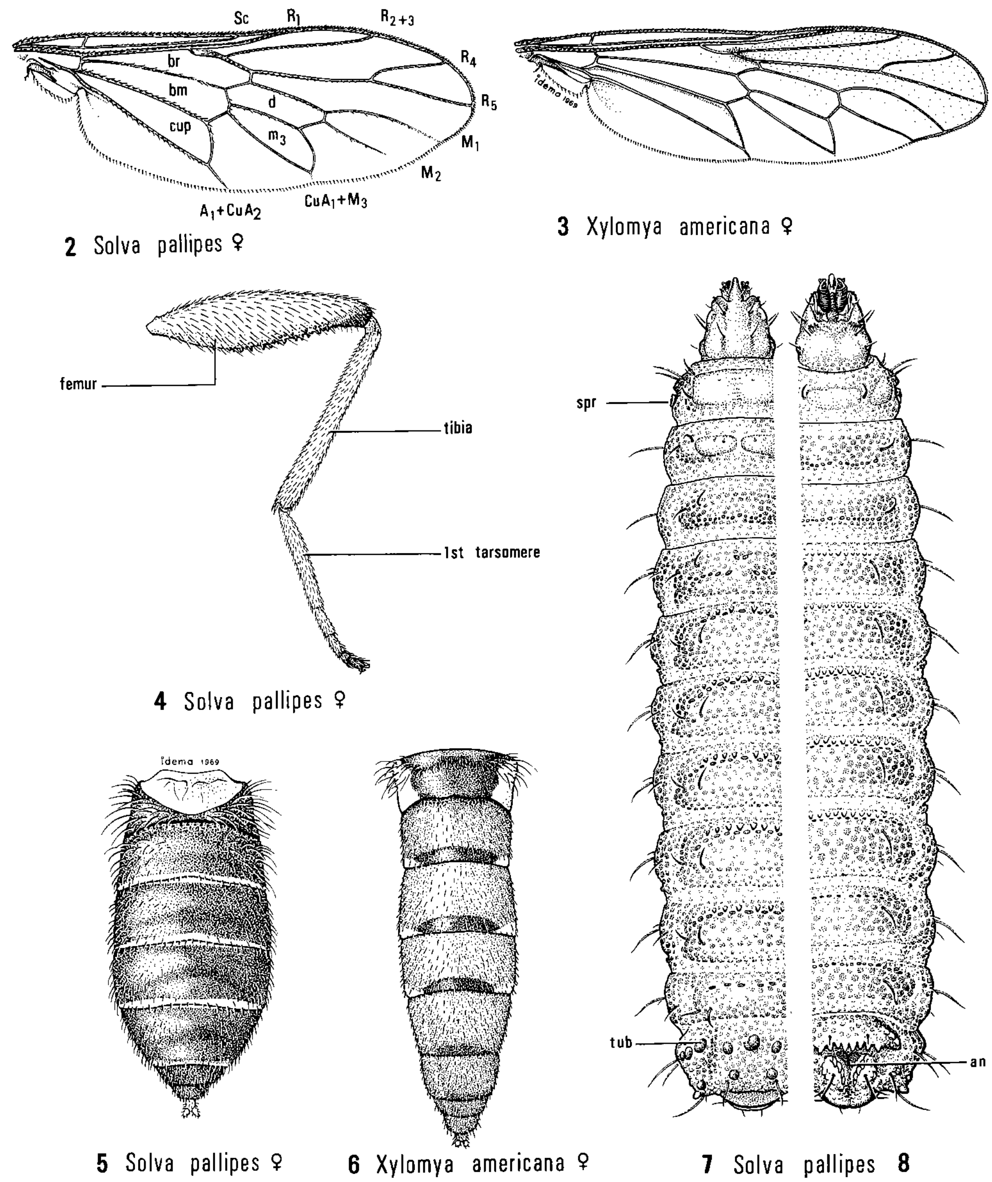
Classification and distribution. This family is considered by many workers as a subfamily of the Stratiomyidae; others have made it a part of the Rhagionidae or have united it with the Xylophagidae. The affinities are, definitely, with the Stratiomyidae; the larval structure and method of pupation within the last larval skin, if considered alone, would definitely place it there. Significant larval differences between the two families occur, however, and along with adult differences, these justify separate familial consideration for each.

In Europe, the Xylomyidae are known to occur in Baltic amber (Paleocene). In America Melander (1949) records two species of *Xylomya* Rondani from the Florissant shales of Colorado.

Keys to genera

Adult

1. Hind femur swollen and armed below with minute teeth (Fig. 4). Second abdominal tergite with large basal membranous area, permitting upward flexing of abdomen (Fig. 5). CuA and A_1 in American species with stiff microsetulae (Fig. 2), as on anterior veins............***Solva*** Walker
2 spp.; widespread; Steyskal 1947



Figs. 35.2–8. *Solva pallipes* (Loew) and *Xylomya americana* (Wiedemann): wing of (2) *S. pallipes* and (3) *X. americana*; (4) hindleg of *S. pallipes*; dorsal view of abdomen of (5) *S. pallipes* and (6) *X. americana*; larva of *S. pallipes* (7) in dorsal view and (8) in ventral view.
Abbreviations: an, anus; spr, spiracle; tub, tubercle.

Hind femur elongated, not swollen nor armed with teeth. Second abdominal tergite (Fig. 6) without a basal membranous area. CuA and A_1 with only soft pubescence (Fig. 3) .... ***Xylomya*** Rondani

8 spp.; widespread; Steyskal 1947, Vasey 1977

Larva

(after McFadden 1967)

1. Prothorax with a tubercle (Figs. 7, 8) anterior to spiracle, giving a cleft-like appearance to margin. Terminal abdominal segment with a transverse row of shining low tubercles on dorsum (Fig. 7) .... ***Solva***

   Prothorax without a tubercle anterior to spiracle. Terminal abdominal segment without shiny tubercles on dorsum .... ***Xylomya***

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STRATIOMYIDAE 36

MAURICE T. JAMES

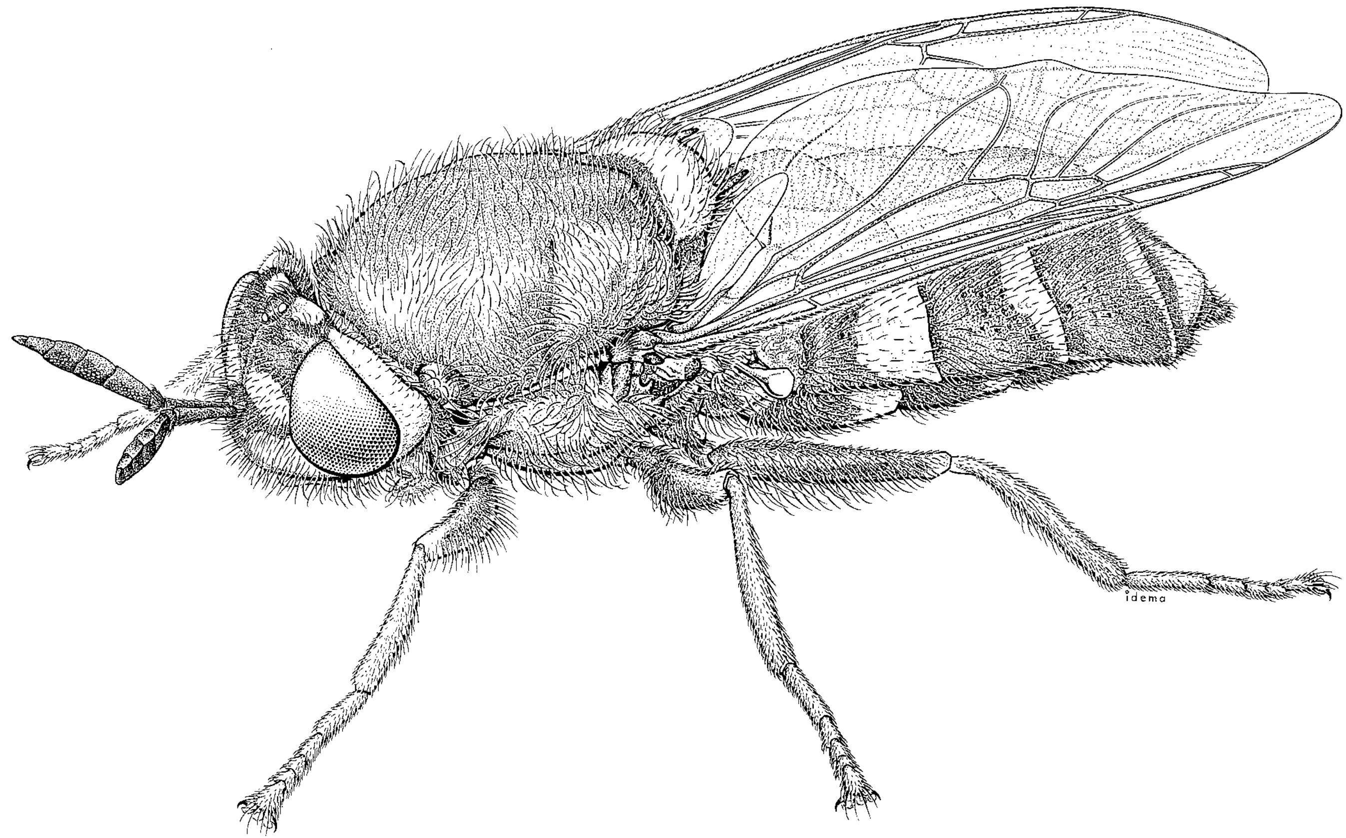


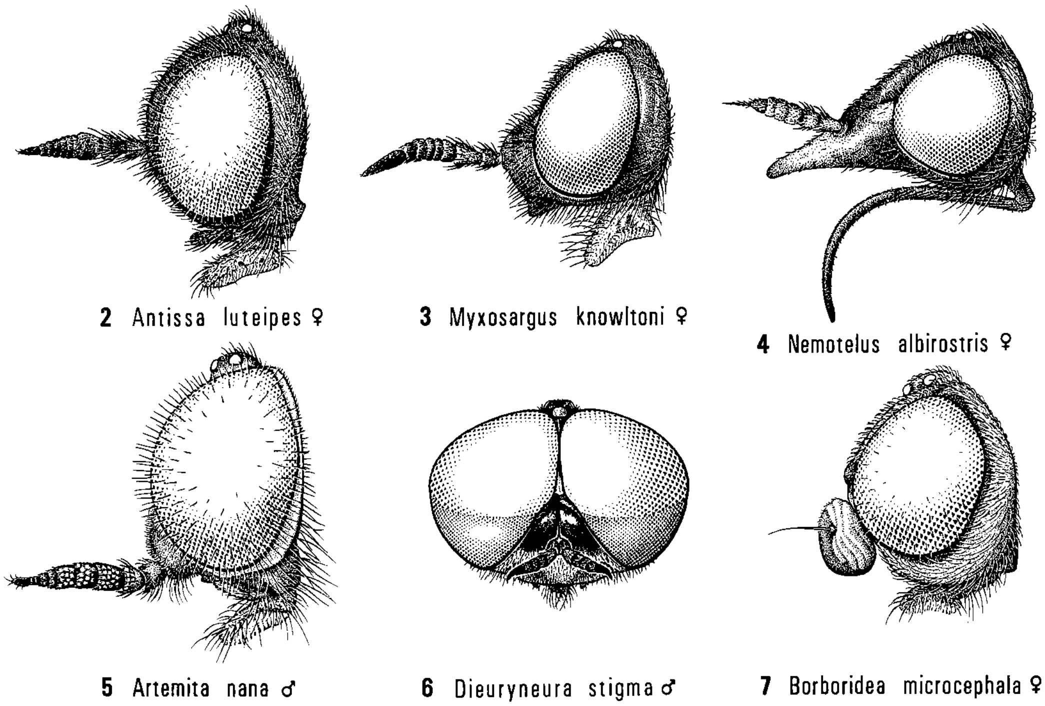
Fig. 36.1. Female of *Stratiomys barbata* Loew.

Slender to quite robust flies (Fig. 1), 2–18 mm long. Color usually yellow, green, blue, or black, sometimes metallic, frequently with variegated color patterns particularly on abdomen. Bristles not developed, though body, especially thorax, sometimes densely pilose.

Adult. Head: usually as broad as thorax but sometimes broader, hemispherical to spherical (Figs. 2–7), sometimes elongated by being produced forward into a cone, sometimes tuberculate or protruding below antennae, sometimes produced downward at lower facial margin. Occipital (postocular) orbit often well-developed, especially in female. Eyes ranging from bare to densely hairy, widely separated in female, more narrowly separated or contiguous in male, each eye in male often divided into an upper area comprising large facets and a lower area of small facets; ocelli present. Antenna inserted at or below middle of head; scape and pedicel unmodified except in respect to elongation; flagellum consisting of five to eight flagellomeres; flagellomeres unmodified or with a stylus or an apical or subapical arista (Figs. 8–26). Proboscis usually fleshy, sometimes atrophied, sometimes elongated, never adapted for sucking blood; palpus one- or two-segmented, not conspicuous.

Thorax: rectangular–oval in dorsal outline, sometimes elongated. Scutellum (Figs. 47–53) sometimes with one to three pairs of apical spines. Wing well-developed (rarely absent, but never in Nearctic species) (Figs. 27–37); C not reaching beyond apex of wing; stronger veins crowded anteriorly; branches of R always meeting wing margin well before wing apex; Rs usually arising from R_1 shortly before base of cell d or dm; R_4 short, often indistinct or wanting; veins toward posterior margin of wing weak, tending to evanesce; cell d or dm always present in Nearctic species. Legs simple (Figs. 43–45), at most with certain segments or tarsomeres inflated or elongated, never densely pilose; fore coxa never unusually elongated; pulvilli and empodia padlike; tibial spurs only rarely developed.

Abdomen: composed of five to eight visible segments, with the remaining segments telescoped into visible ones or forming terminalia; outline from dorsal view varying



Figs. 36.2–7. Heads: (2) *Antissa luteipes* (Williston), lateral view; (3) *Myxosargus knowltoni* Curran, lateral view; (4) *Nemotelus albirostris* Macquart, lateral view; (5) *Artemita nana* (Bellardi), lateral view; (6) *Dieuryneura stigma* (Giglio-Tos), anterior view; (7) *Borboridea microcephala* (Kraft & Cook), lateral view.

from almost round to elongate–oval, sometimes petiolate or spatulate; vestiture moderate, never dense (Figs. 38–42, 46). Male terminalia usually small, rather simple; surstylus simple and ventral; aedeagus two- or three-pronged; cercus simple. Terminal female segments forming at most a simple weakly developed ovipositor.

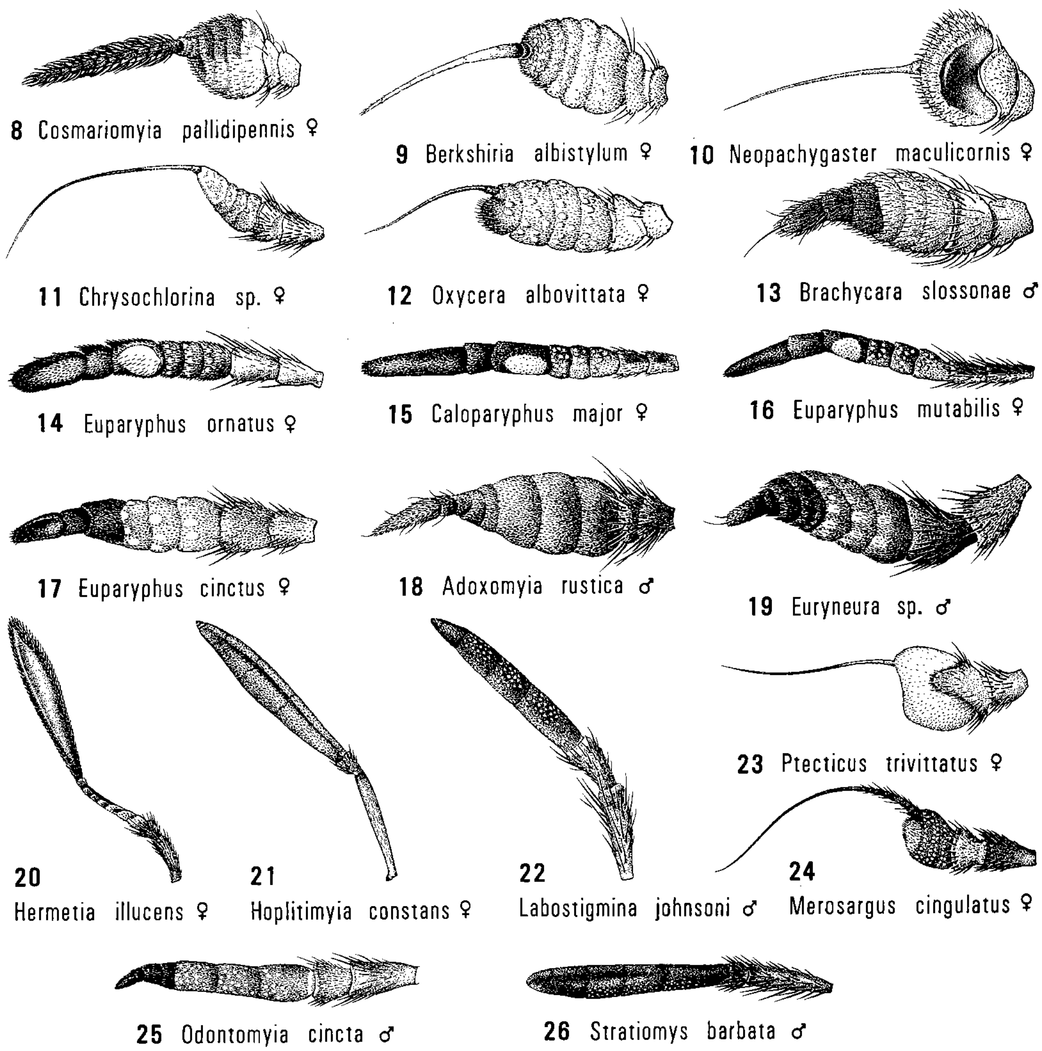
Larva. Elongated, flattened, composed of head capsule and 11 body segments (Figs. 71–75, 84). Integument shagreened from deposit of calcium carbonate plates. Head and body bearing setae that are sometimes taxonomically important.

Head capsule well-developed (Figs. 57–70), although broadly open posteroventrally, retracted more than half its length within thorax, but not functionally retractile; anterior exposed portion elongated and narrow except for ocular prominences, broadened posteriorly. Mandible and maxilla more or less completely fused, operating vertically; maxillary palpus distinct; no free pharyngeal skeleton within head capsule. Antenna usually located anterolaterally.

Prothorax broader than head, with remainder of body either parallel-sided to near apex or attaining maximum width at abdominal segment 2. Prominent lateral spiracles present on prothorax; lateral spiracles sometimes present on metathorax and on abdominal segments 1–6 or 1–7, but small and probably not functional; posterior spiracles functional, located in a transverse cleft on terminal abdominal segment; transverse cleft fringed with hydrofuge hairs in aquatic forms. Prolegs lacking, although ventral hooks sometimes present, especially on penultimate or antepenultimate segment, or both. Pupation occurring within last larval integument. Larval description based mainly on McFadden (1967).

Biology and behavior. Adults of the Stratiomyidae are frequently found resting on vegetation or feeding on flowers such as willow (*Salix*), hawthorn (*Crataegus*), Umbelliferae, or Compositae. Some species hover in the fashion of syrphids. Many can be collected by sweeping in grasses, sedges (*Carex*), cattails (*Typha*), or other vegetation in boggy areas or near the margins of streams or ponds. Some species can be caught effectively in a Malaise trap.

Larvae of the Stratiomyinae are aquatic; some of these can endure highly saline waters or the high temperature of hot springs. The other subfamilies are terrestrial. They breed mostly in decaying plant or animal materials, in excrement, or under the bark of fallen trees; most of those living under bark (Pachygastrinae) are predacious, and some are natural enemies of bark beetles. Some Chiromyzinae, at least, feed on the roots of grasses; one introduced species damages lawns in California. Several Australian species are sugar cane pests. *Hermetia illucens* (Linnaeus) has been involved in human enteric myiasis; however, it is also beneficial to man by successfully breeding in competition with the



Figs. 36.8–26. Antennae: (8) *Cosmariomyia pallidipennis* (Williston); (9) *Berkshiria albistylum* Johnson; (10) *Neopachygaster maculicornis* (Hine); (11) *Chrysochlorina* sp.; (12) *Oxycera albovittata* Malloch; (13) *Brachycara slossonae* (Johnson); (14) *Euparyphus ornatus* Williston; (15) *Caloparyphus major* (Hine); (16) *Euparyphus mutabilis* Adams; (17) *Euparyphus cinctus* (Osten Sacken); (18) *Adoxomyia rustica* (Osten Sacken); (19) *Euryneura* sp.; (20) *Hermetia illucens* (Linnaeus); (21) *Hoplitimyia constans* (Loew); (22) *Labostigmina johnsoni* (Curran); (23) *Ptecticus trivittatus* (Say); (24) *Merosargus cingulatus* Schiner; (25) *Odontomyia cincta* Olivier; (26) *Stratiomys barbata* Loew.

house fly (*Musca domestica* Linnaeus) and controlling its numbers. Several scavengers breed in decaying cactus in southwestern United States and Mexico.

Classification and distribution. The classification used here is that of McFadden (1967), except that the Xylomyinae are excluded from the Stratiomyidae. McFadden's excellent study of the larvae has clarified greatly the subfamilial and tribal classification of the Stratiomyidae. A partial review of the Canadian species is given by McFadden (1972).

In comparison with other families of Diptera in the Nearctic region, the taxonomy of the Stratiomyidae is fairly satisfactory. Species numbering 254 in 42 genera are known as adults, but of these the larvae of only 53 species in 24 genera are known. The immature forms obviously need further study, and the larval key given here is only of limited value. Adult classification is much more satisfactory, although at least one undescribed genus and several undescribed species occur, and the taxonomy of certain genera and species complexes needs clarification. As is true for most other Diptera, few studies have been made on an infraspecific level.

Fossil stratiomyids are known as early as the Cretaceous era, with several extinct related families going back to the Jurassic period. Eight species in eight genera are known from North America; six of these are from the Florissant deposits in Colorado (James 1937, Melander 1949), one is from amber in the Chiapas deposits in Mexico (James 1971), and the last is from Canadian amber (Teskey 1971).

Key to genera

Adult

1. Abdomen usually elongate, with seven or eight visible abdominal tergites (Figs. 38, 39); those beyond tergite 5 not retracted except sometimes in *Antissa* 2

Abdomen with five visible abdominal tergites (Figs. 40–42, 46); a sixth sometimes visible, but usually those beyond tergite 5 retractile into the fifth 6

2. Proboscis vestigial; palpus button-like. Scutellum unspined. Abdomen of female broadest at base, gradually tapering to apex ....................CHIROMYZINAE....***Inopus*** Walker

1 sp., *rubriceps* (Macquart); introduced, California

Proboscis well-developed; palpus elongated though sometimes small and slender. Scutellum with four or six spines, or unspined. Abdomen in both sexes oval, not tapering 3

3. Scutellum unspined. Eye bare or at most with short inconspicuous scattered hairs ....BERIDINAE, in part ...***Allognosta*** Osten Sacken

4 spp.; east of Rocky Mountains; James 1939*b*

Scutellum with four or six spines (Figs. 49, 50). Eye with thick long hairs 4

4. Mid tibia with a small but distinct apical spur (Fig. 43). Abdomen (Fig. 39) broad; segments 6–8 very short, sometimes telescoped into segment 5; segment 6 of female more closely associated with ovipositor than with those segments preceding terminalia ....................CLITELLARIINAE, in part ...***Antissa*** Walker, in part

2 spp.; 1 sp. western, other widespread; James 1939*b* (as *Hexodonta*)

Mid tibia without spur. Abdomen rather slender (Fig. 38); segments 6–8 not telescoped; segment 6 of female more closely associated with segments preceding terminalia than with ovipositor ....BERIDINAE, in part 5

5. Scutellum with four spines (Fig. 49). Hind tibia inflated (Fig. 44). Palpus long, extending almost to apex of labella with proboscis in normal position. Eyes widely separated in both sexes ....***Actina*** Meigen

1 sp., *viridis* (Say); widespread

Scutellum with six spines (Fig. 50). Hind tibia not inflated (Fig. 45). Palpus very small, though slender. Eyes of male contiguous ....***Beris*** Latreille

3 spp.; boreal; James 1939*b*

6. Scutellum with four or six usually long spines 7

Scutellum with two long spines, or with a series of spinules, or unarmed 8

7. Scutellum with four spines. Three veins arising from cell dm. Antenna arising from apex of truncated cone-like prominence formed on ventral part of frons (Fig. 5) ....................PACHYGASTRINAE, in part...***Artemita*** Walker

1 sp., *inornata* (Williston); southern Texas

Scutellum with six spines. Four veins arising from cell dm. Frons not produced (Fig. 2), so consequently antenna not arising from a prominence ....................CLITELLARIINAE, in part...***Antissa*** Walker, in part

see couplet 4

8. Crossvein m-cu absent; cell dm present (Figs. 27–31) 9

Crossvein m-cu present; cell d present (Figs. 32–37) 32

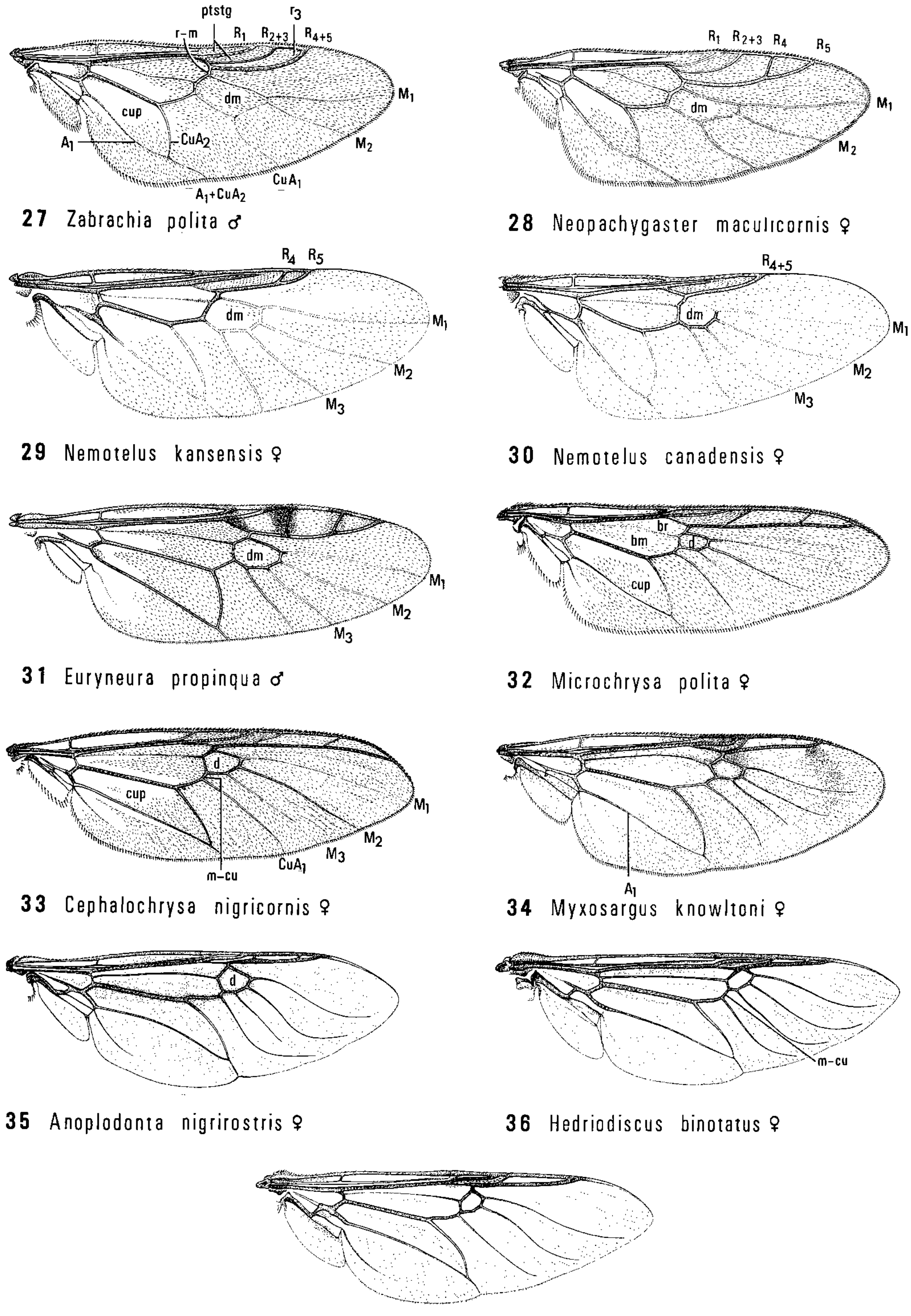
9. Three veins arising from cell dm; that is, M_3 lacking, not even represented by fold in membrane (Figs. 27, 28). Antenna with two-segmented arista; basal four flagellomeres compact. Scutellum unspined ....................PACHYGASTRINAE, in part....10

Four veins arising from cell dm; M_3 represented at least by fold in membrane (Figs. 29–31). Antenna various. Scutellum unspined or spined 17

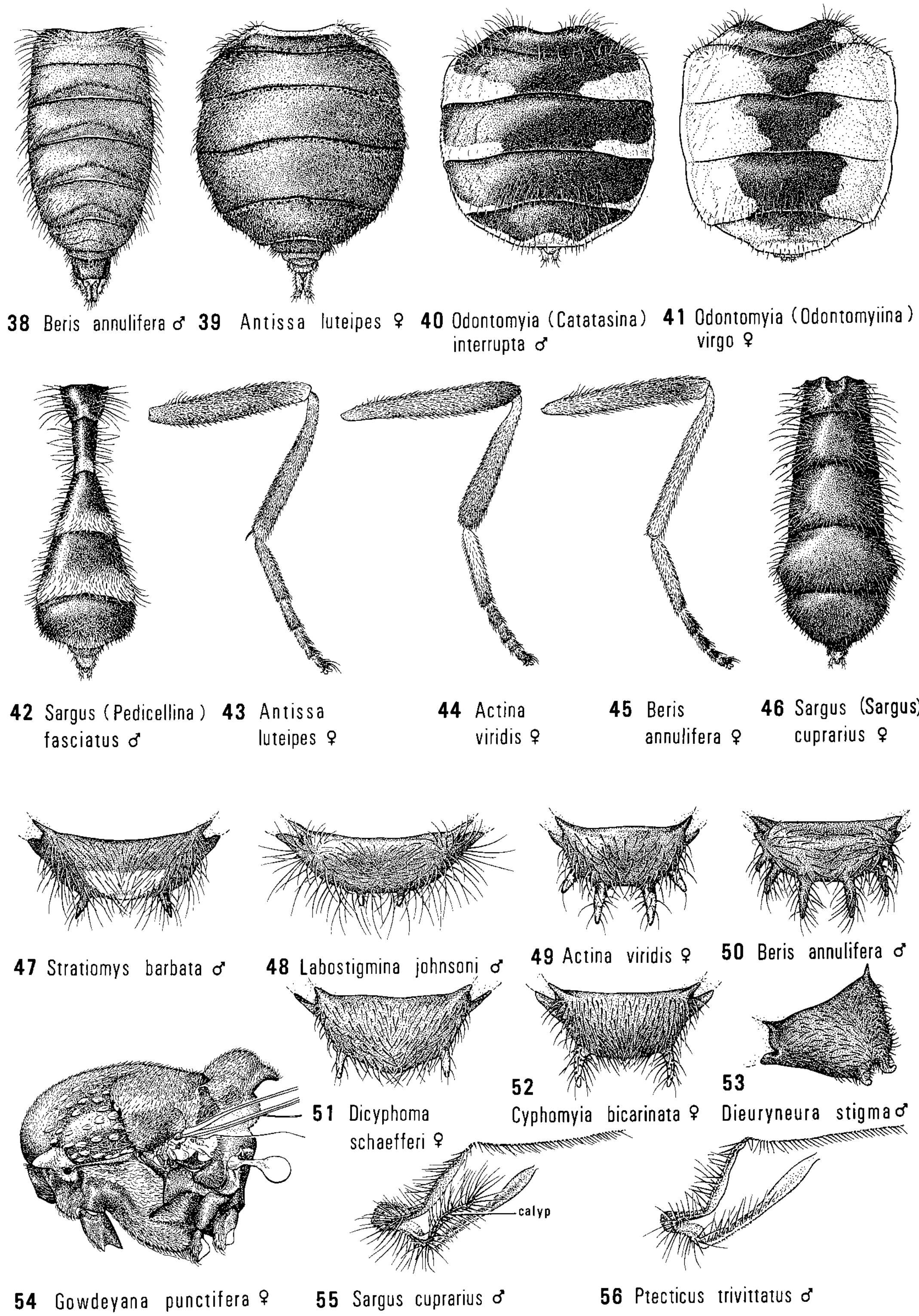
10. Arista (Fig. 8) with dense black hairs that give it superficial appearance of a vane-like stylus ....***Cosmariomyia*** Kertész

1 sp., *pallidipennis* (Williston); Ohio

Arista (Figs. 9, 10) bare or with only very short pubescence 11



Figs. 36.27–37. Wings: (27) *Zabrachia polita* Coquillett; (28) *Neopachygaster maculicornis* (Hine); (29) *Nemotelus kansensis* Adams; (30) *Nemotelus canadensis* Loew; (31) *Euryneura propinqua* Schiner; (32) *Microchrysa polita* (Linnaeus); (33) *Cephalochrysa nigricornis* (Loew); (34) *Myxosargus knowltoni* Curran; (35) *Anoplodonta nigrirostris* (Loew); (36) *Hedriodiscus binotatus* (Loew); (37) *Odontomyia pilimana* Loew.
Abbreviation: ptstg, pterostigma.



Figs. 36.38–56. Abdomens, legs, thoraces, and posterior wing bases: abdomen of (38) *Beris annulifera* (Bigot), (39) *Antissa luteipes* (Williston), (40) *Odontomyia* (*Catatasina*) *interrupta* Olivier, (41) *Odontomyia* (*Odontomyiina*) *virgo* (Wiedemann), and (42) *Sargus* (*Pedicellina*) *fasciatus* Fabricius; (43) midleg of *Antissa luteipes*; (44) hindleg of *Actina viridis* (Say) and (45) *Beris annulifera*; (46) abdomen of *Sargus* (*Sargus*) *cuprarius* (Linnaeus); dorsal view of scutellum of (47) *Stratiomys barbata* Loew, (48) *Labostigmina johnsoni* (Curran), (49) *Actina viridis*, (50) *Beris annulifera*, (51) *Dicyphoma schaefferi* (Coquillett), (52) *Cyphomyia bicarinata* Williston, and (53) *Dieuryneura stigma* (Giglio-Tos); (54) lateral view of thorax of *Gowdeyana punctifera* (Malloch); posterior wing base of (55) *Sargus cuprarius* and (56) *Ptecticus trivittatus* (Say).
Abbreviation: calyp, calypter.

11. Basal complex of flagellum (Fig. 9) longer than wide, not disc-shaped or reniform, composed of five distinct flagellomeres .... ***Berkshiria*** Johnson

1 sp., *albistylum* Johnson; east of Rocky Mountains

Basal complex of flagellum (Fig. 10) disc-shaped or reniform, as high as or higher than long, apparently composed of four flagellomeres that are often difficult to distinguish 12

12. R_4 and R_5 fused (Fig. 27) 13

R_4 and R_5 separate (Fig. 28) 14

13. Frontal area of head, at least in female (Fig. 7), strongly flattened. Cell r_3, measured along the costal margin, as long as pterostigma. Scutellum massive, not margined, on a line with plane of scutum .... ***Borboridea*** Kertész

1 sp., *microcephala* (Kraft & Cook); Texas; James 1965

Frontal area of head not distinctly flattened above. Cell r_3, measured along costal margin, shorter than pterostigma (Fig. 27). Scutellum of ordinary size, frequently margined, more or less set at an angle with plane of scutum .... ***Zabrachia*** Coquillett

10 spp.; predominantly western; Kraft and Cook 1961, James 1965

14. Antennal flagellum (Fig. 10) with smooth dark shiny area on inner surface .... ***Neopachygaster*** Austen

4 spp.; widespread; Kraft and Cook 1961

Antennal flagellum without such an area 15

15. Scutellum without distinct posterior rim; sides of scutum with only ordinary hairs as on rest of scutum .... ***Pachygaster*** Meigen

3 spp.; widespread; Kraft and Cook 1961

Scutellum with thin wide posterior rim; sides of scutum, before suture, with either single conspicuous flattened hairs or with small groups of these hairs aligned in longitudinal rows (Fig. 54) 16

16. Antenna inserted at middle of head in lateral view. Scutellum in lateral view strongly convex above .... ***Gowdeyana*** Curran

1 sp., *punctifera* (Malloch); widespread in U.S.A.

Antenna inserted below middle of head. Scutellum only moderately convex above .... ***Eidalimus*** Kertész

2 spp.; widespread; James 1965

17. Scutellum without spines 18

Scutellum with a pair of spines 23

18. Face, below antennae, produced forward into an elongate cone (Fig. 4). Small flies, predominantly black but sometimes varied with white or orange .... NEMOTELINAE, in part 19

Face sometimes produced forward but never into an elongate cone, sometimes with a short cone extending downward. Size and color various 21

19. Eyes of male separated. No females keyed here .... ***Akronia*** Hine, in part

1 sp., *frontosa* Hine; Ohio

Eyes of male contiguous. All females keyed here .... ***Nemotelus*** Geoffroy, in part 20

20. R_4 separate from R_5 (Fig. 29) .... ***Nemotelus*** (***Nemotelus*** Geoffroy)

12 spp.; widespread; James 1936*a*

.... ***Akronia*** Hine, in part

see couplet 19

R_4 fused with R_5 (Fig. 30) .... ***Nemotelus*** (***Camptopelta*** Williston)

26 spp.; widespread; Hanson 1963

21. Terminal flagellomere (Fig. 11) forming an arista that is distinctly longer than remainder of antenna. Eyes widely separated in both sexes .... CHRYSOCHLORINAE .... ***Chrysochlorina*** James

1 sp., *quadrilineata* (Bigot); Florida

Terminal flagellomere forming a stylus that is usually no longer than rest of flagellum, at most shorter than remainder of antenna. Eyes widely separated in both sexes, or contiguous in male .... CLITELLARIINAE, in part 22

22. Antenna longer than head; terminal flagellomere (Fig. 20) vane-like, flattened, usually as long as and sometimes longer than rest of flagellum; basal complex of flagellum grooved toward apex on inner side. Eyes widely separated in both sexes .... HERMETIINI....*Hermetia* Latreille

12 spp.; south and southwest with 1 sp. widespread; James and Wirth 1967

Antenna shorter than head; terminal flagellomere (Fig. 13) cylindrical and shorter than basal complex; groove on inner side of basal complex lacking. Eyes of male contiguous .... CLITELLARIINI, in part....*Brachycara* Thomson

2 spp.; southern; James 1962

23. Scutellar spines short, blunt, hook-like, directed downward but recurved upward at apex (Fig. 53). Pair of well-developed frontal calli in female; frontal triangle of male callus-like (Fig. 6). Body black in background .... CLITELLARIINI, in part....*Dieuryneura* James

1 sp., *stigma* (Giglio-Tos); U.S.A.

Scutellar spines straight and moderately long. Neither sex with well-developed frontal calli. Body black, variegated with yellow or orange 24

24. Antennal flagellum composed of six flagellomeres. Branches of M often weakened. Body variegated in background .... STRATIOMYINAE, in part; OXYCERINI....25

Antennal flagellum composed of eight flagellomeres; terminal two or three flagellomeres forming a distinct stylus. Branches of M strong and distinct. Body entirely black in background .... CLITELLARIINI, in part....31

25. Antenna short; last two flagellomeres forming a distinctly preapical arista (Fig. 12) .... *Oxycera* Meigen

7 spp.; widespread in east with 1 sp. to Alaska; Malloch 1917

Antenna usually elongated, sometimes with a terminal stylus but never aristate (Figs. 14–17)..26

26. Antennal pedicel elongated, at least as long as basal three flagellomeres combined .... *Glariopsis* Lindner

1 sp., *decemmaculatus* (Osten Sacken); southwestern

Antennal pedicel of ordinary length, much shorter than basal three flagellomeres combined 27

27. R_4 fused with R_5; cell r_3 fairly short and broad, with membrane no more than four to five times as long as its maximal width. Aedeagus bifid .... *Euparyphus* Gerstäcker, in part....28

R_4 separate from or fused with R_5; if R_4 fused with R_5, membrane of cell r_3 at least six but usually eight to ten times as long as its maximal width. Aedeagus bifid or trifid 29

28. Veins outlining cell dm apical to CuA_2 and crossvein r-m feeble, concolorous with membrane .... *Euparyphus* (*Aochletus* Osten Sacken)

5 spp.; widespread; Quist and James 1973

Veins outlining cell dm, both on its basal and apical parts, distinct and usually more heavily pigmented than membrane .... *Euparyphus* (*Parochletus* Quist)

2 spp.; southwestern; Quist and James 1973

29. Spines of scutellum usually separated at base by a distance at least as great as length of spines; if not, apical one-fourth of wing with only scattered microtrichia and with extensive bare areas along veins. Aedeagus trifid. Flies robust; abdomen usually black, either with median spots or with transverse usually interrupted bands .... *Caloparyphus* James

9 spp.; widespread; James 1939*a*

Spines of scutellum always closer together at base than length of spines; apical one-fourth of wing thickly and uniformly covered with microtrichia. Aedeagus bifid. Flies more slender than above; abdomen not marked as above .... *Euparyphus* Gerstäcker, in part....30

30. Penultimate flagellomere of antenna much shorter than preceding one (Fig. 14) (except in *patagius* Quist). Facial pattern (except in *pygmaea* James) characteristic; mid face with a black or brown median area or vitta and with a yellow lateral margin; female facial orbit also yellow .... *Euparyphus* (*Nigriparyphus* Quist)

7 spp.; western; Quist and James 1973

Penultimate flagellomere of antenna subequal to preceding one (Fig. 16). Facial pattern variable, but not as described above .... *Euparyphus* (*Euparyphus* Gerstäcker)

9 spp.; widespread; Quist and James 1973

31. Eye densely long–pilose. Antenna with last three flagellomeres developed into an acute stylus that is several times as long as wide (Fig. 18). Wing hyaline or uniformly clouded .... ***Adoxomyia*** Kertész

11 spp.; western with 1 sp. in east; James and McFadden 1969

Eye bare. Antenna with last two flagellomeres developed into a blunt stylus that is no longer than wide (Fig. 19). Wing patterned (Fig. 31) .... ***Euryneura*** Schiner

1 sp., *propinqua* Schiner; southwestern

32. Face below antenna produced forward into a distinct cone (Fig. 4). Flies small, black, marked with white........................ NEMOTELINAE, in part.... ***Nemotelus*** Geoffroy, in part

see couplet 20

Face receding, tuberculate, or produced downward, never extending forward. Size and color variable 33

33. Antennal flagellum composed of eight flagellomeres with at most the last one forming a stylus. Venation strong; three branches of M and crossveins r-m and m-cu all strong. Abdomen sometimes bicolored but not patterned .... CLITELLARIINAE; CLITELLARIINI, in part....34

Antennal flagellum composed of five or six flagellomeres, either with or without development of an arista or stylus. Venation and abdominal coloration variable 35

34. Eighth flagellomere forming a poorly defined stylus. Scutellar spines small, widely separated, and subapical; tips of spines barely reaching apex of scutellum (Fig. 51) .... ***Dicyphoma*** James

1 sp., *schaefferi* (Coquillett); southwestern

Eighth flagellomere not stylus-like. Scutellar spines strong, approximated, apical (Fig. 52) .... ***Cyphomyia*** Wiedemann

2 spp.; Florida, southwestern; James 1940

35. Antenna aristate (Figs. 23, 24) 36

Antenna not aristate, with or without a terminal stylus (Figs. 21, 22, 25, 26) .... STRATIOMYINAE, in part....43

36. Arista terminal. A_1 slightly though distinctly sinuous. Scutellum two-spined .... STRATIOMYINAE; MYXOSARGINI, in part.... ***Nothomyia*** Loew

2 spp.; Florida, Ohio (probably adventitious in Ohio); James 1936

Arista at least slightly dorsal. A_1 not sinuous. Scutellum unspined .... SARGINAE....37

37. Eye densely pilose .... ***Chloromyia*** Duncan

1 sp., *formosa* (Scopoli); introduced, New York

Eye bare........................ 38

38. Lower calypter with a strap-like prolongation near outer end (Fig. 55) 39

Lower calypter transverse, without such a prolongation (Fig. 56) 42

39. Ocellar triangle approximately equilateral, situated less than its length from posterior margin of head. Eyes holoptic in male 41

Ocellar triangle situated at least its length from posterior margin of head; distance from anterior ocellus to posterior ones greater than distance between posterior ocelli, usually considerably so. Eyes holoptic or dichoptic in male .... ***Sargus*** Fabricius....40

40. Eyes holoptic in male. Abdomen, especially in male, clavate (Fig. 42) .... ***Sargus*** (***Pedicellina*** James)

1 sp., *fasciatus* Fabricius; east of Mississippi River

Eyes dichoptic in male. Abdomen ovoid (Fig. 46) .... ***Sargus*** (***Sargus*** Fabricius)

5 spp.; widespread; James 1936*b*

41. Wing with cell d small; branches of M weak, evanescent toward wing margin; cell cu*p* as broad as combined basal cells (Fig. 32) .... ***Microchrysa*** Loew

2 spp.; both introduced but well-established and widespread; James 1936*b*

Wing with cell d of usual size; branches of M, or at least M_1 and M_2, evident to wing margin; cell cu*p* about two-thirds combined width of basal cells (Fig. 33) .... ***Cephalochrysa*** Kertész

4 spp.; widespread; James 1936*b* (as *Isosargus*)

42. Pedicel of antenna prolonged finger-like into inner side of flagellum (Fig. 23). Nearctic species predominantly yellow .... ***Ptecticus*** Loew

4 spp.; widespread; McFadden 1971

Pedicel of antenna at most gently convex on inner side of adjoining flagellum (Fig. 24). Nearctic species predominantly metallic blue or green .... ***Merosargus*** Loew

2 spp.; widespread; James 1941

43. A_1 slightly though distinctly sinuous (Fig. 34). Face produced angularly downward at lower margin (Fig. 3). Abdomen relatively slender, no more than two-thirds as wide as long, not patterned .... MYXOSARGINI, in part.... ***Myxosargus*** Brauer

4 spp.; widespread; James 1942

A_1 not at all sinuous. Face sometimes tuberculate or somewhat produced forward, but never downward. Abdomen at least three-quarters as wide as long, usually patterned 44

44. Scutellum without spines. Venation strong; M_1, M_3, and crossvein r-m all present and distinct (Fig. 35) .... ***Anoplodonta*** James

1 sp., ***nigrirostris*** (Loew); Rocky Mountain area

Scutellum with spines; spines in some *Labostigmina* sometimes minute. Venation variable 45

45. Antenna with six flagellomeres; last two flagellomeres forming a short but distinct stylus; ratio of scape to pedicel usually not more than 1.5:1 (Fig. 25). Venation somewhat reduced; either crossvein r-m absent or at least M_3 reduced to a stump or weak fold, sometimes virtually absent .... ODONTOMYIINI.... 46

Antenna with five flagellomeres, and without a stylus; ratio of scape to pedicel more than 2:1 (Fig. 26). Venation variable .... STRATIOMYINI.... 49

46. Wing with crossvein r-m absent; M_1 and M_3 strong and distinct nearly to wing margin (Fig. 36) .... ***Hedriodiscus*** Enderlein

7 spp.; widespread; James 1936*c* (as *Odontomyia*, in part)

Wing with crossvein r-m present; M_3 and sometimes M_1 weak, reduced to a stump or fold, or virtually absent (Fig. 37) .... ***Odontomyia*** Meigen.... 47

James 1936*c*

47. Pleural, postpronotal, and supra-alar regions in female and usually in male marked with distinct yellow areas .... ***Odontomyia*** (***Odontomyia*** Meigen)

15 spp.; widespread

Pleural, postpronotal, and supra-alar regions wholly black or without distinct yellow areas in both sexes 48

48. Abdomen black in background, with transverse paired yellow or green linear or triangular markings at apices of tergites (Fig. 40) .... ***Odontomyia*** (***Catatasina*** Enderlein)

9 spp.; widespread

Abdomen yellow or green in background, usually with a median longitudinal black stripe dorsally; this stripe sometimes occupying most of dorsum but leaving broad lateral margins pale (Fig. 41) .... ***Odontomyia*** (***Odontomyiina*** Enderlein)

7 spp.; widespread

49. Face receding. Scutellar spines strong, located on outer corners and outside median third (Fig. 47) .... ***Stratiomys*** Geoffroy

26 spp.; widespread; James and Steyskal 1952

Face produced or tuberculate; if tuberculate, tubercle involving area of antennal insertion. Scutellar spines more nearly approximate (Fig. 48) 50

Figs. 36.57–70. Larval heads: (57) dorsal, (58) ventral, and (59) lateral views of *Odontomyia cincta* Olivier; (60) dorsal view of *Caloparyphus major* (Hine); (61) dorsal view of *Euparyphus limbrocutris* Adams; (62) dorsal view of *Adoxomyia* sp.; (63) dorsal view of *Dicyphoma schaefferi* (Coquillett); (64) dorsal view of *Microchrysa polita* (Linnaeus); (65) dorsal view of *Sargus cuprarius* (Linnaeus); (66) ventral view of *Inopus rubriceps* (Macquart); (67) ventral view of *Cyphomyia bicarinata* Williston; (68) ventral view of *Neopachygaster maculicornis* (Hine); (69) ventral view of *Hermetia* sp.; (70) ventral view of *Sargus cuprarius*.

Abbreviations: ant, antenna; lab, labium; spn, spine.

50. Flagellum flattened, or triangular in cross section; scape 4–5 times as long as pedicel (Fig. 21). Head wider than thorax. Scutellar spines strong .... ***Hoplitimyia*** James
3 spp.; western; James and Steyskal 1952

Flagellum cylindrical or almost so; scape 1.25–2.5 times as long as pedicel (Fig. 22). Head not wider than thorax. Scutellar spines weak or evanescent .... ***Labostigmina*** Enderlein
18 spp.; widespread; James and Steyskal 1952

Larva

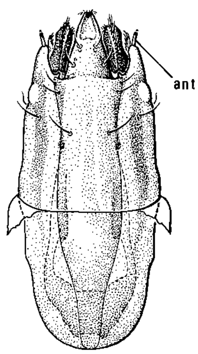
(modified from McFadden 1967)

1. Terminal abdominal segment with a terminal or dorsal coronet of very short or long hydrofuge (plumose or pinnate) setae on margin of spiracular cleft (Figs. 74, 83, 84, 86) 2

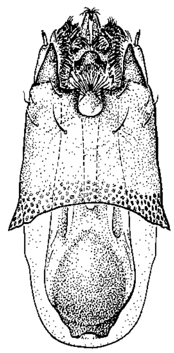
Terminal abdominal segment without a coronet of hydrofuge setae 12

2. Coronet of hydrofuge setae apical in position (Figs. 74, 84, 86) .... STRATIOMYINAE 3

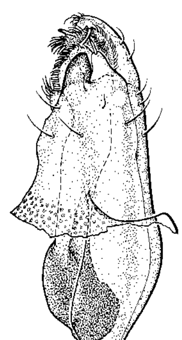
Coronet of hydrofuge setae dorsal in position (Fig. 83) .... NEMOTELINAE .... ***Nemotelus***



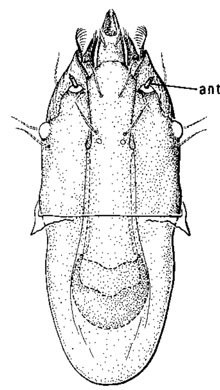
57 Odontomyia cincta



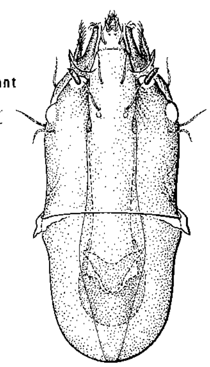
58 Odontomyia cincta



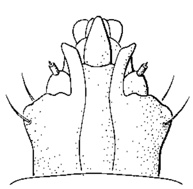
59 Odontomyia cincta



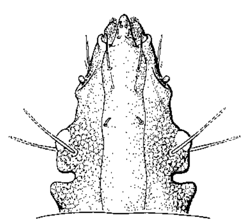
60 Caloparyphus major



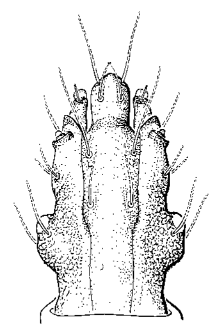
61 Euparyphus limbrocutris



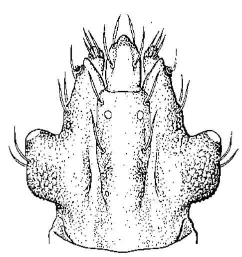
62 Adoxomyia sp.



63 Dicyphoma schaefferi

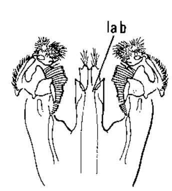


64 Microchrysa polita

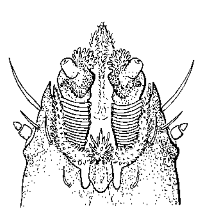


65 Sargus cuprarius

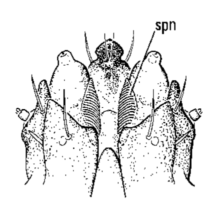
66 Inopus rubriceps



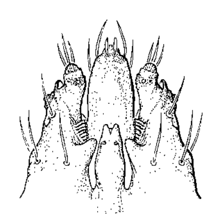
67 Cyphomyia bicarinata



68 Neopachygaster maculicornis

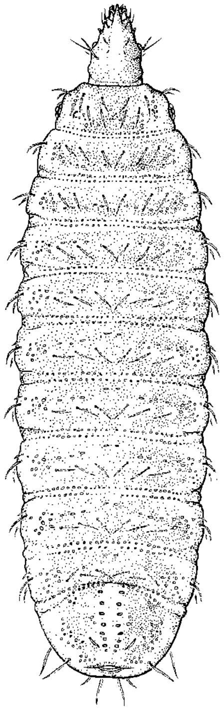


69 Hermetia sp.

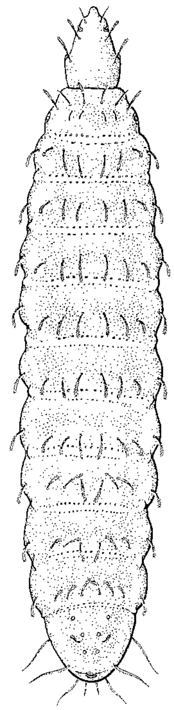


70 Sargus cuprarius

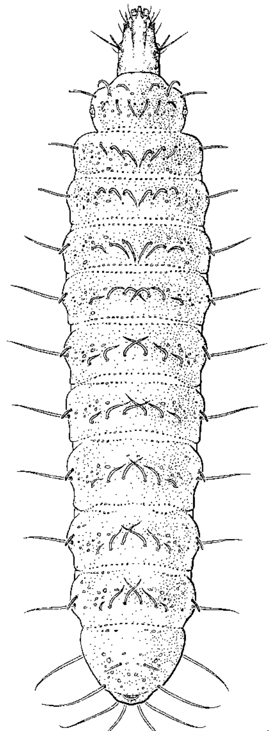
3. Abdominal sternite 7 with one or more pairs of sclerotized hooks (Fig. 75) 4
   Abdominal sternite 7 without paired sclerotized hooks 10



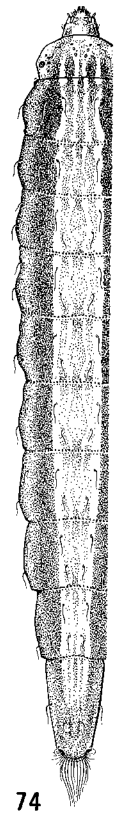
71 Berkshiria albistylum



72 Pachygaster pulchra



73 Zabrachia polita



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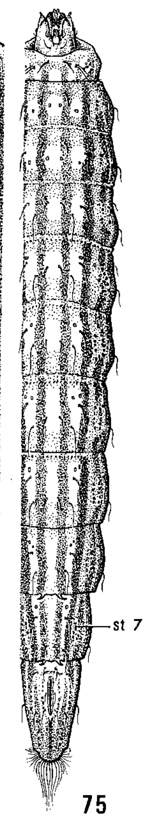

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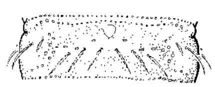
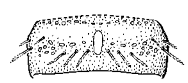
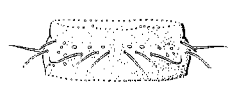
Odontomyia cincta



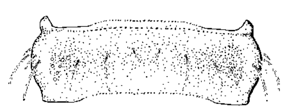
76 Berkshiria albistylum



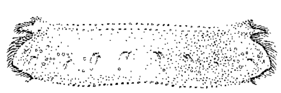
77 Neopachygaster maculicornis



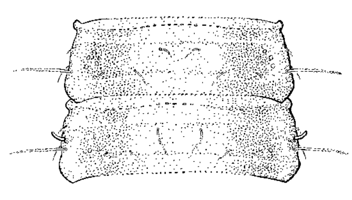
78 Zabrachia polita



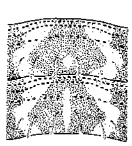
79 Adoxomyia sp.



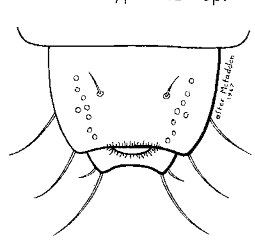
80 Allognosta sp.



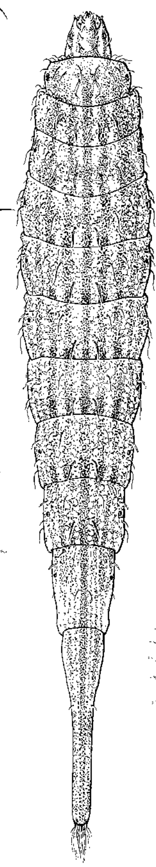
81 Dicyphoma sp.



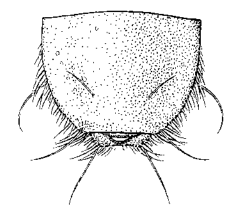
82 Ptecticus trivittatus



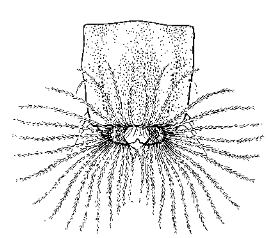
83 Nemotelus kansensis



84 Stratiomys norma



85 Beris annulifera



86 Myxosargus nigricornis

4. Sclerotized hooks present on venter of each of first seven abdominal sternites; hooks on sternite 7 larger than those on others .... ***Euparyphus* (*Aochletus*)**
   Sclerotized hooks absent from first five or six abdominal sternites 5
5. Hydrofuge setae on terminal abdominal segment arising from two lobate structures on lower lip of spiracular cleft (Fig. 86); anterior spiracle located at anterior corner of terminal abdominal segment .... ***Myxosargus***
   Hydrofuge setae arising from straight edge of lower lip; spiracular cleft lacking lobate structures; anterior spiracle not located in anterior corner of segment 6
6. Antenna dorsal, not at apex of ocular lobe (Figs. 60, 61). Anterior spiracle elevated or stalked .. 7
   Antenna at apex of ocular lobe (Figs. 57–59). Anterior spiracle neither elevated nor stalked 8
7. Anterior spiracle on long stalk. Distance from antenna to eye prominence more than twice length of antenna (Fig. 60) .... ***Caloparyphus*, in part**
   Anterior spiracle on short stalk or nearly sessile. Distance from antenna to eye prominence approximately equal to length of antenna (Fig. 61) .... ***Euparyphus* (*Euparyphus*)**
8. Only abdominal sternite 7 with sclerotized hooks .... ***Odontomyia* (*Odontomyiina*)**
   Both abdominal sternites 6 and 7 with sclerotized hooks (Fig. 75) 9
9. Body segments with broad dorsal vittae (Fig. 74), fine white pubescence, or multiple hooks .... ***Odontomyia* (*Odontomyia*)**
   Body segments not as described above .... ***Hedriodiscus***
10. Antenna located at apex of ocular lobe (as in Fig. 57) 11
    Antenna not located at apex of ocular lobe (Fig. 60) .... ***Caloparyphus*, in part**
11. Integument covered with minute peltate scales .... ***Odontomyia* (*Catatasina*)**
    Integument lacking peltate scales .... ***Stratiomys***
12. Mouthparts highly sclerotized, foreshortened, without setae or bristles; mandible well-developed (Fig. 66) .... CHIROMYZINAE .... ***Inopus***
    Mouthparts with a combination of characters other than that given above 13
13. Setae of dorsal transverse rows each surrounded by smaller setae (Fig. 80). Larva uniformly colored .... BERIDINAE, in part 14
    Setae of dorsal transverse rows not surrounded by smaller setae. Larva either colored uniformly or with a pattern 17
14. Larva robust; when mature, longer than 10 mm .... CLITELLARIINAE, in part ... ***Antissa***
    Larva smaller; when mature, shorter than 10 mm .... BERIDINAE, in part 15
15. Abdominal segments with lateral margin bilobate; anterior lobe smaller than posterior one (Fig. 80) .... ***Allognosta***
    Abdominal segments with lateral margin straight 16
16. Terminal abdominal segment not indented apically, fringed apically and laterally with fine setae (Fig. 85) .... ***Beris***
    Terminal abdominal segment broadly indented apically, not fringed .... ***Actina***
17. Labium well-developed (Fig. 67) .... CLITELLARIINAE, in part; CLITELLARIINI 18
    Labium weakly developed or absent 20
18. Head without a distinct notch posterior to eye prominence (Fig. 62). Series of setae on first abdominal tergite transverse, perpendicular to body axis; median seta shorter than other two setae (Fig. 79) .... ***Adoxomyia***

Figs. 36.71–86. Larvae: (71) dorsal view of *Berkshiria albistylum* Johnson; (72) dorsal view of *Pachygaster pulchra* Loew; (73) dorsal view of *Zabrachia polita* Coquillett; (74) part dorsal and (75) part ventral view of *Odontomyia cincta* Olivier; ventral view of abdominal segment 6 of (76) *Berkshiria albistylum*, (77) *Neopachygaster maculicornis* (Hine), and (78) *Zabrachia polita*; dorsal view of abdominal segment 1 of (79) *Adoxomyia* sp. and (80) *Allognosta* sp.; (81) dorsal view of abdominal segments 1 and 2 of *Dicyphoma* sp.; (82) ventral view of abdominal segments 5 and 6 of *Ptecticus trivittatus* (Say); (83) dorsal view of terminal segment of *Nemotelus kansensis* Adams; (84) dorsal view of *Stratiomys norma* Wiedemann; dorsal view of terminal segments of (85) *Beris annulifera* (Bigot) and (86) *Myxosargus nigricornis* Greene.
Abbreviation: st, sternite.

Head with a distinct notch posterior to eye prominence (Fig. 63). Series of setae on first abdominal tergite oblique, set on a line on each side diagonal to body axis (Fig. 81) 19

19. Median seta longer than other two in diagonal series on first abdominal tergite .... ***Cyphomyia***

Median seta no longer than other two in diagonal series on first abdominal tergite .... ***Dicyphoma***

20. Mandibular–maxillary complex of mouthparts (Fig. 68) in part strongly sclerotized. Species small; mature larva not exceeding 7 mm long .... PACHYGASTRINAE 21

Mouthparts lacking sclerotized areas (Figs. 69, 70). Species with some exceptions larger; mature larva usually 9–22 mm long 26

21. Teeth along anal opening prominent; setae on margin of terminal segment short, no longer than one-fourth as long as width of segment (Fig. 71) 22

No prominent teeth along anal opening; setae on margin of terminal segment long, at least one-third as long as width of segment (Fig. 72) 23

22. Ventromedial line of abdominal segment 6 with a round sternal patch (Fig. 76) located anterior to transverse row of setae; eight or more pairs of conspicuous plaques along dorsomedial line of terminal segment (Fig. 71) .... ***Berkshiria***

Sternal patch of ventromedial line of abdominal segment 6 oval (Fig. 77), located between inner setae of transverse row; no more than three or four pairs of conspicuous plaques along dorsomedial line of terminal segment (as in Fig. 72) .... ***Neopachygaster***

23. Each thoracic leg group with two setae 24

Each thoracic leg group with three setae 25

24. Each of first seven abdominal tergites with a row of transverse setae of approximately equal length .... ***Gowdeyana***

Each such row with outermost seta shorter than others .... ***Eidalimus***

25. Abdominal segments 1–7 each with nine pairs of setae; two of these pairs located laterally (Fig. 72) .... ***Pachygaster***

Abdominal segments 1–7 each with 10 pairs of setae; the additional pair located laterally on dorsum (Figs. 73, 78) .... ***Zabrachia***

26. Mouthparts simple; setae restricted to a linear patch on inner margin of mandibular–maxillary complex (Fig. 69). Larva robust, 17–22 mm long when mature, uniformly colored .... CLITELLARIINAE; HERMETIINI .... ***Hermetia***

Mouthparts more elaborate; setae present on mandibular–maxillary complex in addition to linear patch on its inner margin (Fig. 70). Larva more slender, smaller, when mature 5–15 mm long, usually with a vittate pattern .... SARGINAE 27

27. A sternal patch on each of abdominal segments 5 and 6; patch on segment 6 extending almost whole length of sternite (Fig. 82) .... ***Ptecticus***

No sternal patch on abdominal segment 5; patch on segment 6 much shorter than length of sternite 28

28. Dorsolateral margin of each thoracic segment and each of abdominal segments 1–7 with a series of dark plaques arranged in a circular pattern; each thoracic segment with a transverse band of these plaques connecting the two lateral circles; five vittae present on dorsum, with median vitta markedly the broadest .... ***Sargus* (*Pedicellina*)**

Dorsolateral margin of thoracic segment and abdominal segments 1–7 not as described above 29

29. Lateral margin of head (Figs. 64, 65) with a protruding tubercle; head constricted posterior to tubercle 30

Lateral margin of head lacking a protruding tubercle; head continuing to widen posteriorly, though impressed immediately behind eye prominence .... ***Sargus* (*Sargus*)**, in part

30. Eye prominence anterior to protruding lateral tubercle .... ***Merosargus***

Eye prominence on protruding lateral tubercle 31

31. Head elongated, narrow, with the part anterior to eye prominence as long as greatest width of head (Fig. 64) .... ***Microchrysa***

Head shorter and broader, with the part anterior to eye prominence much shorter than greatest width of head (Fig. 65) .... ***Sargus* (*Sargus*)**, in part

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THEREVIDAE

37

MICHAEL E. IRWIN AND LEIF LYNEBORG

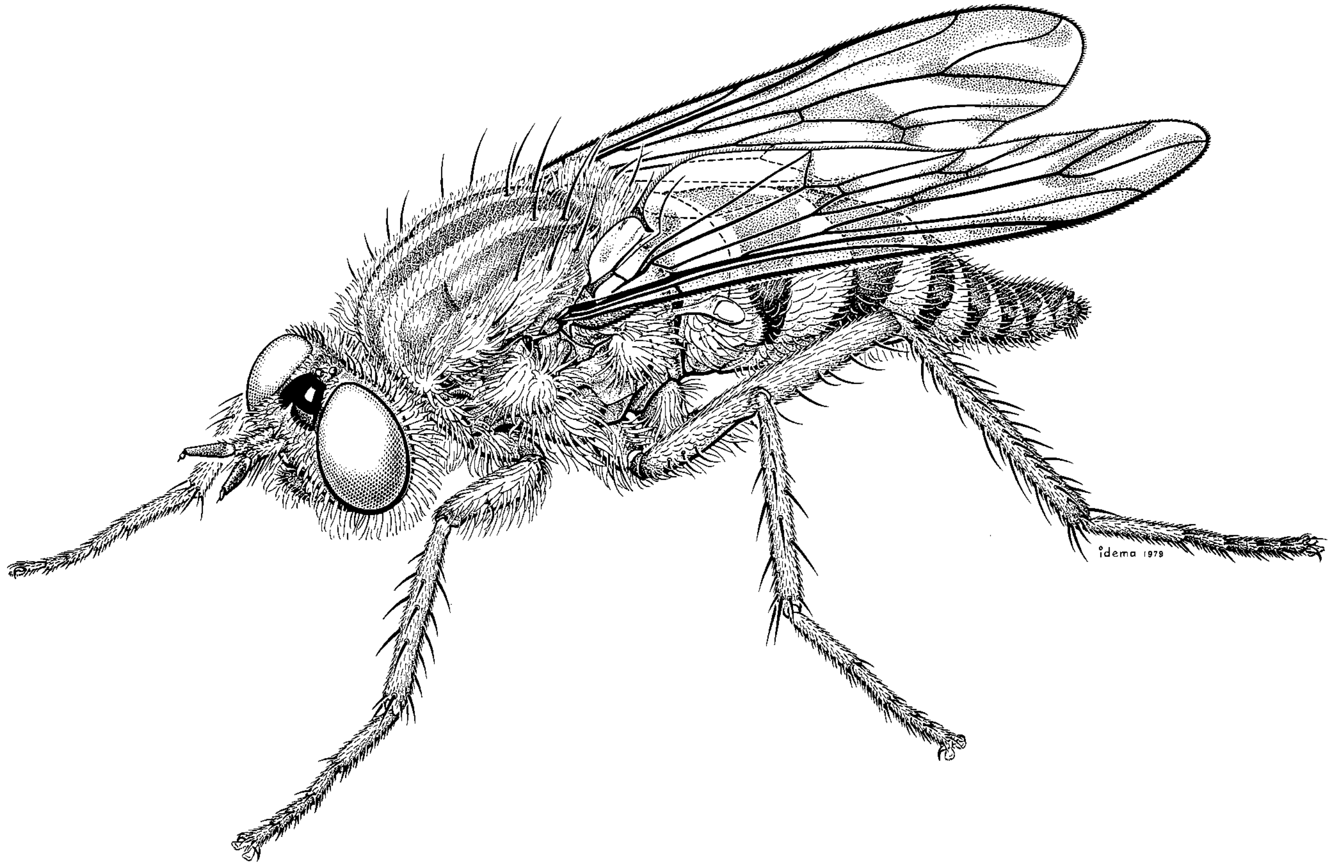


Fig. 37.1. Female of *Thereva fucata* Loew.

Slender to moderately thick-bodied flies (Fig. 1); length, excluding antennae, 2.5–15 mm. Background color light yellow to black. Body wholly or partly pilose, tomentose, and pruinose; setae usually prominent. Wing venation constant; R_4 elongate, sinuous; cell d elongate, with three veins extending from its apex; crossvein m-cu present.

Adult. Head: hemispherical, not depressed at vertex, hypognathous (Fig. 1) to prognathous (Figs. 2, 3). Eyes dichoptic in female, holoptic in most males, usually without hairs in both sexes. Frons of female wide, reaching ocellar tubercle, often covered variously with pollen and scattered hairs; frons of male usually small, acutely to broadly triangular, pruinose to bare, often without hairs. Three prominent ocelli set at vertex or slightly anterior to vertex. Antenna three-segmented, sometimes set on prominent frontal protuberance; scape usually setose, especially ventrally; pedicel usually with a ring or two of short setae; first flagellomere without setae, or with setae usually confined to basal third; stylus comprising one or two flagellomeres and a terminal or subterminal bristle, and set apically or subapically on basal flagellomere; bristle elongate and prominent in some genera, but almost undetectable in others (Figs. 2–7). Face often pruinose; lateral area hairy or not; gena hairy or not, often with a darkened pruinose, tomentose, or bare stripe; occiput finely pruinose, often densely hairy from midpoint ventrally and strongly setose dorsally; postocular setae usually present, though often weak. Palpus one- or two-segmented, usually hairy and not prominent, set beside proboscis in subcranial cavity; proboscis slightly longer than palpus, and usually carried within subcranial cavity.

Thorax: scutum varying from nearly square to elongate rectangular when viewed from above, often sparsely to densely tomentose or pilose, or both. Scutellum prominent, often without hairs, but almost always pruinose and often tomentose. Pleuron variously pilose; upper portion usually densely pruinose; lower portion sometimes without pollen. Chaetotaxy: one pair postalar setae; one to six pairs notopleural setae, or more; one or two pairs supra-alar setae; usually from zero to two pairs dorsocentral setae, but three or more in a few species; zero to three, rarely four, pairs scutellar setae.

Legs usually fairly long and slender; hindleg longer than other two. Fore coxa with none to several setae on anterior surface; all femora bare to heavily setose especially postventrally, often with long scale-like pile along dorsal surface; tibiae and tarsi setulose in definite longitudinal rows; fore tibia lacking setae anteroventrally. Five tarsomeres present; first tarsomere longest, and sometimes swollen; claw with two pulvilli and a seta-like central empodium, or with empodium absent.

Wing venation generally uniform (Figs. 13, 14); R_1 setose or not; R_4 elongate, often sinuate; cell d elongate, with M_1, M_2, and M_3 arising from apex; CuA_1 not meeting posterior margin of cell d; crossvein m-cu present; cell cu*p* closed behind; cell m_3 open or closed; abnormalities common in wing venation. Pterostigma usually well-developed. Wing hyaline to infuscate, sometimes banded or spotted, with veins often surrounded by darker infuscation. Microtrichia very sparse to dense. Calypter well-developed. Halter large and well-developed.

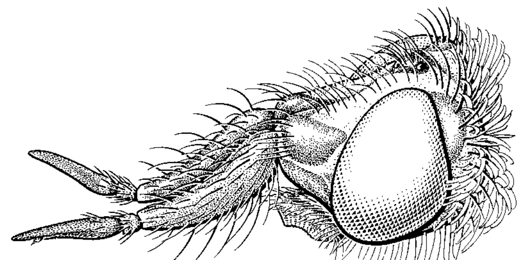
Abdomen: usually convex to flattened dorsally and tapering at apex, sometimes laterally compressed, always with eight well-developed pregenital segments. Fine silvery pollen often adorning abdomen, covering it completely in male of many species and in patterns on female. Tomentum and pile present or absent, usually longer and denser on male.

Female terminalia characterized by a large conspicuous sternite 8, functioning variously as a digging–anchoring apparatus for oviposition, as a floor for the genital chamber, and as a guide for aedeagal insertion during copulation (Figs. 21, 22). Sternite 9, or genital fork, acting as a roof of the genital chamber, completely internal, with two lateral sclerites fused posteriorly to a sclerotized bar that contains a membranous central sheath through which pass ducts of spermathecae and accessory glands. Three unsclerotized spermathecae (sclerotized in *Apsilocephala* Kröber) and two accessory glands present. Tergite 8 generally unmodified. Tergite 9 usually a single sclerite, and generally with extended lateral margins fused to posterolateral margins of genital fork. Tergite 10 always divided, though often fused with tergite 9; digging–anchoring spines often present posterodorsally and anterolaterally (Fig. 22), although reduced in Phycinae (Fig. 21). Sternites 10 and 11 (hypoproct, subanal plate) usually a single plate, usually heavily sclerotized though more thinly so in some genera of Phycinae (*Apsilocephala* with paired sclerites). Cerci disc-shaped, attached to tergite 10 in most groups, but fused into a single sclerite in *Pherocera* group.

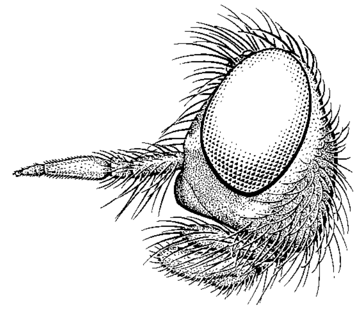
Male terminalia (Figs. 15–20) fairly uniform in plan. Sclerites forming sternite 8 and tergite 8 unmodified to narrowly constricted. Tergite 9, the epandrium, acting as a large covering for terminalia, variously haired, often with surstyli or lateral surstylar-like lobes of various sizes and shapes; hypoproct and cerci borne apically. Sternite 9, the hypandrium, large in a few genera, narrow to absent in others. Gonocoxites variously free from or fused to sternite 9, fused together at bases or free, each often extending as a broad to narrow lobe well beyond insertion of gonostylus, and usually with one or more other appendages; these appendages consisting of paired ventromedial lobes that sometimes appear to function as an aedeagal guide, and dorsolateral processes, the parameres, connecting through thickened ridges along lateral edges of gonocoxites to short parameral apodemes. Gonostylus variously shaped, moving in a dorsoventral or oblique direction and not opposed, often appearing to lie within the genital cavity. Aedeagus consisting of a short to long variously twisted distiphallus (coiled in *Apsilocephala*), an elongate or vestigial dorsal aedeagal apodeme, a simple or forked ventral apodeme sometimes having an extension toward tip of distiphallus, and a variously shaped ejaculatory apodeme (Figs. 15–20); aedeagus attached at one or more of three sites, namely by anterior edge of intersegmental membrane below epandrium (usually as a basal extension of hypoproct) to distal portion of aedeagal apodeme, by parameral apodeme to lateral portion of dorsal aedeagal apodeme, or by ventral lobe to base of phallus.

Egg. Ovoid to bluntly ovoid, shining milky-white, 0.4–0.8 mm long, lacking reticulation, and often with sand particles adhering to chorion.

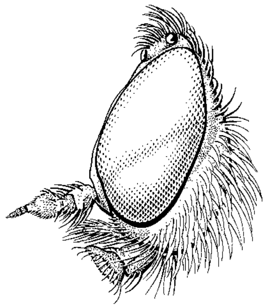
Larva. Elongate, cylindrical, similar in form to Scenopinidae (Fig. 38.16), tapering anteriorly toward head and apex of abdomen (Fig. 23). Head small, with cranium well-sclerotized and divided into two portions (Fig. 24); anterior portion exposed and strongly tapered anteriorly toward mouthparts; posterior portion a long apically spatulate metacephalic rod, flexibly articulated to posterior dorsal margin of anterior cranial portion and projecting into thorax. Mouthparts comprising a median slender tapered labrum flanked by curved pointed mandibles, and laciniae and palpi of maxillae, with elements of labium ventrally; labium consisting of a large postmentum closing the ventral part of the cranial cavity, a fused pair of labial palpi usually bearing several pairs of setae, and a prementum anteriorly (Fig. 26). Cranium exteriorly with several sensory cells both dorsally and ventrally, with antennae set in crescent-shaped cups on anterodorsal surface, with one pair of elongate dorsal setae and two pairs of elongate ventral setae, with heavily sclerotized postmentum ventrally, and dorsally with some weakly sclerotized portions called white areas; two pairs of heavy tentorial arms present internally.



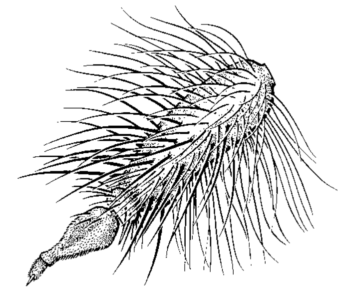
2 Nebritus pellucidus ♂



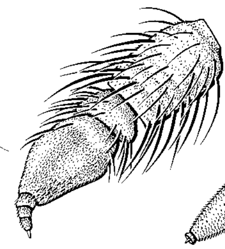
3 Parapherocera wilcoxi ♂



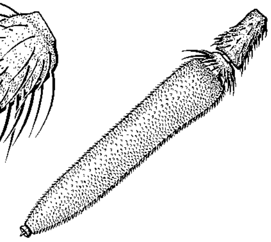
4 Litolinga acuta ♂



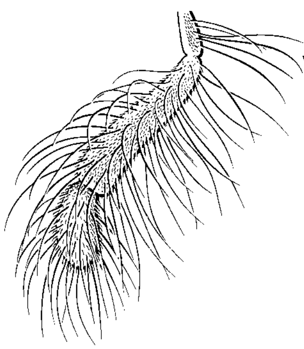
5 Pallicephala willistoni ♂



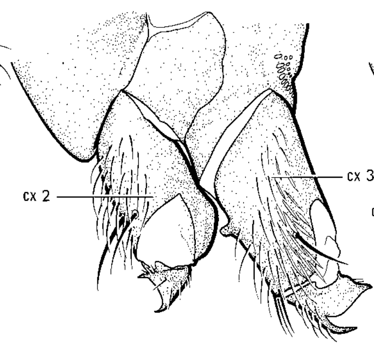
6 Breviperna placida ♀



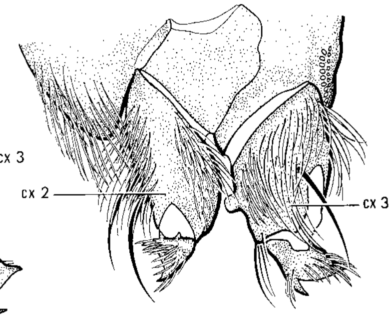
7 Henicomyia hubbardii ♂



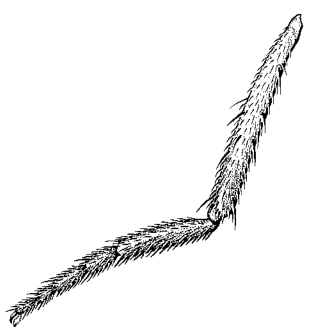
8 Rhagioforma maculipennis ♂



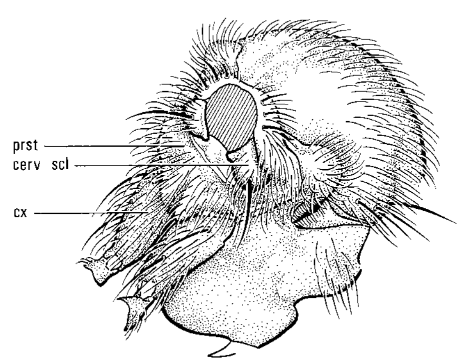
9 Cyclotelus rufiventris ♂



10 Brachylinga cinerea ♀



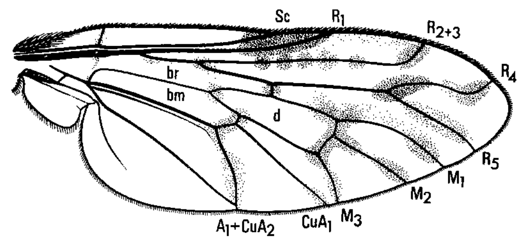
11 Cyclotelus rufiventris ♂



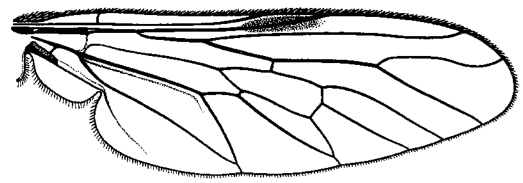
12 Megalinga insignata ♂

Figs. 27.2–12. Details of head and thorax: lateral view of head of (2) *Nebritus pellucidus* Coquillett, (3) *Parapherocera wilcoxi* Irwin, and (4) *Litolinga acuta* (Adams); antenna of (5) *Pallicephala willistoni* (Cole), (6) *Breviperna placida* (Coquillett), and (7) *Henicomyia hubbardii* Coquillett; (8) palpus of *Rhagioforma maculipennis* (Kröber); mid and hind coxae of (9) *Cyclotelus rufiventris* (Loew) and (10) *Brachylinga cinerea* (Cole); (11) fore tibia and tarsus of *Cyclotelus rufiventris*; (12) oblique anterior view of thorax of *Megalinga insignata* Irwin & Lyneborg.

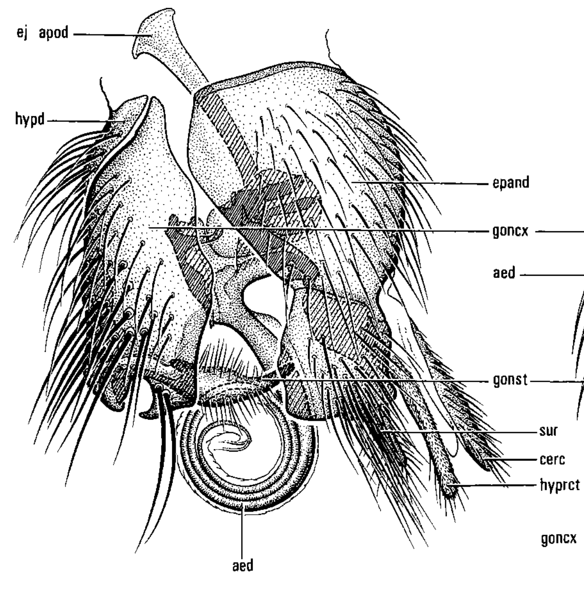
Abbreviations: cerv scl, cervical sclerite; cx, coxa; prst, prosternum.



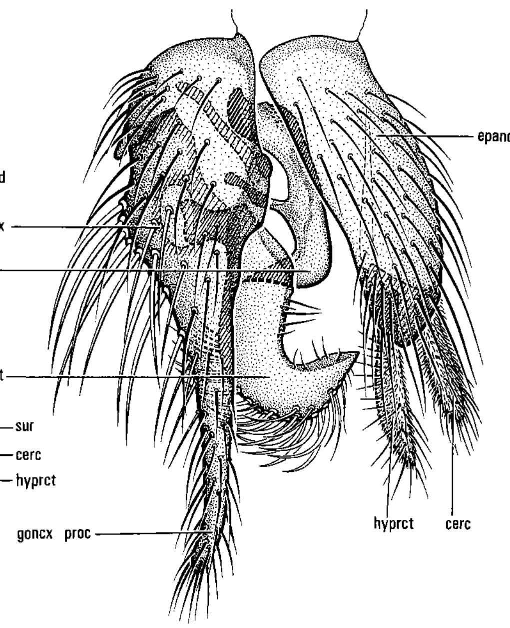
13 Megalinga insignata ♂



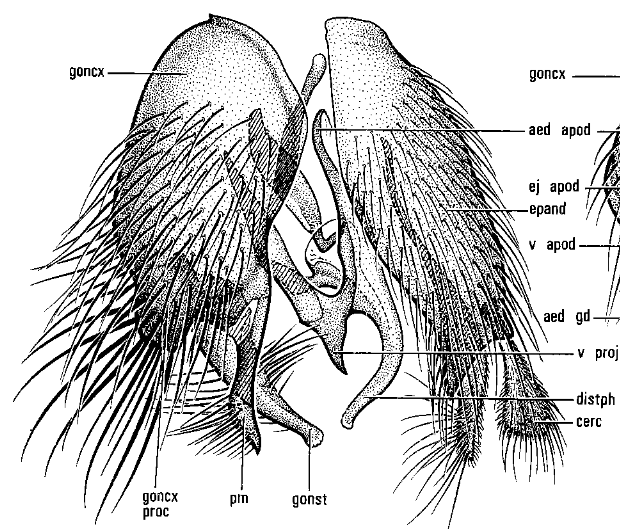
14 Ozodiceromyia signatipennis ♀



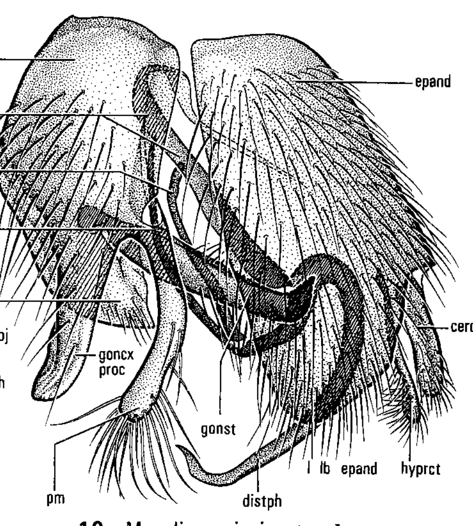
15 Apsilocephala sp. ♂



16 Brachylinga cinerea ♂



17 Acrosathe pacifica ♂



18 Megalinga insignata ♂

Figs. 37.13–18. Wings and terminalia: wing of (13) *Megalinga insignata* Irwin & Lyneborg and (14) *Ozodiceromya signatipennis* (Cole); lateral view of male terminalia of (15) *Apsilocephala* sp., (16) *Brachylinga cinerea* (Cole), (17) *Acrosathe pacifica* (Cole), and (18) *Megalinga insignata* (gonocoxite and epandrium of 17 and 18 separated to show aedeagus).

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; cerc, cercus; distph, distiphallus; ej apod, ejaculatory apodeme; epand, epandrium; goncx, gonocoxite; goncx proc, gonocoxal process; gonst, gonostylus; hypd, hypandrium; hyprct, hypoproct; l lb epand, lateral lobe of epandrium; pm, paramere; sur, surstylus; v apod, ventral apodeme; v proj, ventral projection of aedeagus.

Thorax with a pair of dorsolateral setae on each segment; anterior spiracle distinct, with two or three spiracular openings on specimens examined (Fig. 25*a*). Abdominal segments 1–8 secondarily constricted, giving appearance of two segments each, which with three thoracic segments appear as 19 segments in all (Fig. 38.16); posterior spiracles on antipenultimate segment, apparently with eight spiracular openings (Fig. 25*b*); terminal segment ending in a pair of retractable finger-like processes called prolegs (Fig. 23).

Pupa. Head with pair of antennal horns or sheaths visible; ventral labral sheath and lateral proboscial sheath visible ventrally. A tubular thoracic area situated dorsally just behind head sheath, and bearing a pair of bumps or spines called wing processes; leg sheaths and wing sheaths visible ventrally next to proboscial sheath. Abdominal sheath terminating in pair of caudal spines laterally (Fig. 27).

Biology and behavior. Therevid bioecology is only beginning to be explored. Most of the accumulated knowledge stems from accounts by Lundbeck (1908), Collinge (1909), Verrall (1909), Cole (1923), English (1950), Cole and Schlinger (1969), and Irwin (1972, 1973, 1976, 1977). Irwin (1971, 1977) reviewed the biology of adult and immature Therevidae and dealt with environmental biology, plant and animal associates, ovipositional and egg-hatching sequences, larval movement, larval feeding and cannibalism, pupation sites, adult flight patterns, and phenology and related phenomena for the three phycine genera *Pherocera* Cole, *Parapherocera* Irwin, and *Schlingeria* Irwin.

Adult therevids are diurnal, and many can live for several months under favorable environmental conditions. They often alight in sunny patches on trails and paths, the males usually awaiting passing females. Resting substrates are often specific for a given species or genus and include sand, rock, grass-blades, leaves, stems, and tree trunks. Most therevids have a rapid flight of short duration, but one genus, *Lyneborgia* Irwin from southern Africa, contains flightless females and males with slow, almost fluttering flights. A few species of therevids mimic various wasps (Nicholson 1927, Irwin 1971). Adults are not predacious; most species imbibe water. Members of the *Phycus* group, *Pherocera* group, and *Cyclotelus* group (*Ozodiceromya* Bigot, *Chromolepida* Cole, and others) take nourishment in the form of plant nectars, plant exudates, insect excretions, and insect secretions. Several groups of insects prey on therevids. Their most important predators are probably other therevid larvae during the larval stages, and asilids and predatory wasps like *Bembex* Fabricius and *Oxybelus* Latreille (Peckham *et al.* 1973) during the adult stage. Vertebrate predators (birds, frogs, toads, lizards) probably have a minimal impact on adult populations. The only known parasitoid is a species of Bombyliidae (English 1950). Ovipositional and egg-hatching sequences (Irwin 1973, 1976, 1977) seem characteristic of subfamilial and tribal groupings. Although females average about 50 eggs each, some have laid up to 90 and others as few as 25 (M. E. Irwin, unpublished data). The pupal stage lasts from 6 to 14 days, averaging about 10 days depending on species and environmental conditions. The pupa is especially vulnerable to desiccation and to attack by predators.

As far as is known, there are five larval stadia, the last of which either pupates or goes into a diapause. Even though the diapause can persist for 2 yr (Irwin 1971), therevids are usually univoltine. The snake-like larvae are most often found burrowing through sandy to sandy–loam soils, but larvae of some species can be found under rotting tree bark, in decaying fruit or fungus, and under heavy stones. Larvae are well adapted to fossorial life and move rapidly through loose soils. Therevid larvae are voracious predators, feeding on many active, fossorial arthropods and earthworms; they prefer larvae of Coleoptera, especially those of the families Elateridae, Scarabaeidae, and Tenebrionidae. Therevids play an important, though as yet unascertained, role in the suppression of actual and potential fossorial target-pest larvae in agroecosystems and should be considered as potential biological control agents.

Classification and distribution. At present approximately 129 species are known in 29 genera from America north of Mexico. The number of described genera is a fair reflection of the diversity encountered in this region and probably will not increase drastically. The number of described species represents from a half to a third of the total number actually occurring in the region.

Until very recently the Therevidae was without an internal hierarchy; the characters used for separating genera were highly convergent and resulted in an unnatural, polyphyletic classification. This old classification was still in use when the last cataloging of the Diptera of North America (Stone *et al.* 1965) was completed. That work is now superceded by the work of Irwin and Lyneborg (1980), who presented a monophyletic classification of the North American genera of Therevidae based mainly on synapomorphous attributes.

Based on material from the Afrotropical, Palaearctic, Nearctic, and Neotropical regions, Irwin and Lyneborg (1980) divided the Therevidae into two subfamilies, Phycinae and Therevinae. Irwin (1976) and Irwin and Lyneborg (1980) do not regard *Apsilocephala* Kröber as belonging to the Therevidae *sens. str.*, and this genus is included here only for convenience. It is known from a single species, *A. longistyla* Kröber, and is restricted to the deserts of western North America. It seems to be related to some of the heterotropine Bombyliidae, especially *Caenotus* Cole, but clearly does not belong to the Bombyliidae *sens. str.*

Tribal divisions have been delayed until more information about the composition of other faunal regions can be obtained and evaluated.

The two subfamilies of Therevidae have distinct distributional patterns. The Phycinae has an Afrotropical–Neotropical–Nearctic pattern, whereas the Therevinae has a Neotropical–Nearctic–Palaearctic pattern. Within the Phycinae, the *Xestomyza* group is confined to southern Africa except for the single genus *Henicomyia* Coquillett, which is Neotropical and extends northward into Arizona and New Mexico (Lyneborg 1972). The *Phycus* group at present contains two genera: *Phycus* Walker, occupying the Middle East area southward to eastern and southern Africa (Lyneborg 1978) and eastward to the Philippines, and also in Mexico and southern California; and *Ataenogera* Kröber, extending through the Neotropical region. The *Ruppellia* group occurs in the Mediterranean area, the Near East, and southward to southern Africa. The *Pherocera* group occurs in North America west of the Rocky Mountains and extends into western and central Mexico (Irwin 1971, 1977). Within the Therevinae the genera allied with *Cyclotelus* have a strong Central American base with ties to genera in North America and South America; the genera allied with *Brachylinga* are centered in the Caribbean region with a strong group of genera in South America and another, less dominent group in North America; the genera allied with *Thereva* show strong affinities between North America and the Palaearctic region.

Most fossil Therevidae recorded from North America are from the Miocene shales of Florissant, Colo., and were described by Cockerell (1909*a*, 1909*b*, 1916, 1927). Cockerell placed two of these species, *scudderi* Cockerell and *hypogaea* Cockerell, under the genus *Psilocephala* Zetterstedt *sens. lat.* and a third species, *vagabunda* Cockerell, under the Old World genus *Ruppellia* Wiedemann. Another species, *simplex* Cockerell, was placed under a new genus *Eothereva* Cockerell (Cockerell 1921). None of these species have been accurately placed into existing genera.

Key to genera

1. Five or more pairs of dorsocentral setae. Male aedeagus elongate, coiled (Fig. 15) .... ***Apsilocephala*** Kröber
   1 sp., *longistyla* Kröber; southwestern U.S.A., northwestern Mexico

   Four or fewer pairs of dorsocentral setae. Male aedeagus short, not coiled 2

2. Mid coxa with pile on posterior surface (Fig. 10) 3

   Mid coxa without pile on posterior surface (Fig. 9) or with only a few appressed scale-like hairs 21

3. Prosternum with pile in and around central depression (Fig. 12) 4

   Prosternum without pile in and around central depression 16

4. Lower frons in both sexes entirely shiny; head strongly protruding anteriorly; compound eyes of male separated by more than width of ocellar tubercle (Fig. 2) .... ***Nebritus*** Coquillett
   2 spp.; western U.S.A.

   Lower frons at least partially tomentose; head not so strongly protruding anteriorly (Fig. 1); compound eyes of male separated by at most width of ocellar tubercle 5

5. Lateral portion of face, or at least its upper part, without pile 6

   Lateral portion of face, or at least its upper part, with pile 14

6. Paired cervical sclerites anterior to prosternum each with a strong black seta in addition to whitish pile (Fig. 12). R_{2+3} and R_4 with a deep curve before wing margin (Fig. 13). Distiphallus deeply cleft at apex (Fig. 18) .... ***Megalinga*** Irwin & Lyneborg
   1 sp., *insignata* Irwin & Lyneborg; southwestern U.S.A.

   Paired cervical sclerites anterior to prosternum without a strong black seta, with only whitish pile present. R_{2+3} usually with no more than a gentle curve before wing margin (Fig. 14) except in *Litolinga*. Distiphallus not cleft 7

7. Macrosetae of mesonotum all pale. Paramere well-developed, enlarged, and modified distally (Fig. 19). Cell m_3 closed .... ***Arenigena*** Irwin & Lyneborg
   3 spp.; southwestern U.S.A., northwestern Mexico

   Macrosetae of mesonotum usually all black; if macrosetae pale (some *Lysilinga*), then cell m_3 open. Paramere absent, or present and simple. Cell m_3 only rarely closed 8

8. Scape in lateral view distinctly wider than first flagellomere (Fig. 5); pile of scape long and dense 9

   Scape in lateral view narrower than or as wide as first flagellomere (Fig. 4); pile of scape shorter and sparser 10

9. Male frons with long pile; female frons with pile also on lower part above antennal bases. Fore and mid femora without setae. Hypandrium absent .... ***Dialineura*** Rondani
1 sp., *gorodkovi* Zaitzev; Manitoba

Male frons without pile; female frons without pile on lower part. Fore and mid femora usually with several anteroventral setae. Hypandrium present as a small narrow transverse sclerite basal to gonocoxites (as in Figs. 19, 20) .... ***Pallicephala*** Irwin & Lyneborg
5 spp.; western, northwestern, and northeastern North America

10. One pair of scutellar setae present, and genal area with darkened wedge or stripe; ocellar tubercle very prominent, especially in male .... ***Litolinga*** Irwin & Lyneborg
3 spp.; southeastern and southern U.S.A.

Two pairs of scutellar setae present, or genal area not darker than lower portion of occiput and uniform in color and texture; ocellar tubercle normal 11

11. Palpus constricted a short distance before apex (Fig. 8). Wing strongly maculated. Male frons prominent, with long dense black pile. Female abdomen yellowish brown with median row of dark spots .... ***Rhagioforma*** Irwin & Lyneborg
1 sp., *maculipennis* (Kröber); southwestern U.S.A., northwestern Mexico

Palpus not constricted apically. Wing not strongly maculated. Male frons with or without long dense pile. Female abdomen variously colored, usually brownish to grayish, without median row of dark spots 12

12. Pile of fore femur pale and erect, composed of long uniform thin hairs. Male with a large paramere, and with a simple slender gonostylus .... ***Pandivirilia*** Irwin & Lyneborg, in part
1 sp., *bussi* (James); western Canada

Pile of fore femur composed of appressed whitish scaly hairs and slender erect hairs that are whitish or blackish. Male without a paramere, and with a hook-shaped gonostylus bearing groups of setae (Fig. 16) 13

13. Dorsocentral setae absent. Abdomen orangish to reddish brown in both sexes. Aedeagus only about half as long as gonocoxite; distiphallus subapical and projecting downward .... ***Lysilinga*** Irwin & Lyneborg
3 spp.; southwestern U.S.A.

One or two pairs of dorsocentral setae present. Abdomen gray or black. Aedeagus usually more than half as long as gonocoxite; distiphallus apical (Fig. 16) .... ***Brachylinga*** Irwin & Lyneborg
10 spp.; Bahamas, southern United States to northern Mexico

14. Frons in both sexes with dense appressed pile of whitish scaly hairs. Macrosetae of mesonotum pale. A circular blackish area usually present in and around each anterior tentorial pit .... ***Ammonaios*** Irwin & Lyneborg
1 sp., *niveus* (Kröber); southwestern U.S.A., northwestern Mexico

Frons in both sexes with pile of erect normal hairs. Macrosetae of mesonotum black. Area in and around anterior tentorial pits not differently colored from rest of face 15

15. Male with epandrium as long as or longer in midline than wide; aedeagus with twin ventral projections adjoining distiphallus (Fig. 17). Male abdomen entirely whitish pilose. Female frons with pattern of dull pale or dark tomentum, not with subshining to shiny calli .... ***Acrosathe*** Irwin & Lyneborg
6 spp.; western North America, southern U.S.A.

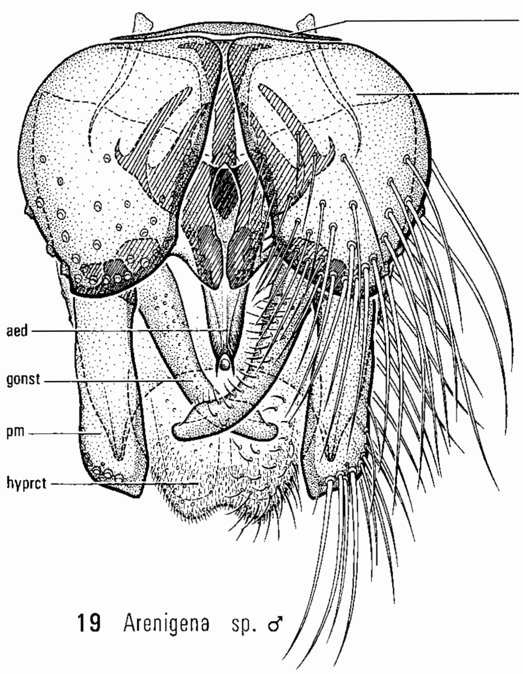
Male with epandrium much shorter in midline than wide; aedeagus without ventral projections adjoining distiphallus. Male abdomen entirely whitish pilose only in a few species. Female frons in most species with a large shiny black callus, or calli, or at least subshiny on middle .... ***Thereva*** Latreille
29 spp.; western and northern North America

16. Scape distinctly longer and wider than first flagellomere. Head strongly protruding anteriorly 17

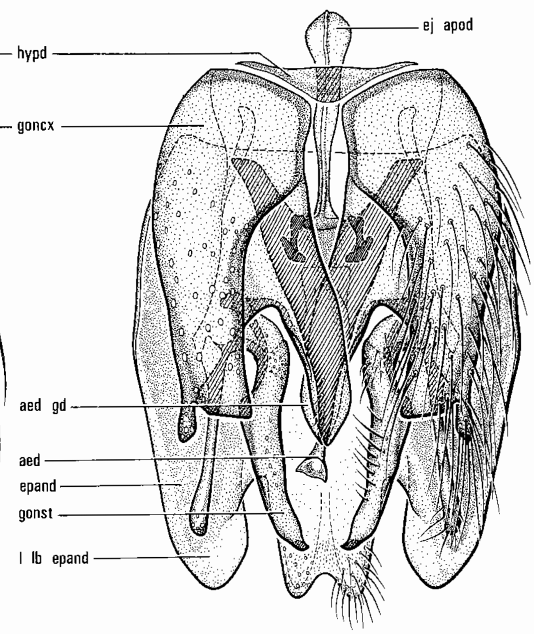
Scape not longer or wider than first flagellomere. Head not strongly protruding anteriorly 18

17. Male with compound eyes separated by at least width of anterior ocellus. Two supra-alar setae and one dorsocentral seta present. Cell m_3 broadly open. Paramere without free distal portion .... ***Tabuda*** Walker
3 spp.; northern, eastern, and western U.S.A.

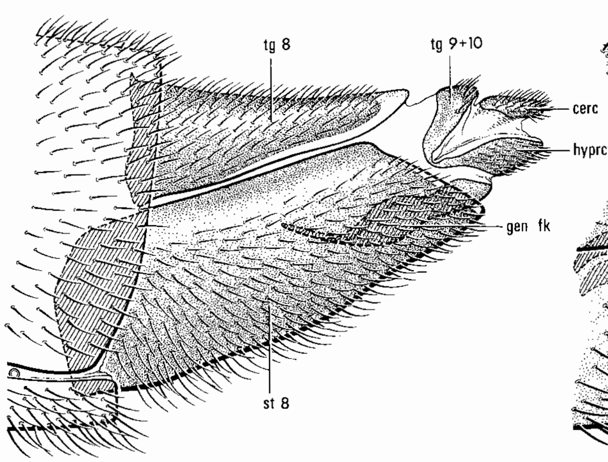
Male with compound eyes separated by less than width of anterior ocellus. One supra-alar seta present; dorsocentral setae absent. Cell m_3 closed or narrowly open. Paramere with free distal portion .... ***Tabudamima*** Irwin & Lyneborg
1 sp., *melanophleba* (Loew); southwestern U.S.A.



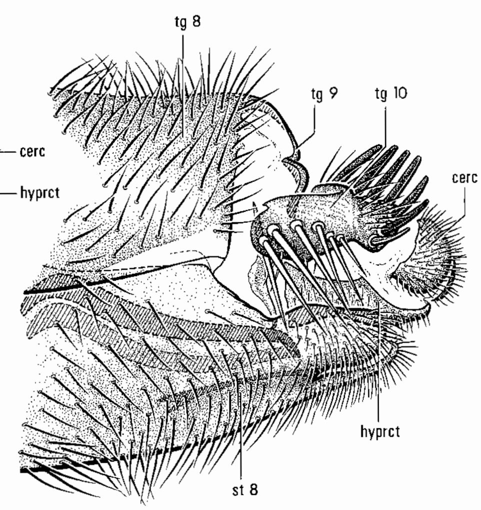
19 Arenigena sp. ♂



20 Spiriverpa candidata ♂



21 Pherocera flavipes ♀



22 Cyclotelus rufiventris ♀

Figs. 37.19–22. Terminalia: ventral view of male terminalia of (19) *Arenigena* sp. and (20) *Spiriverpa candidata* (Loew); lateral view of female terminalia of (21) *Pherocera flavipes* Cole and (22) *Cyclotelus rufiventris* (Loew).

Abbreviations: aed, aedeagus; aed gd, aedeagal guide; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; gen fk, genital fork; goncx, gonocoxite; gonst, gonostylus; hypd, hypandrium; hyprct, hypoproct; l lb epand, lateral lobe of epandrium; pm, paramere; st, sternite; tg, tergite.

18. Mesonotal pile of male short, sparse, and appressed; hairs shorter than width of scape. Hind femur with sparse appressed pile, and with many short scattered black setae on entire ventral surface in addition to normal row of strong anteroventral setae .... ***Viriliricta*** Irwin & Lyneborg

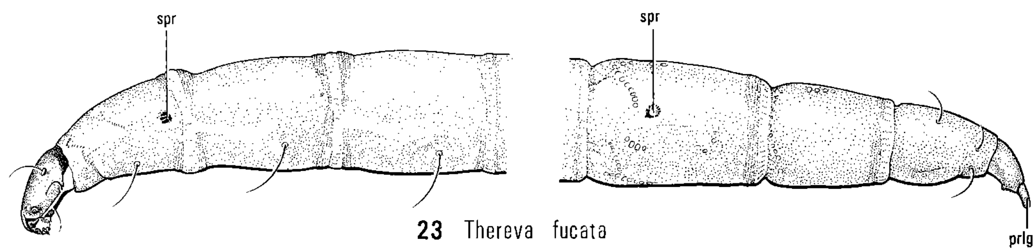
    3 spp.; northern, eastern, and western U.S.A.

    Mesonotal pile of male long, abundant, and erect; hairs distinctly longer than width of scape. Hind femur with more numerous usually more erect pile, and with at most a few short black posteroventral setae in apical part in addition to the usual row of strong anteroventral setae 19

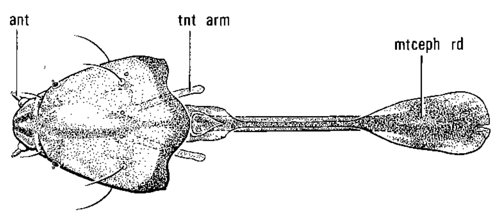
19. Male compound eyes separated by at least width of anterior ocellus. Female with black or blackish brown tibiae. Female with tergite 4 entirely shiny black .... ***Dichoglena*** Irwin & Lyneborg

    4 spp.; western, eastern, and northern U.S.A.

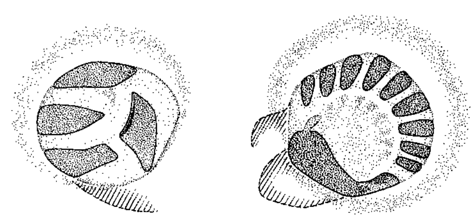
    Male compound eyes separated by less than half width of anterior ocellus. Female with yellowish brown tibiae. Female with tergite 4 at least partly tomentose 20



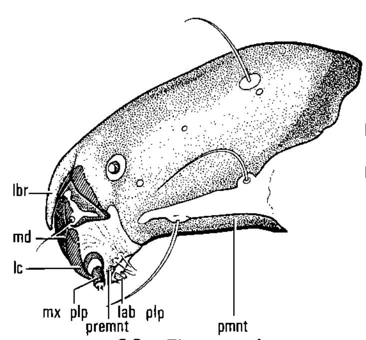
23 Thereva fucata



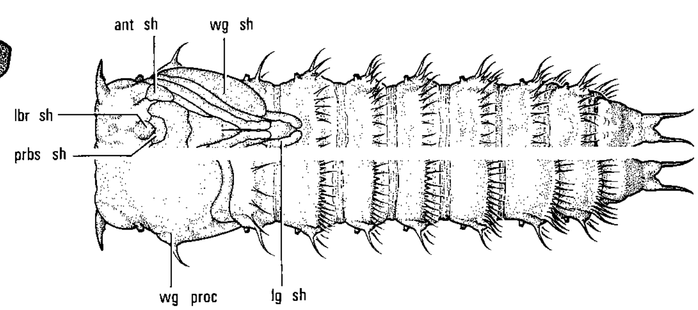
24 Thereva fucata



25 Thereva fucata



26 Thereva fucata



27 Spiriverpa candidata

Figs. 37.23–27. Immature stages: larva of *Thereva fucata* Loew showing (23) lateral view of head and thoracic segments and terminal segments, (24) dorsal view of head capsule, (25) anterior and posterior spiracles, and (26) ventrolateral view of head capsule without metacephalic rod; (27) pupa of *Spiriverpa candidata* (Loew), half dorsal and half ventral views.

Abbreviations: ant, antenna; ant sh, antennal sheath; lab plp, labial palpus; lbr, labrum; lbr sh, labral sheath; lc, lacinia; lg sh, leg sheath; md, mandible; mtceph rd, metacephalic rod; mx plp, maxillary palpus; pmnt, postmentum; prbs sh, proboscial sheath; premnt, prementum; prlg, proleg; spr, spiracle; tnt arm, tentorial arm; wg proc, wing process; wg sh, wing sheath.

20. Lower frons of both sexes with whitish pile; upper lateral portion of face with long whitish pile. Hypandrium present; distiphallus long, its tip twisted (Fig. 20) .... ***Spiriverpa*** Irwin & Lyneborg
9 spp.; Canada, northern and eastern U.S.A.

Lower frons of both sexes either without pile or with blackish pile; upper lateral portion of face in most species without pile, but if pile present then black. Hypandrium absent; distiphallus shorter, its tip not twisted .... ***Pandivirilia*** Irwin & Lyneborg, in part
3 spp.; western North America

21. Prosternum with pile in and around central depression 22
Prosternum without pile in and around central depression 25

22. A pair of shiny black raised calli on upper face below antennal bases. Thorax and abdomen clothed with totally appressed broad scales in addition to normal pile ......***Chromolepida*** Cole
2 spp.; western U.S.A., western Mexico

Face without shiny calli. Pile of thorax and abdomen composed of semiappressed scaly hairs and erect normal hairs...23

23. Cell m_3 broadly open. Male frons entirely tomentose and without pile; female frons entirely tomentose. Fore tibia with at most two or three very short posteroventral setae; fore tibia and first tarsomere very slender ....***Penniverpa*** Irwin & Lyneborg
1 sp., *festina* (Coquillett); southern U.S.A., West Indies

Cell m_3 closed (Fig. 14), or narrowly open (in some *Breviperna*). Male frons usually partly shining, and with pile; female frons usually shining (not in *Breviperna*). Fore tibia with several strong posteroventral setae; fore tibia and first tarsomere not very slender................24

24. Entire frons in both sexes covered with tomentum, without shiny areas. Male dichoptic. Large broadly built species with short broad antennae (Fig. 6).................................***Breviperna*** Irwin
1 sp., *placida* (Coquillett); southwestern U.S.A., northern and western Mexico

Frons in both sexes at least partly shiny. Smaller and more slenderly built species, with more slender antenna..***Ozodiceromya*** Bigot
34 spp.; North America south to Venezuela and Ecuador

25. Hind femur with appressed scaly hairs, usually also with some anteroventral setae. Tergite 10 of female strongly spinose; distal spines stouter, shorter, projecting dorsally and laterally; basal spines slimmer, longer, projecting ventrally (Fig. 22)..26

Hind femur with erect normal hairs, without anteroventral setae. Tergite 10 of female weakly spinose; spines of only one kind (Fig. 21) ....PHYCINAE....27

26. First tarsomere of foreleg swollen (Fig. 11). Scutellum short, with pile on margin only; katepisternum without pile. Male terminalia partly telescoped, concealed within abdomen, and usually yellowish. Paramere not projecting beyond apex of gonocoxite...***Cyclotelus*** Walker
6 spp.; eastern and southern U.S.A. southward to Argentina

First tarsomere of foreleg not swollen. Scutellum longer, with long pile on disc; katepisternum with long pale pile. Male terminalia strongly projecting, polished black; paramere extending well beyond dorsolateral edge of gonocoxite ....***Psilocephala*** Zetterstedt
3 spp.; Canada, northern U.S.A.

27. Scutellar setae absent...28
One pair scutellar setae present 29

28. One or two pairs of notopleural setae present; anepisternum without pile. Flagellum much longer than scape (Fig. 7). Mid and hind tarsi with very short setae. Genital opening of female dorsally directed ....***Henicomyia*** Coquillett
1 sp., *hubbardii* Coquillett; southwestern U.S.A., Mexico

Three pairs of notopleural setae; anepisternum with long pile. Flagellum only slightly longer than scape. Mid and hind tarsi with very long thin setae. Genital opening of female posteriorly directed..***Schlingeria*** Irwin
1 sp., *ammobata* Irwin; southwestern U.S.A., northwestern Mexico

29. Palpus distinctly two-segmented, with apical segment shorter. Hind femur with very short uniform hairs. Cerci of male each slightly longer than hypoproct. Antenna distinctly longer than head length ....***Phycus*** Walker
1 sp., unnamed; southwestern U.S.A., northwestern Mexico

Palpus one-segmented. Hind femur with elongate hairs. Each cercus and hypoproct of male about equal in length. Antenna shorter than or about as long as length of head 30

30. Antenna at least as long as length of head; shining raised callus present between antennal base and subcranial cavity (Fig. 3); male dichoptic ....***Parapherocera*** Irwin
3 spp.; southern California, northern Baja California in Mexico

Antenna shorter than length of head; no raised callus between antennal base and subcranial cavity; male holoptic (except for a single undescribed species from Mexico)....***Pherocera*** Cole
4 spp.; western U.S.A., northwestern Mexico

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SCENOPINIDAE

L. P. KELSEY

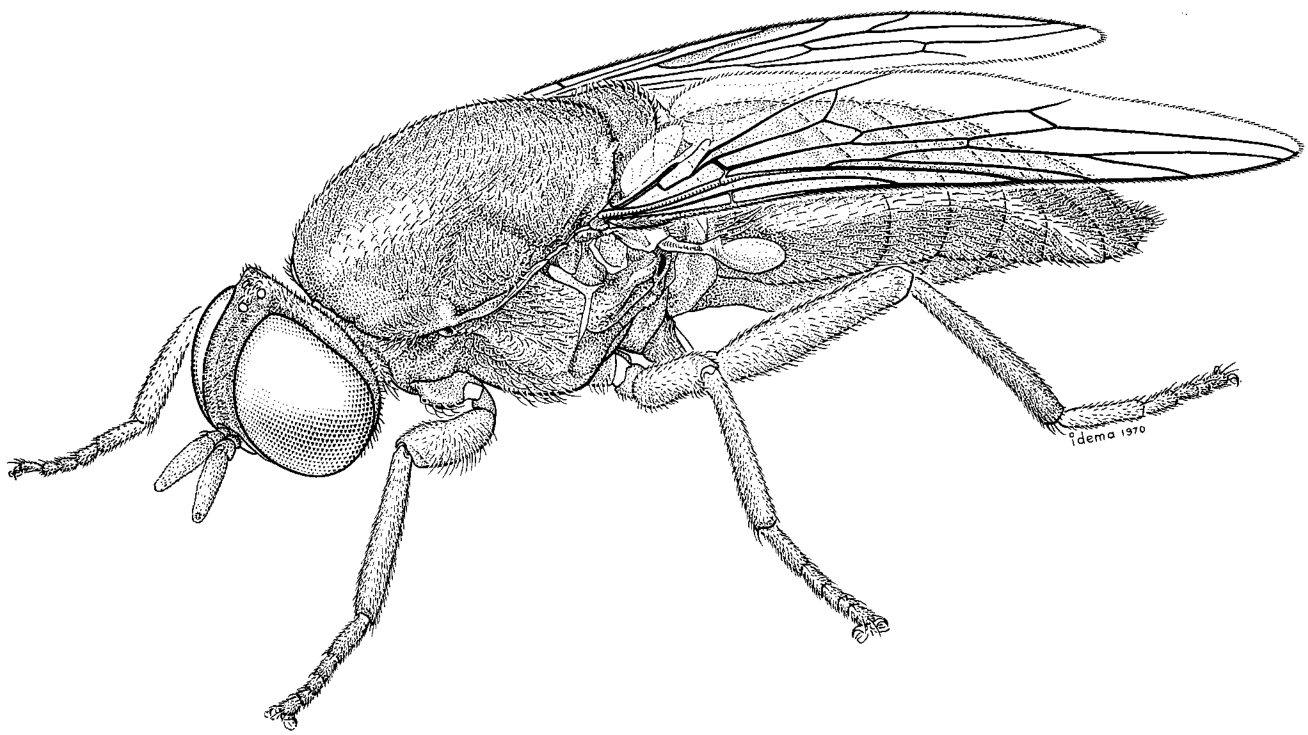

Fig. 38.1. Female of *Scenopinus fenestralis* (Linnaeus).

Flies moderate to small, of variable color but usually dark (Fig. 1).

Adult. Head: situated low on thorax. Frons of female not excavated; female face short and broad, bare of bristles but sometimes with short pubescence or flattened scale-like hairs; ocelli present. Eyes of male holoptic, with facets of upper field of each eye coarse and those of lower field finer and usually darker in color; frons of male reduced to a small triangle above antennae. Antennae (Figs. 6–10) approximate at base; each three-segmented, with stylus; scape and pedicel short; first flagellomere variable, from long and slender to short and oval, often with a bifurcate tip with a median peg-like stylus. Mouthparts generally well-developed and held in oral cavity; palpus generally cylindrical, but occasionally broad and flattened.

Thorax: rather long, moderately convex above, without bristles but often sparsely clothed with short to long hairs or flattened scale-like hairs; entire surface of thorax pruinose. Scutellum short and broad, convex above, unarmed. Legs short; empodia absent. Wing venation (Figs. 2–5) simple; R_4 separate and ending in leading edge of wing; cell r_5 open to end of wing, or closed and stalked.

Abdomen: broad, flattened or elongate, cylindrical, composed of 10 segments; last two segments short and incomplete. Female sternite 8 elongate, enclosing bursa. Male segment 8 short, ring-like, hidden by segment 7; segment 9 enlarged, containing accessory copulatory organs and visible portion of aedeagus. For positive identification terminalia of both sexes should be examined.

Larva. Only the larva of *Scenopinus fenestralis* (Linaeus) has been described. It resembles larvae of the Therevidae very closely.

Head capsule conical, exserted, articulated posteriorly with a slender metacephalic rod lying within prothorax (Fig. 12). Body long, slender, eel-like, with 19 apparent segments, first three being thoracic and remainder comprising usual eight abdominal segments that have undergone secondary division (Fig. 11). Conspicuous long setae present on head, on segments 1, 2, and 3, and on terminal segment. Respiratory system amphipneustic;

both pairs of spiracles with four oval openings (Figs. 13, 14); posterior spiracles situated laterally on antepenultimate segment.

Pupa. Species in several genera reared. Head and thorax fairly smooth, lacking prominent spines or tubercles at least anteriorly (Fig. 15). Antennal sheath projected laterally; leg sheaths sometimes extended slightly beyond wing sheath (Fig. 16). Anterior and abdominal spiracles sessile. Each abdominal segment girdled by a row of short to long spines; terminal abdominal segment with two apical processes.

Biology and behavior. The larvae are predacious and have been recorded in association with wood-boring larvae, termites, woodrat nests, bird's nests, and carpet beetle larvae. Carpet beetle larvae are a common host of *S. fenestralis* and *S. glabrifrons* Meigen, which are world wide in distribution.

Classification and distribution. The adults, though not common in most collections, are well represented in the Nearctic region by nearly one-half of the described species. The greatest concentration of species is found in the southwest, west of the Rocky Mountains in arid or semiarid localities. The family was extensively revised by Kelsey (1969), who gave keys to the species and presented illustrations of head, antennae, wings, and terminalia. Several new Nearctic species of Scenopinidae have since been described (Kelsey 1971, 1974).

Key to genera

1. Cell r_5 open to tip of wing (Figs. 2, 3) .... ***Scenopinus*** Latreille....2
   Cell r_5 closed and petiolate (Figs. 4, 5) 3
2. Adult large, robust, over 4 mm long. Antenna usually long, slender (Fig. 7). R_4 branching from R_5 before middle of cell r_5 (Fig. 1) .... ***Scenopinus*** [***fenestralis*** (Linnaeus) group]
   8 spp.; 2 spp. widespread, remainder primarily western
   Adult medium to small, usually under 4 mm long. Antenna short, oval (Fig. 6). R_4 branching beyond middle of cell r_5 (Fig. 3) .... ***Scenopinus*** [***velutinus*** (Kröber) group]
   40 spp.; mainly western
3. Adult small, predominantly light in color or with distinctively marked patterns. Thorax pruinose. R_4 branching from basal third of cell r_5 (Fig. 4) .... ***Brevitrichia*** Hardy
   43 spp.; west of Rocky Mountains
   Adult large and robust or long and slim, usually dark-colored. Thorax not pruinose. R_4 usually branching from beyond basal third of cell r_5 (Fig. 5) 4
4. Body robust with flattened scale-like hairs. Area of frons that bears antennae projecting anteriorly beyond eye profile (Fig. 8) .... ***Metatrichia*** Coquillett
   1 sp., *bulbosa* (Osten Sacken); widespread
   Body elongate, hairy or naked, but without flattened scale-like hairs. Area of frons that bears antennae scarcely visible in lateral view (Figs. 9, 10) 5
5. Head usually longer than high, with well-developed mouthparts (Fig. 9). Body without hairs .... ***Pseudatrichia*** Osten Sacken
   37 spp.; western
   Head higher than long, with atrophied mouthparts (Fig. 10). Thorax clothed with short to very long hairs .... ***Belosta*** Hardy
   7 spp.; western

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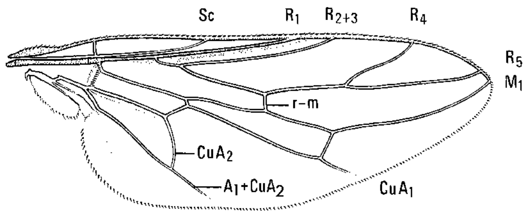
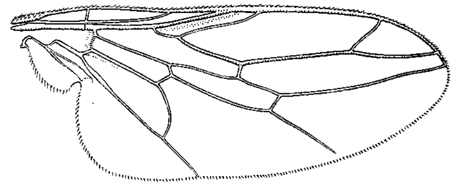
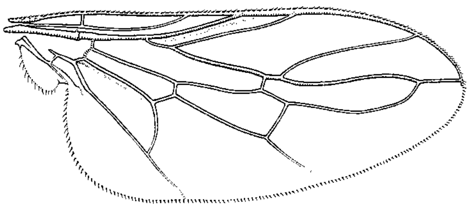


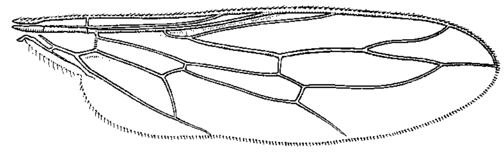
2 Scenopinus fenestralis ♀



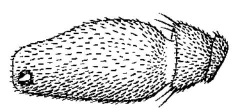
3 Scenopinus pecki ♂



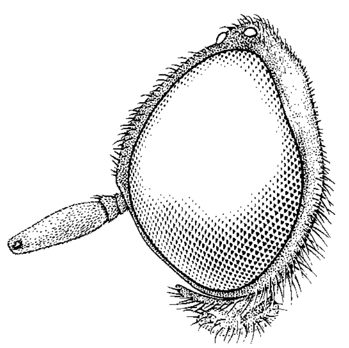
4 Brevitrichia schlingeri ♀



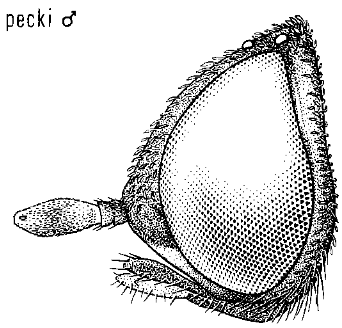
5 Pseudatrichia howdeni ♀



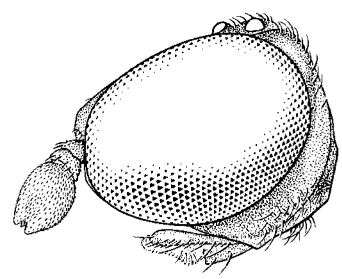
6 Scenopinus pecki ♂



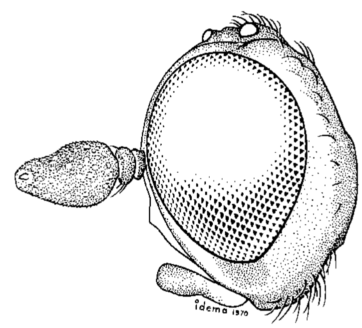
7 Scenopinus fenestralis ♀



8 Metatrichia bulbosa ♀

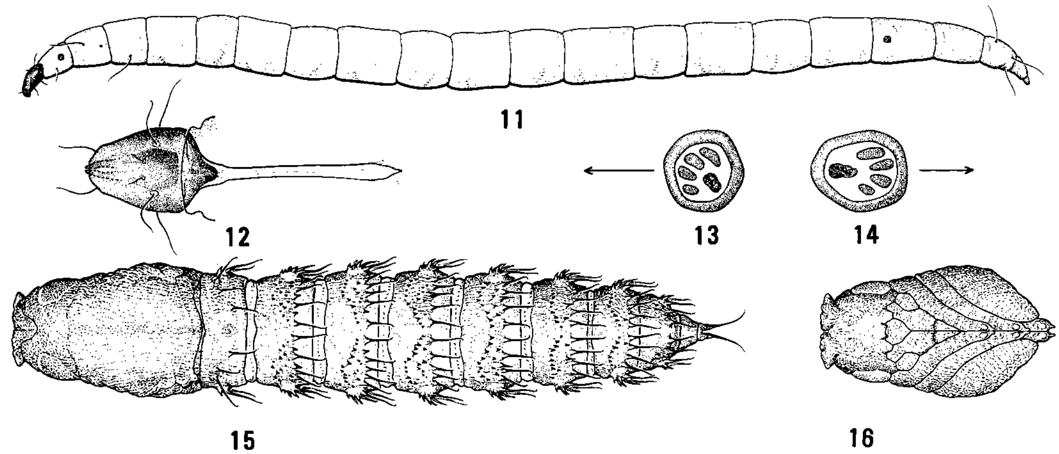


9 Pseudatrichia howdeni ♀



10 Belosta albipilosa ♀

Figs. 38.2–10. Wings and details of head: wing of (2) *Scenopinus fenestralis* (Linnaeus), (3) *Scenopinus pecki* Kelsey, (4) *Brevitrichia schlingeri* Kelsey, and (5) *Pseudatrichia howdeni* Kelsey; (6) antenna of *Scenopinus pecki*; lateral view of head of (7) *Scenopinus fenestralis*, (8) *Metatrichia bulbosa* (Osten Sacken), (9) *Pseudatrichia howdeni*, and (10) *Belosta albipilosa* Hardy.



Figs. 38.11–16. Immature stages of *Scenopinus* sp.: (11) lateral view of larva; (12) dorsal view of larval head capsule; (13) anterior and (14) posterior spiracles of larva; (15) dorsal view of pupa; (16) ventral view of head and thorax of pupa.

VERMILEONIDAE

H. J. TESKEY

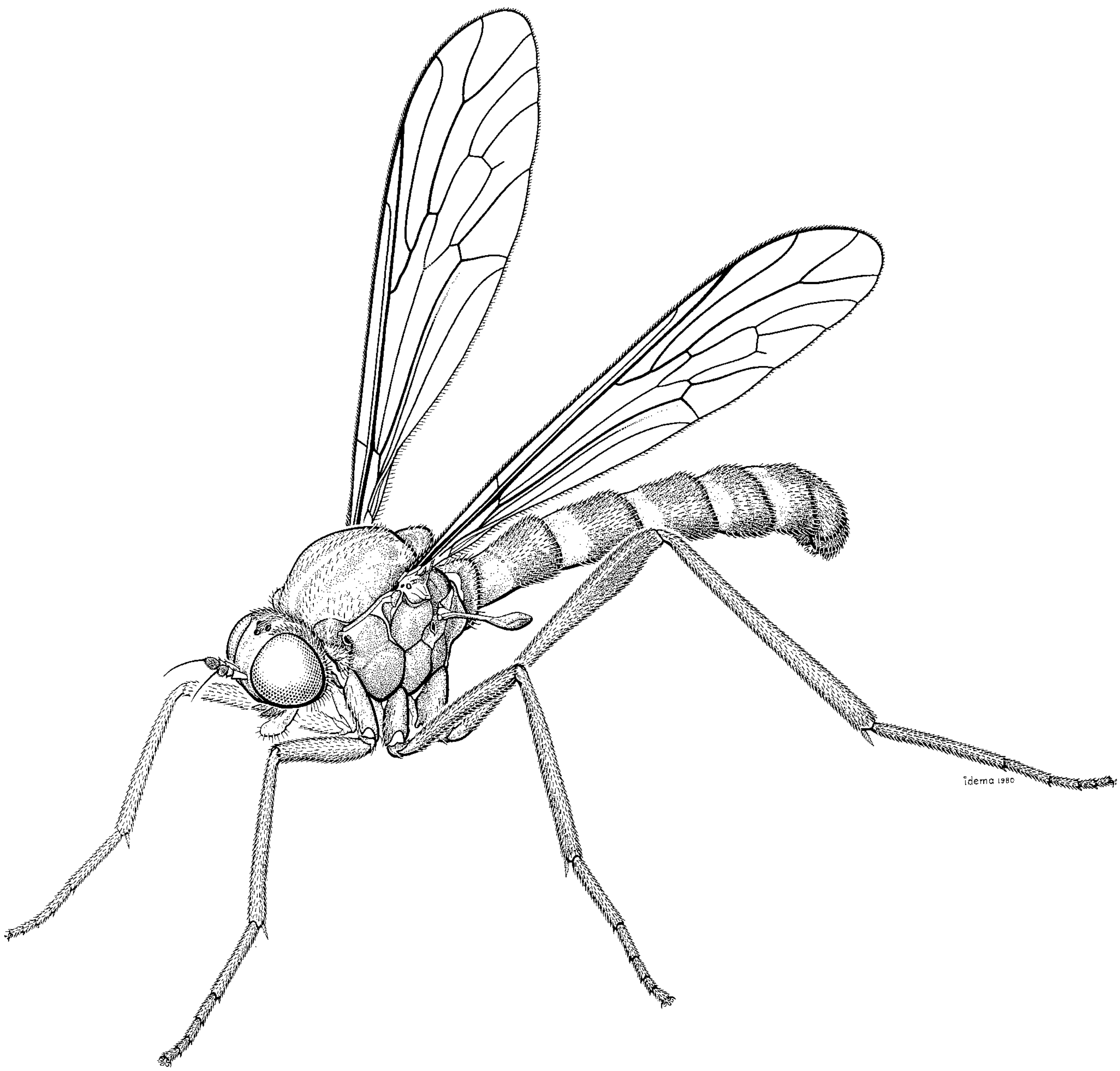


Fig. 39.1. Female of *Vermileo comstocki* Wheeler.

Slender almost hairless flies, with stylate antenna, subpetiolate abdomen, and slender legs (Fig. 1). Wing (Fig. 2) with nearly complete venation, weakly developed anal angle, and no alula.

Adult. Head: as wide as thorax, hemispherical in lateral and dorsal views, nearly round in anterior view. Eyes large, hairless, dichoptic; ommatidia of uniform size in both sexes. Frons usually almost parallel-sided although somewhat tapered below in some *Vermileo* Linnaeus, usually higher than wide, slightly narrower in male than in female, on same plane or only slightly depressed below eye level, more or less deeply indented at vertex on either side of prominent ocellar tubercle.

Face parallel-sided, composed mainly of clypeus, with parafacials narrow to obsolete; clypeus strongly projecting snout-like in *Lampromyia* Macquart, elevated only slightly above eye level and not convex in other genera. Antenna simple, arising near or above middle of head; scape longer than pedicel; flagellum with three to eight flagellomeres and with apical one to three flagellomeres forming a slender apical or subdorsal stylus. Labium short with broad labella (*Vermileo, Vermitigris* Wheeler), or as much as three-quarters length of body, slender, and with small labella (*Lampromyia*); mandible absent; maxilla reduced, with two-segmented palpus.

Thorax: higher than long, longer than wide. Scutum lacking almost all vestige of transverse suture; scutellum small, flattened dorsally, with a rather sharply rounded caudal margin; mediotergite of postnotum large, at least half as long as greatest width, usually well-exposed as result of small scutellum and slender abdomen; pleural suture gently sinuate with result that anterior margin of anepimeron bowed and not strongly angulated. Legs relatively long and slender; hindleg distinctly larger than midleg or foreleg; hind femur moderately enlarged apically; tibial spur formula 1:2:2; first tarsomere of each leg longer than combined length of remaining tarsomeres; empodia pulvilliform although in *Lampromyia* pulvilli and empodia extremely reduced.

Wing strongly tapered basally, sometimes with prominent dark markings; anal angle gently rounded and alula lacking (Fig. 2). Venation relatively complete; cells m_3 and cu*p* closed or strongly narrowed at margin; R_3 strongly curved anteriorly in *Lampromyia* and *Vermitigris*. Calypter small.

Abdomen: slender, usually narrowest at segment 2, moderately enlarged apically especially in males.

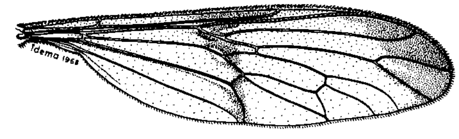
Male terminalia (Fig. 3) with gonocoxites and perhaps sternite 9, the hypandrium, fused, or with hypandrium absent; fusion sometimes extending to apices of gonocoxites; gonocoxite often with ventromedial extension beyond point of articulation of gonostylus; gonostylus simple, folding dorsomedially within genital cavity; transverse bridge-like sclerite joining dorsobasal edges of gonocoxites, serving for attachment of proctiger and articulation of aedeagal guide (fused parameres), sometimes with short paired apodemes projecting anterodorsally to articulate with gonocoxal apodeme. Tergite 9, the epandrium, usually relatively large and indented apically. Tergite 10 absent or fused with tergite 9; cercus sometimes partially or entirely hidden beneath posterior margin of epandrium.

Female terminalia of *Vermileo* not retractile. Tergite 9 much smaller than tergite 8. Tergite 10 absent. Cercus two-segmented; basal segment largest, with a lateral protuberance.

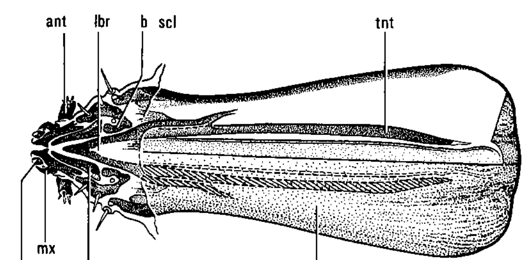
Larva. Head capsule (Fig. 4) almost completely and permanently retracted within thorax; only anterior portion containing mouthparts and one-segmented antennae exposed; this anterior portion externally membranous, with sclerites of maxillary portion of mandibular–maxillary complex appearing to support this membranous covering in a skeletal manner; retracted portion of head capsule covered dorsally by prominent sclerotized cranium, but broadly open ventrally. Cranium about twice as long as greatest width, moderately tapered anteriorly, truncate posteriorly, convex dorsally and more abruptly curved near lateral margins, resembling an inverted shallow scoop. Internally paired plate-like tentorial phragmata descending from cranium to either side of midline anteriorly, with tentorial arms extending posteriorly from their caudoventral margin nearly to end of cranium; sclerotized pharynx between tentorial arms and apparently attached to them anteriorly; salivary duct entering cibarium anteriorly. Mouthparts comprising a mandibular–maxillary complex of sclerites on either side of an acutely tapered median labrum; labium absent; mandibular–maxillary sclerites comprising a complexly formed V-shaped basal sclerite, a mandible, and a maxilla; mandible slender, curved, apically serrate, and articulated anteriorly on the median arm of the V; maxilla in form of a curved apically branched bar, with palpus in membranous area at apex of branch, and articulating with outer arm of V; basal sclerite articulated with cranium firstly via a ventral extension of median arm with anteroventral extremity of tentorial phragmata, and secondly through outer arm of basal sclerite with anterolateral corner of cranium.

Body (Fig. 5) slender anteriorly, gradually increasing in size to obliquely truncated posterior end, 11-segmented; integument thin, pliable, covered with microtrichia. Boundaries of anterior segments (Fig. 4) indistinct because of transverse wrinkling of integument; wrinkling producing more or less distinct secondary annulations on thoracic segments; secondary annulations of thorax particularly evident laterally as a row of papillae each bearing a seta. Similar setae systematically positioned on all aspects of most abdominal segments, but those situated laterally usually the largest and most prominent. First abdominal segment ventrally with a median short eversible proleg with apical setae; arrangement of these setae distinctive of the few known larvae of the family. Abdominal segment 7 posterodorsally with conspicuous transverse comb-like series of recurved flattened spines. Abdominal segment 8 apically with a transverse row of four triangular lobes fringed with short setae. Respiratory system amphipneustic; spiracles laterally on prothorax and dorsally on terminal segment; both spiracles with curved fan-shaped row of short linear spiracular openings bordering ecdysial scar; anterior spiracles with five or six openings and posterior spiracles with 10–12 openings. Anus opening in a longitudinal slit.

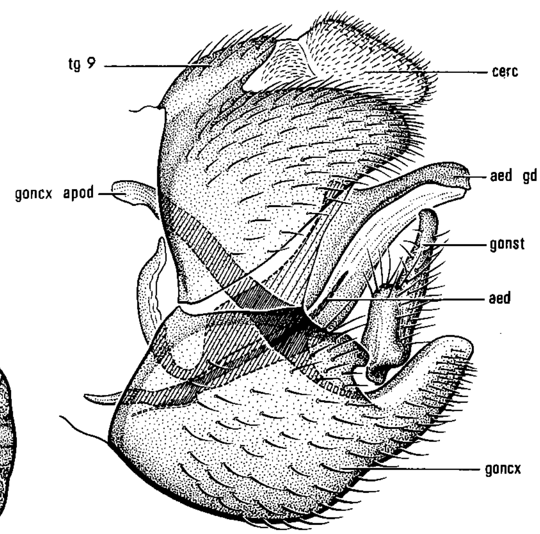
Pupa. Exarate; wing and leg sheaths folded close to thorax but obviously not adherent in any way. Head showing to some extent features of adult such as head shape, eye conformation, antennal form, and proboscis length. Thorax relatively short. Spiracles of thorax and abdomen inconspicuous; anterior spiracle situated dor-



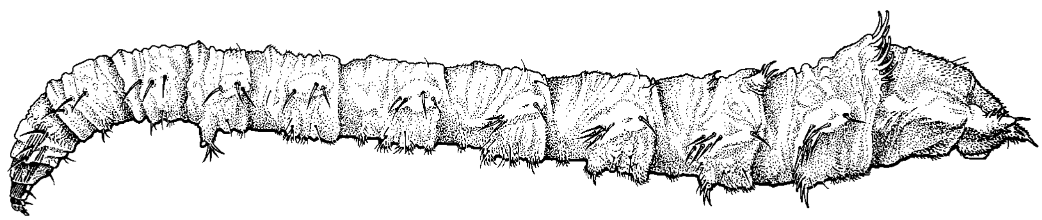
2 Vermileo tibialis ♂



4 Vermileo comstocki



3 Vermileo opacus ♂



5 Vermileo comstocki

Figs. 39.2–5. *Vermileo* spp.: (2) wing of *Vermileo tibialis* (Walker) (not Nearctic); (3) male terminalia of *Vermileo opacus* (Coquillett); (4) larval head capsule of *Vermileo comstocki* Wheeler; (5) larva of *Vermileo comstocki*.

Abbreviations: aed, aedeagus; aed gd, aedeagal guide; ant, antenna; b scl, basal sclerite; cerc, cercus; cr, cranium; goncx, gonocoxite; goncx apod, gonocoxal apodeme; gonst, gonostylus; lbr, labrum; md, mandible; mx, maxilla; mx plp, maxillary palpus; tg, tergite; tnt, tentorium.

solaterally behind head and not at base of wing sheath as shown by Green (1926). Abdomen lacking setae or spines; terminal segment with blunt para-anal lobes. Last larval skin remaining attached to posterior end of pupa.

Biology and behavior. Larvae of the Vermileonidae are the well-known worm lions that construct pitfall traps for the purpose of capturing prey. Their life history and behavior are discussed extensively by Wheeler (1930) and Engel (1929) and in a series of papers by Hemmingsen and co-workers culminating in Hemmingsen (1977).

The adult female deposits eggs singly or in clusters beneath the surface of sand or dust where the larvae form their pits. Incubation requires about 1 wk. The newly hatched larva constructs a trap by throwing the sand or dust particles from the pit with its head. Favored locations for traps include the mouths of caves or the bases of trees or walls. The larva lies in wait in the bottom of the trap to capture prey, most commonly ants, which happen to fall into the trap. The prey is seized and drawn down into the sand, where the softer parts are consumed. The empty cadaver is then thrown from the pit by the larva. Maturation of the larva normally requires about a year. Pupation occurs in the sand and takes approximately a month. Adults feed on nectar. Members of *Lampromyia* insert a long proboscis into deep flowers, whereas members of *Vermileo*, with a short proboscis, are confined to flat, open umbelliferous flowers.

Classification and distribution. The family comprises three genera: *Vermileo* with two species in the Mediterranean region and six New World species (two Nearctic), *Lampromyia* comprising 19 species in the southern Palaearctic and Ethiopian regions, and *Vermitigris* with three species from the Oriental region. Although the close relationship of the three genera appears assured, their position among the lower Brachycera has been the subject of some speculation. They have most commonly been placed in the Rhagionidae (Wheeler 1930; Leonard 1930; Stuckenberg 1960; James 1965, 1968), but apparently only for want of a more suitable placement. Stuckenberg (1960) questioned the association with the Rhagionidae. All features shared with the Rhagionidae are plesiomorphic. There are more convincing reasons to consider a relationship among the Asilomorpha. But because the evidence of this relationship is not indicative of placement in any one family, the above three genera are here recognized as a separate family as did Nagatomi (1977).

Adults of Vermileonidae bear a close resemblance to certain members of the Leptogastrinae (Asilidae), particularly in their rounded head and slender petiolate abdomen, and in the weak anal angle and alula of the wing and the narrowing of both cells m_3 and cu*p* at the wing margin. The similarity extends to a parallel-sided, relatively flat facial region composed almost exclusively of clypeus with no parafacial area, and a gently sinuate pleural suture resulting in the anteroventral margin of the anepimeron being rounded and not strongly angulated as in most Tabanomorpha. The male terminalia of Vermileonidae most closely resemble the Therevidae. Both families apparently lack sternite 9 and have the gonocoxites extensively fused ventrally with their inner subapical margins produced lobe-like, all apomorphic features not found in the Tabanomorpha. These features are also present in the Hilarimorphidae and many Bombyliidae.

The larval mouthparts of the Vermileonidae bear remarkable similarities to some of the Empidoidea (compare Fig. 4 with Figs. 48.41 and 48.43), especially in the configuration of the mandibular–maxillary sclerites and the membranization of the lateral covering of the head that bears the antennae and maxillary palpi. The retracted cranial portions of the head capsule have retained a more primitive, extensively sclerotized condition.

Keys for the identification of the New World species of *Vermileo*, only two of which have been found in the Nearctic region, are provided by Pechuman (1938). Most of the species of *Lampromyia* can be identified using the paper of Stuckenberg (1960).

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MYDIDAE 40

J. Wilcox

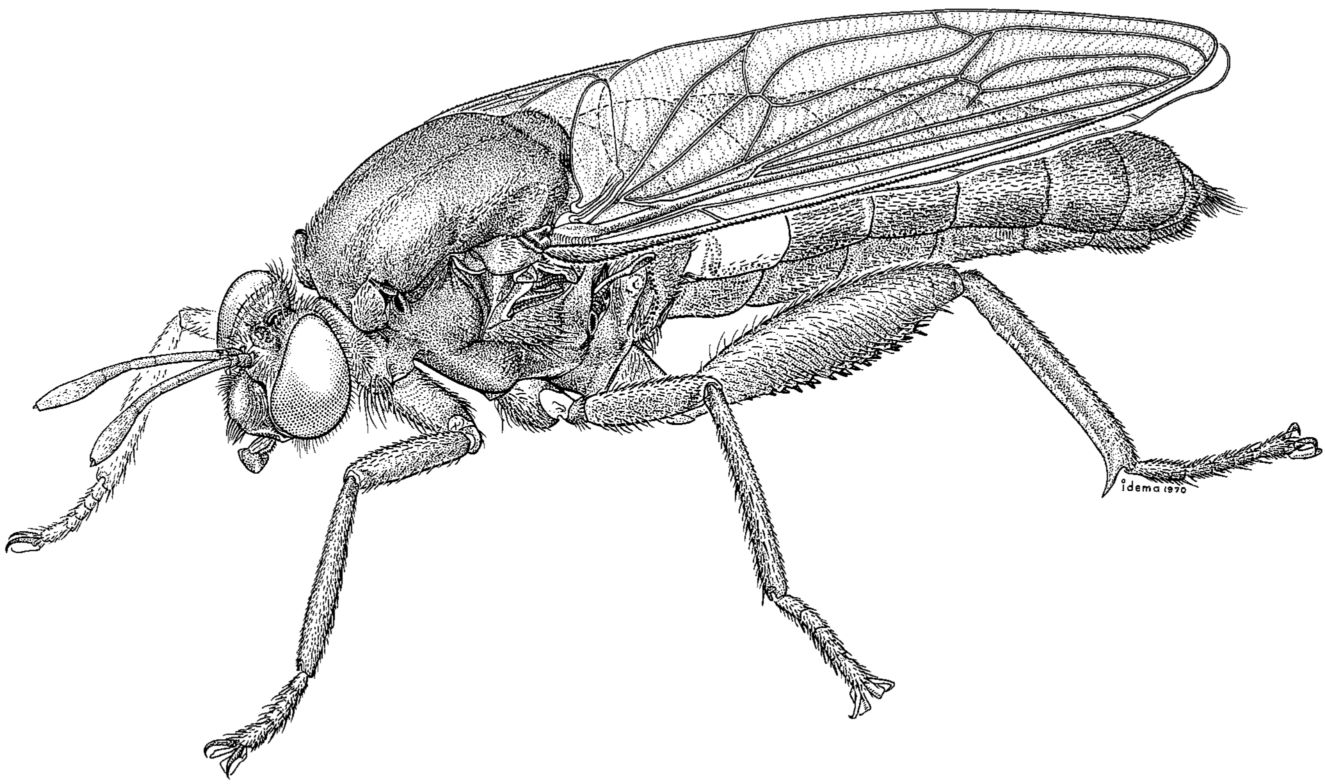
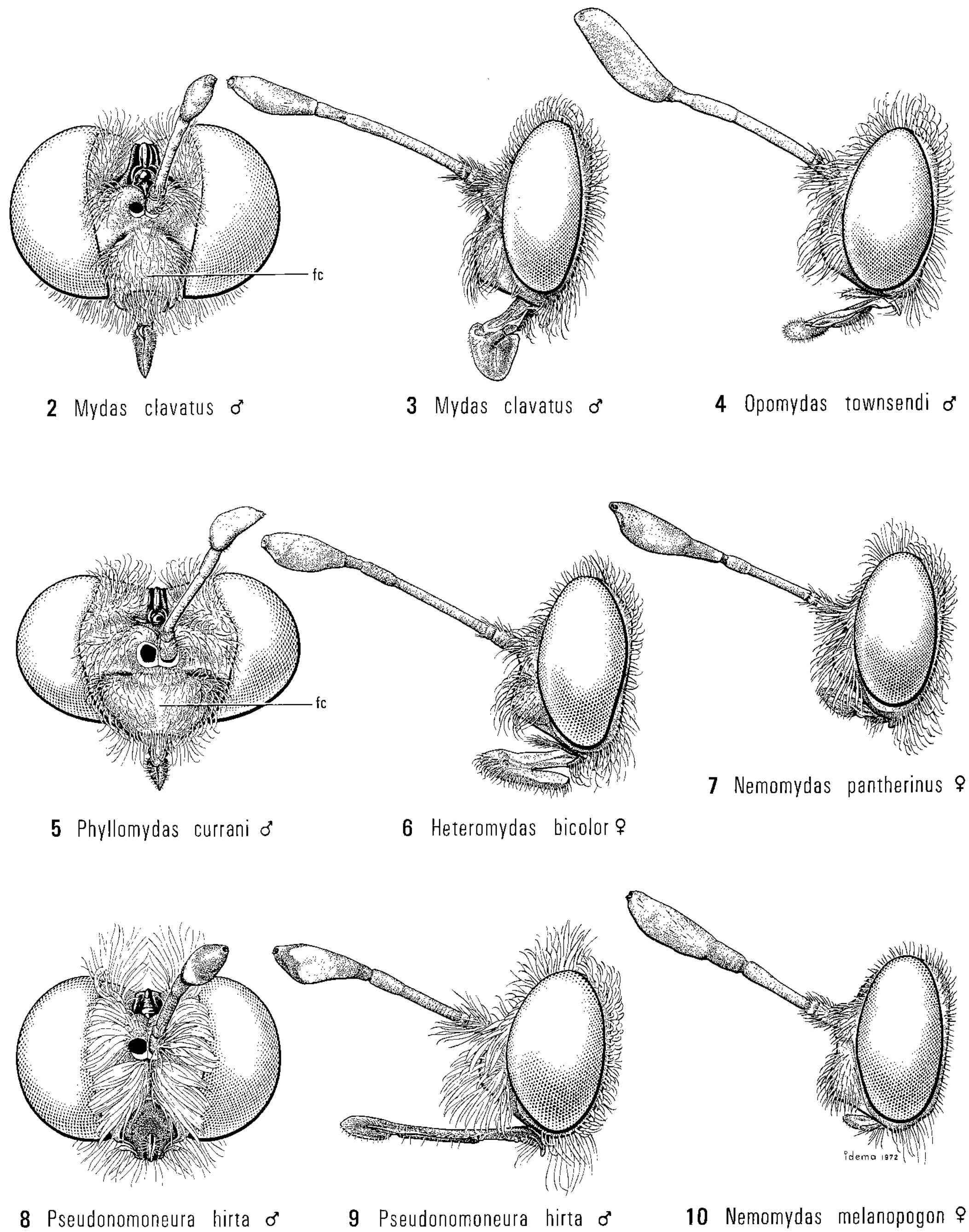


Fig. 40.1. Female of *Mydas clavatus* (Drury).

Medium to very large flies, 9–60 mm long, usually sparsely pilose, and without bristles except on legs (Fig. 1). Second flagellomere of antenna clubbed (Figs. 2–10). Abdomen long, cylindrical, and slightly tapered apically in male, but usually widest at segment 4 in female. Hindleg much longer and stronger than midleg and foreleg; hind femur usually swollen, with ventral spines (Figs. 15, 16); hind tibia with apical spur or bristles. Wing long, narrow to wide (Figs. 11–14); most veins ending in upper margin before apex.

Adult. Head: wider than high in anterior view (Figs. 2, 5, 8). Face at level of antennae one-third to one-half width of head, narrower at level of lower eye margin, and slightly narrower at vertex; large central part of face gibbous and pilose, with the hairs forming a mystax; narrow sides of face bare of hairs and usually pruinose. Frons slightly depressed; narrow central (ocellar) area usually shining black, with a single ocellus above antennae; sides usually pruinose and pilose, frequently with conspicuous tufts to sides of antennae and on vertex. Occiput pruinose and pilose, sometimes densely so on upper part. Anterior subcranial margin situated at level of lower eye margin (*Mydas* Fabricius, *Phyllomydas* Bigot), or varying from one-fourth to one-half distance from lower eye margin to base of antenna so that subcranial cavity is oblique in lateral view (Figs. 6, 7, 9). Proboscis usually with short mentum and well-developed labella, together usually subequal to length of subcranial cavity but sometimes varying from one-half to three times its length (*Nemomydas* Curran, *Pseudonomoneura* Bequaert). Palpus one-segmented, usually not much longer than broad, frequently not visible, or up to four times as long as broad and one-half length of subcranial cavity (*Opomydas* Curran, *Heteromydas* Hardy). Compound eye with uniformly small facets.

Scape cylindrical, about twice as long as broad, with few to many hairs; pedicel about as long as broad, with sparse short hairs. First flagellomere usually slender, three or more times as long as scape and pedicel combined, with apical one-fourth slightly wider. Second



Figs. 40.2–10. Heads: (2) frontal view of *Mydas clavatus* (Drury); left lateral view of (3) *Mydas clavatus* and (4) *Opomydas townsendi* (Williston); (5) frontal view of *Phyllomydas currani* Hardy; left lateral view of (6) *Heteromydas bicolor* Hardy and (7) *Nemomydas pantherinus* (Gerstäcker); (8) frontal view of *Pseudonomoneura hirta* (Coquillett); left lateral view of (9) *Pseudonomoneura hirta* and (10) *Nemomydas melanopogon* Steyskal.

Abbreviation: fc, face.

flagellomere often club-shaped, but shape varying among genera and between sexes; inner apical one-fourth (sensory area) usually depressed and pruinose; apex with a minute spine. A membranous area allowing for movement of club usually present between flagellomeres 1 and 2.

Thorax: postpronotum elevated and truncate posteriorly, pilose, frequently pruinose. Scutum usually bare of pollen but sometimes completely or partly pruinose; hairs usually confined to lateral and posterior margins and to dorsocentral rows. Scutellum small, bare to mainly pruinose, and usually with short sparse hairs;

lateral arms (axillary cords) bare of pollen, and with a few short hairs. Postnotum smooth or rugose, usually pruinose, usually bare of hairs; anatergite occasionally pilose (*Opomydas*, *Heteromydas*, and some species of *Pseudonomoneura*). Pleural areas usually thinly pruinose with dense spots in some genera; proepisternum, metepisternum, and mesepimeron pilose; posterior margin of anepisternum, katatergite, and katepimeron sometimes pilose; hairs much shorter and inconspicuous in female of some species.

Fore coxa usually twice as long as wide but sometimes about as long as wide, sparsely to densely pilose, sometimes pruinose. Trochanters with short sparse hairs; hind trochanter with two to five short stout spines (Fig. 15) (*Opomydas* and *Heteromydas*). Foreleg and midleg short and slender; femora usually not much wider than tibiae, and usually with long sparse hairs; tibiae and tarsi usually with short recumbent hairs but at times with long dense hairs. Hindleg much longer and stronger than anterior ones; femur wider than tibia and often greatly swollen (Fig. 16); venter with a few sharp spines to numerous short stout tuberculate spines; hairs usually short recumbent, but long erect on dorsum in male of some species. Hind tibia cylindrical with apical bristles, or widened with a ventral keel and a terminal spur (Figs. 15, 16); spur varying from long and curved to a mere stump in female of some species, with one or more basal bristles; hairs usually short recumbent. Hind tarsus cylindrical, with short dense recumbent hairs and sparse bristles; first tarsomere about three times as long as wide and subequal in length to second and third tarsomeres in most genera, but five times as long as wide and subequal in length to second, third, and fourth tarsomeres in *Opomydas* and *Heteromydas*. Claws strong, with curved tips. Pulvilli nearly as long as claws, usually with one rib or ridge (Bequaert 1961) in contrast to two ribs or ridges in Asilidae; empodia absent.

Wing varying from long and narrow to quite broad (Figs. 11–14); color hyaline, yellow, orange, and various shades of brown in most combinations. Cell br very long (Fig. 11); stem of Rs very short; R_1 to R_5, M_1, and sometimes M_2 ending before wing apex; R_5 usually ending in R_1 thereby closing cell r_4 (Figs. 11, 13, 14) or ending in C (Fig. 12) with cell r_4 open. M_1 usually ending in C (Figs. 11, 12) with cell r_5 open, but ending in R_1 with cell r_5 closed in some species of *Nemomydas* (Figs. 13, 14), *Mitrodetus*, and *Pseudonomoneura*; distal portion of M_2 fusing with CuA_1 and reaching hind margin of wing in most genera (Figs. 11, 12) but distal portion absent, atrophied, or perhaps fused with M_1 in a few species of *Mydas*, *Nemomydas* (Fig. 13), and *Pseudonomoneura*; M_2 sometimes reaching anterior margin of wing (Fig. 14). Halter and alula similar in color in *Mydas*; fringe varying from long, dense, and squamose in most species of *Mydas* to short, fine, and sparse in *Nemomydas*.

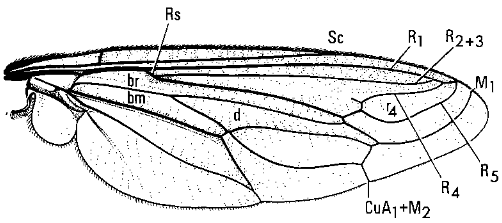
Abdomen: cylindrical in male and tapering from base to apex, but in female usually widest at segment 3 or 4 from which it narrows toward apex. Eight segments present, but tergite 8 usually hidden by tergite 7. Anterior part of tergite 1 bare, ovately tuberculate, and situated posterior to halteres in *Mydas*, but slightly rounded in other genera, bare of hairs to densely pilose, and bare of pollen to densely pruinose; posterior part always pilose with hairs usually longer and more numerous than on remaining tergites, and sometimes bare of pollen or completely or partly pruinose. Tergite 2 on each side of posterior margin having oval or elongate smooth areas, or bullae (Bezzi 1924); bulla usually of contrasting color, sensory in function, and usually larger in male than in female. Tergites 2–7 usually with short sparse recumbent hairs; hairs dense in male of some species, erect or retrorse on apical segment in female of some species. Sternites usually with very sparse short hairs; male sternite 8 short to long, frequently with numerous longer hairs.

Male terminalia (Figs. 21–26) rigid but free enough for slight movement. Epandrium divided into two parts, usually broader at base than apex, and with an apical lateral spur in most species of *Mydas*; cerci extended up or caudally between apices of epandrium, and bearing long hairs. Hypandrium hemispherical in most genera and connected to apically divided gonocoxites (Karl 1959), but slightly curved, partly split apically, and fused to gonocoxites in *Nemomydas* and *Pseudonomoneura* (Hardy 1944), and separated from gonocoxites in *Opomydas* and *Heteromydas* (Wilcox and Papavero 1971); aedeagus usually short and stout, with a large opening (Hardy 1944), but large basally and usually narrowing to an erect slender tube in *Nemomydas* except for a few species in which preapical part is enlarged, or with a broad base in *Pseudonomoneura*, or narrowed into a rounded flattened posteriorly directed tube, or greatly enlarged, folded over itself, and narrowed to an anteriorly directed point in *Opomydas* (Hardy 1944).

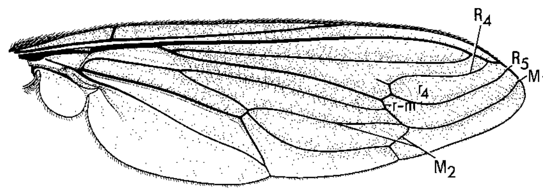
In female of *Mydas* (Fig. 18) and *Messiasia*, segment 9 narrower at apex than at base, with short hairs directed posteriorly. Tergite 8 with a posterior semicircular less-chitinized area, bare of hairs. Tergite 9 in *Phyllomydas* (Fig. 19) much wider at apex than at base, and fluted. Numerous erect or retrorse hairs present on segment 8 and sometimes on segment 7 in *Phyllomydas*. Circlet of strong blunt spines on tergite 10 (Fig. 20), with numerous erect or retrorse hairs on tergite 8 and sometimes on tergites 7 or 6 in other genera.

Larva. Only a few North American species are known in the larval stage. The following description is modified in part from Green (1917) and Teskey (1976).

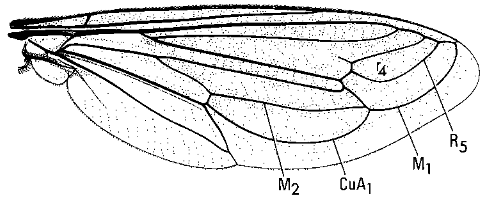
Mature larva (Fig. 28) robust, long, nearly cylindrical, rather narrowly pointed anteriorly, broader and more rounded posteriorly; largest of known species, *Mydas heros* (Perty) from South America, reaching about 75 mm long and about 10 mm wide. Body with 12 segments exclusive of head; cuticle smooth, creamy white.



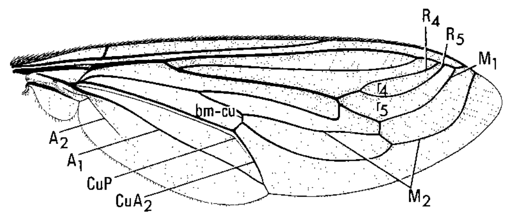
11 Opomydas townsendi ♂



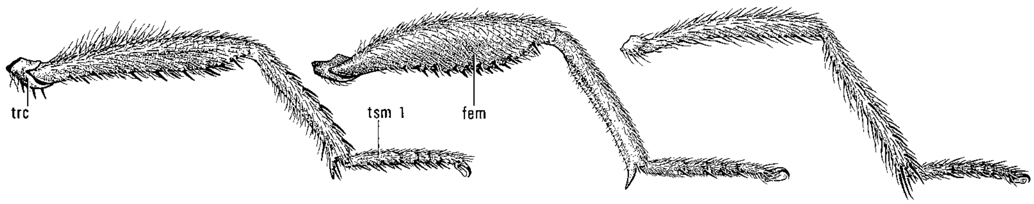
12 Heteromydas bicolor ♂



13 Nemomydas pantherinus ♂



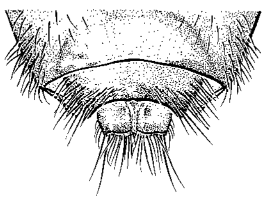
14 Mitrodetus dentitarsus ♂



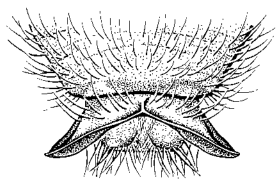
15 Opomydas townsendi ♂

16 Mydas clavatus ♂

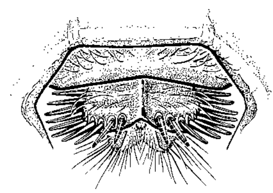
17 Nemomydas melanopogon ♂



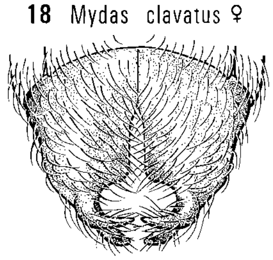
18 Mydas clavatus ♀



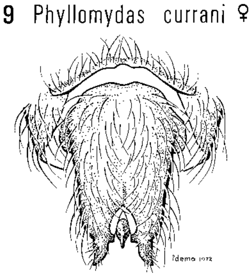
19 Phyllomydas currani ♀



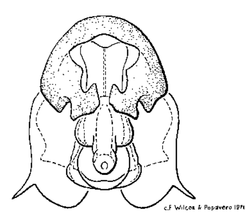
20 Opomydas townsendi ♀



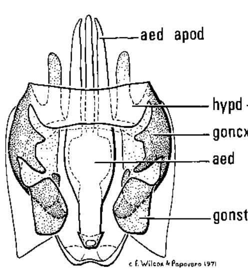
21 Nemomydas pantherinus ♂



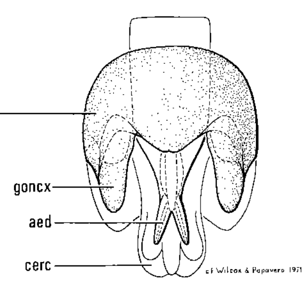
22 Pseudonomoneura hirta ♂



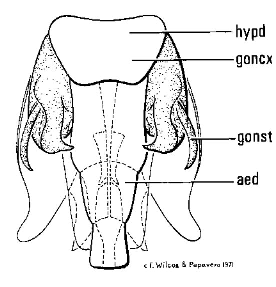
23 Mydas heros ♂



24 Ectyphus armipes ♂



25 Syllegomydas daltoni ♂



26 Opomydas limbatus ♂

Head capsule (Fig. 29) conical, relatively small but well-developed and heavily sclerotized, partially retractile within first thoracic segment. Mandible slender, rather straight, sharply pointed, overlaid by maxilla; maxilla compressed laterally, strongly tapering anteriorly, with a small single segmented palpus. Club-shaped metacephalic rod and paired tentorial arms articulating with anterior portion of cranium and extending posteriorly deep into thorax.

Abdominal segments 1–7 each with a transverse series of four slender proleg-like ridges near anteroventral margin; posterior margin of terminal segment with a ridge that is somewhat pointed posteromedially. Respiratory system amphipneustic, consisting of a pair of biforous anterior spiracles and a pair of larger rounded spiracles on penultimate segment, each having a series of peripheral openings; body segments 3–10 each with a pair of small vestigial spiracles. Body segments 1–3 each with a pair of long slender bristles ventrally; terminal segment with a pair of similar bristles ventrally near apex and with a more lateral subapical pair.

Pupa. Elongate (Fig. 27) and mobile as in Asilidae. Head with one pair of spine-like dorsal cephalic processes and two pairs of smaller but somewhat similar antennal processes.

Leg sheaths visible; sheath of hindleg extending to middle of abdominal segment 3. Abdomen with nine segments. Anterior margin of tergite 1 with transverse row of about 14 erect but apically recurved spines dorsally; posterior margin with about six posteriorly directed spines on each side. Abdominal segments 2–8 with a row of posteriorly directed spines along posterior margins. Tergites 1–7 each with a pair of bilobate rounded processes on each side; sternites 1–7 with a row of posteriorly directed spines along posterior margins. Terminal segment with an elongate spine-like process on each side.

Biology and behavior. Little is known of the immature stages of the Mydidae. The larva and pupa of *Mydas clavatus* (Drury) were described and illustrated by Malloch in 1917, and the larva and pupa of *Mydas heros* Perty were illustrated by Wilcox and Papavero in 1971. Larvae of *Mydas* spp. were reported feeding on coleopterous larvae in stumps or logs (Westwood 1841, Walsh 1864, Malloch 1917) and on scarabaeid larvae in sandy grass sod in Florida (Genung 1959). Zikán (1942, 1944) extensively observed *Mydas heros* in Brazil and found it ovipositing in the large nests of sauba ants (species of *Atta* Fabricius); he believed that the larvae feed on dynastid larvae (species of *Coelosis* Hope), which inhabit the garbage pits in these nests. *Messiasia pertenuis* (Johnson) was reared from a larva collected in a kangaroo rat nest in Arizona. The adult mydid is essentially a flower feeder; however, Zikán (1944) did not find the female of *M. heros* coming to flowers, and species of *Nemomydas* and *Pseudonomoneura* with atrophied mouthparts may not feed as adults. Olivier (1811) and Paramonov (1950) believed that the adults prey on other insects. Zikán (1944) observed that the male of *M. heros* would try to copulate with females of other species, with other males, or with large black Hymenoptera, which it seems to mimic. This activity might be interpreted as predation. Séguy (1951) described *Midacritus kuscheli* Séguy from Chile that was taken *in copula* with *Mitrodetus microglossa* Séguy.

Classification and distribution. These rare flies are world wide in distribution but most numerous in warm, dry climates. About 340 species have been described: 160 from the Ethiopian region; 70 Neotropical; 40 Nearctic; 30 Australian; 30 Palaearctic; and 10 Oriental.

The Mydidae are now divided into nine subfamilies. The Diochlistinae, Mydinae, and Syllegomydinae were proposed by Bequaert (1961, 1963); the Ectyphinae by Wilcox and Papavero (1971); and the Anomalomydinae, Apiophorinae, Cacatuopyginae, Leptomydinae, and Rhopalinae by Papavero and Wilcox (1974).

Fossil Mydidae of the Oligocene epoch were reported from Florissant, Colo., by Scudder (1881, 1890), and one species of *Mydas* was described by Cockerell (1913).

Figs. 40.11–26. Wings, legs, and abdomens: wing of (11) *Opomydas townsendi* (Williston), (12) *Heteromydas bicolor* Hardy, (13) *Nemomydas pantherinus* (Gerstäcker), and (14) *Mitrodetus dentitarsus* (Macquart); hindleg of (15) *Opomydas townsendi*, (16) *Mydas clavatus* (Drury), and (17) *Nemomydas melanopogon* Steyskal; apex of female abdomen of (18) *Mydas clavatus*, (19) *Phyllomydas currani* Hardy, and (20) *Opomydas townsendi*; views of sternite 9 of male of (21) *Nemomydas pantherinus* and (22) *Pseudonomoneura hirta* (Coquillett); ventral view of male terminalia of (23) *Mydas heros* (Perty), (24) *Ectyphus armipes* Bezzi, (25) *Syllegomydas daltoni* Séguy, and (26) *Opomydas limbatus* (Williston) (23–25 not Nearctic).

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; goncx, gonocoxite; gonst, gonostylus; hypd, hypandrium; fem, femur; trc, trochanter; tsm, tarsomere.

Key to genera

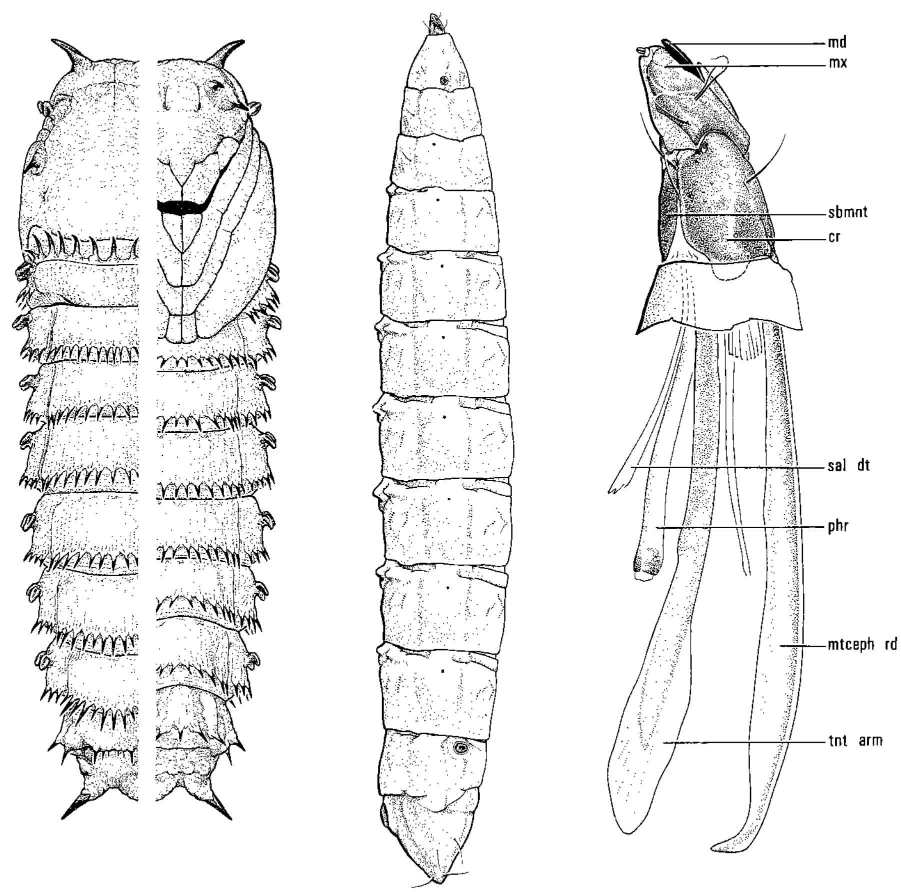
1. First tarsomere of hindleg five times as long as wide, and subequal in length to tarsomeres 2–4 (Fig. 15); hind trochanter with two to five short stout spines. Palpus slender and about one-half length of subcranial cavity. Anatergite pilose. Female abdomen with apical circlet of strong spines (Fig. 20) .... ECTYPHINAE....2

   First tarsomere of hindleg about three times as long as broad, and subequal in length to tarsomeres 2 and 3 (Figs. 16, 17); hind trochanter with fine hairs. Palpus short, one or two times as long as wide. Anatergite usually bare. Female abdomen with or without apical circlet of spines 3

2. Prementum subequal in length to subcranial cavity; labella short and slightly wider than mentum (Fig. 4). Cell r_4 closed (Fig. 11). Hind tibia with slender apical spur and several bristles; spur small in female of some species. Length 18–25 mm .... ***Opomydas*** Curran
   3 spp.; southwest U.S.A., northern Mexico

   Prementum about one-half length of subcranial cavity; labella attached to prementum near its midpoint, and subequal in length to subcranial cavity (Fig. 6). Cell r_4 usually broadly open (Fig. 12). Hind tibia with apical spur and a bristle at base. Length 22–29 mm .... ***Heteromydas*** Hardy
   1 sp., *bicolor* Hardy; California; Hardy 1944

3. Laterotergite bare on both anatergite and katatergite. CuA_1 joining with M_2 distally and ending in hind margin of wing (Figs. 11, 12). Hind tibia with ventral keel and usually with an apical spur (Fig. 16). Proboscis subequal in length to subcranial cavity; labella broad. Apex of female abdomen with hairs (Figs. 18, 19) .... MYDINAE....4



27 Mydas ventralis 28 Mydas clavatus 29 Mydas clavatus

Figs. 40.27–29. Immature stages: (27) pupa of *Mydas ventralis* Gerstäcker in dorsal (*left*) and ventral (*right*) views; (28) larva of *Mydas clavatus* (Drury); (29) head capsule of larva of *Mydas clavatus*.

Abbreviations: cr, cranium; md, mandible; mtceph rd, metacephalic rod; mx, maxilla; phr, pharynx; sal dt, salivary duct; sbmnt, submentum; tnt arm, tentorial arm.

Laterotergite pilose on anatergite or katatergite or on both; hairs short and inconspicuous in female of some species. CuA_1 ending in M which runs to anterior margin of wing as M_1 or M_2 or even as $M_1 + M_2$ (Figs. 13, 14). Hind tibia cylindrical, with apical bristles (Fig. 17). Apex of female abdomen with circlet of strong spines (as in Fig. 20). Proboscis one-half to three times length of subcranial cavity, with small apical labella (Figs. 7, 9) .... LEPTOMYDINAE....6

4. Prementum about one-half length of subcranial cavity; labella attached to prementum near its midpoint, and subequal in length to subcranial cavity (as in Fig. 6); anterior margin of subcranial cavity situated at about two-fifths distance from lower eye margin to base of antenna. Length 15–29 mm .... ***Messiasia*** d'Andretta
   2 spp.; southwest U.S.A.; d'Andretta 1951, Wilcox and Papavero 1975

   Prementum subequal in length to subcranial cavity; labella attached to mentum near its apical one-half, and extending out at about a 90° angle (Fig. 3); anterior subcranial margin level with lower eye margin 5

5. Face about as broad as high (Fig. 2). Female tergite 9 narrower at apex than at base (Fig. 18). Length 15–60 mm .... ***Mydas*** Fabricius
   17 spp.; southern Ontario to California and Massachusetts; Johnson 1926, d'Andretta 1951

   Face about 1.5 times as broad as high (Fig. 5). Female tergite 9 wider at apex than at base, and fluted (Fig. 19). Length 12–29 mm........................ ***Phyllomydas*** Bigot
   7 spp.; southern U.S.A.; Hardy 1943, Wilcox 1978

6. Antennal club shorter than or subequal in length to basal flagellomere (Fig. 9). Male sternite 9 divided apically; each arm with a single spur (Fig. 22). Length 9–20 mm........................ ***Pseudonomoneura*** Bequaert
   4 spp.; western; Hardy 1951

   Antennal club longer than basal flagellomere (Fig. 10). Male sternite 9 divided basally; each arm with two apical prongs (Fig. 21). Length 12–23 mm .... ***Nemomydas*** Curran
   11 spp.; British Columbia south to California and Georgia; Hardy 1951, Steyskal 1956

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APIOCERIDAE 41

B. V. PETERSON

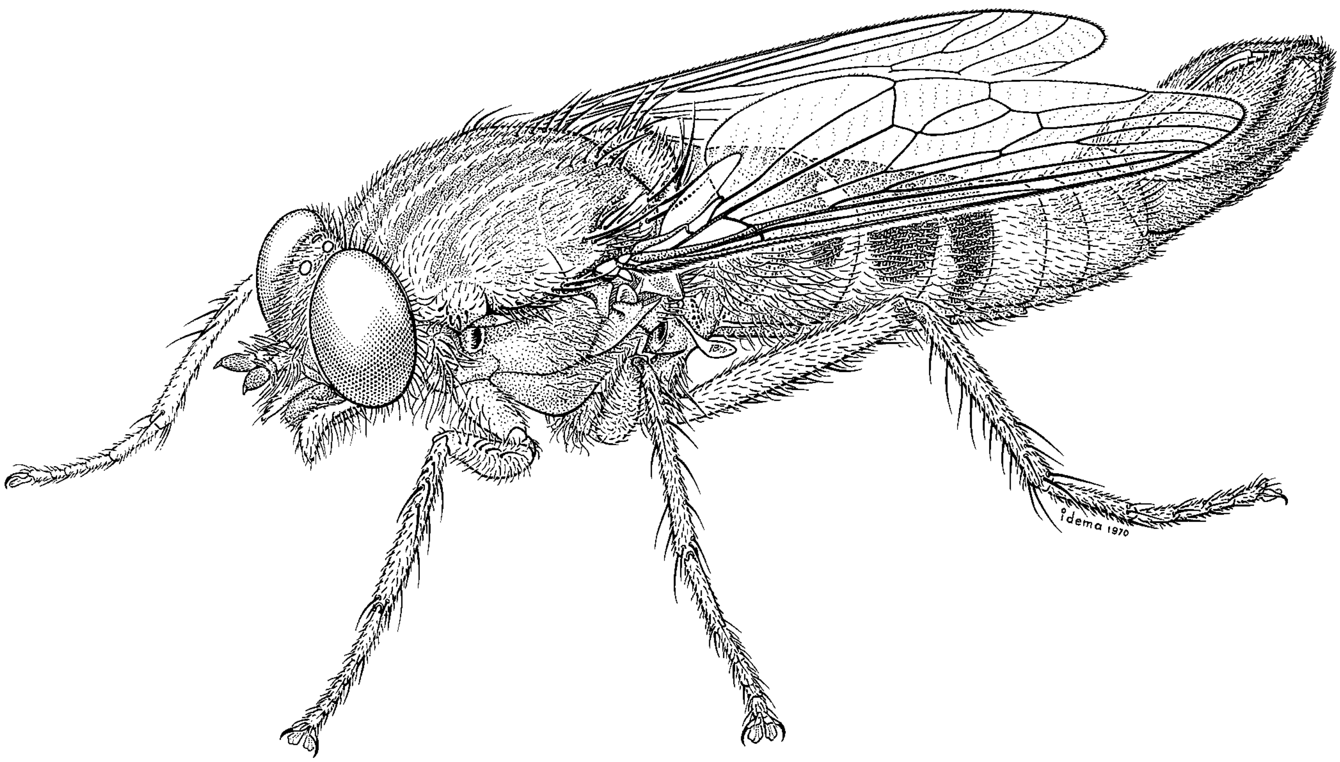


Fig. 41.1. Male of *Apiocera haruspex* Osten Sacken.

Medium to large flies, 7.5–35.0 mm long, with most species ranging between 12.0 and 20.0 mm (Fig. 1). Body stout, nearly bare to moderately setose, usually dull in color. Abdomen often elongate, tapering posteriorly; male terminalia often enlarged; tergite 10 of female with series of stout spines.

Adult. Head: short and wide, two or three times as wide as long, flattened posteriorly, usually with a series of stout occipital bristles; vertex usually shallowly depressed between eye and ocellar tubercle. Eyes large, bare, usually dichoptic in both sexes but holoptic in male of *Tongamya* Stuckenberg. Ocelli well-developed (apparently absent in *Megascelus* Philippi); anterior ocellus often somewhat larger and more rounded than dorsal ocelli. Frons flattened, wider in female than in male, bare or variously setose. Antennae porrect, inserted close together near mid level of eye, rather short, about as long as or slightly longer than length of head; pedicel short and globular, bearing long fine setae or bristles or both; flagellum enlarged, rather ovoid, often as long as or longer than basal two segments combined, often rather densely covered dorsally with coarse and fine punctations, and with a small terminal two-segmented stylus or a minute apparently single-segmented spine-like process or sensory fovea. Face short, bare or sparsely setose; a suboval aperture present in *Tongamya*, situated slightly lateroventral to base of antenna, and passing through head via a hollow slightly curved tentorial arm. Palpus well-developed, one- or two-segmented (two-segmented in all North American species examined, but segments sometimes imperfectly separated); apical segment small, or large and blade-like. Proboscis generally projecting forward horizontally, ranging from about as long as head to about five times as long as head (Fig. 4), rudimentary in *Tongamya*; maxillae and hypopharynx moderately elongate and stylet-like in *Rhaphiomidas* Osten Sacken, fitting inside a greatly elongated labium that is closed proximodorsally by a shorter labrum and that bears small partially sclerotized labella at its apex; in *Apiocera* Westwood maxillae and hypopharynx short and not stylet-like, and labella large and fleshy.

Thorax: large and stout. Antepronotum narrow and collar-like dorsally, often bearing a row of stout bristles; postpronotum small, often with a patch or a series of moderately strong bristles. Scutum only moderately convex, often patterned but with pattern sometimes dull and rather indistinct, often bearing a row of notopleural bristles, a series of supra-alar and postalar bristles, and sometimes a few prescutellar dorsocentral bristles, but sometimes nearly bare or densely covered with fine moderately long setae. Scutellum rather short and broad, partly concealing postnotum, with or without setae and marginal bristles. Postnotum short; mediotergite bare; anatergite sometimes covered by fine setae; katatergite sometimes slightly swollen to strongly produced as a conical lobe. Thoracic pleurites without bristles, but anepisternum and katepisternum often fully covered by fine setae or partly covered by patches of fine setae; anepimeron usually bare but sometimes with a few fine setae; katepimeron bare.

Legs long, moderately stout, with at least a few bristles in addition to a rather dense covering of setae on nearly all segments; tibiae with spurs and several strong apical bristles. Claws rather long and stout, strongly curved apically; pulvilli well-developed; empodia bristle-like or absent.

Wing (Figs. 2, 3) moderately long, usually shorter than abdomen but sometimes approaching tip of abdomen, rather narrow; both lying flat over abdomen in resting position; alula usually well-developed but reduced in some species; membrane usually smooth but sometimes somewhat wrinkled, usually hyaline, occasionally yellowish, brownish, or grayish tinged, sometimes with a variably developed pattern. Veins mostly well-developed but in some species and particularly in *Tongamya miranda* Stuckenberg distal portions of posterior veins weak, colorless, and difficult to discern; C continuing around margin of wing including alula, but sometimes reduced or evanescent; Sc long, usually extending over half length of wing; R_1 strong, joined by R_{2+3} near apex and also by R_4 before or at junction with C; R_5, M_1, and even M_2 sometimes also joining R_1 apically; R_4, R_5, and M_1, and occasionally M_2, curving forward to end before apex of wing; M_2 also sometimes terminating behind apex of wing; M_3 sometimes absent (*Tongamya*), but usually joining distally with CuA_1 thus forming cell m_3 (often called subdiscal cell); distal portion of petiole and basal portion of fork of M often weakened and pale (thyridium of Paramonov 1953); CuA_2 joined by A_1 apically or meeting at margin of wing; CuP distinctly or faintly indicated; A_2 usually short and faint; MA (arculus) well-developed. Cell br and cell bm elongate; cell d well-developed except in *Tongamya*; cell m_3 usually present; cell cu*p* long, reaching or nearly reaching wing margin. Halter with moderately long to long stem and relatively small knob, variable in color. Calypter moderately large, with dense fringe of setae.

Abdomen: broad basally, elongate or long ovoid, tapering posteriorly, often with an indistinct dull pattern, and with eight pregenital segments. Usually seven abdominal spiracles present (Fig. 5); an eighth auxiliary spiracle, with a closely associated tiny pale seta, present on each side of tergite 8 in female of some (perhaps all) species of *Rhaphiomidas* (Fig. 7). Tergites and sternites usually heavily sclerotized, variously clothed with moderately long stiff setae some of which are sometimes directed anteriorly; tergite 7 and sternite 7 sometimes with a median rod-like sclerotization extending posteriorly through segmental membrane nearly to base of tergite 8 and sternite 8.

Female terminalia as in Figs. 6 and 8–12. Tergite 9 sometimes emarginate posteriorly, but with a distinct raised median keel-like process; lateral lobes (hemitergites) often enlarged, sometimes bearing few to many setae, and sometimes overlapping and fused with lateral lobes of tergite 10, or sometimes closely abutting lobes of tergite 10. Tergite 10 with lateral lobes (hemitergites, sometimes termed acanthophorites) bearing a series of long stout spines wrongly attributed in most previous descriptions to tergite 9; cercus free, varying considerably in size, variously covered with rows of stiff setae. Sternite 8 moderately sclerotized, often weakly so medially; distal membranous portion variously emarginate medially or produced as a short tongue-like median lobe, in all cases variously setose. Sternite 9 (furca) varying in size and shape, often an inverted U- or V-shaped structure that is fused or articulated with sternite 10 (Figs. 11, 12). Sternite 10 variously developed, usually with at least a few setae, and ranging from a small partially bilobate plate to an enlarged anchor-shaped sclerite that is sometimes fused laterally or articulated with ventrolateral margins of tergite 10. Hypoproct small. Three spermathecae present; capsule or gland rather small, weakly sclerotized, globular to elongate; duct long and slender, with a slightly enlarged pump-like basal section that diminishes in size just before union of duct with other two ducts into a larger common duct apparently opening into oviduct between arms of sternite 9.

Male terminalia (Figs. 13–16) greatly enlarged in North American genera, but small and somewhat retracted in *Neorhaphiomidas* Norris and *Megascelus*. Tergite 9, or epandrium, produced as two large lobes (sometimes referred to as upper forceps) surrounding unsclerotized segment 10, cerci, and anus; these lobes sometimes notched apically, and bearing secondary internal lobes as well as tiny spines and long setae or bristles; cercus usually rather small, free or partially fused with paraproct, variously setose. Sternite 9, or hypandrium, usually large, usually fused or partially fused with gonocoxites, rarely entirely free, often with various accessory lobes on its internal (dorsal) surface, and sometimes having a patch of dense setae on its external surface; gonocoxites usually at least partially fused with hypandrium, and varying in shape from digitiform lobes of variable size to large lamelliform lobes; gonostyli ventral to lateroventral in position, varying in shape from digitiform to lamelliform lobes of variable size but similar in form to respective gonocoxites, and at least partially fused with gonocoxites; parameres fused, varying in shape from a solid heavily sclerotized simple conical sheath through which aedeagus moves to a partially membranous and partially sclerotized sheath bearing various apical lobes or processes; aedeagus only moderately long, strongly sclerotized, lance-like, tapering to a fine point; aedeagal apodeme short and broad (Fig. 14). Sternite 10 evident as two sclerotized rods surrounded by membrane, and appearing to fuse with base of parameres.

Egg. Elongate, ovoid to slightly reniform in shape, with ends bluntly rounded to slightly pointed, and varying from about 0.66 to 2.1 mm long and 0.17 to 1.0 mm wide. Chorion smooth and shiny, without pattern but wrinkling somewhat with age and degree of larval development; color varying from pearly white to pale yellowish to bright orange.

Larva. Known only for *Apiocera maritima* Hardy from Australia (English 1947), and for first instar larvae of *A. painteri* Cazier from Arizona (Cazier 1963) and *Tongamya miranda* from South Africa (Irwin and Stuckenberg 1972).

First instar larva slender, 1.18–4.0 mm long, pale white to yellowish white in color. Head rather cylindrical, slightly angled ventrally. Thorax with three rather uniform segments. Abdomen apparently with nine segments; abdominal cuticle smooth, without strong setae except on terminal segment.

Mature larva of *Apiocera maritima* (English 1947) white, long, and slender, reaching maximum length of 51.0 mm and width of 3.0 mm. Head well-developed, elongate, retractable for about half its length into prothorax; mandible slender, heavily sclerotized, fitting into a groove in dorsal part of maxilla. Thoracic segments 1 and 2 longer than segment 3; segment 1 with a thickened anterior collar bearing tiny tubercles; each segment with a pair of short ventral setae situated in a ventral cuticular furrow. Abdominal segments 1–5 somewhat bead-like, broad anteriorly, tapering posteriorly; segments 6–8 more cylindrical; segment 9 short, with its ventral surface sharply curving dorsally almost as a straight transverse keel, with anal opening situated on ventral surface, and with four pairs of setae of which posterior pair is longest. Ventral surface of segments 2–6 with a trace of paired processes delimited more by semicircular depressions than by actual protuberances; thoracic and abdominal segments with longitudinal striations, and with a pair of lateral furrows that become deeper and more pronounced anteriorly; two semicircular furrows present laterally near posterior margin of each abdominal segment, crossing each lateral furrow to form a small raised area. All spiracles placed between lateral furrows; anterior spiracle distinct, situated near posterior margin of prothoracic segment; posterior spiracle large, lying near anterior margin of segment 8; small spiracles also present on metathorax and abdominal segments 1–7. For details of head structure and mouthparts see English (1947).

Pupa. Large, varying from about 18.0 to 30.0 mm in length, and from 3.0 to 7.0 mm at greatest width, with female apparently somewhat larger than male; cuticle heavily sclerotized, variously rugose in texture, yellowish brown in color (Fig. 19). Head variously armed with a few strong bristles or spines; spines free or fused basally onto a common protuberance; sheath of proboscis short (*Apiocera*), or long and extending nearly to tips of sheaths of anterior legs (*Rhaphiomidas*). Thorax with sheaths of legs varying from distinctly longer than sheath of wing to about as long as sheath of wing; a prominent spine present at base of sheath of wing, and similar spines sometimes present at base of each leg sheath; thoracic spiracle prominent. Abdomen with eight apparent segments and seven spiracles (*Rhaphiomidas*) (Hogue 1967), or with nine apparent segments and eight spiracles (*Apiocera*) (English 1947); segments with a row of stout bristles or bristle-like spines both dorsally and ventrally; terminal segment with (*Rhaphiomidas*) or without (*Apiocera*) bristles or spines. This description based on pupal features of *Apiocera maritima* (English 1947) and *Rhaphiomidas terminatus* Cazier (Hogue 1967), the only two species described of the four or five known.

Biology and behavior. There is a paucity of biological data for the Apioceridae. In fact, only four papers have been published that contain significant biological information for the family. These include the notes by English (1947) on the Australian species *Apiocera maritima*, observations on *A. painteri* from Arizona (Cazier 1963), the data of Irwin and Stuckenberg (1972) on *Tongamya miranda* from South Africa, and the work of Lavigne (1975) on the Mexican species *Apiocera clavator* Painter; a few scattered observations have appeared elsewhere.

Most species occur in arid or semiarid regions, or in sandy areas on or near ocean beaches. Adults are usually found on or near the vegetation of these areas. The flies are most active from about midmorning to middle or late afternoon, walking or running between plants, or resting on the ground in the shade. *Apiocera painteri* and *A. clavator* usually fly very rapidly with a loud buzzing sound (Cazier 1963, Lavigne 1975), whereas *A. maritima* was reported to fly lazily from place to place (English 1947) and *Tongamya miranda* was reported to be slow of flight with the female seemingly flying into clumps of grass without reducing speed (Irwin and Stuckenberg 1972). Adults intermittently touch their mouthparts to the soil surface. Cazier (1963) suggested this behavior was for obtaining moisture, but Lavigne (1975) suggested it might be a foraging maneuver because the structure of their mouthparts indicate that these flies are scavengers. Mating apparently occurs without elaborate courtship maneuvers; it takes place in the tail-to-tail position with the two partners facing in opposite directions and lasts from about 2 to 19 min. In all known instances, oviposition takes place in loose soil or sand, sometimes near the stems of bushes. The eggs are deposited about 2.5–4.0 cm below the soil surface, and according to Cazier (1963) two to five eggs are laid in each batch, with each female producing a total of about 38 eggs. English (1947) found 69 large eggs and several small eggs in the abdomen of a female of *Apiocera maritima*; Irwin and Stuckenberg (1972) reported that a single female of *Tongamya miranda* laid 56–150 eggs in each cluster with each female capable of producing upwards of 1000 eggs. Larval development requires 15–24 days, and the hatching sequence an average of 70 min (usually varying from about 44 min to 97 min or more). The developing larva lies doubled over within the egg. At the time of hatching, larval movements within the egg ruptures the chorion. The break is irregular and occurs near one end of the egg. Irwin and Stuckenberg (1972) claim the larva leaves the egg head first, but Cazier (1963) observed that emergence of the larva was by the caudal end first. Larvae apparently are carnivorous and may even be cannibalistic. Pupae are found in the larval habitats and apparently wriggle out of the loose soil or sand, or at least partly protrude, to enable the adults to successfully emerge. A male and a female of *Apiocera maritima* reared in the laboratory (English 1947) required 20 and 21 days, respectively, to complete their development and emerge.

Classification and distribution. This small family of relatively large flies has had a jumbled taxonomic history. Its first species was named and described in the Asilidae as *Laphria brevicornis* Wiedemann (=*Apiocera brevicornis*) from Australia. Other species have been included in the Mydidae and the Therevidae, and even under the name Pomaceridae (=Apioceridae).

The family has a wide but disjunct distribution. It consists of two subfamilies and five genera. The Apiocerinae contains *Apiocera* (North America, Mexico, Chile, Australia, Borneo, Sri Lanka, and South Africa) with 94 species and *Rhaphiomidas* (United States and Mexico) with 13 species; and the Megascelinae contains *Megascelus* (Chile) with five species, *Neorhaphiomidas* (Australia) with seven species, and *Tongamya* (South Africa) with the single species *miranda*. Only the first two genera with about 29 species are represented in the Nearctic region.

The generic review and revision of the North American species by Cazier (1941) put the family classification on a firm foundation. Other important works on the Nearctic fauna include those of Painter (1932, 1936) and Cazier (1954, 1963). Useful extralimital papers include those of Norris (1936), Hardy (1940), Carrera and d'Andretta (1948), Paramonov (1950, 1953), Stuckenberg (1966), and Artigas (1970, 1973).

The Apioceridae is generally considered to be an archaic family and one that is in its declining stages of evolution. Despite the suggested antiquity of this relict family there are no known fossil remains.

Keys to genera

Adult

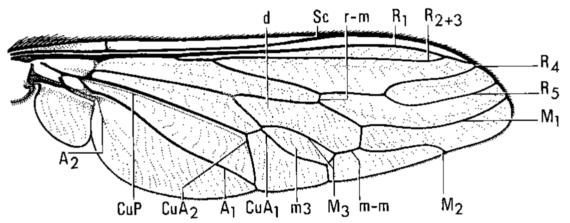
1. Proboscis long, up to five times longer than head (Fig. 4). Laterotergite of postnotum with a strongly produced conical projection. Gonostylus ventral in position (Fig. 16) .... ***Rhaphiomidas*** Osten Sacken
   9 spp.; southwestern U.S.A.

   Proboscis short, about as long as head. Laterotergite of postnotum without a strongly produced conical projection, at most slightly swollen. Gonostylus lateroventral in position (Figs. 13, 15) .... ***Apiocera*** Westwood
   20 spp.; western, British Columbia south to Texas and Mexico

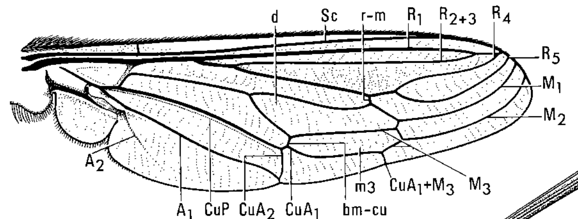
Pupa

1. Sheath of proboscis long, nearly as long as those of legs. Sheaths of legs and wings subequal in length (Fig. 18). Terminal abdominal segment with at least a pair of posteriorly directed apical spines (Fig. 17) .... ***Rhaphiomidas***

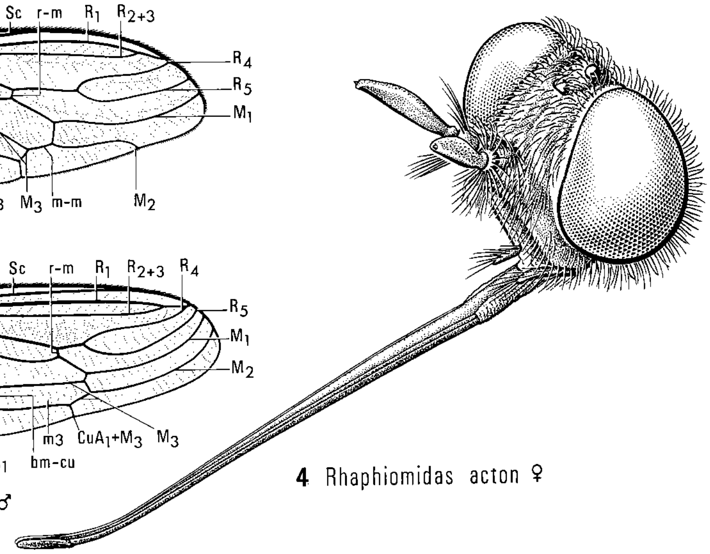
   Sheath of proboscis short, much shorter than those of legs. Sheaths of legs longer than those of wings. Terminal abdominal segment without bristles or spines .... ***Apiocera***



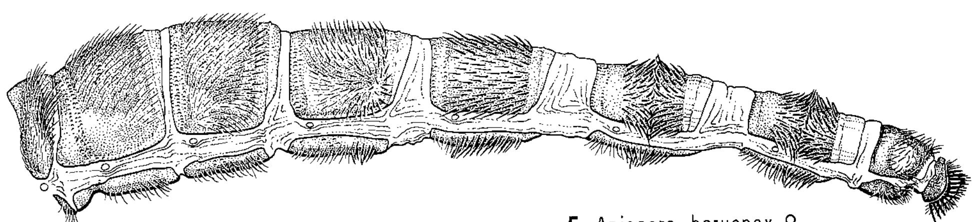
2 Apiocera haruspex ♂



3 Rhaphiomidas acton ♂



4 Rhaphiomidas acton ♀



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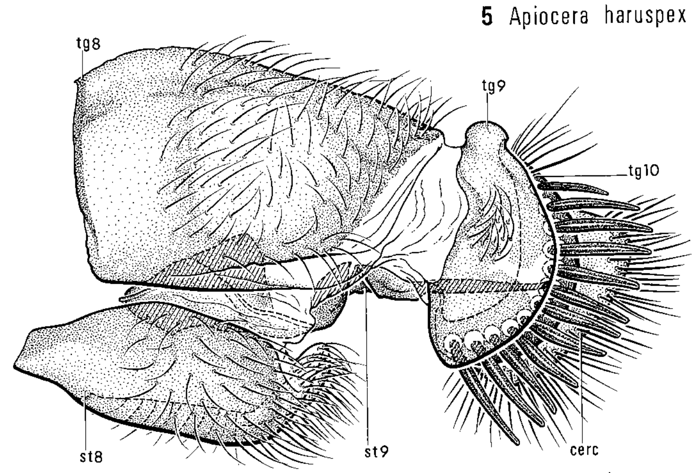
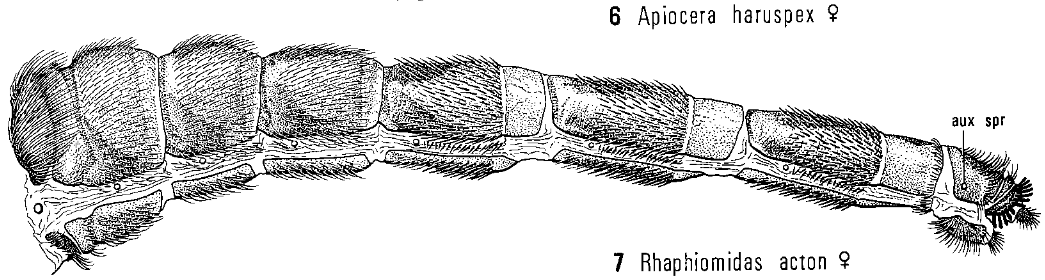


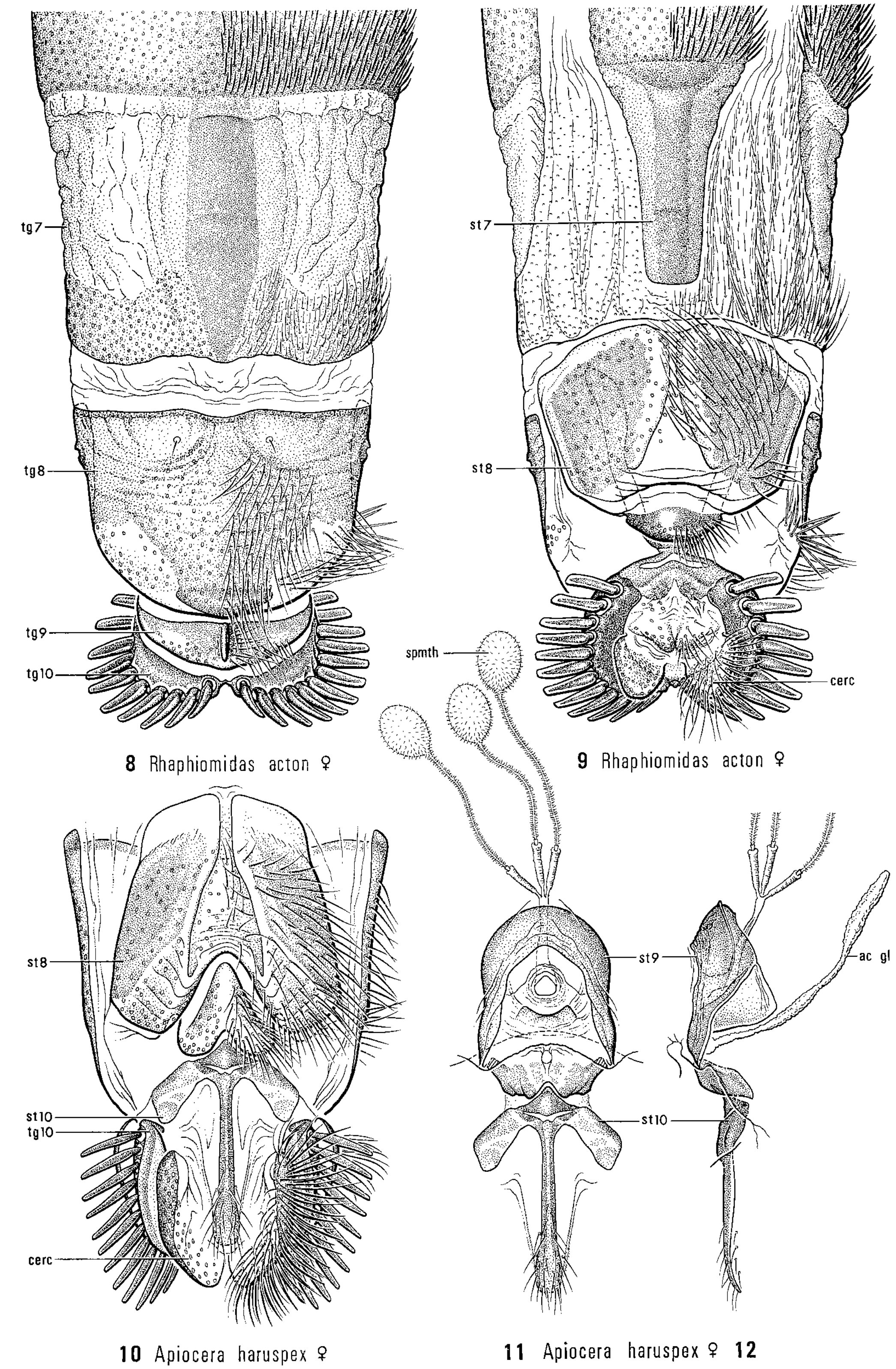
6 Apiocera haruspex ♀



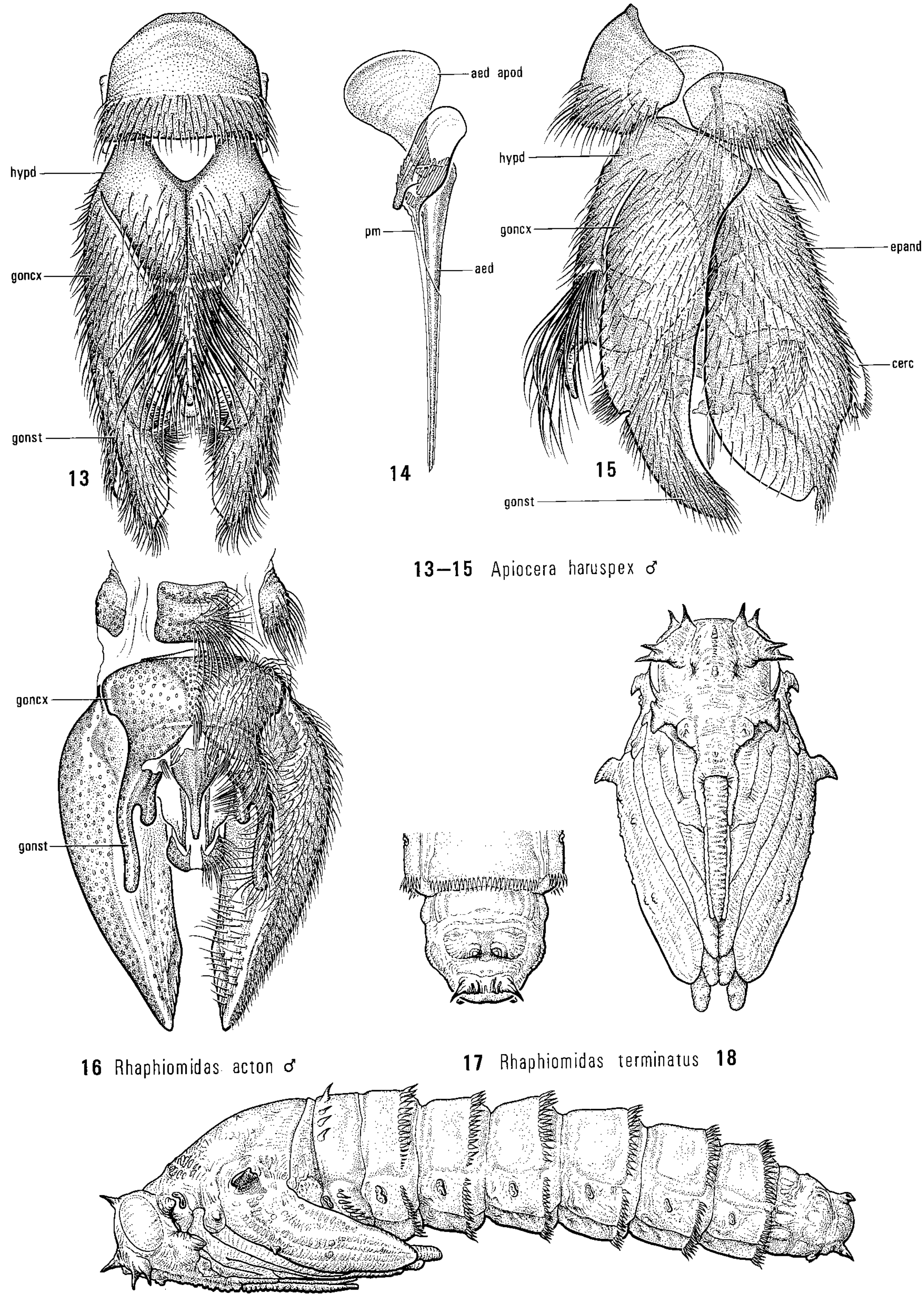
7 Rhaphiomidas acton ♀

Figs. 41.2–7. Wings, head, and abdomens: wing of male of (2) *Apiocera haruspex* Osten Sacken and (3) *Rhaphiomidas acton* Coquillett; (4) head of female of *Rhaphiomidas acton*; (5) abdomen of female of *Apiocera haruspex*; (6) enlarged view of female terminalia of *A. haruspex*; (7) abdomen of female of *Rhaphiomidas acton*.

Abbreviations: aux spr, auxiliary spiracle; cerc, cercus; st, sternite; tg, tergite.



Figs. 41.8–12. Details of abdomen of female: (8) dorsal view and (9) ventral view of abdomen of female of ***Rhaphiomidas acton*** Coquillett; terminalia of female of ***Apiocera haruspex*** Osten Sacken showing (10) external structures in ventral view, (11) internal structures in ventral view, and (12) internal structures in lateral view.
Abbreviations: ac gl, accessory gland; cerc, cercus; spmth, spermatheca; st, sternite; tg, tergite.



Figs. 41.13–19. Male terminalia and pupa: terminalia of male of *Apiocera haruspex* Osten Sacken showing (13) external structures in ventral view, (14) internal structures in lateral view, and (15) external structures in lateral view; (16) male terminalia of *Rhaphiomidas acton* Coquillett in ventral view; pupa of *Rhaphiomidas terminatus* Cazier showing (17) terminal segments in dorsal view, (18) head and thorax in ventral view, and (19) full lateral view.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; epand, epandrium; goncx, gonocoxite; gonst, gonostylus; hypd, hypandrium; pm, paramere.

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ASILIDAE 42

GRACE C. WOOD

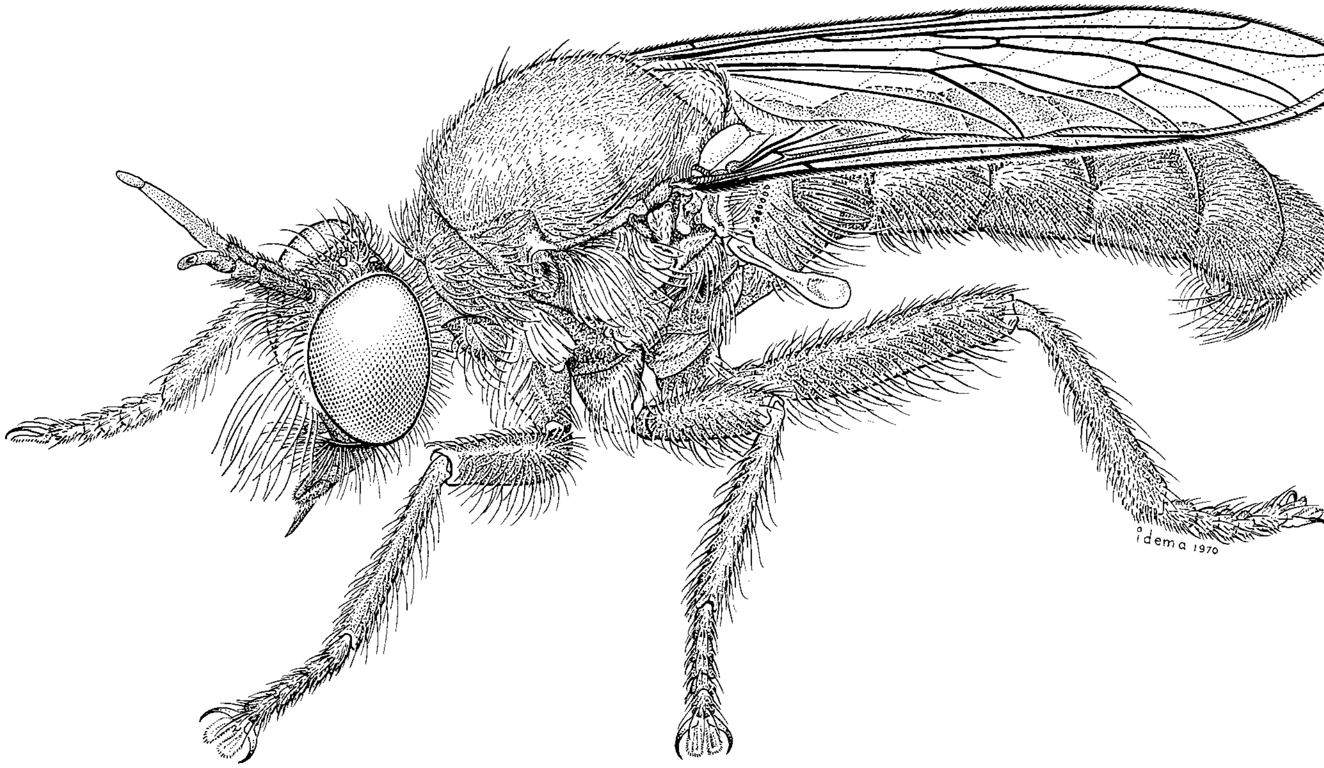


Fig. 42.1. Male of *Dicolonus sparsipilosum* Back.

Small (3 mm) to very large (over 50 mm) flies, averaging 9–15 mm in length (Fig. 1), long and slender to short, robust, and bee-like.

Adult. Head: compound eyes large, usually widely separated, equally so in both sexes; eye facets enlarged medially; eye extending dorsally above level of vertex, causing vertex to appear excavated when viewed anteriorly (Figs. 24–35); ocellar tubercle prominent; median ocellus enlarged; vestiture of ocellar tubercle of fine pile, often mixed with bristles. Frons short in Laphystiini, Laphriini, and Atomosiini, but higher in Stichopogonini, varying from a narrow transverse band to half height of head. Face more extensively developed than in other Asilomorpha, exceptionally high in most species, often convexly protuberant (gibbous); facial protuberance, or gibbosity, with a characteristic group of stout anteroventrally directed hairs or bristles, the mystax, arranged as a cluster on lower part of face; mystax in some genera extending over entire face to antennal bases, in others reduced to a transverse row along lower margin of face. Clypeus reduced, concave or flat, folded posteroventrally below lower facial margin.

Antenna held erect (Figs. 36–44); scape and pedicel each usually with long or short pile (Figs. 45–59), often with stout bristles; first flagellomere elongate or oval, clavate in a few genera, pubescent or tomentose but without pile or bristles, usually longer than either scape or pedicel especially in Dasypogoninae. A bent apical or subapical stylus usually present on first flagellomere, typically two-segmented (the very small second and more elongate third flagellomeres), occasionally one-segmented, apparently absent in Laphriinae; shape varying widely throughout the family, elongate and thickened in most Dasypogoninae, forming a long bristle-like structure in Asilinae, elongate and as thick as first flagellomere in *Myelaphus* Bigot and *Ceraturgus* Wiedemann, and plumose in the asiline tribe Ommatiini. A minute spine, often in a pit, present at apex of antenna on either the first or succeeding flagellomeres.

Mouthparts (Figs. 2.53–54) similar in both sexes, unlike those of the biting (bloodsucking) Nematocera and Tabanomorpha, uniquely adapted for stabbing and sucking prey. Mandible absent; stabbing function performed by needle-like hypopharynx that injects a paralyzing saliva. Proboscis elongate, heavily sclerotized, formed from ventromedial fusion of prementum and labella as a continuous tube open at apex and dorsomedially, and enclosing maxillae and hypopharynx; tip of labella pointed or rounded, usually surrounded with sensory hairs; ventral surface of labella and most of prementum pilose. Palpus usually slender or clavate, setose, two-segmented in all Dasypogoninae with a small basal segment hidden among dense vestiture of the subcranium and with an elongate clavate or lamellate apical segment, or one-segmented in all Asilinae and Leptogastrinae with the basal segment missing or fused to the apical segment.

Thorax: sclerites varying somewhat in shape, fusion, vestiture, and chaetotaxy. Antepronotum often with a transverse furrow separating an anterior ridge on which bristles or pile are located; postpronotum bare in some genera, with pile or long bristles in others; prosternum fused with proepisternum either forming a precoxal bridge in Laphystiini, Laphriini, Atomosiini, and some genera of other groups (Fig. 61), or separated by membrane (Fig. 62) in the remaining genera. Notopleural, supra-alar, and postalar bristles almost always present; dorsocentral bristles usually present. Scutellum usually pruinose but sometimes shiny, almost always with hairs or bristles along its margin especially at apex; katatergite almost always with a row or group of bristles (absent in subgenus *Stenopogon* Loew); anatergite (lateral slope of metanotum of Hull 1962) bare in most Dasypogoninae and in one group of Asilinae (Fig. 64) (*Promachus* Loew, *Efferia* Coquillett and allied genera), or with hairs or bristles in most other Asilinae (Fig. 63). Metepimeron usually with pile on its posterodorsal corner, occasionally bare (Stichopogonini and a few other genera); posterior edges of metepimera sometimes extended posteromedially to meet and fuse in midline forming a postmetacoxal bridge (Fig. 60) in Atomosiini, Ommatiini, and isolated genera in Dasypogoninae; postmetacoxal region membranous in other genera.

Legs, as befits a predatory insect, raptorial, stout, frequently with numerous stout bristles (Figs. 66–69); all tibiae with several stout bristles at apices; a modified apical bristle, usually termed fore tibial spine, present on fore tibia of some members of Dasypogoninae (Dasypogonini *sensu* Hull 1962), either stout, thickened, and arising from a spine-like process on the apex as in *Saropogon* Loew (Fig. 20), or thin and twisted as in *Cophura* Osten Sacken (Fig. 22). First tarsomere of hindleg enlarged in a few genera, much longer and wider that succeeding segments (e.g. *Holopogon* Loew); claws strong and sharp in most groups (Fig. 71), but blunt in the asiline genus *Mallophora* Macquart and allied genera (Fig. 72); pulvilli usually present, although absent in Leptogastrinae and in a few genera of Dasypogoninae (e.g. *Ablautus* Loew); empodia bristle-like, lost in the leptogastrine genus *Psilonyx* Aldrich and in some *Leptogaster* Meigen.

Wing venation (Figs. 2–19) much as in Tabanidae, Rhagionidae, and Therevidae, not highly modified; R always four-branched, with R_{2+3} unbranched; recurrent spur or stump vein occasionally extending proximally toward base of wing from R_4 near base, incomplete in some genera (e.g. *Efferia,* Fig. 17) but extending proximally to meet R_{2+3} in *Promachus* (Fig. 18) and a few related genera; all veins proceeding to wing margin independently in many Dasypogoninae and most Leptogastrinae; cell r_1 closed, i.e. R_{2+3} joining R_1 before reaching C in Asilinae and Laphriinae (Figs. 3, 14–19); in the latter three groups M_3 meeting CuA_1, and CuA_2 meeting A_1, before the wing margin, thereby closing cells m_3 and cu*p*; in Dasypogoninae and Leptogastrinae, some genera with either cell cu*p* or cell m_3 closed (Figs. 7–13) [e.g. *Holcocephala* Jaennicke (Damalini), some *Prolepsis* Walker], occasionally with both closed [e.g. *Microstylum* Macquart (Fig. 10)]; sometimes, in various genera throughout family except Leptogastrinae, M_1 joining R_5 before reaching wing margin [e.g. *Perasis* Hermann (Fig. 9), *Cerotainiops* Curran (Fig. 15), and some *Mallophorina* Curran]; rarely, M_2 or M_3 not reaching wing margin, reducing number of cells as in *Itolia* Wilcox (Fig. 12) and *Townsendia* Williston (Fig. 7) (Dasypogoninae). Strongly thickened costa-like hind margin absent in a few genera (e.g. *Itolia*). Alula well-developed except in Leptogastrinae and a few genera of Dasypogoninae (e.g. absent in *Dioctria* Meigen). Wing most often hyaline, but partly infuscated in many genera (e.g. *Asilus* Linnaeus), or completely darkened in a few genera, or patterned with spots on crossveins and bifurcations as in *Nicocles* Jaennicke and *Eucyrtopogon* Curran.

Abdomen: hemicylindrical, often tapering, sometimes clavate, often slightly narrower at junction with thorax and widest at segments 2–4, gradually narrowing distally to apex, in some groups (e.g. *Mallophora* and related genera) stout, widened, and shortened mimicking various bees or wasps, and in Leptogastrinae usually slender, very elongate, and clavate. Pile on abdominal tergites somewhat sparse except in groups mimicking bees, longer on posterolateral corners, most abundant on tergite 1 which usually has differentiated external bristles, and often reduced or absent on second and succeeding tergites. Eight segments usually present in both male and female, with the remaining two segments incorporated into terminalia. In male, tergite 8 often shortened and somewhat telescoped inside tergite 7; sternite 8 modified in shape also; segment 8 vestigial in a few groups (Laphriini and Atomosiini) in which segment 7 is also reduced, partly or totally concealed behind segment 6; only six segments visible in male of Laphystiini. In female of Asilinae and Laphriinae segment 8 incorporated into terminalia; sometimes segments 7 and 6 incorporated as well, as in *Neoitamus* Osten Sacken; in Laphriinae segment 7 shortened and narrowed; in most Dasypogoninae, sternite 8 modified in shape, with tergite 8 sometimes included in terminalia; in Leptogastrinae segment 8 not included, sometimes shortened but not otherwise much modified.

Male terminalia (Figs. 74, 75) unrotated at emergence, except in Laphriini and Atomosiini in which they are rotated 180° permanently; rotation variable, up to 90° occurring during copulation in most Dasypogoninae or occurring before copulation in remaining Dasypogoninae, never rotated in Leptogastrinae and Asilinae. Epandrium entire, lobed or divided medially as epandrial lobes (superior forceps of Hull 1962). Hypandrium well-developed, secondarily reduced or absent; gonostylus arising from gonocoxite apically in Laphriini, basally in Asilinae, reduced or absent in Atomosiini; parameres fused to form an aedeagal sheath; aedeagus bulb- or funnel-shaped at base, narrowed to apex, single-tubed in most Dasypogoninae, trifid in Atomosiini, Laphriini, and most Asilinae, bifid in a few asiline genera, or with lateral tubes reduced or nonfunctional as in *Polacantha* Martin (Martin 1975). Surstyli (paralobus of Hull 1962) present or absent, separate or fused medially; cerci (lamellae or proctiger of Hull 1962) partly to completely fused.

Female terminalia with tergite 8, or epigynium, reduced in size but unmodified in shape in most Dasypogoninae, incorporated into terminalia in Asilinae. Sternite 8, or hypogynium, bearing a pair of lobes, the hypogynial valves (interpreted by some authors, e.g. Cole and Wilcox 1938, as sternite 9). A pair of sclerites (interpreted as remnants of sternite 9 by Adisoemarto and Wood 1975) lying on either side of vagina, in some genera joined to each other by their anterior ends; tergite 9 obsolete medially, reduced to a pair of small sclerites (Adisoemarto and Wood 1975). Tergite 10 in most Dasypogoninae divided midlongitudinally into two plates called acanthophorites bearing five or more pairs of stout spines probably used for digging; in a few genera of Asilinae cerci with stout spines for depositing eggs in soil.

Egg. Shape subspherical (*Leptogaster* spp., *Dioctria* spp.) to long oval, more than three times as long as wide (*Efferia* spp.); but shape in most species semioval, two to two and one-half times as long as wide. Length 0.29–2.2 mm; width 0.25–0.72 mm. Chorion smooth, without ornamentations in most genera (six genera viewed with scanning electron microscope, 2000×, Dennis and Lavigne 1975), or with characteristic elevated ridges (*Cerotainia*, Scarbrough 1978) (some European species of *Dioctria* and *Laphria* Meigen, Melin 1923). Color usually creamy white, varying to orange, amber, or brownish. Description based on eggs of 22 species in 12 genera from North America and three species of *Dioctria* from Europe (Melin 1923, Knutson 1972, Dennis and Lavigne 1975, Scarbrough 1978).

Larva. Elongate, subcylindrical to somewhat dorsoventrally flattened, often tapering at each end (Figs. 76, 77). Color white to yellowish, sometimes with a few fine longitudinal streaks. Four instars in the few forms studied. Head capsule much narrower than prothorax, usually exerted, directed ventrally. Nine abdominal segments apparently present, with eighth and ninth partly fused; length of segments increasing toward seventh. Respiratory system functionally amphipneustic, although vestigial spiracles are present on first seven abdominal segments.

Head capsule (Figs. 78, 79) with light to dark brown sclerotized cranium bearing one to three pairs of bristles laterally and medially. Antenna small to minute, arising from anterolateral corner of head capsule. Metacephalic rod sclerotized, sometimes deeply forked posteriorly, attached to posterior edge of cranium and extending posteriorly through prothorax. A small sclerotized oblong plate usually present ventrally. Maxilla broad, triangular, flattened dorsoventrally, apparently two-segmented; cardo with two or three bristles; endite long, flattened dorsoventrally, scoop-shaped, somewhat toothed above palpus in Laphriinae, laterally incised below palpus in Leptogastrinae, Dasypogoninae, and Laphriinae; palpus attached about midway on endite. Mandible narrow, heavily sclerotized, lying in concavity in median face of maxilla, not extending to apex of maxilla, strongly reduced or lacking in Leptogastrinae. Labrum slender, wedge-like.

Thorax sometimes broader than abdomen, but not usually strongly differentiated. Each segment with one pair of bristles ventrolaterally; smallest bristles on first segment. Prothorax sometimes encircled apically by a narrow roughened ring-like welt; remaining two thoracic segments also sometimes with a similar though narrower ring. Anterior spiracle oriented dorsolaterally in distal quarter of prothorax.

Abdominal segments 1–7 each with a small nonfunctional spiracle laterally, and with one pair of contractile warts anteroventrally (except in *Laphria* and *Andrenosoma* Rondani in which segments 1–6 each have four pairs of contractile warts) (Fig. 77); other callosities also often present anterodorsolaterally and laterally on first seven segments. Segment 8 short (except in Leptogastrinae), often depressed slightly, bearing posterior spiracles dorsolaterally near distal edge. Segment 9 tapering, with two pairs of long bristles laterally at midsection, and with two pairs of terminal bristles; one pair of these terminal bristles arising dorsal to anus and one pair ventral to anus sometimes surrounding a small terminal spine. Up to 10 additional sclerotized processes in *Dioctria*; one to three conical or spine-like processes arranged on a terminal plate (*Laphria*), or with a lateral sclerotized keel (*Andrenosoma*, Asilinae). Anus in form of a small longitudinal ventral slit.

Pupa. Mobile, not enclosed in skin of last larval instar. General color white at formation, darkening to yellow, brown, or dark brown; processes darker, brownish or reddish brown. Antennal sheath with several stout pointed spines called antennal processes; one pair of large sharply pointed anterior antennal processes arising on vertex, directed anteriorly and somewhat curved ventrally (blunt or truncate and ridged in Leptogastrinae); one group of three to five posterior antennal processes also present, acuminate or subacuminate apically, with confluent bases (absent or reduced to a crenulate ridge in Leptogastrinae). One pair of truncate dorsal cephalic processes present in Megapodini. Lower facial area with one or two pairs of short spine-like processes in Megapodini and Laphriinae, absent in other subfamilies; two or three suborbital spines above base of anterior coxal sheath in Megapodini. Mouthpart sheaths well-developed; labral, maxillary, and hypopharyngeal sheaths smooth or with rugose areas, often with small tubercles distally.

Anterior margin of thorax midlaterally with oval anterior spiracle, basally surrounded with thickened cuticle, occasionally hidden under fold. Leg sheaths visible, including anterior coxal sheath, posterolateral to hypopharyngeal sheath; hindleg sheath extending to middle of abdominal segment 3. A pair of anterior mesothoracic spines present laterally above base of midleg sheath, absent in *Doryclus* Jaennicke (Megapodini), in Leptogastrinae evident as a bristle only; posterior mesothoracic spine usually present on callosity at base of wing sheath; this spine absent in *Doryclus* and *Stenopogon*, evident only as one or two bristles in *Leptogaster*, *Dioctria*, and *Heteropogon* Loew; one or two pairs of small bristles occasionally present on dorsum of thorax.

Abdomen usually flexed ventrally, with nine segments, but with eighth and ninth partly fused; each segment except the ninth with a lateral spiracle. Anterior margin of abdominal tergite 1 with transverse row of 6–16 long spines; these spines usually apically recurved, but shorter, weaker, and more numerous in *Doryclus* and *Laphria*. Tergites 2–7 with median transverse row of spines; these spines usually alternating long and short, but in *Leptogaster* spines exceptionally long and hair-like alternating with short stout spines. Sternites 2–7 usually with posterior transverse row of bristles; sometimes this row incomplete or absent. Pleurites 2–7 each with transverse row of elongate spines or bristles arising dorsolaterally; number varying from 1 to 14, absent in *Heteropogon* and *Stenopogon*, usually fewer than five in Dasypogoninae, usually five or more in other subfamilies. Abdominal segment 8 with encircling ring of long spines, often with fewer spines than in previous segments. Abdominal segment 9 with one to four pairs of strongly sclerotized terminal caudal hooks; the dorsolateral pair of hooks always present, occasionally toothed or branched (*Lasiopogon* Loew, *Leptogaster*); the ventrolateral pair present in all subfamilies except Leptogastrinae; smaller ventromedial processes present in Laphriinae, Asilinae, and a few Dasypogoninae, but absent in most Dasypogoninae, Megapodini, and Leptogastrinae; one or two pairs of tubercles also sometimes present, spine-like or rounded, size varying with sex.

Biology and behavior. Adult asilids, both male and female, are noted for their rapacious attacks on other insects, including stinging insects such as bees and wasps. This behavior has earned them the name 'bee catchers' (Bromley 1934). They are usually found in open and sunny habitats ranging from grassland and brush, valleys and draws, to open glades in woodland. They are seldom found in deep woods where it is dark. Their flight activity occurs mainly during the hottest part of the day. The activity-threshold temperature, though undoubtedly different for each species, is relatively high; Dennis and Lavigne (1975) set it at above 20°C for most species. Their activity is greatly reduced or absent in overcast weather, as is the activity of the other insects upon which they prey. Their general habit is to perch in open sunlit areas where they presumably command a good view of passing insects, then to fly out to catch a suitable prey. Some asilids take up stations on exposed branches, others on logs or stones, still other species on the ground itself, each species showing a preference for type of perch and height from the ground. Most species capture prey as it flies by, but members of the Leptogastrinae capture stationary prey while themselves in flight, as do damselflies (Scarbrough and Sipes 1973). A few dasypogonine species capture prey that is crawling on the ground (Lavigne 1963). Immediately upon making a capture, the asilid stabs its prey with its hypopharynx in the neck between the head and thorax, at the junction of thorax and abdomen, through the eyes, or between the sclerites at the end of the abdomen (Dennis and Lavigne 1975, Scarbrough 1978). The prey is then injected with saliva containing neurotoxic and proteolytic enzymes, which rapidly immobilize the prey and liquify its tissues; in a relatively short time the asilid is able to suck out the contents.

A wide variety of insects of most orders are taken as prey. Occasionally other invertebrates, especially spiders, are captured. Species of some genera show a preference for one type of prey; for example species of *Mallophorina* attack Hymenoptera almost exclusively (Linsley 1960). Others, however, are more opportunistic, capturing whatever insects are available. In an extensive study of the ethology of 10 species of asilids, Dennis and Lavigne (1975) found that five were stenophagic, exhibiting a strong preference for prey of one or two orders, and five were euryphagic, taking prey from a broader range of orders. However, even some stenophagic species were observed to be opportunistic, switching their prey to another order when some particular insect was especially abundant. Scarbrough (1978) found that although 67% of all prey of the stenophagic *Cerotainia albipilosa* Curran belonged to Diptera and Hemiptera–Homoptera, these orders were also the most abundant at the study site.

The size of prey taken varies widely with each species of predator. Dennis and Lavigne (1975) found that the mean size ratio of predator to prey was 2.6:1, varying between 1.8:1 for larger predators and 3.7:1 for smaller predators. The smaller asilid species had larger predator to prey ratios, presumably because they were weaker and would not be able to subdue larger prey. An asilid may fly out after a prey that is much too large but he avoids it just before capture, or grasps it for a few seconds then releases it again (Scarbrough 1978). Females of some species take larger prey than do males of the same species, but no sex differences have been noted for other species. Females also spend more time seeking prey than do males, possibly because of their reproductive requirements.

Courtship behavior varies in the Asilidae. The male may perform a simple chase, capturing the female in the air, or he may undertake short searching flights before catching the female. In some species a more elaborate courtship has also been observed, in which the male searches for the female then hovers in front of her, with legs extended displaying ornamented tarsi, waving the abdomen before mounting and mating. Mating position may be tail to tail (most Dasypogoninae studied) or male over female, both facing the same way or with bodies at an angle (Dennis and Lavigne 1975).

The method of egg laying has been correlated with the structure of the ovipositor (Melin 1923). In most species of Dasypogoninae the tip of the ovipositor is buried in soil, probably with the help of the row of spines on each half of tergite 10 (acanthophorites). The female of *Dioctria,* however, releases the eggs one at a time while in flight. The female of *Leptogaster* deposits them individually as it crawls along a twig or other perch. The female of *Laphria*, which has a short conical ovipositor with no digging spines, oviposits in easily accessible crevices in rotten wood or among pine needles on the ground. The ovipositors of many Asilinae also lack spines and are more or less pointed for probing into dry crevices such as flower heads or leaf sheaths. However, some genera, for example, *Philonicus* Loew and *Proctacanthus* Macquart, have reacquired spines on the cerci rather than on tergite 10, and they oviposit in sandy soil. Melin (1923) also pointed out that the color of the eggs is orange, amber, or brown in genera that lay eggs in exposed places (e.g. *Leptogaster*, *Dioctria*, and *Laphria*), whereas egg color is white or creamy white in genera with buried or hidden eggs.

Because the immature stages of Asilidae are cryptic, living in soil or in rotting wood, very few immature specimens of the 5000 or so species have been found and studied. Melin (1923) summarized what was known of the biology of immature stages and added his own observations to these. Lucas (1848) first suggested that asilid larvae are predacious on other larval insects. However, because no species had been reared through its complete development, some controversy arose on this point. Melin (1923) presented evidence, partly circumstantial and partly based on the structure of larval mouthparts, that the larvae are primarily phytophagous, with secondary sporadic predation possible. Recent studies by several workers, however, have shown conclusively that the larvae are predators of the eggs, larvae, and pupae of other insects. Knutson (1972) has provided an excellent review of these studies. Of the three species that have been reared completely from egg to pupa, *Promachus yesonicus* Bigot was found to be a free-living predator of larval scarabaeids whereas the young larvae of *Mallophora media* Clements & Bennett and *M. ruficauda* (Wiedemann) are ectoparasites of larval Scarabaeidae. As the larva of *M. media* grows, it either becomes a free-living predator in the soil or continues to feed as an ectoparasite; *M. ruficauda* remains ectoparasitic on the host throughout development. Other workers have also observed ectoparasitism, at least by young larvae. Most host records have been larvae of Scarabaeidae, but larvae of other Coleoptera, Hymenoptera, Diptera (including a record of cannibalism), and Orthoptera [eggs of *Schistocerca gregaria* (Forskål)] have also been recorded as prey.

Classification and distribution. The present key includes 87 genera and subgenera, representing 983 species. Genera and species not known to occur north of the border of the United States and Mexico are excluded. Coverage is therefore equivalent to that given by Martin and Wilcox (1965).

The Asilidae as here recognized are based on several synapomorphies. By far the most distinctive of these is the feeding mechanism and predatory behavior of the adult. The labella and prementum are fused to form a heavily sclerotized, tube-like proboscis enclosing the needle-like hypopharynx that is used to stab the prey and inject it with saliva. The sexes are not dimorphic in this respect, unlike the Tabanomorpha and Nematocera. The mystax, a row or group of stout bristles along the lower edge of the face, is also peculiar to the Asilidae. The Mydidae, which are probably the sister group of the Asilidae, have a fleshy, pad-like labella, the primitive situation in the Diptera. Both families share a well-developed face and a sunken vertex, but the Mydidae lack a mystax. The Asilidae have retained the primitive number of three ocelli, whereas the mydids have only one. The larvae of both asilids and mydids are rather similar, especially in having a broadened paddle-like or scoop-like maxilla. However, in the Asilidae, the palpus arises in a notch situated laterally on the maxilla, not at the apex as in the Mydidae; also, the mandible does not extend as far forward as the apex of the maxilla but is hidden in a concavity along the median edge of the maxilla.

The Leptogastrinae, in spite of their many distinctive features (autapomorphies), share with the rest of the Asilidae the synapomorphies mentioned in the previous paragraph, namely the modified proboscis and predatory behavior of the adult and the modifications of the larval maxilla and mandible. Although Martin (1968*a*) proposed that the group be accorded full family rank, Oldroyd (1969) argued that there were insufficient grounds for separating them from the Asilidae. Further to Oldroyd's arguments, some of the autapomorphic characters of the Leptogastrinae, such as absence of the alula and the pulvilli, absence of acanthophorites of the tenth abdominal segment of the female, and absence of larval mandibles, must be considered, in the context of other Asilomorpha and Tabanomorpha, to be derived characters. Most other features of the Leptogastrinae such as their slender shape, their inclination to capture resting prey, their peculiar egg-laying habits, their helicopter-like flight, and their propensity to inhabit grassy habitats are autapomorphic; these features indicate only the distinctness of the Leptogastrinae as a group, not their phylogenetic position relative to other Asilidae or to the asilomorph families.

The Asilidae have been classified into a varying number of subfamilies and tribes (reviewed by Papavero 1973). Hull (1962) recognized five subfamilies, Dasypogoninae, Leptogastrinae, Laphriinae, Megapodinae, and Asilinae. With the exception of the Megapodinae, which are not found north of Mexico, Martin and Wilcox (1965) adopted the same arrangement as did Hull (1962). More recently, Papavero (1973*a*, 1973*b*) recognized eight subfamilies of Asilidae, not including *Leptogaster* and its allies which he considered as a separate family, following Martin (1968*a*). Papavero split the Asilinae into three subfamilies, Apocleinae, Asilinae, and Ommatiinae. The basis for separation of the Apocleinae seems to be the absence of hairs or bristles on the anatergite. Most species of *Asilus* have these hairs, but a few species, e.g. *auriannulatus* Hine and *blantoni* Bromley, lack them and would therefore have to be placed in the Apocleinae. Although there may be some phylogenetic basis for the inclusion of most of these genera into a single taxon, it would probably be more convenient to group them at the tribal level. The Asilinae in a broad sense (*sensu* Hull 1962) is probably a monophyletic group as well as a useful and readily recognized taxon; this interpretation is therefore used here, including the tribes Apocleini and Ommatiini.

The Laphriinae also seem to form a monophyletic group, reasonably distinct from the Dasypogoninae in the immature stages as well as in the adult, but they may be an offshoot of some branch of the Dasypogoninae, such as the Laphystiini (no Laphystiini are known from the immature stages). The Dasypogoninae (*sensu* Hull 1962) are a diverse group and are probably paraphyletic. Papavero restricted the Dasypogoninae to those forms with a stout sigmoid spine on the fore tibia. However, *Ablautus* and *Omniablautus* Pritchard, which are otherwise quite similar, differ in the presence or absence of this spine; likewise some specimens of a species that lack the spine and thus ought to belong to *Wilcoxia* James appear otherwise conspecific with specimens of *Cophura* which possess the spine; therefore the spine may be present or absent in the same or closely related species. Hull (1962) has also remarked on the close similarity of some species that have the spine and those which lack it that would therefore be placed by Papavero in his Stenopogoninae.

The European species of *Asilus* were divided by Loew (1849) into several subgenera that were later raised to genera by subsequent authors. These taxa are similar to each other and are not readily separated. Theodor (1976) found differences in the internal terminalia of both sexes of some of these Palaearctic species that corresponded with the subgeneric arrangements proposed by Loew (1849). However, attempts by North American workers such as Hine (1909) to place the Nearctic species in these European genera have not been entirely successful because many species are intermediate. Martin and Wilcox (1965) also attempted to place the Nearctic species into European genera, but left 38 species in *Asilus* (*sens. lat.*), even though they believed that these species were not congeneric with the type species of *Asilus*. Working with the fauna of Mexico and the southwestern United States, Martin (1975) erected six new genera (including four occurring in the United States) for some of the species unassigned except to *Asilus* (*sens. lat.*) by Martin and Wilcox (1965), and regrouped other species into older genera. Nevertheless, some of these species did not fit readily into any of the categories. Most of the genera proposed by Martin (1975) were separated only by characters of the male terminalia; good characters are not available to separate most of the females. Because of the uncertainty concerning the placement of so many species, and because the characters for separation of the various genera are restricted to the terminalia, usually of the male alone, a conservative approach has been taken here, with most of the species, totaling 74, relegated to *Asilus*.

Asilids of all four subfamilies are found in all continents except Antarctica, and they are particularly abundant in the warm temperate and tropical areas of the world. The Neotropical region and the Australian region both have an especially rich and interesting fauna, whereas New Zealand has very few species. Of the 447 genera and subgenera in Hull's (1962) world list, 93 genera or 20% are recorded from the Nearctic region north of the Mexican border and probably close to 100 genera are present if the area includes that portion of Mexico north of Mexico City. Twelve genera, *Blepharepium* Rondani, *Archilestris* Loew, *Holcocephala*, *Plesiomma* Macquart, *Prolepsis*, *Lampria* Macquart, *Promachina* Bromley, and *Eccritosia* Schiner, and all the Atomosiini except *Atomosiella* Wilcox, are essentially Neotropical but each is represented by one or two species in the Nearctic region. Twelve additional genera, *Diogmites* Loew, *Taracticus* Loew, *Cophura*, *Townsendia*, *Ceraturgus* Wiedemann, *Sintoria* Hull, *Orthogonis* Hermann, *Efferia*, *Mallophora*, *Proctacanthus*, *Orrhodops* Hull, and *Leptopteromyia* Williston, are more evenly represented in both the Neotropical and Nearctic regions, with a few species in the Oriental region. Eleven genera are Holarctic, these being *La-*

siopogon, *Stenopogon*, *Laphystia* Loew, *Dioctria*, *Myelaphus*, *Cyrtopogon* Loew, *Holopogon*, *Heteropogon*, *Andrenosoma* (*Pogonosoma* Rondani), *Philonicus*, and *Rhadiurgus* Loew. Twelve genera, *Leptogaster*, *Saropogon* Loew, *Stichopogon* Loew, *Microstylum*, *Laphria*, *Andrenosoma*, *Ommatius* Wiedemann, *Promachus*, *Neoitamus*, *Asilus*, *Cerdistus* Loew (including *Neomochtherus* Osten Sacken), and *Machimus* Loew (including *Tolmerus* Loew) are world wide in distribution. The remaining 45 genera, 48% of the total, are confined to the Nearctic region.

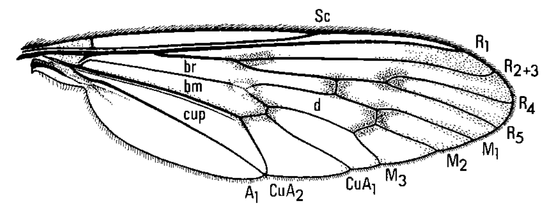
In North America, asilids range from the tree line in northern Canada and Alaska south into Mexico, but only a few species are found as far north as Alaska and the Yukon. However, by far the greatest number of species occur in the southwestern and central United States and adjacent Mexico, as might be expected in view of their preference for dry, sandy areas. Semidesert and savanna areas support the most species. However, some genera, notably *Lasiopogon*, *Cyrtopogon*, and *Laphria*, are predominantly forest species where they are active at sunlit edges or in clearings.

Fossil asilids have been found in formations as early as those of the Eocene. Two of the three found have been assigned to nonextant genera. Both the major subfamilies are represented; one genus, *Stenocinclis* Scudder, is from the Dasypogoninae and two are from the Asilinae. One of the fossil asilines, *Asilopsis* Cockerell, is known only as a fossil, and the other is assigned to the modern genus *Asilus*. From the Oligocene of central and northern European formations, 11 species representing five modern genera have been recovered, namely one species assigned to *Holopogon* of the Dasypogoninae, one to *Proctacanthus*, one to *Machimus*, seven to *Asilus*, and the first fossil representative of *Leptogaster*. The number of asilid species found increases greatly in the Miocene, mostly from the Colorado Florissant shales, with three species of *Asilus* and one of *Leptogaster* from European formations. All except one dasypogonine genus, *Paleomolobra* Hull, belong to modern genera. Represented are 10 genera of Dasypogoninae, namely *Holopogon*, *Dioctria*, *Nicocles*, *Taracticus*, *Cophura*, *Saropogon*, *Microstylum*, *Lestomyia* Williston, and *Ceraturgopsis* Johnson; two species representing *Leptogaster*; and 12 species representing three genera of Asilinae, namely *Asilus*, *Philonicus*, and *Senoprosopis* Macquart. No Damalini, Laphistiini, or Laphriinae have yet been found as fossils.

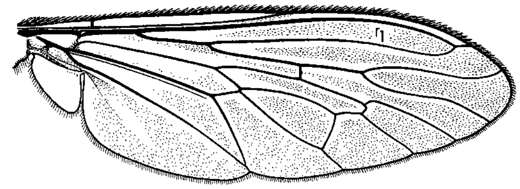
Key to genera

1. R_{2+3} ending in C (Fig. 2) 2
   R_{2+3} joining R_1 proximal to end of R_1, with cell r_1 thus separated from wing margin (Fig. 3) 63
2. Abdominal segment 2 five or more times as long as wide. Alula and pulvilli lacking. Abdominal sternite 1 either absent or extending about halfway back under tergite 2 .... LEPTOGASTRINAE 3
   Abdominal segment 2 no more than four times as long as wide. Usually both alula and pulvilli present, but occasionally one or other absent. Abdominal sternite 1 confined beneath tergite 1 8
3. Anal angle of wing absent; CuA unbranched; A_1 absent (Fig. 4). First flagellomere spherical, with a long slender arista arising apicodorsally. Halter as long as mesonotum .... ***Leptopteromyia*** Williston
   1 sp., *americana* Hardy; Texas
   Anal angle of wing reduced but not absent; CuA branched to form CuA_1 and CuA_2; A_1 present (Figs. 5, 6). First flagellomere elongate, with arista arising apically. Halter much shorter than mesonotum .... ***Leptogaster*** Meigen[1] 4
4. Middle of abdominal tergite 2 with transverse band of long hairs. Base of M_2 closing cell d short, not more than 1.5 times length of crossvein m-m; crossvein m-cu present but short, or M_3 and CuA_1 narrowly united with each other, the union shorter than length of crossvein r-m (Fig. 6) 5
   Abdominal tergite 2 without transverse band of hairs. Base of M_2 long, twice or more length of crossvein m-m; crossvein m-cu absent; M_3 and CuA_1 broadly united, the union longer than length of crossvein r-m (Fig. 5) 6

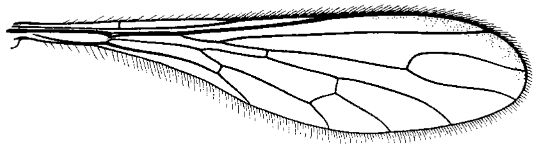
[1] The genera recognized by Martin (1957) are treated here in a subgeneric sense; good characters for separating all specimens have not been found.



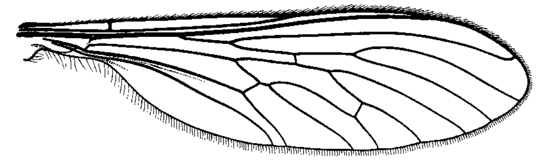
2 Eucyrtopogon sp. ♀



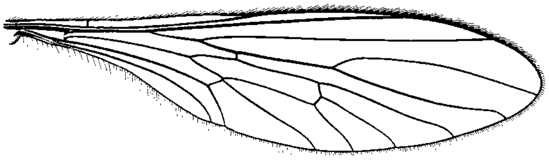
3 Machimus sp. ♀



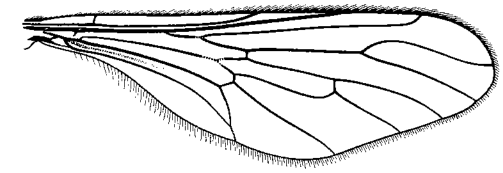
4 Leptopteromyia americana ♂



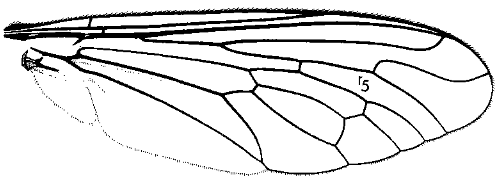
5 Leptogaster cylindrica ♂



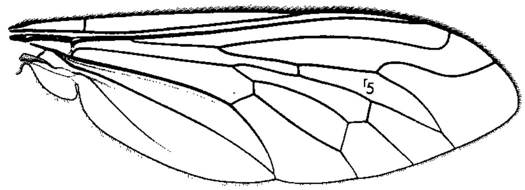
6 Psilonyx annulatus ♂



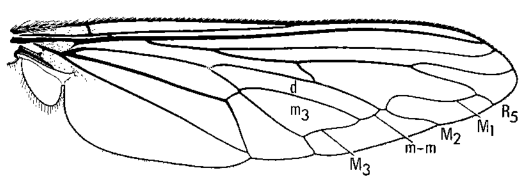
7 Townsendia sp. ♂



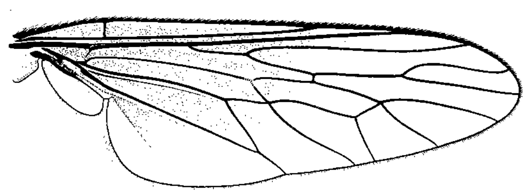
8 Laphystia sexfasciata ♀



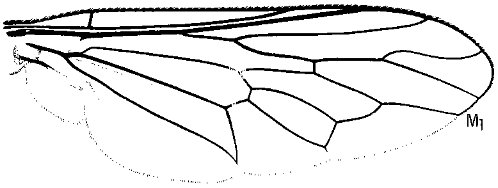
9 Perasis argentifacies ♀



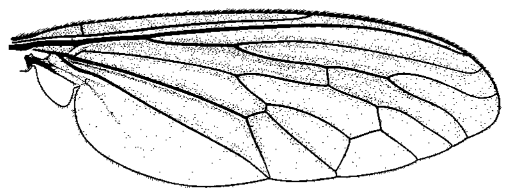
10 Microstylum galactodes ♀



11 Orrhodops americanus ♂



12 Itolia maculata ♂



13 Prolepsis tristis ♂

Figs. 42.2–13. Wings: (2) *Eucyrtopogon* sp.; (3) *Machimus* sp.; (4) *Leptopteromyia americana* Hardy; (5) *Leptogaster cylindrica* (De Geer), not Nearctic; (6) *Psilonyx annulatus* (Say); (7) *Townsendia* sp.; (8) *Laphystia sexfasciata* (Say); (9) *Perasis argentifacies* (Williston); (10) *Microstylum galactodes* Loew; (11) *Orrhodops americanus* (Curran); (12) *Itolia maculata* Wilcox; (13) *Prolepsis tristis* (Walker) (*continued*).

5. Empodia lacking. Epandrial lobe of male deeply divided, almost to base, forming narrow dorsal and wider ventral lobes. Width of face at narrowest point no wider than diameter of an adjacent eye facet .... ***Leptogaster*** **(*Psilonyx*** Aldrich)
   1 sp., *annulatus* (Say); eastern

   Empodia usually present. Epandrial lobe of male at most shallowly notched. Width of face at narrowest point 1.5–3 times as wide as diameter of an adjacent eye facet .... ***Leptogaster*** **(*Beameromyia*** Martin)
   15 spp.; widespread; Martin 1957

6. Hind femur with distal swelling arising gradually, beginning at or before mid length. Scutellar margin with bristles or (*crinita* Martin) with hairs on disc as long as crossvein r-m. Epandrial lobe of male deeply divided almost to base, with ventral branch subequal in length to and narrower than dorsal branch .... ***Leptogaster*** **(*Apachekolos*** Martin)
   5 spp.; mostly western, one eastern; Martin 1957

   Hind femur with distal swelling arising abruptly at about two-thirds or more the distance from the base. Scutellar margin and disc bare or with a few small hairs. Epandrial lobe of male undivided, or if divided, with the ventral branch longer and wider than the dorsal lobe (*Leptogaster*), or with both branches of equal width (*Tipulogaster*) 7

7. Flagellum 2.5 times as long as preceding two segments and one-sixth as wide as long (Fig. 45) .... ***Leptogaster*** **(*Tipulogaster*** Cockerell)
   1 sp., *glabrata* Wiedemann; eastern and central

   Flagellum not more than twice as long as preceding two segments and one-quarter as wide as long (Fig. 46) .... ***Leptogaster*** **(*Leptogaster*** Meigen)
   30 spp.; widespread; Martin 1957

8. One of the apical spines on the ventral side of the fore tibia differentiated, enlarged and stouter than remaining spines, or if not noticeably larger, twisted and sigmoid (Figs. 20–23) 9

   All apical spines on fore tibia straight, or if one is slightly curved, it is not thickened or sigmoid 19

9. Differentiated fore tibial spine stout, hooked, arising from a large basal tubercle, and opposing a group of denticles or a raised denticulate area on first tarsomere of foreleg (Figs. 20, 21) 10

   Fore tibial spine thin, sigmoid, often inconspicuous, not arising from a large basal tubercle, and not meeting a modified area on first tarsomere of foreleg (Figs. 22, 23) 13

10. Lower two-thirds of face with a pronounced haired swelling or gibbosity (as in Fig. 41). Strong presutural dorsocentral bristles present .... ***Lestomyia*** Williston
    6 spp.; western; Curran 1942

    Face flattened, without gibbosity; facial hair confined to lower one-third or less of face. Presutural bristles absent 11

11. M_3 extending to wing margin, i.e. cell m_3 open. Two flagellomeres; the second one small, with an apical pit enclosing spine at apex (Fig. 47) .... ***Saropogon*** Loew
    19 spp.; southwestern; Wilcox 1966*b*

    M_3 joining CuA_1 before terminating in wing margin, i.e. cell m_3 closed. One flagellomere only, with pit and enclosed spine at apex (Fig. 48) 12

12. At least one pair of scutellar bristles .... ***Diogmites*** Loew
    26 spp.; widespread; Bromley 1936, Artigas 1966

    No scutellar bristles .... ***Blepharepium*** Rondani
    1 sp., *secabile* (Walker); Arizona

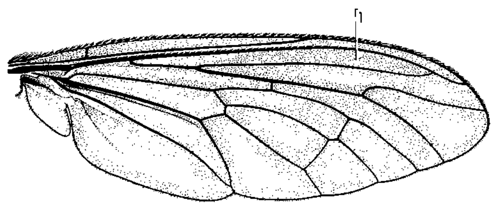
13. Pulvilli present 14

    Pulvilli absent 17

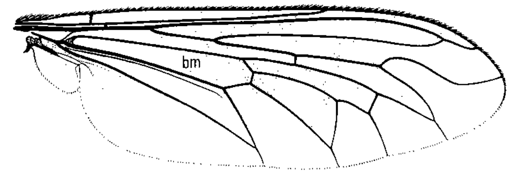
14. Face with pronounced gibbosity on lower two-thirds or more (as in Fig. 41). Scutum with a midlongitudinal 'mane'-like crest of hairs .... ***Comantella*** Curran
    4 spp.; western; James 1937

    Face plane or slightly rounded. Scutum without such crest of hairs 15

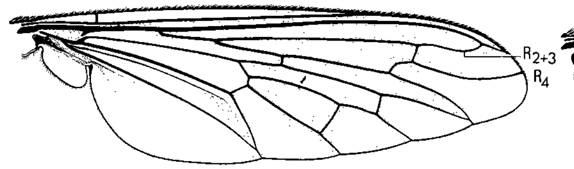
15. First flagellomere more than twice as long as scape and pedicel combined, without apical stylus, but with a small spine arising from a notch near middle of dorsal surface (Fig. 49). Abdomen pitted .... ***Taracticus*** Loew
    3 spp.; widespread; Pritchard 1938*b*



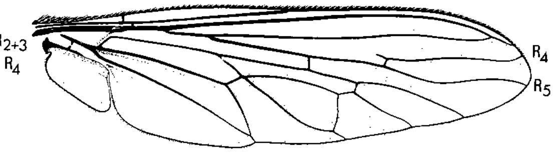
14 Orthogonis stygia ♂



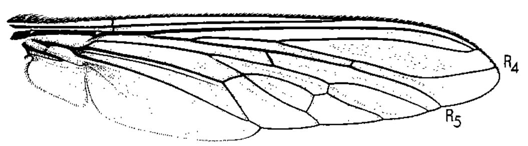
15 Cerotainiops sp. ♀



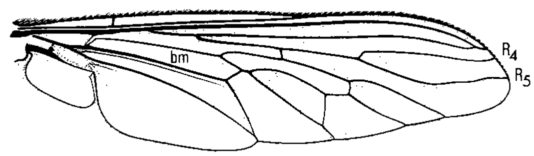
16 Andrenosoma (Pogonosoma) ridingsi ♀



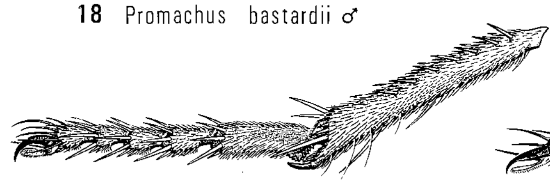
17 Efferia aestuans ♀



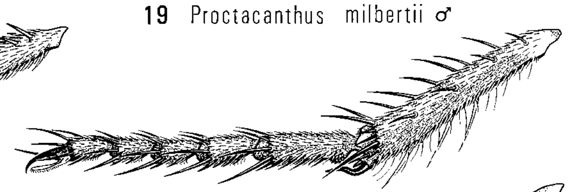
18 Promachus bastardii ♂



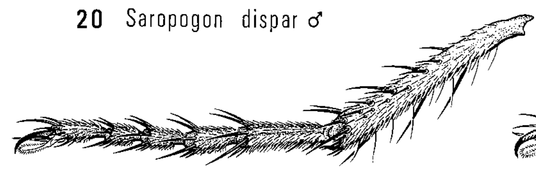
19 Proctacanthus milbertii ♂



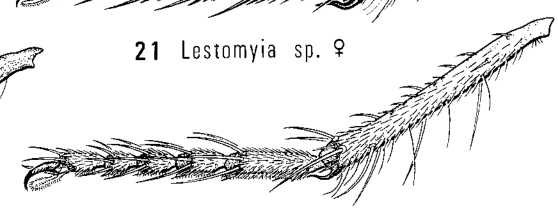
20 Saropogon dispar ♂



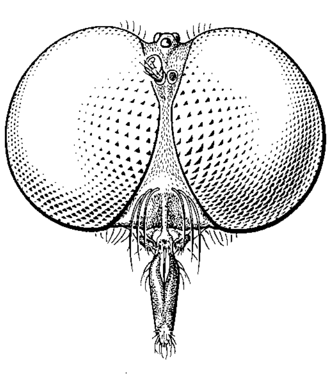
21 Lestomyia sp. ♀



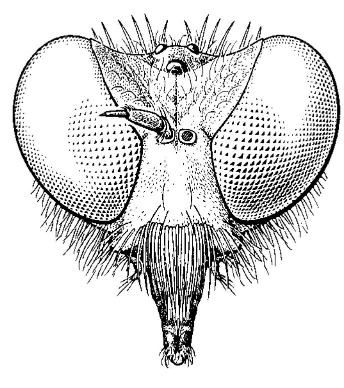
22 Cophura brevicornis ♀



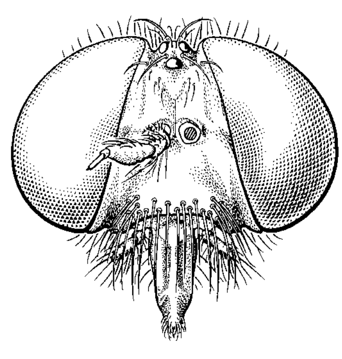
23 Taracticus octopunctatus ♀



24 Psilonyx annulatus ♂



25 Stichopogon trifasciatus ♀



26 Plesiomma unicolor ♂

Figs. 42.14–26. Wings (*concluded*), forelegs, and heads: wing of (14) *Orthogonis stygia* (Bromley), (15) *Cerotainiops* sp., (16) *Andrenosoma* (*Pogonosoma*) *ridingsi* (Cresson), (17) *Efferia aestuans* (Linnaeus), (18) *Promachus bastardii* (Macquart), and (19) *Proctacanthus milbertii* Macquart; anterior view of tibia and tarsus of right foreleg of (20) *Saropogon dispar* Coquillett, (21) *Lestomyia* sp., (22) *Cophura brevicornis* (Williston), and (23) *Taracticus octopunctatus* (Say); anterior view of head of (24) *Psilonyx annulatus* (Say), (25) *Stichopogon trifasciatus* (Say), and (26) *Plesiomma unicolor* Loew (*continued*).

First flagellomere unnotched, approximately twice as long as scape and pedicel combined, and with apical stylus; abdomen normal, not pitted 16

16. Male with only six visible abdominal tergites; last two tergites widened, covered with dense silvery pollen; terminalia usually hidden beneath this segment. Wing spotted, brown at crossveins and bifurcations [pattern pale in male of *pictus* (Loew)] or brown almost to apex, including bifurcation of R_4 and R_5 ....***Nicocles*** Jaennicke
14 spp.; widespread; Wilcox 1946

Male with seven visible abdominal tergites; last tergite not modified as above. Wing hyaline or basal two-thirds brown, not spotted as above ....***Cophura*** Osten Sacken
24 spp.; western; Pritchard 1943, Wilcox 1959

17. Prescutal dorsocentral bristles lacking, although scutum usually with short appressed scale-like white hairs; postpronotum without bristles, at most with fine hairs. Pedicel with a long strong bristle; scape with only weaker hairs ....***Hodophylax*** James
4 spp.; western; Wilcox 1961

Long prescutal dorsocentral bristles present; postpronotum with two to four bristles. Either pedicel without a long ventral bristle or both pedicel and scape with long strong bristles 18

18. Facial hairs dense, strongly appressed, extending almost to bases of antennae. Scape and pedicel each with long ventral bristles. Frons either nearly bare or with some scattered appressed scale-like hairs. Short acrostichal hairs present ....***Omniablautus*** Pritchard
5 spp.; western; Wilcox 1966*a*

Facial hairs sparse, coarse, erect, extending two-thirds to three-fourths distance to bases of antennae. Scape with two long bristles, but pedicel without bristles. Frons with row of three or four coarse bristles near eye margin. Acrostichal hairs absent ....***Parataracticus*** Cole
5 spp.; California, Arizona; Wilcox 1967

19. Frons greatly expanded toward vertex; vertex, measured from above between eyes, at least 1.7 times as wide as face at level of antennae (Fig. 25) 20

Sides of frons usually more or less parallel or converging toward vertex, but if expanded, only slightly so 23

20. Face strongly inflated on lower three-fourths, with hair of mystax on lower half or more ....***Lasiopogon*** Loew
38 spp.; widespread; Cole and Wilcox 1938

Face plane or slightly convex, with mystax confined to its lower margin (Fig. 25) 21

21. M_3 absent beyond cell d (Fig. 7). Postmetacoxal bridge sclerotized (as in Fig. 60). Mystax sparse, consisting of five or six pairs of widely spaced slender bristles in a transverse row........ ....***Townsendia*** Williston
3 spp.; New Jersey to New Mexico

M_3 present from cell d to wing margin. Postmetacoxal area membranous. Mystax dense, consisting of six to twelve pairs of straight moderately stout bristles 22

22. Prosternum fused to proepisternum (Fig. 61). First flagellomere tapering, not wider than pedicel. Postsutural dorsocentral bristles weak or absent; 6–15 long fine hairs on katatergite.. ....***Stichopogon*** Loew
10 spp.; widespread; Wilcox 1936*c*

Prosternum dissociated from proepisternum by membranous area (as in Fig. 62). First flagellomere oval, 1.5–2 times width of pedicel. Two to four strong postsutural dorsocentral bristles; no long hairs on katatergite ....***Willistonina*** Back
1 sp., *bilineata* (Williston); western

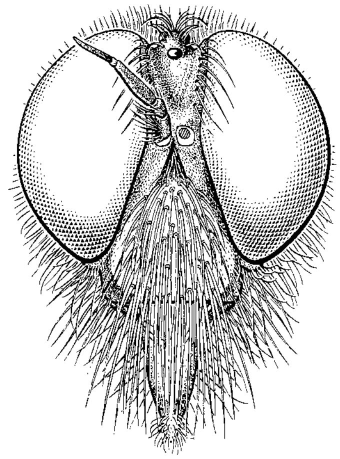
23. Head very narrow, as high as wide, appearing more or less circular in frontal view (Fig. 27) ....***Stenopogon*** Loew....24

Head wider than high (Figs. 28, 29) 26

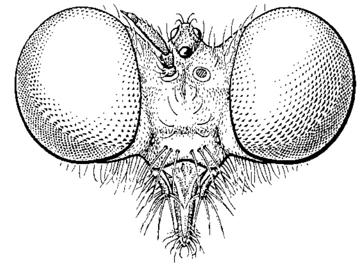
24. Katatergite without hairs or bristles..***Stenopogon*** (***Stenopogon*** Loew)
48 spp.; western; Wilcox 1971

Katatergite with hairs, bristles, or both 25

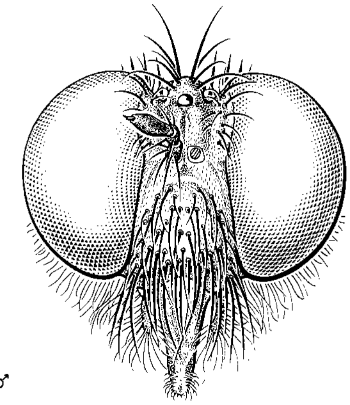
25. First flagellomere less than 1.75 times combined length of scape and pedicel; scape 1–1.5 times length of pedicel; second and third flagellomeres forming an apically pointed stylus, with a short spine at apex. Wing usually hyaline................................***Stenopogon*** (***Scleropogon*** Loew)
15 spp.; western; Martin 1970, Wilcox 1971



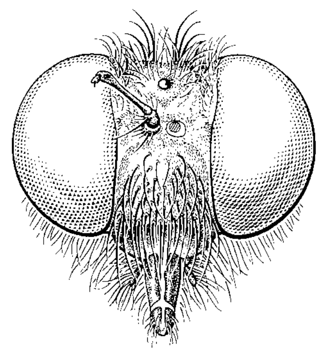
27 Stenopogon inquinatus ♂



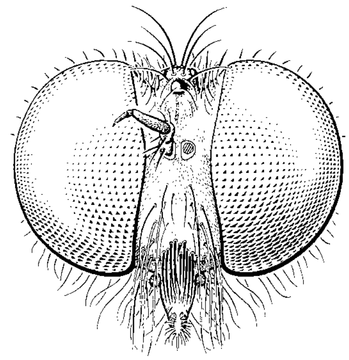
28 Holcocephala abdominalis ♂



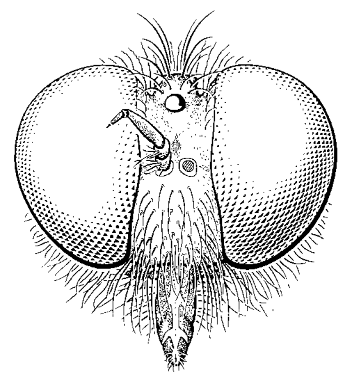
29 Coleomyia setigera ♂



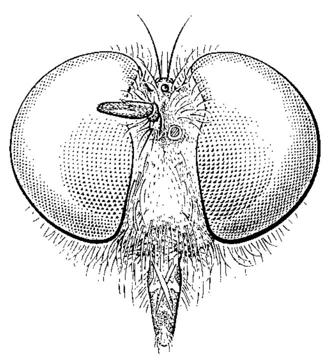
30 Nannocyrtopogon neoculatus ♂



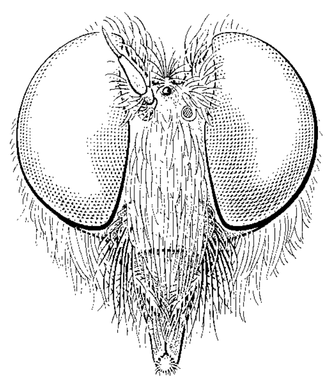
31 Hadrokolos cazieri ♂



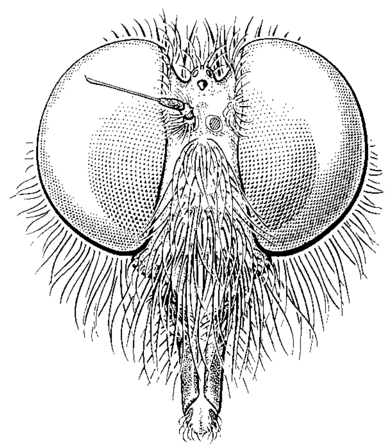
32 Wilcoxia martinorum ♂



33 Atomosia puella ♀



34 Mallophorina frustra ♂



35 Promachina trapezoidalis ♂

Figs. 42.27–35. Anterior views of head (*concluded*): (27) *Stenopogon inquinatus* Loew; (28) *Holcocephala abdominalis* (Say); (29) *Coleomyia setigera* (Cole); (30) *Nannocyrtopogon neoculatus* Wilcox & Martin; (31) *Hadrokolos cazieri* Martin; (32) *Wilcoxia martinorum* Wilcox; (33) *Atomosia puella* (Wiedemann); (34) *Mallophorina frustra* Pritchard; (35) *Promachina trapezoidalis* (Bellardi).

First flagellomere two or more times combined length of scape and pedicel; scape twice or more as long as pedicel; second and third flagellomeres absent, or if present, truncate at apex with spine arising from pit. Wing usually brown............................***Stenopogon*** (***Ospriocerus*** Loew)
22 spp.; western; Martin 1968*b*, 1970

26. Apical portion of M_3 in line or nearly so with crossvein m-m (Fig. 10). Very large flies, 35–50 mm long..........27
Apical portion of M_3 at an angle to crossvein m-m. Smaller flies, less than 28 mm long............28

27. M_{1+2} branching at or beyond apex of cell d; M_1 strongly arched forward after branching from M_{1+2} (Fig. 10). Anatergite with hair (as in Fig. 63)............................***Microstylum*** Macquart
2 spp.; Arizona to Kansas; Martin 1960
M_{1+2} branching before apex of cell d; M_1 normal, slightly curved. Anatergite bare ....***Archilestris*** Loew
1 sp., *magnifica* (Walker); Arizona

28. M_2 absent beyond cell d; C on posterior wing margin, between wing base and M_1, unthickened and membranous; remaining wing veins not reaching wing margin (Fig. 12). Scutum gray, strongly humped, with three broad shiny longitudinal black stripes ....***Itolia*** Wilcox
3 spp.; Arizona, California; Martin 1966
M_2 present; C continuing around posterior wing margin to wing base; all veins or fused veins reaching wing margin (Fig. 8). Scutum not as above 29

29. Apex of R_{2+3} directed sharply forward meeting C at an angle of about 90°, ending either at distal end of R_1 (cell r_1 closed) or a short distance along C (cell r_1 open) (Fig. 8); R_4 strongly sinuate and arched forward after separation from R_5; cell cu*p* and cell m_3 closed before wing margin. Prosternum fused to proepisternum (as in Fig. 61). Male with only six abdominal tergites visible dorsally..........LAPHYSTIINI....30
Apex of R_{2+3} not directed sharply forward before ending in C; R_4 not unusually arched and sinuate (Fig. 11); cell cu*p* and cell m_3 open to wing margin, or one of the two closed (except in some *Myelaphus* and *Prolepsis*). Prosternum separated from proepisternum by membrane (as in Fig. 62), except in Damalini (see couplet 33). Male with seven or eight tergites visible dorsally 33

30. R_5 and M_1 each ending separately in wing margin, thus cell r_5 open (Fig. 8), rarely closed in margin. All abdominal tergites with bristles 31
M_1 ending in R_5, thus cell r_5 closed (Fig. 9). Third and succeeding abdominal tergites without bristles 32

31. Face wide, about width of eye. Antenna with stylus. C extending only to end of cell cu*p*, leaving margin of anal angle membranous (Fig. 8). Scutellum without bristles ....***Laphystia*** Loew
30 spp.; widespread; Wilcox 1960
Face narrower, two-thirds width of eye. Antenna without stylus. C extending around entire wing margin. Scutellum with at least one pair of bristles ....***Psilocurus*** Loew
7 spp.; central; Curran 1931

32. Face convex, with many long bristly hairs overall. Scutellum with many long weak bristles. C extending around entire wing margin ....***Zabrops*** Hull
2 spp.; western
Face flat, sloping outward and downward, with long strong bristles at lower margin and short appressed hair on remainder. Scutellum without bristles. C extending only to end of R_4; remainder of wing margin membranous (Fig. 9)..........***Perasis*** Hermann
1 sp., *argentifacies* (Williston); Arizona

33. Face with pronounced tentorial pits or grooves extending well above lower facial margin; face not produced beyond eye margin when viewed in profile. Eye large, rounded, making head width 1.7–2.0 times head height (Fig. 28). Scutum high, arched, with a height to length ratio of 0.5–0.6. Abdomen very short, usually three-quarters or less length of wing. Prosternum fused to proepisternum (as in Fig. 61). Wing with CuA_2 and A_1 fused before wing margin, but with M_3 and CuA_1 ending separately (Fig. 11)..........DAMALINI....34
Face without pronounced tentorial pits, except in *Myelaphus* and *Plesiomma* which have face produced beyond eye margin in profile. Head narrower, its width less than 1.7 times height. Scutum of normal height, with a height to length ratio of 0.44 or less except in *Metapogon*,

which has a ratio of 0.44–0.5. Abdomen longer than three-quarters length of wing. Prosternum dissociated from proepisternum (as in Fig. 62). Wing with CuA_2 and A_1 ending separately, except in *Myelaphus* and *Holopogon* 37

34. Mystax sparse, covering lower two-thirds or less of face. Crossvein bm-cu as long as crossvein r-m. First flagellomere at least 1.25 times combined length of scape and pedicel; second and third flagellomeres forming a short stylus not longer than first flagellomere (Fig. 57) 35

Mystax covering entire face. Crossvein bm-cu almost lacking, much shorter than crossvein r-m. First flagellomere as short as combined length of scape and pedicel; second and third flagellomeres forming a long thin bristle-like stylus 1.3 times length of first flagellomere (Fig. 58) 36

35. Face with pronounced transverse groove about one-fourth distance between lower facial margin and antennae (Fig. 28); face with four to six bristles along lower margin and a few fine reclinate hairs in middle .... ***Holcocephala*** Jaennicke
3 spp.; eastern; Pritchard 1938*a*

Face without transverse groove; face with pale proclinate bristles or hairs on lower two-thirds .... ***Haplopogon*** Engel
7 spp.; southwestern; Wilcox 1966*d*

36. Small species, about 8 mm in length. Basal part of M_2, closing cell d, very short or lacking (Fig. 11). Tentorial groove extending not more than one-third distance from lower margin of face to base of antenna .... ***Orrhodops*** Hull
1 sp., *americanus* (Curran); Arizona

Larger bee-like species, about 18 mm long. Basal part of M_2 closing cell d two-thirds or more length of crossvein m-m. Tentorial groove extending almost to antenna .... ***Bromleyus*** Hardy
1 sp., *flavidorsus* Hardy; Arizona

37. Lower margin of face wider than eye. Face and frons converging strongly to vertex (Fig. 26) .... ***Plesiomma*** Macquart
1 sp., *unicolor* Loew; New Mexico, Texas

Face and frons not strongly converging dorsally 38

38. Face haired over lower one-third or less; upper two-thirds of face bare, or with a tuft of hairs at antennal base separated from mystax by a bare area, or with a row of weak hairs along eye margin. Abdominal tergite 10 of female without strong bristles .... DIOCTRIINI ... 39

Mystax occupying lower half or more of face, but without separate tuft or row of hairs. Abdominal tergite 10 of female with strong bristles 47

39. Hind femur and hind tibia each club-shaped, enlarged apically; first tarsomere of hindleg as long as subsequent three tarsomeres (Fig. 66). R_4 ending posterior to wing tip. Ocellar tubercle without bristles. Alula absent .... ***Dioctria*** Meigen ... 40

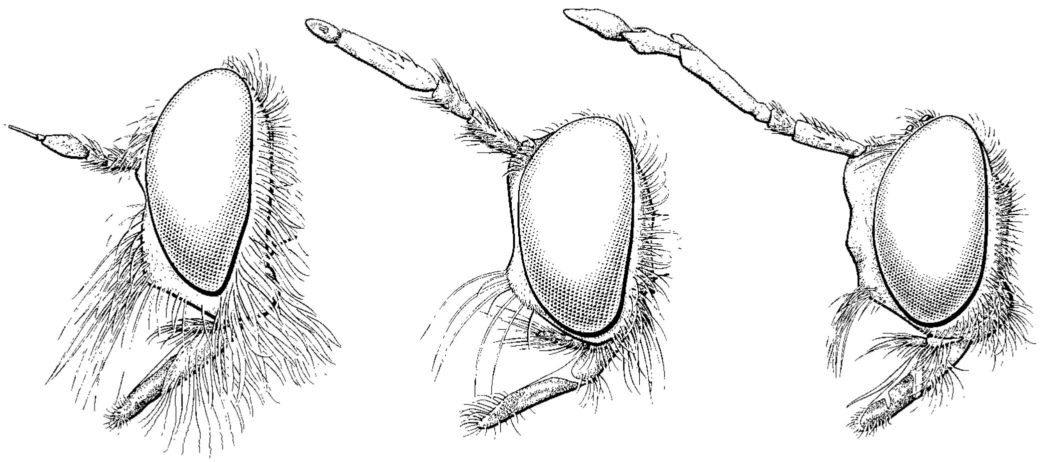
Hind femur thickest subbasally, at middle, or only gradually enlarged apically (Fig. 1); first tarsomere of hindleg as long as subsequent two tarsomeres. R_4 ending anterior to wing tip. Ocellar tubercle with bristles or with moderately long hairs curving forward over frons. Alula present 41

40. Antennal bases not raised on tubercle, hidden behind eye margin in profile; second flagellomere short and narrow, one-fifth as long as first flagellomere, subtruncate or cup-shaped .... ***Dioctria*** (***Nannodioctria*** Wilcox & Martin)
2 spp.; California, Florida; Adisoemarto and Wood 1975

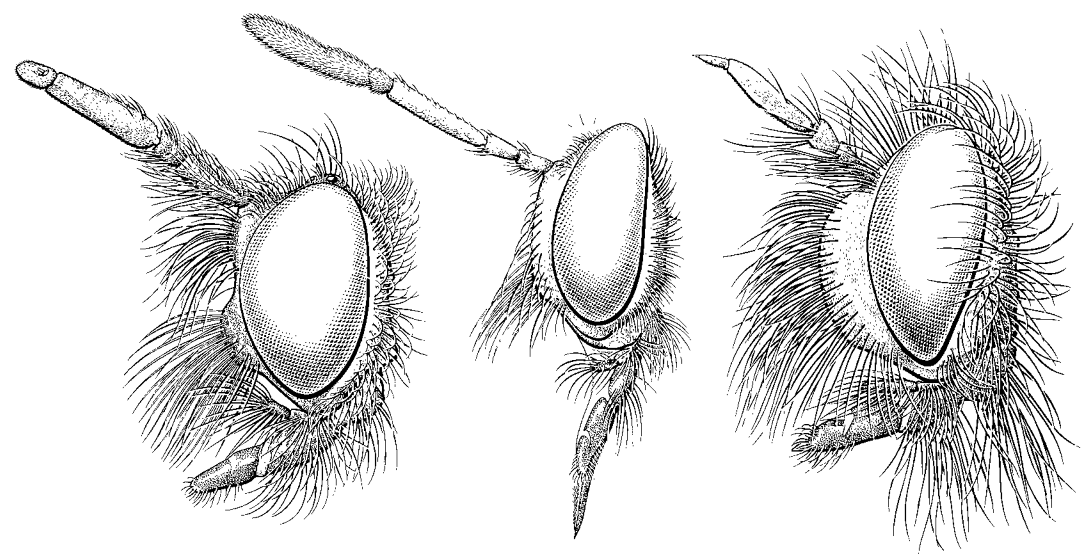
Antennal bases raised on tubercle visible in profile; second flagellomere long, subequal in width to first flagellomere, one-third to one-half as long as first flagellomere, more or less boat-shaped .... ***Dioctria*** (***Dioctria*** Meigen)
6 spp.; mostly western; Adisoemarto and Wood 1975

41. Mystax a narrow band of short straight bristles along lower margin of face. Antenna long, with three prominent flagellomeres; bases of second and third flagellomeres each enclosed by leaf-like extensions of preceding flagellomere (Fig. 38) .... ***Myelaphus*** Bigot
2 spp.; western; Adisoemarto and Wood 1975

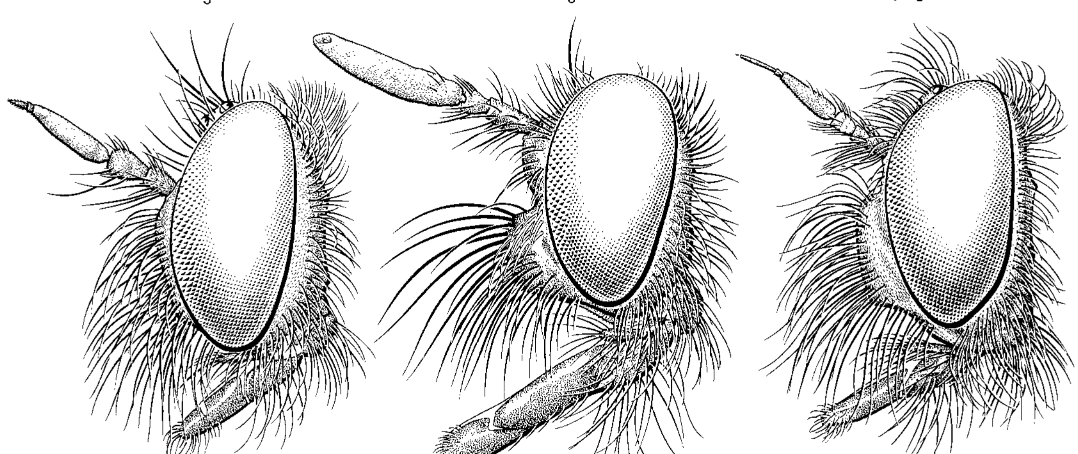
Mystax a cluster of curved bristles on lower one-fourth to one-third of face. Antenna usually with two flagellomeres; second flagellomere cup-shaped, or, if three flagellomeres present, the last two not enclosed by leaf-like extensions at base 42



36 Proctacanthella cacopiloga ♂ 37 Dioctria baumhaueri ♂ 38 Myelaphus melas ♂



39 Dicolonus nigricentrum ♀ 40 Ceraturgus cruciatus ♀ 41 Cyrtopogon willistoni ♀



42 Sintoria emeralda ♀ 43 Laphria sadales ♀ 44 Neoitamus orphne ♀

Figs. 42.36–44. Lateral views of head: (36) *Proctacanthella cacopiloga* (Hine); (37) *Dioctria baumhaueri* Meigen; (38) *Myelaphus melas* Bigot; (39) *Dicolonus nigricentrum* Adisoemarto & Wood; (40) *Ceraturgus cruciatus* (Say); (41) *Cyrtopogon willistoni* Curran; (42) *Sintoria emeralda* Hull; (43) *Laphria sadales* Walker; (44) *Neoitamus orphne* (Walker).

42. Upper half of face and frons prominently swollen, bearing the antennae and a brush of abundant long hairs below their bases; these hairs extending ventrally along lateral margin of face (Fig. 39). Anatergite haired (as in Fig. 63) .... ***Dicolonus*** Loew
5 spp.; western; Adisoemarto and Wood 1975

Swelling at antennal base less well-marked or nearly absent; upper part of face either bare or with only a single row of hairs along eye margin [except *Metadioctria* (n. subg.) with a group of hairs below antennal bases]. Anatergite bare (as in Fig. 64) 43

43. Upper part of face bare. Abdominal tergite 2 with a groove about one-third to one-quarter distance from base of segment; groove expanding laterally, thus separating a shiny raised cresent-shaped area on the first third of the segment (Fig. 65) 44

Upper part of face with a few weak hairs beside eye and occasionally with a few under antennal bases. Abdominal tergite 2 without a groove, or with the groove close to proximal margin and not separating off a crescent-shaped area 45

44. Scutellar margin with moderately long erect hair, as long as scutellum; disc of scutellum with appressed short hair. Anepisternum covered with recumbent hair .... ***Echthodopa*** Loew
3 spp.; widespread; Adisoemarto and Wood 1975

Scutellar margin without long hair; disc of scutellum bare or at most with minute hairs. Anepisternum pilose on upper one-third and along posterior margin .... ***Eudioctria*** Wilcox & Martin
14 spp.; widespread; Adisoemarto and Wood 1975

45. Antenna with three flagellomeres (Fig. 59). R_{4+5} branching distal to end of cell d. Abdominal tergite 2 without groove. Notopleural and supra-alar bristles absent .... ***Metadioctria*** (undescribed subgenus)
2 spp.; western

Antenna with two flagellomeres. R_{4+5} branching proximal to end of cell d. Abdominal tergite 2 with groove close to proximal end. Notopleural and supra-alar bristles present 46

46. Abdominal tergites strongly arched dorsally, rounded in cross section, making abdomen chrysidid-like. Scutum bare, or with sparse minute hairs; scutellar margin with very short appressed hair. Frons and occiput pruinose .... ***Bohartia*** Hull
6 spp.; western; Adisoemarto and Wood 1975

Abdominal tergites flattened dorsally. Scutum and scutellar margin with long fine hair. Frons and occiput shining black .... ***Metadioctria*** (***Metadioctria*** Wilcox & Martin)
1 sp., *rubida* (Coquillett); California

47. Pulvilli lacking. Thorax, legs, pronotum, and base of C with appressed white scale-like hairs .... ***Ablautus*** Loew
13 spp.; western; Wilcox 1966*a*

Pulvilli present. Body, legs, and wing without scale-like hairs 48

48. Stylus absent; first flagellomere very long, about three times combined length of scape and pedicel, with apical pit and spine. Cell m_3 closed or occasionally narrowly open at wing margin; wing dark brown .... ***Prolepsis*** Walker
1 sp., *tristis* (Walker); southern U.S.A.; Lamas 1973*a*

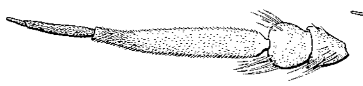
Stylus present; first flagellomere shorter. Cell m_3 open to margin, usually widely open; wing hyaline, lightly infuscated, or spotted, not dark brown 49

49. Mid tibia with a pair of moderately strong ventral bristles at apex directed proximally at an angle of 60–90° (Fig. 70) .... ***Callinicus*** Loew
4 spp.; western; Wilcox 1936*b*

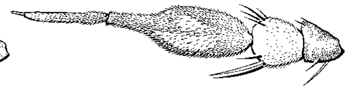
Mid tibia with bristles directed distally 50

50. Antenna with three flagellomeres; flagellomeres elongate, not stylus-like; second and third flagellomeres as wide as or wider than first flagellomere. Face in profile produced beyond eye margin, with antennal bases on raised area (Fig. 40) .... ***Ceraturgus*** Wiedemann
9 spp.; eastern; Brimley 1924

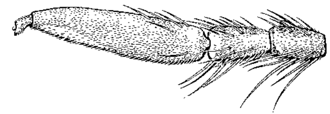
Second flagellomere of antenna stylus-like, narrowing apically, often with a spine. Face sometimes produced, but antennal bases never on raised area 51



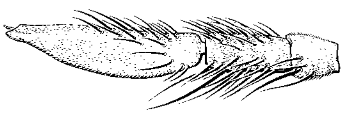
45 Leptogaster (Tipulogaster) glabrata ♂



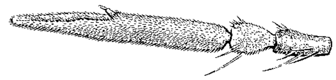
46 Leptogaster (Leptogaster) cylindrica ♂



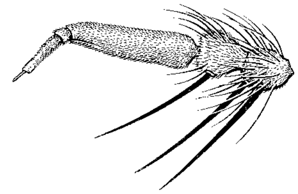
47 Saropogon combustus ♂



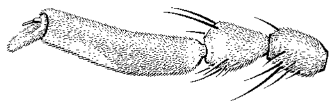
48 Diogmites basalis ♂



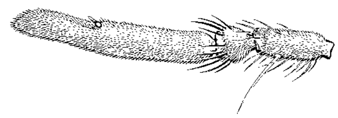
49 Taracticus octopunctatus ♂



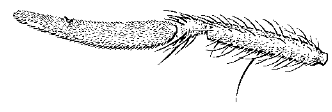
50 Backomyia limpidipennis ♂



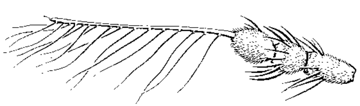
51 Atoniomyia duncani ♀



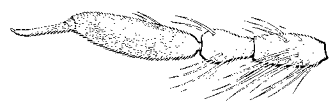
52 Atomosiella antennata ♀



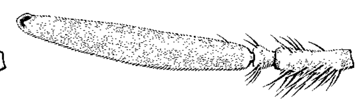
53 Cerotainia macrocera ♀



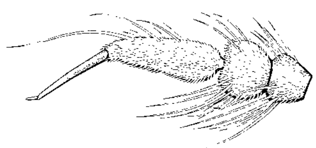
54 Ommatius tibialis ♂



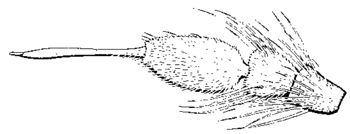
55 Stenopogon (Scleropogon) helvolus ♂



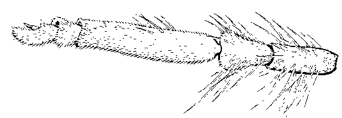
56 Stenopogon (Ospriocerus) abdominalis ♂



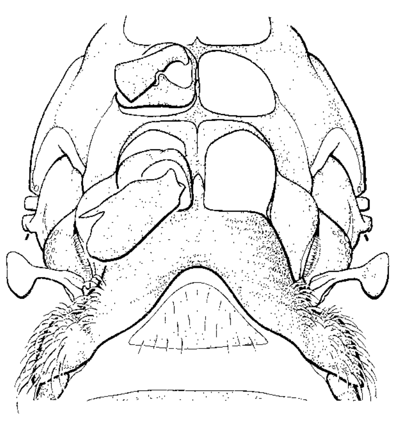
57 Haplopogon sp. ♂



58 Orrhodops americanus ♂

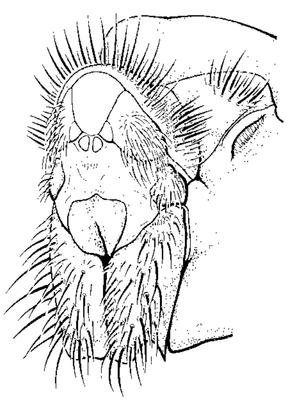


59 Metadioctria resplendens ♂



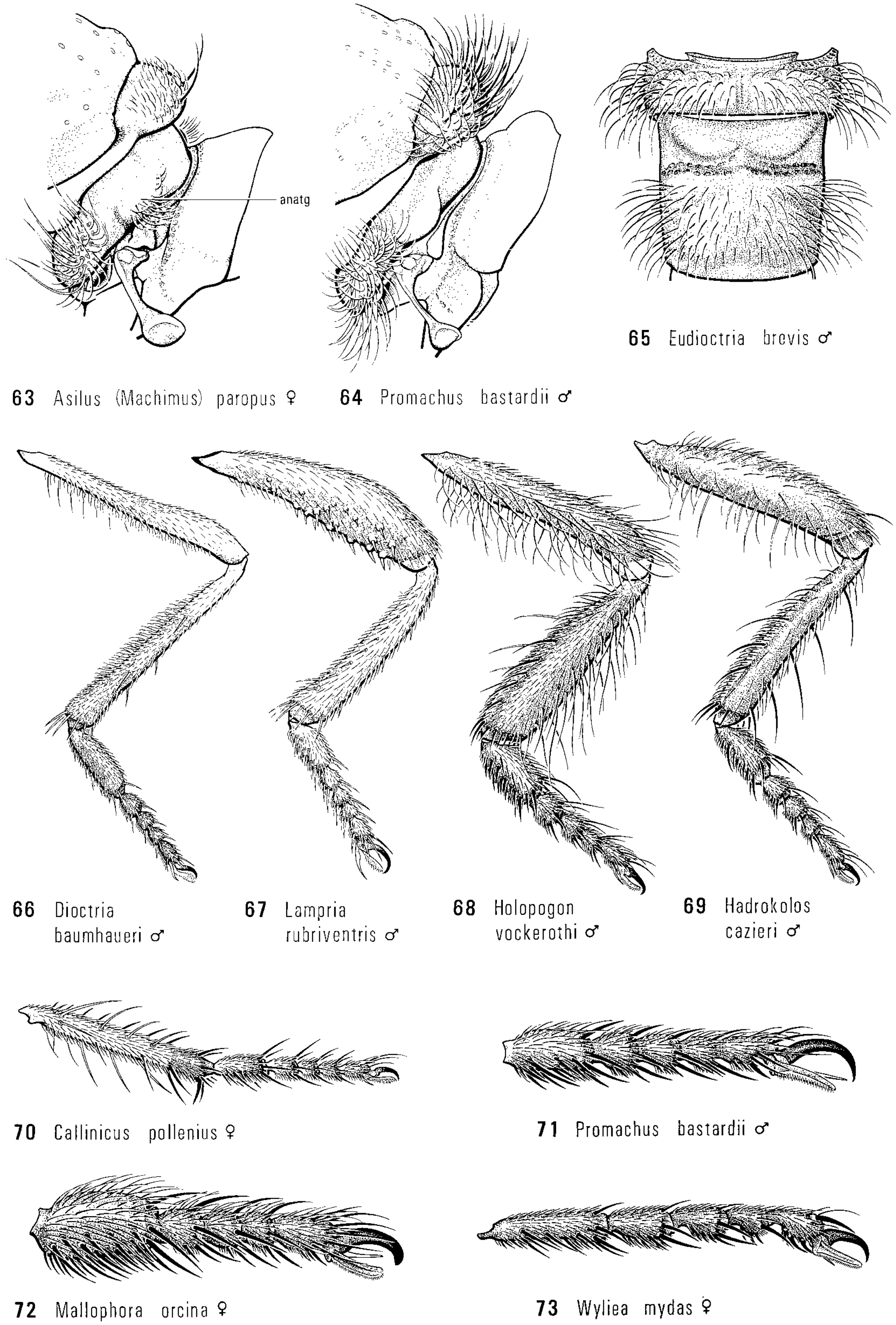
60 Atomosia puella ♀

61 Stichopogon trifasciatus ♂



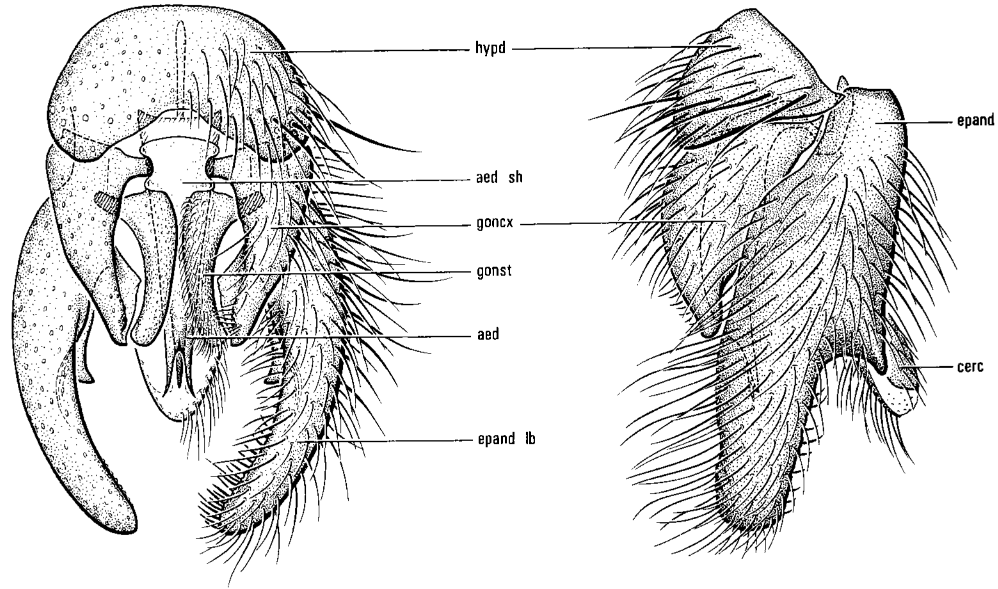
62 Microstylum galactodes ♂

Figs. 42.45–62. Antennae and thoraces: antenna of (45) *Leptogaster* (*Tipulogaster*) *glabrata* Wiedemann, (46) *Leptogaster* (*Leptogaster*) *cylindrica* (De Geer), (47) *Saropogon combustus* Loew, (48) *Diogmites basalis* (Walker), (49) *Taracticus octopunctatus* (Say), (50) *Backomyia limpidipennis* (Wilcox), (51) *Atoniomyia duncani* (Wilcox), (52) *Atomosiella antennata* (Banks), (53) *Cerotainia macrocera* (Say), (54) *Ommatius tibialis* Say, (55) *Stenopogon* (*Scleropogon*) *helvolus* (Loew), (56) *Stenopogon* (*Ospriocerus*) *abdominalis* (Say), (57) *Haplopogon* sp., (58) *Orrhodops americanus* (Curran), and (59) *Metadioctria* (undescribed subgenus) *resplendens* (Loew); (60) postmetacoxal bridge of *Atomosia puella* (Wiedemann); prosternum of (61) *Stichopogon trifasciatus* (Say) and (62) *Microstylum galactodes* Loew.

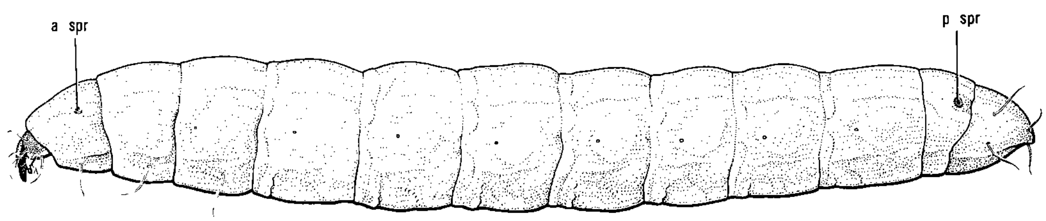


Figs. 42.63–73. Details of thorax, abdomen, and legs: (63) side view of thorax of *Asilus* (*Machimus*) *paropus* Walker; (64) anatergite and postscutellum of *Promachus bastardii* (Macquart); (65) dorsal view of abdominal tergites 1 and 2 of *Eudioctria brevis* (Banks); left hindleg, anterior view, of (66) *Dioctria baumhaueri* Meigen, (67) *Lampria rubriventris* (Macquart), (68) *Holopogon vockerothi* Martin, and (69) *Hadrokolos cazieri* Martin; (70) left mid tibia and tarsus, anterior view, of *Callinicus pollenius* (Cole); left hind tarsus, anterior view, of (71) *Promachus bastardii* (Macquart) and (72) *Mallophora orcina* (Wiedemann); (73) right fore tarsus, posterior view, of *Wyliea mydas* (Brauer).

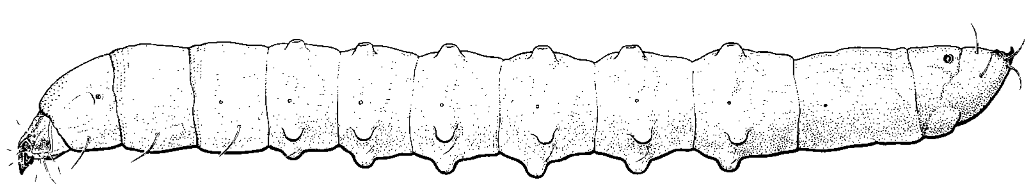
Abbreviation: anatg, anatergite.



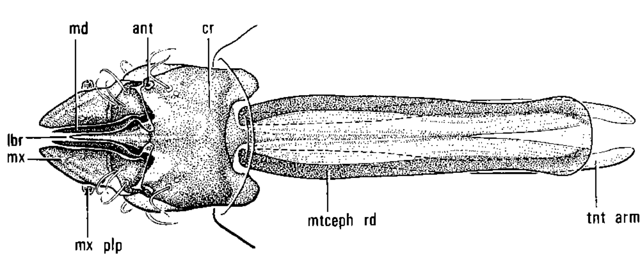
74 Philonicus sp. ♂ 75 Philonicus sp. ♂



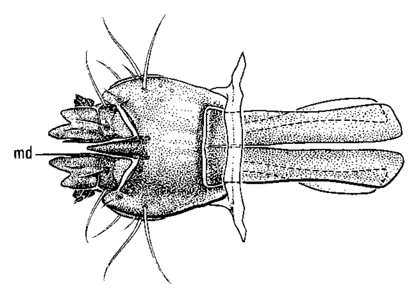
76 Promachus sp.



77 Laphria sp.



78 Promachus sp.



79 Laphria sp.

Figs. 42.74–79. Male terminalia and larvae: (74) ventral and (75) lateral views of terminalia of *Philonicus* sp.; lateral view of larva of (76) *Promachus* sp. and (77) *Laphria* sp.; dorsal view of head capsule of larva of (78) *Promachus* sp. and (79) *Laphria* sp.

Abbreviations: aed, aedeagus; aed sh, aedeagal sheath; ant, antenna; a spr, anterior spiracle; cerc, cercus; cr, cranium; epand, epandrium; epand lb, epandrial lobe; goncx, gonocoxite; gonst, gonostylus; hypd, hypandrium; lbr, labrum; md, mandible; mtceph rd, metacephalic rod; mx, maxilla; mx plp, maxillary palpus; p spr, posterior spiracle; tnt arm, tentorial arm.

51. Wing with brown spots at crossvein r-m, at bifurcation of R_4 and R_5, and at apex of cell d (Fig. 2) (other spots often present as well); bifurcation of R_4 and R_5 proximal to or level with apex of cell d, except in *Metapogon gilvipes* Coquillett 52

Wing hyaline or infuscated, or if brown spots are present (some *Cyrtopogon* and *Heteropogon*) they are not in the three positions given above; bifurcation of R_4 and R_5 distal to apex of cell d 54

52. Presutural dorsocentral bristles prominent and coarse; otherwise, hair on scutum sparse; scutum strongly arched, with height to length ratio of 0.44–0.5; marginal scutellar bristles strong, coarse, not more than two pairs; scutellar disc bare, or with sparse short pile .... ***Metapogon*** Coquillett
11 spp.; western; Wilcox 1964, 1972*b*

Presutural dorsocentral bristles lacking, but hair on scutum abundant; scutum not strongly arched, with height to length ratio of 0.30–0.42; marginal scutellar bristles hair-like, six or more; scutellar disc with moderate to abundant long pile 53

53. Anepisternum haired. Bristles on scape weak. Face wide, two-thirds or more width of one eye .... ***Eucyrtopogon*** Curran
11 spp.; widespread; Curran 1923

Anepisternum bare. Scape with two dark stout bristles (Fig. 50). Face narrow, less than two-thirds width of one eye .... ***Backomyia*** Wilcox & Martin, in part
5 spp.; western; Wilcox and Martin 1957*b*

54. Face strongly convex, in profile extending the length of the scape or more beyond eye margin (Fig. 41) 55

Face flat, slightly raised beyond eye margin, or weakly convex; if depth of convexity approaches length of scape (as in some *Backomyia*), then one or two long strong bristles present on scape 57

55. Dorsocentral bristles coarse, well-developed; little or no pile on scutum, upper occiput, or abdomen; marginal scutellar bristles coarse, with scutellar disc bare of pile or nearly so. Mystax consisting of bristles or of bristles and hairs 56

Dorsocentral bristles lacking; moderate to abundant pile on scutum, upper occiput, and abdomen; marginal scutellar bristles weak, barely differentiated from adjacent pile on disc (if strong marginal bristles present, see couplet 56); mystax consisting of hairs only .... ***Cyrtopogon*** Loew
70 spp.; widespread; Wilcox and Martin 1936

56. Mystax consisting of sparse stout bristles each arising from a tubercle. Frons with row of strong bristles along eye margin. Face narrow, two-thirds or less width of one eye (Fig. 29) .... ***Coleomyia*** Wilcox & Martin
7 spp.; western; Martin 1953

Mystax consisting of hairs and bristles. Frons with abundant fine hairs in tufts. Face wide, three-fourths width of one eye (Fig. 30) .... ***Nannocyrtopogon*** Wilcox & Martin
28 spp.; southwestern; Wilcox and Martin 1957*a*

57. Hind tibia much enlarged, as thick as or thicker than hind femur (Fig. 68). CuA_2 and A_1 joined before wing margin thus making cell cu*p* closed except in one unnamed species .... ***Holopogon*** Loew
17 spp.; widespread; Martin 1959*a*

Hind tibia thinner than hind femur (Fig. 69). CuA_2 and A_1 ending separately in wing margin, thus making cell cu*p* open 58

58. Mystax with dense patch of short bristles in middle of lower margin, and with longer less densely spaced bristles on remainder of face (Fig. 31) .... ***Hadrokolos*** Martin
3 spp.; southcentral North America; Martin 1959*a*

Mystax sparse or dense, but without dense patch of short bristles on lower margin 59

59. Hairs plumose (the plumosity visible under 25× magnification) on pronotum, upper occiput, and side of thorax. Frons with tufts of hair laterally .... ***Heteropogon*** Loew
24 spp.; widespread; Wilcox 1965*a*

Hairs straight or crinkly, not plumose. Frons with a lateral row of fine hairs 60

60. Large vespid mimic, over 2.5 cm long, with scutum and abdomen prominently striped and banded with black and yellow. Proboscis long, pointed apically .... ***Pritchardomyia*** Martin
1 sp., *vespoides* (Bigot); California; Wilcox 1965*a*

Smaller species, less than 2.0 cm long, not marked as above. Proboscis short, rounded apically 61

61. Face in profile nearly flat, but produced beyond eye margin with highest point just below antennal base (Fig. 42). Scutum humped. Legs and dorsum of abdomen with green or blue metallic reflections. Side of thorax with sparse hairs .... ***Sintoria*** Hull
4 spp.; southwestern; Wilcox 1972*a*

Face in profile flat or slightly convex, sometimes with swelling on lower half. Scutum not humped. Metallic reflections absent. Side of thorax, except for katepisternum, bare 62

62. Scape with one or two long black bristles as long as first flagellomere (Fig. 50). Frons widening toward vertex .... ***Backomyia*** Wilcox & Martin, in part
see couplet 53

Scape without long heavy black bristles but often with short weak hairs. Frons parallel-sided (Fig. 32) .... ***Wilcoxia*** James
5 spp.; southwestern; Wilcox 1972*b*

63. Antenna blunt apically, without stylus (Fig. 43), or with one or two abruptly tapered short microsegments (Fig. 51). Palpus two-segmented. Crossvein m-cu present; thus apex of cell bm closed by three veins (Fig. 15) 64

Apex of antenna with long slender bristle-like stylus (Figs. 44, 54). Palpus one-segmented. Crossvein m-cu absent, and veins M_3 and CuA_1 joined together; thus apex of cell bm usually closed by only two veins (Fig. 19), except in *Mallophora* and some *Efferia* 74

64. Postmetacoxal region with a transverse heavily sclerotized bridge (Fig. 60). First flagellomere either with a short bristle arising near middle of dorsal surface (Fig. 52), or with a stylus at apex (Fig. 51) .... ATOMOSIINI and ***Dasylechia***....65

Postmetacoxal area membranous. First flagellomere without a stylus, but with an apical pit containing a short spine or bristle (Fig. 43) .... LAPHRIINI except *Dasylechia*....69

65. Species resembling bumblebees, more than 2.5 cm long, with entire face and body densely haired. Anatergite bare; sclerotized part of postmetacoxal region very narrow, with its posterodorsal margin U-shaped .... ***Dasylechia*** Williston
1 sp., *atrox* (Williston); eastern U.S.A., Utah

Small rather bare species, less than 20 mm long, often with punctate mesonotum and abdomen. Anatergite with bristly pile (as in Fig. 63); sclerotized part of postmetacoxal region more extensive, with its posterodorsal margin V-shaped (Fig. 60) 66

66. Lateral margins of frons curved, converging at vertex (Fig. 33) .... ***Atomosia*** Macquart
9 spp.; widespread; Curran 1935

Lateral margins of frons straighter, diverging at vertex 67

67. Entire face, including antennal bases, produced beyond eye margin when viewed laterally. Frons strongly divergent at vertex, with abundant fine long pile. Scape four or more times as long as pedicel (Fig. 53) .... ***Cerotainia*** Schiner
3 spp.; eastern and central; Curran 1934

Face in lateral view produced beyond eye margin on lower one-third. Frons slightly divergent at vertex, pruinose but with only a few fine hairs on lateral margin. Scape not more than twice as long as pedicel 68

68. M_2 absent beyond cell d. First flagellomere greater than 1.5 times combined length of scape plus pedicel; flagellomere without a microsegment at apex but with an inconspicuous spine near middle of dorsal surface (Fig. 52) .... ***Atomosiella*** Wilcox
1 sp., *antennata* (Banks); western

M_2 present beyond cell d. First flagellomere 1.5 times or less the combined length of scape and pedicel; first flagellomere with a microsegment at apex, shorter than length of scape (Fig. 51) .... ***Atoniomyia*** Hermann
2 spp.; Arizona

69. Proboscis laterally compressed, two or more times as wide in profile as when viewed from above (Fig. 43) 70

Proboscis either more or less cylindrical, or dorsoventrally compressed, narrower in profile than when viewed from above 71

70. Hind femur with tubercles on ventral surface (Fig. 67) .... ***Lampria*** Macquart
3 spp.; eastern U.S.A.

Hind femur without tubercles .... ***Laphria*** Meigen
63 spp.; widespread; McAtee 1919

71. Proboscis more or less cylindrical, blunt at tip. Basal portion of M_2 that closes cell d parallel with apical portion of M_3, almost forming a straight line (Fig. 14) .... ***Orthogonis*** Hermann
1 sp., *stygia* (Bromley); southeastern U.S.A.

Proboscis dorsoventrally compressed, boat-shaped and pointed at end in profile. Basal portion of M_2 and apical portion of M_3 not parallel and not forming a straight line 72

72. Hind margin of wing membranous, C ending proximal to wing tip, slightly beyond apex of R_4 (Fig. 15). Upper half of face with appressed pile. Ocellar bristles shorter than flagellomere. Lateral margins of abdominal tergites with very short inconspicuous pile; abdomen short, wide. Male terminalia small, turned under, almost concealed from dorsal aspect .... ***Cerotainiops*** Curran
6 spp.; central to western; Martin 1959*b*

Hind margin of wing thickened, continuous with C. Face with strong erect bristles, at least on lower half. Ocellar bristles as long as or longer than flagellomere. Lateral margins of at least abdominal tergites 1 and 2 with long conspicuous pile. Male terminalia held in normal position parallel to long axis of body, visible from above .... ***Andrenosoma*** Rondani....73

73. R_{2+3} and R_4 connected by a short extra crossvein (Fig. 16) .... ***Andrenosoma*** (***Pogonosoma*** Rondani)
2 spp.; widespread

R_{2+3} and R_4 not connected by an extra crossvein .... ***Andrenosoma*** (***Andrenosoma*** Rondani)
4 spp.; widespread; McAtee 1919

74. Antennal stylus plumose (Fig. 54). Postmetacoxal area heavily sclerotized, forming a complete bridge behind hind coxae (as in Fig. 60) .... OMMATIINI.... ***Ommatius*** Wiedemann
8 spp.; widespread; Wilcox 1936*a*

Antennal stylus bare (Fig. 44). Postmetacoxal area membranous .... ASILINI....75

75. Anatergite bare (Fig. 64) 76

Anatergite pilose (Fig. 63) 85

76. R_4 with a recurrent vein arising near its junction with R_5; recurrent branch sometimes short, ending in cell r_{2+3} (Fig. 17), or sometimes extending toward base of wing until it joins R_{2+3} (Fig. 18) 77

R_4 without an extra vein (Fig. 19) 82

77. Apical half of R_5 subparallel to R_4 (Fig. 17), usually meeting C before wing apex except in *aestuans* group. Posterior basalare bare .... ***Efferia*** Coquillett
100 spp.; widespread; Wilcox 1966*c*

Apical half of R_5 diverging strongly from R_4 (Fig. 18), meeting C well behind wing apex. Posterior basalare haired 78

78. Claws acute (Fig. 71) .... ***Promachus*** Loew
21 spp.; widespread; Hine 1911

Claws blunt (Fig. 72) 79

79. Abdomen slender, as long as or longer than wing. Male terminalia relatively large, about as wide as abdominal tergite 7, and longer than wide 80

Abdomen broad, shorter than wing. Male terminalia small, narrower than abdominal tergite 7, and wider than long 81

80. Face wide, three-fourths width of one eye .... ***Promachella*** Cole & Pritchard
1 sp., *pilosa* (Wilcox); Arizona; Cole and Pritchard 1964

Face narrow, one-third width of one eye (Fig. 35) .... ***Promachina*** Bromley
1 sp., *trapezoidalis* (Bellardi); Texas; Curran 1935

81. Lower half of face prominently bulging; upper half almost bare, shining. Hind femur long, club-shaped, with row of bristles on anterior surface .... ***Mallophora*** Macquart
14 spp.; widespread; Cole and Pritchard 1964

Lower half of face more evenly convex, with pile on upper half (Fig. 34). Hind femur thickened in middle, spindle-shaped, without row of bristles on anterior surface ..***Mallophorina*** Curran
15 spp.; widespread; Cole and Pritchard 1964

82. R_5 reaching wing margin anterior to wing tip (Fig. 19) 83

R_5 reaching wing margin posterior to wing tip 84

83. Abdomen long and slender, tapering, much longer than wing; lateral margins of abdominal tergites 1 and 2 with sparse short pile. Lower three-quarters of face swollen. Species not resembling bumblebees .... ***Proctacanthus*** Macquart
18 spp.; widespread; Curran 1934

Abdomen short and wide, no longer than wing. Lateral margins of abdominal tergites 1–3 with abundant long pile. Lower one-half of face swollen. Bumblebee mimics...... ***Eccritosia*** Schiner
1 sp., *zamon* (Townsend); Arizona, Texas; Lamas 1973*b*

84. Lower part of face only moderately swollen (Fig. 36); face five-sevenths as wide as one eye. Male with large hypandrium as long as or longer than sternite 7. Female with spines on cercus. Scutellum swollen, without groove near margin (as in Fig. 64) ....
.... ***Proctacanthella*** Bromley
5 spp.; western; Wilcox 1965*b*

Lower part of face strongly swollen (as in Fig. 44); face narrow, three-eighths as wide as one eye. Male with small hypandrium. Female without spines on cercus. Scutellum with groove near margin (sometimes difficult to see) (Fig. 63) .... ***Asilus*** Linnaeus, in part
see couplet 88

85. Occipital bristles long, fine; distal one-third strongly proclinate (Fig. 44). Abdominal segment 6 of female incorporated into terminalia .... ***Neoitamus*** Osten Sacken
8 spp.; widespread

Occipital bristles not proclinate at apices, or if slightly so, less than apical one-fourth curved. Abdominal segment 6 of female not incorporated into terminalia 86

86. Fore tarsus with two stout bristles extending dorsally over basal one-third of tarsal claws (Fig. 73). Wing heavily infuscated, orange or brownish orange. Body velvety black ....
.... ***Wyliea*** Martin
1 sp., *mydas* (Brauer); Martin 1975

Fore tarsus lacking stout bristles. Wing hyaline or lightly infuscated, grayish brown or yellowish, not orange. Body color variable, usually gray, brown, or yellowish, not black 87

87. Epandrial lobe excavated on distal one-half to two-thirds of dorsomedial surface beyond dorsomedial tooth; apex thus unusually long and thin, curving toward midline and enclosing hemicircular space beyond proctiger subequal in length to half total length of terminalia (Fig. 74). Abdominal tergite 10 of female with one or more pairs of stout bristles ....
.... ***Philonicus*** Loew
6 spp.; widespread

Epandrial lobe not as above. Female terminalia without strong bristles..88

88. Upper two-thirds of face shining black, not pruinose. Epandrial lobe excavated on distal one-fourth beyond median tooth. Abdominal segment 8 of female short, subequal in length to segment 7; tergite slightly flattened dorsoventrally; sternite rounded........ ***Rhadiurgus*** Loew
1 sp., *variabilis* (Zetterstedt); northern

Upper two-thirds of face pruinose, not shining black. Epandrial lobe not as above, simple, undivided or with one or two rounded lobes distally. Abdominal segment 8 of female short or long, usually flattened laterally to some degree...
.....***Asilus*** Linnaeus (***Machimus*** Loew, ***Negasilus*** Curran, ***Prolatiforceps*** Martin, ***Polacantha*** Martin, ***Dicropaltum*** Martin, ***Neomochtherus*** Osten Sacken, and ***Cerdistus*** Loew)
74 spp.; widespread; Martin 1975, in part

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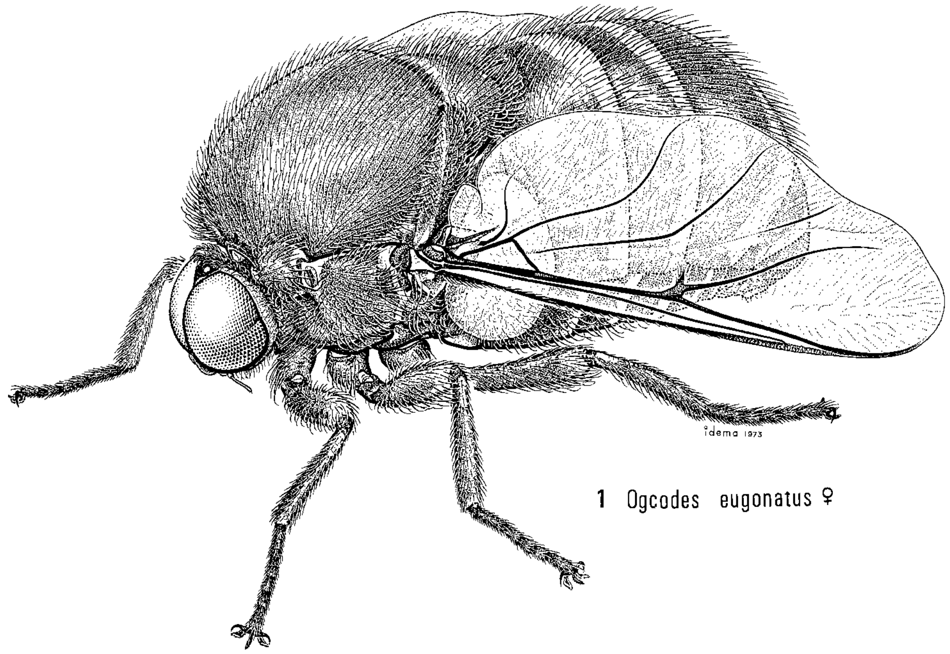
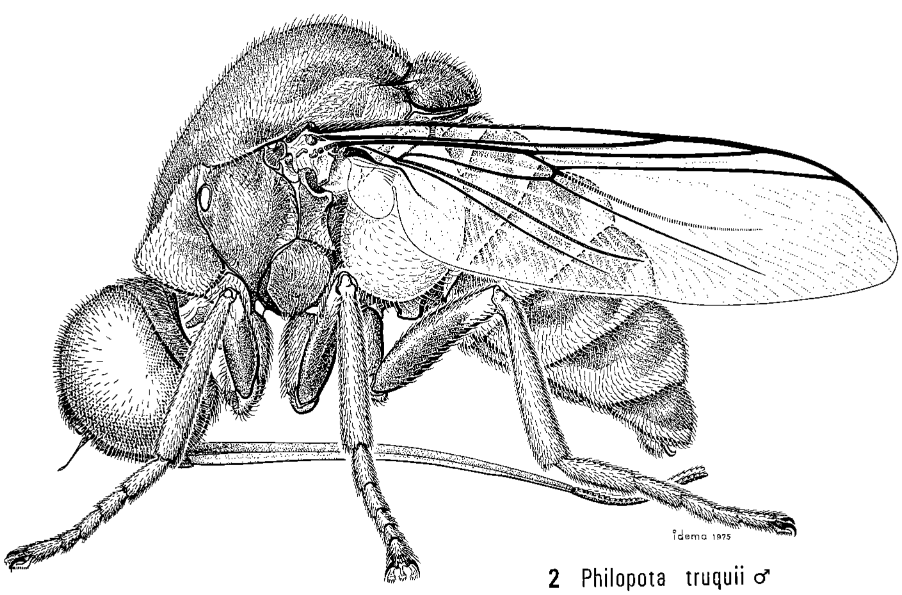
ACROCERIDAE 43

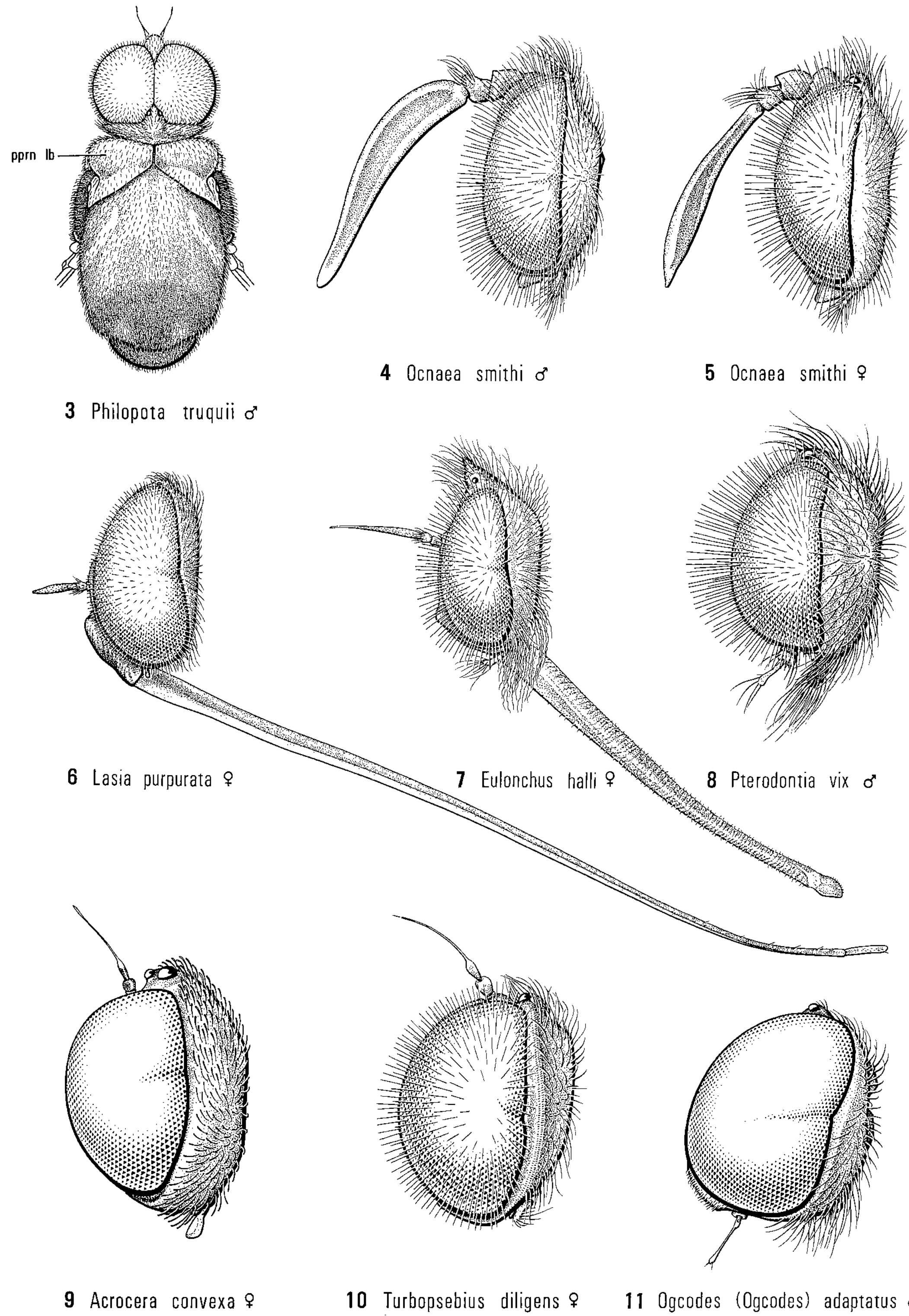
EVERT I. SCHLINGER





Figs. 43.1–2. Adults: (1) female of *Ogcodes eugonatus* Loew; (2) male of *Philopota truquii* Bellardi.

Small to large flies (Figs. 1, 2), 2.5–21 mm long. Head small to medium-sized, consisting mostly of large compound eyes. Abdomen globose, globose–elongate, or narrow and tapering or parallel-sided; color dull or shiny and often bright metallic green, blue, red, or purple, or sometimes brown, black, orange, yellow, or white with maculations on abdomen and with vittae on mesonotum. Some species bee-like, others wasp-like, and some even



Figs. 43.3–11. Heads and thorax: (3) dorsal view of head and thorax of male of *Philopota truquii* Bellardi; lateral view of left side of head of (4) male and (5) female of *Ocnaea smithi* Sabrosky, (6) female of *Lasia purpurata* Bequaert, (7) female of *Eulonchus halli* Schlinger, (8) male of *Pterodontia vix* Townsend, (9) female of *Acrocera convexa* Cole, (10) female of *Turbopsebius diligens* (Osten Sacken), and (11) male of *Ogcodes* (*Ogcodes*) *adaptatus* Schlinger.
Abbreviation: pprn lb, postpronotal lobe.

beetle-like, many appearing to be mimics. Family characterized by following combination of morphological structures: three-segmented antenna, small head, large calypter, pulvilliform empodia, simple unbranched R_2, and body without bristles.

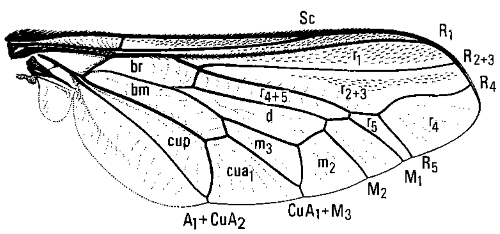
Adult. Head: usually small, round, and placed low on thorax (Fig. 1), but when larger, usually higher than wide (Figs. 2, 3); large compound holoptic eyes occupying most of head, and covered with dense pile (Figs. 4, 5, 7, 8, 10) or fine pubescence (Figs. 2, 6), or bare (Figs. 9, 11). Occiput usually narrow (Figs. 10, 11), but when enlarged, extending laterally beyond eye margin (Fig. 9). Three ocelli usually present, sometimes placed flat on vertex (Fig. 2), or placed to one side of or on top of a raised ocellar tubercle (Fig. 7); median ocellus sometimes absent; rarely all ocelli indistinct. Antenna three segmented, arising from midline anywhere from vertex (Figs. 4, 9, 10) to middle of head (Figs. 6, 7) or on lower part of head (Figs. 8, 11); scape and pedicel short and round (Figs. 7, 32–34), rarely with long seta on pedicel (*Sabroskya* Schlinger, Ethiopian; *Protogcodes* Schlinger, Australian); flagellum usually long, and either laterally compressed (Figs. 4, 5), parallel-sided, or rounded throughout (Figs. 6, 7), setiform or styliform (Figs. 9, 10), or short and terminating with several long setae (Figs. 32, 34); apex of flagellum often with one to five short to minute setae (Fig. 33); sensory pit usually present along inner basal area of flagellum (Figs. 33, 34); base of each antenna approximate, sometimes inserted on or underneath well-raised frons (antennal tubercle) (Figs. 4, 5) or hidden under frons (Fig. 2); scapes of both antennae sometimes fused together into a single structure (*Pialea* Erichson, Neotropical). Mouthparts underdeveloped (Figs. 4, 9–11), partially developed (Fig. 8), or well-developed (Figs. 2, 6, 7); shortened partially developed mouthparts usually in form of a simple setose tube about as long as height of head (*Hadrogaster* Schlinger, Formosa; *Nipponcyrtus* Schlinger, Japan; *Sabroskya*), and usually without palpus or labella; well-developed mouthparts forming a proboscis, usually consisting of large clypeus, minute palpus, labrum, hypopharynx, prementum, lacinia, and labella; prementum extendable, lengthening proboscis to twice normal length (Fig. 7).

Thorax: often humpbacked (Fig. 2) but sometimes flat, covered with long or short dense fine pile, or sometimes nearly bare; pile simple or branched (*Turbopsebius* Schlinger); integument polished, smooth, or finely and densely sculptured to rugose. Cervical region usually hidden behind head and between enlarged postpronota (Fig. 2), sometimes with distinct sclerites (*Sabroskya*; *Meruia* Sabrosky, Ethiopian); postpronota usually enlarged, touching or fused behind head to form prothoracic shield (Philopotinae, Fig. 3), but sometimes close together (*Ocnaea* Erichson) or widely separated (*Ogcodes* Latreille). Scutellum well-developed, often obscuring metanotum; anepisternum swollen; meron often produced into distinct rounded knob, often with a distinct pit behind posterior spiracle.

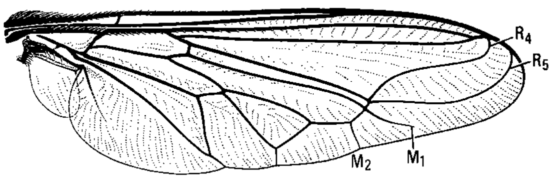
Legs usually simple, often strongly developed, covered with sparse or dense fine pile and pubescence, rarely with foreleg long and thin (*Dimacrocolus* Schlinger, Madagascar); femora sometimes swollen; tibiae sometimes produced into one or two apical spurs (Panopinae, Fig. 37). Tarsomeres usually cylindrical, rarely compressed (*Pialea ecuadorensis* Schlinger); tarsal claws simple, stout; each tarsus with two enlarged pulvilli, usually also with empodium developed pulvilliform (Fig. 36); empodium on each leg much reduced in several genera, or pulvilli and empodium lacking entirely (*Camposella* Cole, Neotropical).

Wing extremely variable in venation, size, and shape (compare Figs. 2, 12–27). Membrane hyaline, lightly or deeply infuscated, rarely spotted, and covered with microtrichia in some genera (*Villalus* Cole, Chile), or with macrotrichia in others (*Archipialea* Schlinger, Chile; *Arrhynchus* Philippi, Chile; *Exetasis* Walker, Neotropical). C sometimes complete (Figs. 12–14, 21, 22), ending at or near wing tip (Figs. 19, 23–27) or before wing tip (Fig. 2); large tuft of hair present at base of C in male of *Dimacrocolus pauliani* Schlinger; costal tooth or projection formed at junction of Sc, with R_1 and R_{2+3} present in male of all species of *Pterodontia* Gray (Fig. 15) and *Turbopsebius sulphuripes* (Loew) (Fig. 22); Sc reaching to middle of wing or beyond; crossvein h present (Figs. 12–16) or absent (Figs. 17–27); R_{2+3}, when present, usually ending in wing margin (Figs. 12, 14, 21), but in Nearctic species of *Lasia* Wiedemann and some species of *Psilodera* Gray (Ethiopian) joining R_1 before wing margin (Fig. 13); wing cells all present, complete, and tabanid-like (Figs. 12, 14), reduced in number (Figs. 15–17), or few to only two in number (Figs. 18, 23–27); an extra crossvein r-m present in most Panopinae and some Acrocerinae forming cells r_{4+5} and r_5 (Figs. 12, 14, 21); cell cu*p* usually closed at or before wing margin (Figs. 12–14, 16), but sometimes open; anal lobe poorly to strongly developed; alula slightly developed or absent. Lower calypter well-developed (Figs. 1, 2), large, usually rounded in outline, either flat or arched, hyaline or infuscated, bare or pilose, with or without distinct rim, freely or strongly attached to thorax, usually completely covering halter. Halter prominent; knob white or colored.

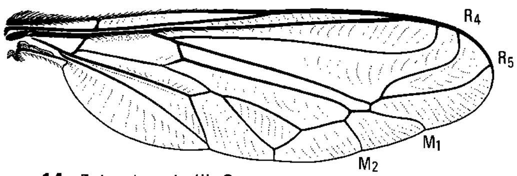
Abdomen: usually globose (most Acrocerinae, Fig. 1), globose-elongate (most Panopinae), or narrow, conical, tapering, or laterally compressed (most Philopotinae, Fig. 2); first few abdominal segments sometimes constricted and caudal segments enlarged, wasp-like (*Leucopsina* Westwood, Australia). Five to eight segments visible; segment 1 often difficult to ascertain; tergites sometimes fused with each other or with their corresponding sternites or both (*Turbopsebius*). Abdominal spiracles located in tergites, sternites, or intersegmental membranes; first spiracle regularly on tergite 1, often with hood-like covering; posterolateral tergal area sometimes produced spine-like (*Thyllis splendens* Brunetti, Madagascar); paired sets of dorsal protuberances sometimes present (*Terphis* Erichson, Neotropical). Vestiture



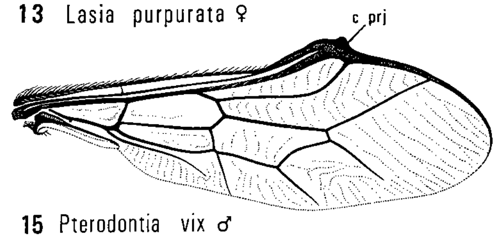
12 Ocnaea smithi ♂



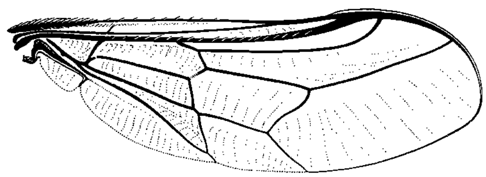
13 Lasia purpurata ♀



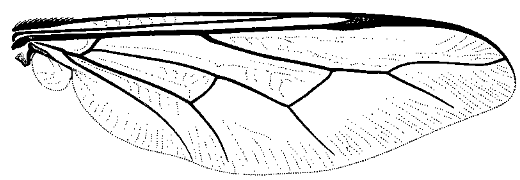
14 Eulonchus halli ♀



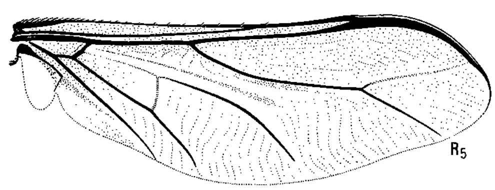
15 Pterodontia vix ♂



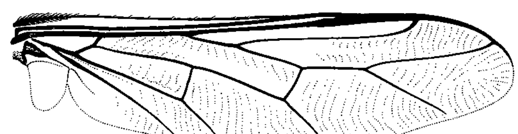
16 Pterodontia misella ♀



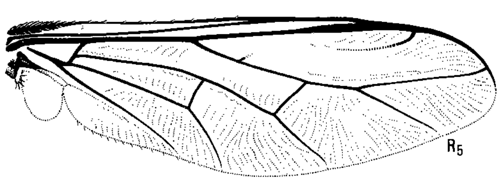
17 Acrocera convexa ♀



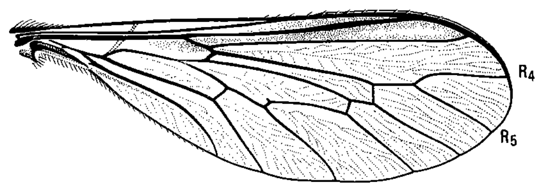
18 Acrocera bulla ♀



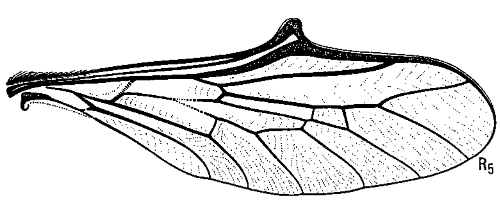
19 Acrocera subfasciata ♀



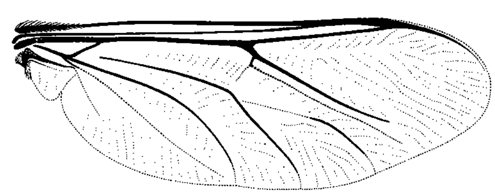
20 Acrocera bimaculata ♀



21 Turbopsebius sulphuripes ♀



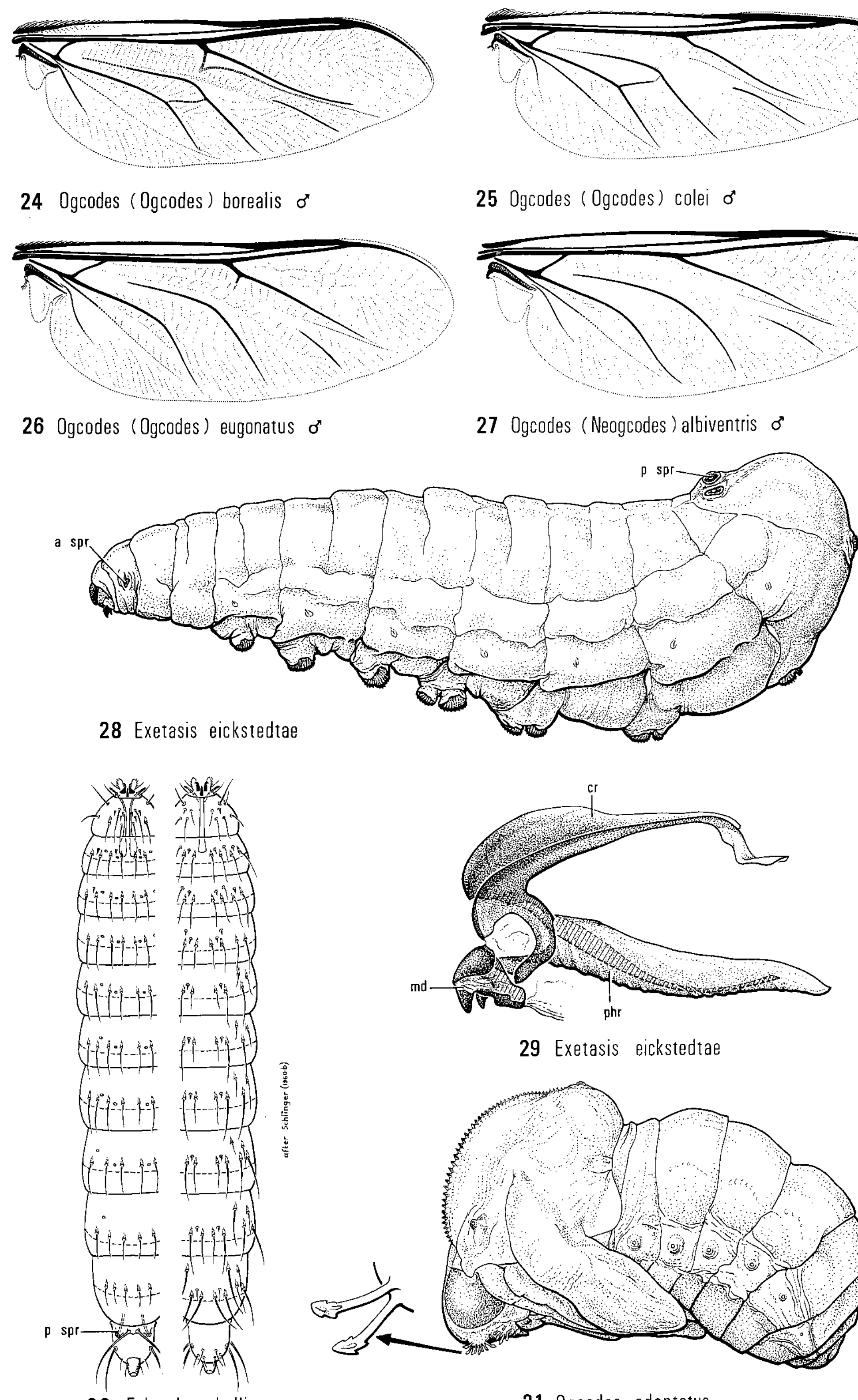
22 Turbopsebius sulphuripes ♂



23 Ogcodes (Ogcodes) adaptatus ♂

Figs. 43.12–23. Wings: (12) *Ocnaea smithi* Sabrosky; (13) *Lasia purpurata* Bequaert; (14) *Eulonchus halli* Schlinger; (15) *Pterodontia vix* Townsend; (16) *Pterodontia misella* Osten Sacken; (17) *Acrocera convexa* Cole; (18) *Acrocera bulla* Westwood; (19) *Acrocera subfasciata* Westwood; (20) *Acrocera bimaculata* Loew; (21) female and (22) male of *Turbopsebius sulphuripes* (Loew); (23) *Ogcodes* (*Ogcodes*) *adaptatus* Schlinger (*continued*).

Abbreviation: c prj, costal projection.



Figs. 43.24–31. Wings (*concluded*) and immature stages: wing of (24) *Ogcodes* (*Ogcodes*) *borealis* Cole, (25) *Ogcodes* (*Ogcodes*) *colei* Sabrosky, (26) *Ogcodes* (*Ogcodes*) *eugonatus* Loew, and (27) *Ogcodes* (*Neogcodes*) *albiventris* Johnson; (28) left side of third larval instar of *Exetasis eickstedtae* Schlinger; (29) left side of cephalopharyngeal skeleton of larva of *Exetasis eickstedtae*; (30) dorsal (*left*) and ventral (*right*) views of first larval instar of *Eulonchus halli* Schlinger; (31) left side of pupa of *Ogcodes adaptatus* Schlinger, with papilliform processes of ventral side of head enlarged at left.

Abbreviations: a spr, anterior spiracle; cr, cranium; md, mandible; phr, pharynx; p spr, posterior spiracle.

usually consisting of dense short pile or pubescence, but sometimes lacking; pile often forming bands or fasciae; fasciae, triangles, or ocellate spots sometimes of integumental coloring; abdomen dull-colored or metallic.

Male terminalia (Fig. 35) variable; structures that are difficult to homologize appearing in different genera, but usually consisting of sternite 9 with gonopods and tergite 9 followed by cerci that more or less surround a well-developed aedeagus; gonocoxite bearing a long bilobate (inner and outer) gonostylus (*Eulonchus* Gerstäcker), or a short and simple hardly differentiated gonostylus (*Ogcodes*); aedeagus generally a long rod-shaped organ, enlarged and sheathed basally by the fused parameres, with the sheath opening on sides and becoming dorsal near apex of aedeagus; apical notch present, with a distinct gonopore lying directly below; ejaculatory apodeme small and concealed by aedeagal sheath (*Eulonchus*), or large or small and extending anterior to aedeagal sheath (*Ogcodes*). Terminalia rotated in most genera 180°, in *Ogcodes* to nearly 360°.

Female terminalia (Fig. 38) usually simple, consisting of enlarged cerci and a cup-shaped, scalloped, or trilobate sternite 8. Terminalia usually in caudoventral position, but in some Panopinae (i.e. *Rhysogaster* Aldrich, Oriental) placed so far forward anteroventrally near thorax that several tergites are in a ventral position.

Larva. Hypermetamorphic, with three larval stages. First instar a planidium, 0.25–1 mm long and 0.05–0.15 mm wide, consisting of a head, three thoracic segments, and nine abdominal segments (Fig. 30). Head with a pair of upwardly curved mandibles, an anterior fleshy lobe or a pair of palpus-like lobes, faint eyespots (or none), a pair of one- or two-segmented antennae, and a buccopharyngeal armature of three or four arms. Body segments well-sclerotized (except in *Acrocera* Meigen), and covered with numerous setae or scales; one or two pairs of longer bristles and a suction disc present caudally. Respiratory system metapneustic; spiracles located on abdominal segment 8 or on base of segment 9.

Second instar poorly known, white, without apparent sclerotized parts, and with a poorly defined head, a small pharyngeal plate, a large unsegmented thoracic area, and six distinguishable abdominal segments. Posterior spiracles large, and located in middle of rounded terminal segment or placed on a sclerotized spiracular plate.

Last instar white, 3–35 mm long, consisting of a distinct head, three thoracic segments, and eight or nine abdominal segments (one less sternite than tergite) (Fig. 28). Mouthparts of *Exetasis eickstedtae* Schlinger comprising an articulated mandible, a condylic pleurostomal ridge, a labrum, and a pharyngeal plate (Fig. 29). Respiratory system peripneustic, with a large pair of dorsolateral eye-like anterior spiracles, with an even larger pair of posterior spiracles placed anteriorly on tergite 8, and with up to seven pairs of small lateral spiracles. Each abdominal sternite bearing one to three bands of minute setae placed on setal platelets.

Pupa. White to brown in color, 3–20 mm long, and consisting of a small head, a swollen thorax with three partially defined segments, and an abdomen with eight or nine visible segments (Fig. 31). Head bearing a row of papilliform processes on each side (*Ogcodes*) or with club-like processes in the two rows forming a V-shaped crest (*Pterodontia*), or without head processes but having a row of dorsomedial spines on thorax (*Astomella* Lamarck). Spiracles present on segments 2–5. Abdominal segment 1 and terminal three segments seemingly not divided into tergites and sternites.

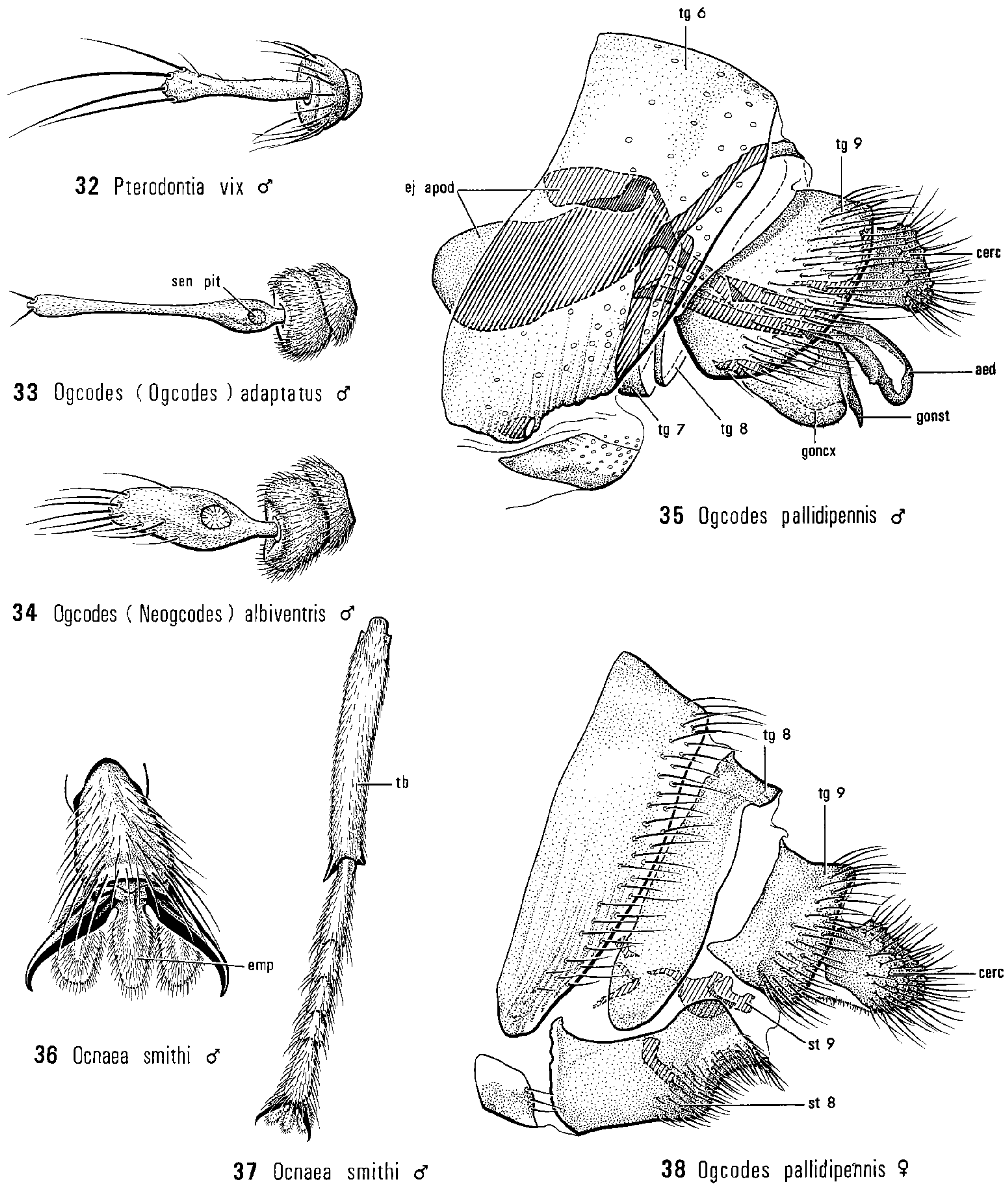
Larval and pupal references used for the above descriptions include those by Lamore (1960), Schlinger (1960*a*, 1960*b*, 1972*a*), and Schlinger (unpublished).

Biology and behavior. All known species of acrocerid flies are internal parasitoids of true spiders (Araneae) during their larval stages. They are usually solitary parasitoids, but several cases of successful duoparasitism are known (Jenks 1940, Schlinger 1972*a*).

Eggs are deposited in large numbers (up to 4000 a female) away from, but in the vicinity of their hosts. Known species of Nearctic genera deposit them as follows. *Ogcodes* spp. place their eggs on dead branches and twigs, and the eggs often appear in large clumps (Schlinger 1960*a*); *Acrocera* spp. place their eggs on green, living grass stems in a linear spiral (Schlinger, in Cole 1969); *Pterodontia* spp. deposit their eggs while in flight upon a vertical surface such as a tree trunk (King 1916); *Eulonchus* spp. deposit their eggs on the ground, while the females are flying (unpublished data), and the same is claimed for *Ocnaea* spp. (Jenks 1938); *Turbopsebius* spp. lay their eggs while in flight (Cole 1919) and have been observed to deposit them on the tops of shrubs. No data on egg deposition are recorded for *Lasia*.

All known species of Nearctic genera have a planidium-like first-instar larva, except *Acrocera* whose larvae lack the sclerotized segments and long setae characteristic of acrocerid planidia. These planidial larvae are capable of crawling and jumping around to search for their spider hosts. When a larva finds a host, it burrows through the spider's integument, usually at an intersegmental area of the leg or on the abdomen just behind the cephalothorax, and attaches itself to the book lung of the spider so that it can breathe outside air. Here it remains from about 4 months to several years in diapause. Species of the Acrocerinae tend to have a short second-instar larval stage, after which they rapidly molt to the third instar, feed voraciously for about 24 h internally, and emerge posteriorly from the host while still feeding internally for several hours. They free themselves from the host, pupate in the spider's premolting web, and emerge as adults in 7–10 days. Species of the Panopinae have similar habits except that: the location of and duration of time spent as a first-instar larva are not fully understood; the second-instar larval stage is long, perhaps even several years, as indicated by the placement of the second-instar larva inside the host spider (which is often a young one); and the feeding time of the third-instar larva is much longer, up to 4–5 days. Nothing has been published on the biology of philopotine species, but larvae of one species of *Megalybus* Philippi from Chile have been reared and they are spider parasitoids (unpublished data of the author).

The spider hosts for acrocerid flies of the world are poorly recorded. Nearctic hosts are recorded for *Ogcodes* (Schlinger 1960*a*), *Turbopsebius* (Schlinger 1952), *Acrocera* (Schlinger, in Cole 1969), *Ocnaea* (Jenks 1938), *Pterodontia* (King 1916), *Eulonchus* (Coyle 1971), and *Lasia* (Baerg 1958). An analysis of



Figs. 43.32–38. Antennae, terminalia, and legs: median view of antenna of (32) *Pterodontia vix* Townsend, (33) *Ogcodes* (*Ogcodes*) *adaptatus* Schlinger showing a small sensory pit on inner side, and (34) *Ogcodes* (*Neogcodes*) *albiventris* Johnson showing a large sensory pit; (35) left lateral view of male terminalia of *Ogcodes pallidipennis* Loew; (36) apex of tarsus and (37) tibia and tarsus of *Ocnaea smithi* Sabrosky; (38) left lateral view of female terminalia of *Ogcodes pallidipennis*.

Abbreviations: aed, aedeagus; cerc, cercus; ej apod, ejaculatory apodeme; emp, empodium; goncx, gonocoxite; gonst, gonostylus; sen pit, sensory pit; st, sternite; tb, tibia; tg, tergite.

these references, together with all other known world records, shows clearly that host specificity, i.e. species to species, rarely occurs. However, a clearer relationship exists between genera of flies and families or family groups of spiders. The more primitive panopine species are restricted to spider hosts in the suborder Orthognatha, whereas the more derived acrocerine species are restricted to the more advanced spiders of the suborder Labidognatha.

The adults of some genera (*Eulonchus, Lasia*) are rapid flyers, and are usually found probing for nectar in flowers; *Eulonchus* spp. have been shown recently to be important pollinators (Schlinger 1960*b*, Grant 1965). Species of other Nearctic genera (except *Philopota*) are not associated with flowers, have small or nonfunctional mouthparts, and vary from good (*Ocnaea, Pterodontia, Turbopsebius*) to poor fliers (*Ogcodes, Acrocera*). *Ocnaea* spp. appear to mimic bees closely, but they are so rare that behavioral observations have not been made.

Some important references dealing with general biology and host records of Nearctic acrocerids are: Lamore (1960) and Schlinger (1960*a*) for *Ogcodes*, Schlinger (1952) for *Turbopsebius*, King (1916) for *Pterodontia*, Schlinger (1960*b*) and Coyle (1971) for *Eulonchus*, Jenks (1938, 1940) for *Ocnaea*, Schlinger in Cole (1969) for *Acrocera*, and Baerg (1958) for *Lasia*.

Classification and distribution. This relict family is cosmopolitan, although species are unknown from any true oceanic island. About 500 described species are contained in 50 genera. Most genera are restricted to a given zoogeographic region; only two genera, *Ogcodes* and *Pterodontia*, are known from all zoogeographic regions. The Nearctic region has 59 described species, but known new species under study will increase this number to about 80.

Since the publication of the Catalog of North American Diptera (Stone *et al.* 1965), the only significant nomenclatural change is with the genus *Opsebius* Costa. The new genus *Turbopsebius* was proposed by Schlinger (1972*b*) for the four American species of *Opsebius*; the genus *Opsebius* was retained for the European and North African species. *Opsebius diligens* Osten Sacken was selected as the type species for *Turbopsebius*. Also, most of the western Nearctic species of this family were treated in some detail by Schlinger in Cole (1969).

The fossil record for Acroceridae is significant, although small. The oldest known acrocerid is *Archocyrtus gibbosus* Ussatchov described from the Upper Jurassic beds of Karatau, Russia, and it was placed in its own subfamily, Archocyrtinae. The known Tertiary Eocene fossils are *Prophilopota succinea* Hennig and *Eulonchiella eocenica* Meunier, both in the subfamily Philopotinae; and *Villalites electrica* Hennig and *Glaesoncodes completinervis* Hennig, both in the subfamily Acrocerinae. The relationships of these Baltic amber acrocerids were discussed fully by Hennig (1966, 1968), but a revised grouping of philopotine genera was proposed by Schlinger (1971). Other fossil flies described as acrocerid-like were *Protocyrtus jurassicus* Rohdendorf from Russia for the family Protocyrtidae (Rohdendorf 1938), which was later declared to belong to the order Hymenoptera (Ussatchov 1968); and *Acrocera hirsuta* Scudder from the Nearctic Oligocene (Scudder 1877, 1890) which, according to his limited description and figure, probably belongs in either the Bombyliidae or the Empididae.

Key to genera

1. Postpronota strongly developed (Fig. 3), coming together dorsally to form a shield in front of scutum .... PHILOPOTINAE.... ***Philopota*** Wiedemann
   3 spp.; Mexican Plateau; Brunetti 1926

   Postpronota weakly or well-developed, but never joining in front of scutum to form a shield 2

2. Tibia on each leg produced on outer apical margin into an acute spur, often with a shorter inner spur (Fig. 37). Antenna with long flagellum that is much longer than scape and pedicel combined, usually rounded or flattened throughout (Figs. 4–7), without distinct terminal styliform seta except in *Pterodontia*, which has long apical setae and a short flagellum. Eyes often not completely holoptic .... PANOPINAE.... 3

   Tibia not produced apically. Antenna usually with styliform flagellum (Figs. 9, 10), or with shortened rod-like flagellum (Figs. 33, 34), with or without apical setae. Eyes holoptic in both sexes .... ACROCERINAE.... 6

3. Proboscis and labella well-developed, functional, with apex extending from level of mid thorax to well beyond tip of abdomen. Antenna placed near middle of head (Figs. 6, 7) 4

   Proboscis barely visible, hidden behind small clypeus. Antenna placed at upper or lower part of head (Figs. 4, 5, 8) 5

4. Eyes widely separated below bases of antennae. Antenna inserted just above clypeus (Fig. 6). Palpus minute .... ***Lasia*** Wiedemann
   2 spp.; Southern Great Plains west to Arizona; Bequaert 1931, 1933

Eyes nearly contiguous below bases of antennae. Antenna inserted in middle of head, well above clypeus (Fig. 7). Palpus distinct .... ***Eulonchus*** Gerstäcker
7 spp.; western North America, Great Smoky Mountains in North Carolina; Sabrosky 1948, Schlinger 1960*b*

5. Antenna placed at or near vertex of head; flagellum long and strap-like or shorter and clavate (Figs. 4, 5), as long as or longer than height of head .... ***Ocnaea*** Erichson
9 spp.; southern U.S.A.; Sabrosky 1948, Aldrich 1932

Antenna placed just above subcranial margin; flagellum short, round or drawn out and thin, beset with several elongate setae (Figs. 8, 32) .... ***Pterodontia*** Gray
6 spp.; widespread; Sabrosky 1948

6. Antenna placed at or near vertex of head, with styliform flagellum (Figs. 9, 10) 7

Antenna placed just above mouthparts on ventral part of head (Fig. 11); flagellum short and rod-like with one to six apical setae (Figs. 33, 34) .... ***Ogcodes*** Latreille.... 8

7. Eye pilose. Antenna placed near vertex, but separated from ocellar tubercle by length of raised antennal tubercle (Fig. 10) .... ***Turbopsebius*** Schlinger
3 spp.; widespread; Sabrosky 1948, Schlinger 1972*b*

Eye bare. Antenna placed at vertex just in front of ocellar tubercle (Fig. 9) ..... ***Acrocera*** Meigen
16 spp.; widespread; Sabrosky 1948, Schlinger in Cole 1969

8. Flagellum long and thin, rod-like, eight to ten times longer than broad, beset with one to three short apical setae (Figs. 11, 33); small sensory pit present at base (Fig. 33). Proboscis hidden by a membrane, not visible in dead specimens .... ***Ogcodes*** (***Ogcodes*** Latreille)
16 spp.; widespread; Schlinger 1960*a*

Flagellum short, about three times longer than broad, beset with five or six long apical setae (Fig. 34); large sensory pit present at base (Fig. 34). Proboscis visible in dead specimens .... ***Ogcodes*** (***Neogcodes*** Schlinger)
1 sp., *albiventris* Johnson; boreal; Schlinger 1960*a*

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NEMESTRINIDAE 44

H. J. TESKEY

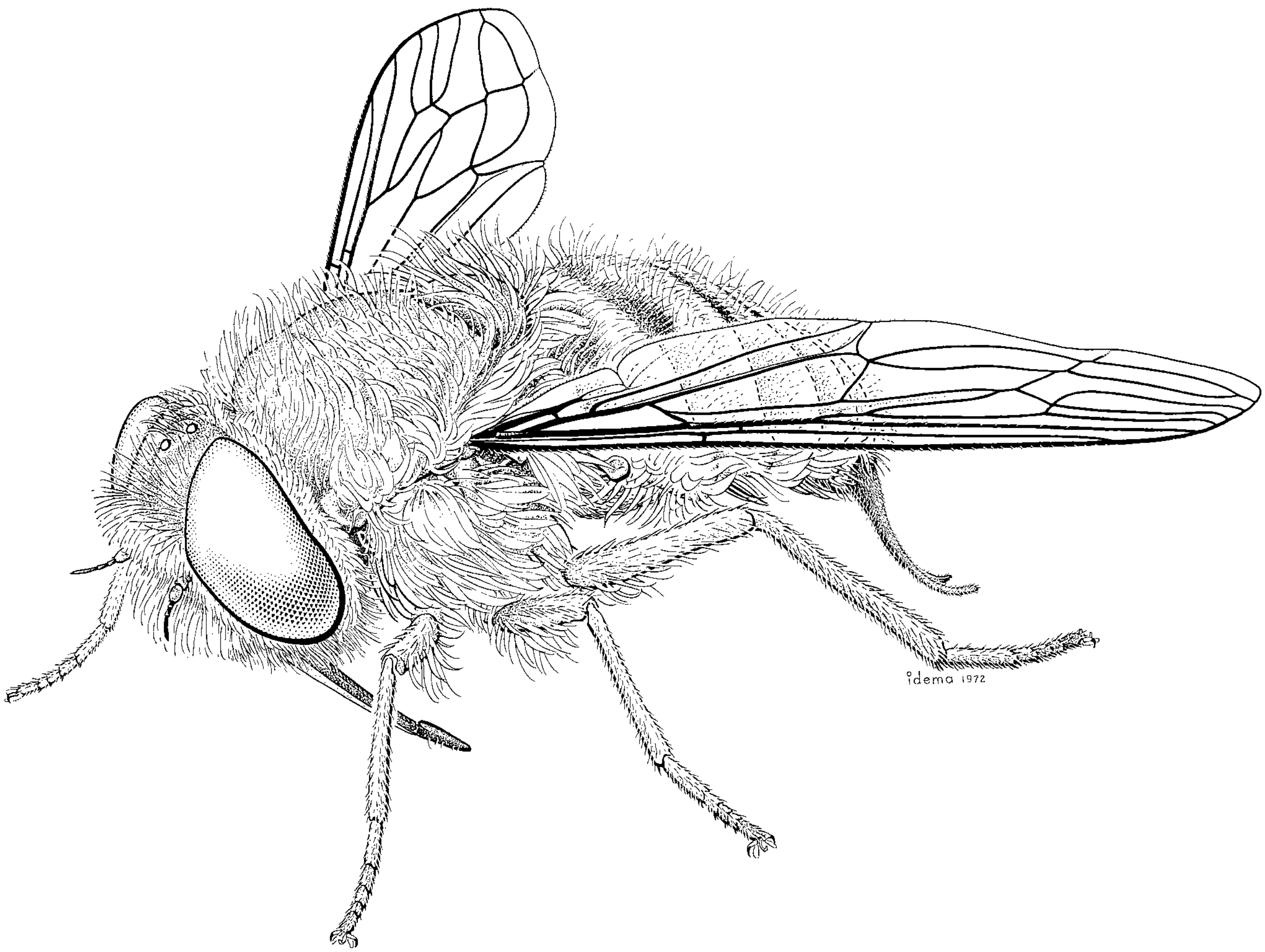


Fig. 44.1. Female of *Neorhynchocephalus sackenii* (Williston).

Moderate to large rather stout flies, variously colored, sometimes with banded or striped thorax and abdomen (Fig. 1). Bristles lacking, but many fine hairs present; hairs sometimes so long and dense as to give a bee-like appearance. Wing hyaline, variously infuscated, or opaque; venation complete, with an oblique linear combination of veins and crossveins crossing apical third of wing, and with radial veins and most medial veins running parallel to hind margin of wing and ending anterior to wing apex.

Adult. Head: narrower to slightly wider than thorax, nearly round to wider than high in anterior view (Fig. 2). Eyes often holoptic or approaching so in male, dichoptic in female (except in some *Hirmoneura* Meigen); each eye densely hairy or bare, moderate to large in size, with upper facets enlarged in male. Ocelli usually well-developed, arranged as an equilateral triangle or with anterior ocellus farther removed; when anterior ocellus not spaced equilaterally, ocellar prominence usually divided by a transverse depression behind anterior ocellus. Frons, at antennae, rather narrow to almost half width of head. Antennae (Figs. 1, 2) situated close together or wide apart in direct relation to frontal width; each antenna moderate to small, consisting of three subequal segments, the scape, pedicel, and first flagellomere, and a terminal stylus usually of three flagellomeres; first flagellomere oval to conical. Facial area fairly narrow and parallel-sided in Hirmoneurinae, broader and more or less strongly diverging ventrally in other groups, and often composed almost totally of the clypeus; clypeus in Nemestrininae often snout-like, but reduced in size in some Trichopsideinae; parafacial sclerites in Trichopsideinae covering up to half of facial area. Proboscis vestigial or fully developed, short with broad labella to long and slender with narrow labella; when long proboscis present, it is hinged basally and when at rest often projecting posteriorly between coxae; palpus two-segmented, with segments subequal and cylindrical.

Thorax: length, width, and height approximately equal; postpronotum small, usually hidden by head; mesonotum convex; postalar callus strongly developed; scutellum short, broad, usually with a submarginal shallow groove; subscutellum often present, sometimes large. Legs rather slender, hairy; midleg and hindleg progressively longer than foreleg; first tarsomere of each leg longer than other tarsomeres, often longer than others combined; tarsal claws well-developed; empodia and pulvilli sometimes very small.

Wing (Fig. 3) well-developed, usually rather slender; anal angle normally rounded; alula poorly or well developed. Venation normally complete, with at least portions of C, Sc, four branches of R, M_1, M_2, M_3, CuA_1, CuA_2, and A_1 usually present, and usually with several cells in addition to cells br, bm and d closed; veins in apical half of wing running parallel to front and hind margins of wing, usually ending anterior to wing apex; so-called diagonal vein present, obliquely crossing wing at apical third of wing length in nearly a straight line, and consisting of a combination of elements of Rs, R_{4+5}, crossvein r-m, M_1, M_2, M_3, and CuA_1.

Abdomen: usually as wide as or wider than thorax, widest near middle, with seven pairs of spiracles. Terminalia in male not rotated; epandrium large, usually shallowly incised posteriorly; cercus well-developed; hypandrium absent in Nearctic genera, but usually present in other genera, although sometimes fused with gonocoxites; aedeagus usually a simple tube. Female with two spermathecae; ovipositor of two types, either with terminalia telescoped and cerci short, or with cerci greatly lengthened, appressed to each other, and shaped like curved sabers.

Larva. Four larval stages. First stage planidiiform, approximately 1–1.5 mm long, metapneustic. Head skeleton very slender, delicate; cranium divided into two slender rods with apices enlarged and darkened; two tentorial arms present ventrally; mandible slender. Body segments usually numbering 11, or 12 if a cephalic division evident; every segment or all but mesothoracic and metathoracic segments with a pair of long slender setiform projections ventrally; projections sometimes hooked apically; terminal abdominal segment also bearing a transverse row of four or six such projections apically.

Second and third stages cigar-shaped, about seven times longer than greatest width, 12-segmented including cephalic segment, and covered in a thin smooth transparent integument. Head skeleton similar in both stages, differing mainly in size, often weakly sclerotized; cranium broad; slender tentorial arms present; mouthparts comprising sharply pointed mandibles and fleshy maxilla bearing minute palpi. Posterior spiracles in second stage each a simple pore, but in third stage comprising 7–12 oval pores arranged in a circle around a central scar.

Fourth stage stout, about three or four times longer than greatest width, 12-segmented including cephalic segment, and covered in a leathery integument (Fig. 4). Head skeleton (Fig. 5) with cranium constricted medially and rounded behind; mandible absent; maxilla darkly sclerotized, broad and spatulate, ventrally somewhat concave, prominently projecting from anterior of larva. Posterior spiracles similar to those of third stage, but each with 18–26 pores encircling an ecdysial scar. Each body segment roughened by wart-like projections arranged in a systematic order; most prominent warts forming a scalloped transverse ridge apically on terminal segment behind and lateral to posterior spiracles (Fig. 4).

Pupa. Obtect. Head narrower and shorter than thorax; thorax narrower and about one-third length of abdomen; wing sheath and leg sheaths of equal length, reaching second abdominal segment. Head usually with sheaths for mouthparts and antennae mirroring size of adult structures, and with two pairs of slightly elevated rough-surfaced calluses anterior to antennal sheaths. Thorax with a callus similar to those on head, and situated laterally near base of each wing sheath. Thoracic and abdominal spiracles bow-shaped slits, mounted on sides of distinctive prominences resembling shiny smooth globules of dark amber; slits located on posterior side of thoracic prominence and on anterior side of abdominal prominences. Abdominal segments 1–7 each encircled by a row of erect spines, three of which on each pleuron are long and hooked apically. Abdominal segment 8 strongly tapered posteriorly to a pair of sclerotized apically compressed and pointed tubercles curving dorsally; stout spines in a transverse row present laterally near base of segment; a pair of spines present ventrally on slightly expanded common base of caudal tubercles.

Biology and behavior. Immature stages for only three genera have been described (Crouzel and Salavin 1943, Fuller 1938, Greathead 1958, Handlirsch 1882, Léonide 1964, Prescott 1955, Spencer 1958): *Neorhynchocephalus* Lichtwardt, *Trichopsidea* Westwood (=*Symmictus*), and *Hirmoneura* Meigen. The descriptions of the larval and pupal stages given above, as well as the life history that follows, are based mainly on these works. Although these described species represent all genera occurring in the Nearctic region, they may not typify the entire family.

At least one species in each of the three genera exhibits hypermetamorphosis. The first of the four larval stages differs notably from the final three as an adaptation to a different, usually terrestrial, environment.

Knowledge of *Hirmoneura* is sparse. Larvae of known species have a different host than do the other two genera. They also differ structurally in their lack of a respiratory tube.

All Nemestrinidae whose larvae are known are parasites. Grasshoppers are the hosts of *Trichopsidea* spp. and *Neorhynchocephalus* spp., and the immature forms of scarabaeid beetles are the hosts of *Hirmoneura* spp. Eggs are deposited in holes or crevices in posts, tree trunks, and other elevated objects near large populations of host insects. Between 4000 and 5000 eggs are laid by a single female. They hatch in about 15 days into minute, planidial larvae, the form in which they are infective. They encounter suitable hosts by chance, aided by wind dispersion at least for *Trichopsidea* and *Neorhynchocephalus*. The larva enters the hemocoel of the host through the intersegmental cuticle on the thorax or abdomen, or through the trachea via a spiracle. The exact site of entry is species specific. The larva molts to the second stage soon after having entered the hemocoel. Apparently essential for the survival of the larvae of *Trichopsidea* and *Neorhynchocephalus* within the hemocoel is the development of a respiratory tube. This tube has a characteristic spiral thickening of its wall. One end opens to the exterior at the point where the larva entered the host, and the other end forms a tight-fitting sleeve around the posterior end of the larva. The respiratory tube is apparently renewed with each molt. The larva always lies with its head directed toward the anterior of the host. It feeds mainly on the fat-body and ovariole tissues of the host. Usually the entire ovary is destroyed, and although the host sometimes survives the parasitism for a brief period after the larva emerges, it is unable to reproduce.

The mature larva leaves the host in the fall, usually through the intersegmental membrane behind the posterior coxae, and enters the soil to overwinter. Pupation occurs the next year. The adult actively oviposits during late June and July. The life-span is fairly short. *Trichopsidea clausa* (Osten Sacken) is apparently incapable of feeding because its mouthparts are vestigial. Other species with well-developed mouthparts have been observed feeding on flowers.

The nemestrinids are important in controlling grasshopper populations. Parasitism of up to 90% has been recorded in large grasshopper populations (Prescott 1960).

Classification and distribution. The family is well known, and its classification is firmly established on Bernardi's (1973) generic revision. Five subfamilies containing 254 world species in 15 genera are recognized. A sixth subfamily contains several fossil species. Members of the family are found in all zoogeographic regions, but best representation occurs in the southern hemisphere, which contains nearly two-thirds of the species in all but three genera. Only six species in three genera are known from the Nearctic region. These are distributed among the subfamilies Nemestrininae, Hirmoneurinae, and Trichopsideinae (Bequaert 1965). However, Bernardi's work resulted in a shift of *Neorhynchocephalus* from the Nemestrininae to the Trichopsideinae as a sister group of *Trichopsidea*.

Fossils of 12 species of Nemestrinidae have been described, five from the Oligocene deposits of Florissant, Colo., six from the Jurassic deposits of Karatau, Kazachstan, and one from the Jurassic deposits of Eichstätt, Germany (Bernardi 1973).

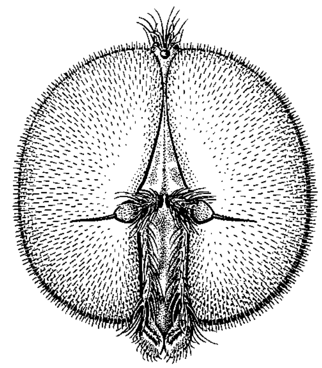
Key to genera

1. Face below antennae at least as wide as eye, and widening below (Fig. 1). Antennae separated by at least half length of one antenna 2

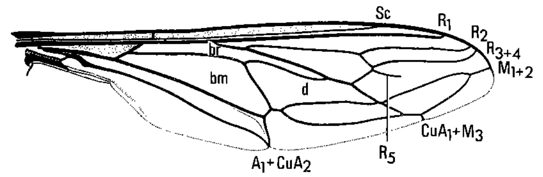
   Face much narrower than width of eye, nearly parallel-sided (Fig. 2). Antennae separated by much less than half length of one antenna .... ***Hirmoneura*** Meigen
   3 spp.; southwestern; Bequaert 1920

2. Proboscis well-developed, longer than head (Fig. 1). Five or six veins reaching C between end of Sc and apex of wing (Fig. 1) .... ***Neorhynchocephalus*** Lichtwardt
   2 spp.; western, south to Florida; Bequaert 1934

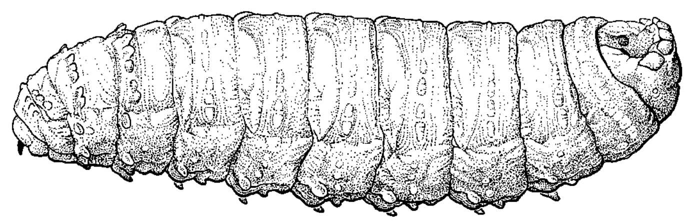
   Proboscis shorter than head, or vestigial. Four veins reaching C between end of Sc and apex of wing (Fig. 3) .... ***Trichopsidea*** Westwood
   1 sp., *clausa* (Osten Sacken); Manitoba and Kansas west, south to Florida



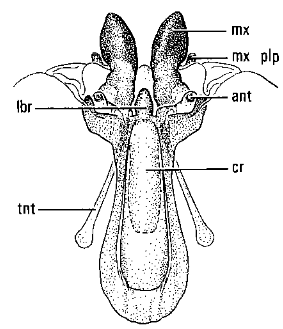
2 Hirmoneura texana ♀



3 Trichopsidea clausa ♂



4 Trichopsidea clausa



5 Trichopsidea clausa

Figs. 44.2–5. Head, wing, and details of larva: (2) head of *Hirmoneura texana* Cockerell; (3) wing of *Trichopsidea clausa* (Osten Sacken); (4) larva and (5) larval head of *Trichopsidea clausa*.
Abbreviations: ant, antenna; cr, cranium; lbr, labrum; mx, maxilla; mx plp, maxillary palpus; tnt, tentorium.

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BOMBYLIIDAE 45

J. C. HALL

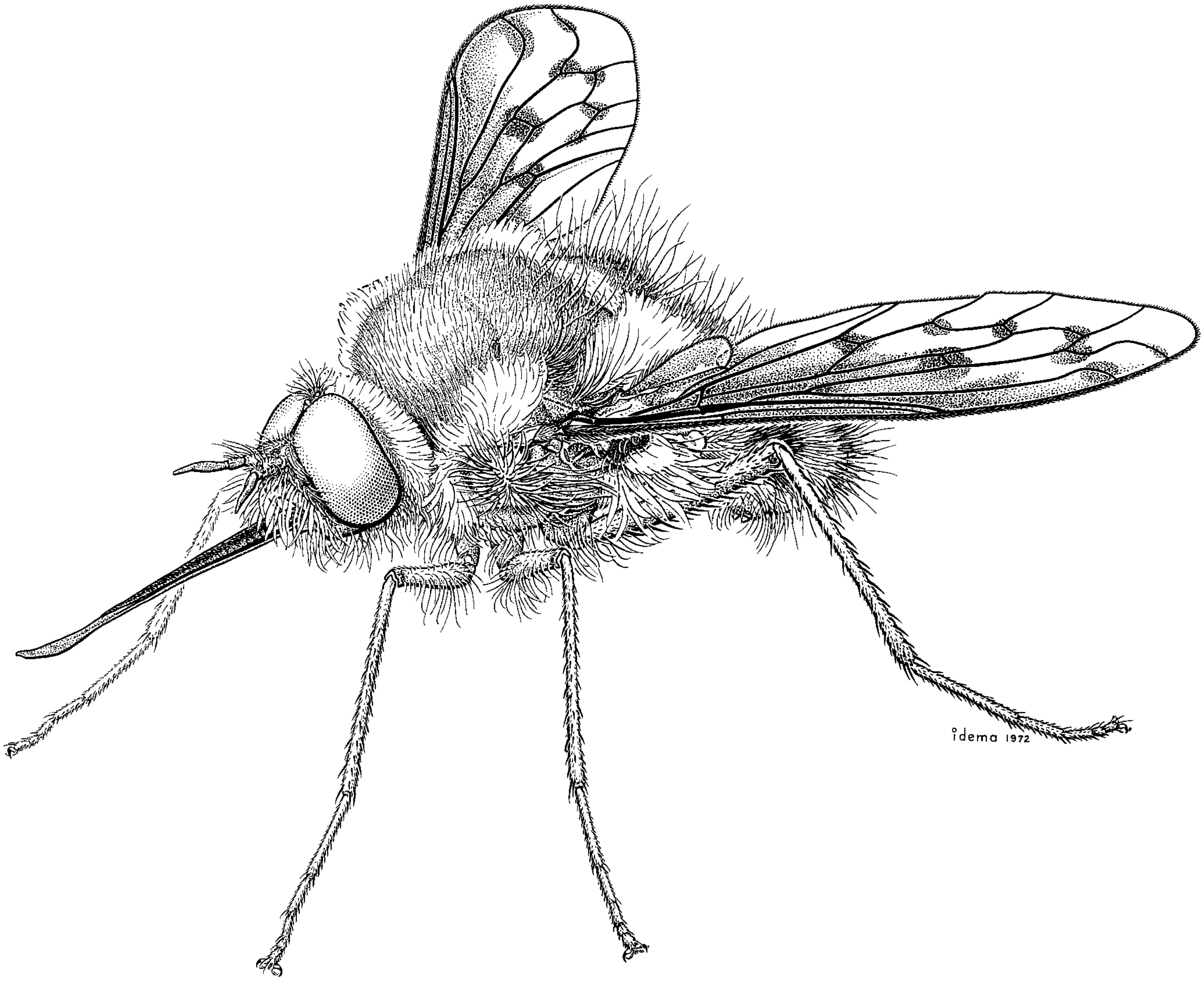


Fig. 45.1. Male of *Bombylius pygmaeus* Fabricius.

Small to large flies, variously hued with bright colors (Fig. 1). Wing often patterned. Body generally covered with delicate hairs or scales, or both. Thoracic bristles rarely strongly developed. Proboscis often very long. Crossvein m-cu always absent.

Adult. Head: round or transverse (Figs. 2–10), narrower than or equal to width of thorax or occasionally wider than thorax. Occiput flat, swollen or concave in middle, but when concave having a deep fovea behind ocellar tubercle; ocelli present. Proboscis either long and porrect with narrow labella or short with large fleshy labella; palpus usually small, one- or two-segmented. Antenna (Figs. 51–58) with one to four flagellomeres; first flagellomere enlarged; remaining flagellomeres forming a stylus, usually terminal (Figs. 57, 58), but if dorsal, arising from a small sulcus (Fig. 52); first flagellomere sometimes also terminating in a tuft of hair (Figs. 55, 56). Eye bare, frequently holoptic in male and dichoptic in female.

Thorax: flattened or humped, with or without bristles; bristles usually not strongly developed (Figs. 49, 50). Scutellum with bristles on posterior margin or without bristles. Pleuron pilose or bare, usually with a few hairs on anepisternum. Legs slender, with or without bristles, almost always with small or large apical tibial bristles; foreleg frequently thinner and shorter than hindleg; pulvilli present or absent. Wing (Figs. 11–48) pictured or hyaline; Rs unbranched in some minute species (Fig. 26), but usually with three branches (R_{2+3}, R_4, and R_5) (Figs. 29–34); occasionally with a crossvein between R_{2+3} and R_4 (Figs. 11, 17) or a partial crossvein (Figs. 12, 18); R_{2+3} usually ending in C toward apex of wing, but sometimes short and terminating in R_1 (Figs. 27, 28); M usually with two free branches (Fig. 11), occasionally with only one either because M_1 ends in R_5 (Figs. 19, 21) or because M_2 is absent (Figs. 14–16); cell dm usually present, but sometimes lacking because of absence of crossvein dm-cu (Fig. 26) or crossvein bm-cu (Fig. 28); cell cu*p* open or closed in wing margin (Fig. 26) or closed before margin and petiolate (Fig. 29); anal lobe enlarged in minute species (Figs. 26–28), reduced in larger ones; alula well-developed or lacking.

Abdomen: short, broad, and elongate or cylindrical, consisting of six to eight visible segments, rarely with bristles, though sometimes densely covered with hair or scales or both, or nearly bare. Ovipositor with or without spines on either side. Male in most genera with terminalia rotated either 90° or 180°; tergite 9 usually large, enclosing most genital parts; gonocoxite usually large and medially divided, but in some genera (*Mythicomyia* Coquillett) small and variously shaped; gonostylus, small, usually apically hooked, one-segmented; aedeagus sometimes one tubular piece, bifid or trifid and of various shapes, with gonopore nearly always terminal; paramere variously shaped; aedeagal apodeme usually ovoid.

Larva. Known for few species. First instar slender, planidiiform, with a pair of long caudal bristles, and amphipneustic although sometimes with abdominal spiracles weakly developed. Mature larva crescentic, tapering at both ends; abdomen with nine segments; integument bare; anterior and posterior spiracles present. Mouthparts (Figs. 59–60) large compared with body, consisting of a median pair of tong-like mandibles and long slender maxillae each bearing a club-shaped palpus tipped with long bristles. Head and thorax each with bristles; those on thorax paired. Small prolegs sometimes present on abdominal segments.

Pupa. Free, somewhat elongated, with several pairs of heavily sclerotized horns or prongs on head (Figs. 61, 62). Each abdominal segment provided dorsally with a row of alternating hooks and long strong bristles; ventrally each segment with a row of short hair; abdomen terminating in one or two pairs of short or long prongs.

Biology and behavior. Very little is known of the life histories of the members of this family. The immature stages, mainly the pupa, are known for only 13 of the 62 described genera from the Nearctic region; seven of these are in the Exoprosopinae. As far as is known all species are either parasitic, feeding on the larvae or pupae or both of various species of Lepidoptera, Hymenoptera, Coleoptera, Diptera, and Neuroptera, or they are predacious on the egg pods of grasshoppers (Acrididae).

Classification and distribution. The Bombyliidae are world wide in distribution, found nearly everywhere except in the colder areas of the north and south. The species are most abundant in the temperate regions of the world. Approximately 800 Nearctic species and subspecies have been described. Many undescribed forms exist.

Key to genera

1. Hind margin of eye entire, at most sinuous, not sharply indented, without a bisecting line dividing facets (Figs. 3, 4, 6, 7). Basal section of Rs (as in Fig. 12) usually short; R_{2+3} usually branching obliquely from R_{4+5} (Figs. 11, 22). Occiput variable .... HOMOEOPHTHALMAE....2

   Hind margin of eye sharply and usually deeply indented, with a narrow line dividing facets (Figs. 2, 5). Basal section of Rs long (as in Fig. 17); R_{2+3} usually branching at a right angle from R_{4+5} (Figs. 38–48). Occiput with a deep central cavity (as in Fig. 8) .... TOMOPHTHALMAE....38

2. Occiput flat or rounded, without a deep central cavity (Fig. 9); occipital fringe typically placed next to eye margin 5

   Occiput somewhat swollen, bilobate above, and with a deep central cavity (Fig. 8); fringe placed on edge of cavity away from eyes .... CYLLENIINAE....3

3. Cell r_{2+3} not divided by a crossvein (Fig. 12). Ocellar tubercle situated near middle of frons or at or near vertex. Body bare or nearly bare 4

   Cell r_{2+3} divided in two parts by a crossvein between R_{2+3} and R_4 (Fig. 11). Ocellar tubercle placed near vertex. Body nearly bare .... ***Amphicosmus*** Coquillett

   4 spp.; western U.S.A.; Hall 1957

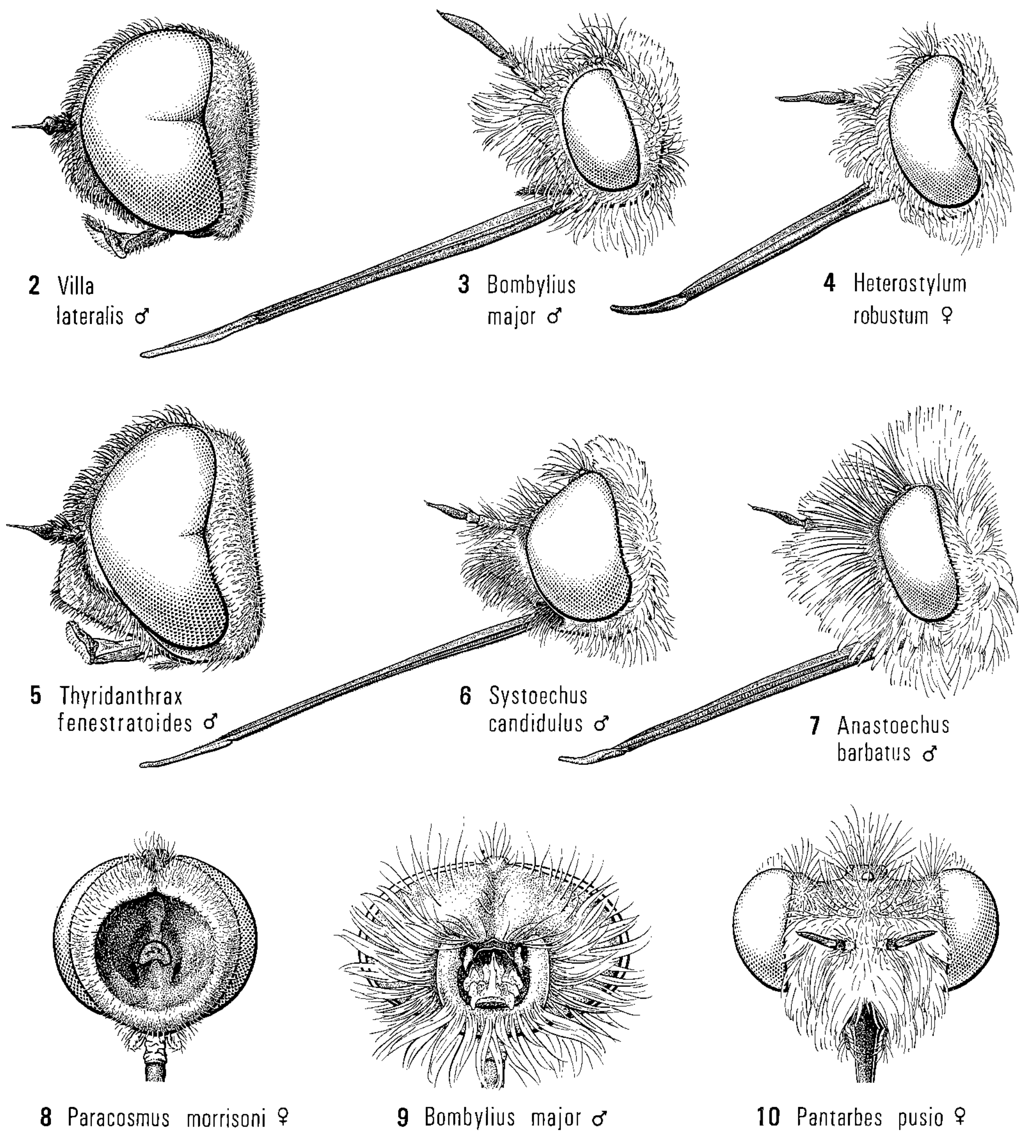
4. Ocellar tubercle situated near middle of frons. First flagellomere rather broad, tapering to apex; apex sometimes narrowly truncate. Body nearly bare. Small species ..***Metacosmus*** Coquillett
   3 spp.; western and eastern U.S.A.; Melander 1950*b*

   Ocellar tubercle situated at or near vertex. First flagellomere distinctly truncate at apex. Body bare or nearly so. Larger species ....***Paracosmus*** Osten Sacken
   5 spp.; western U.S.A.; Melander 1950*b*

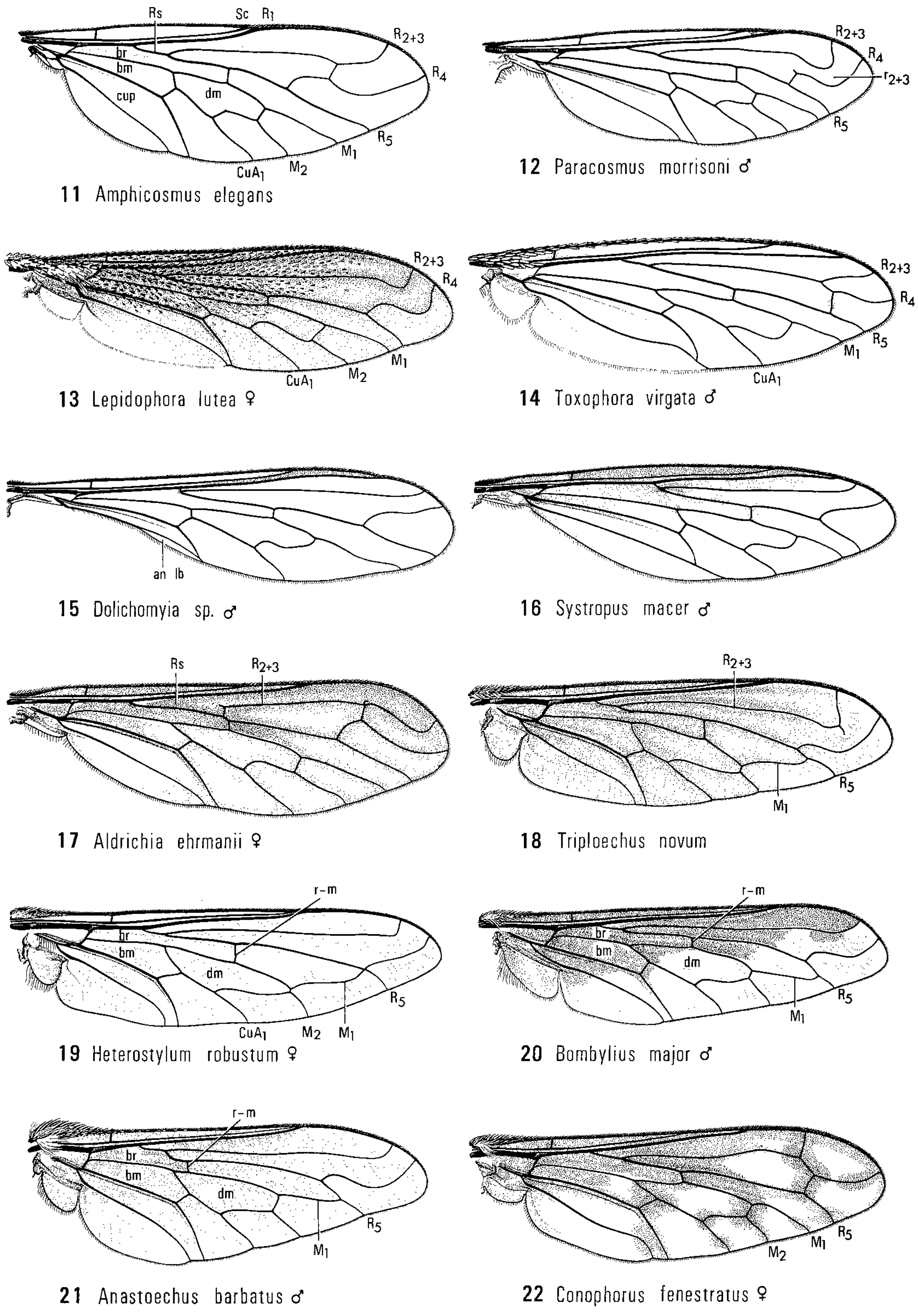
5. Pronotum well-developed, prominent (Fig. 49); thoracic bristles strong, curved posteriorly. Mesonotum more or less humped, covered with scales ........................TOXOPHORINAE....6

   Pronotum not developed, difficult to see (Fig. 50); thoracic bristles not obviously strongly developed 7

6. M_2 present (Fig. 13); R_{2+3} and R_4 not connected by crossvein; scales present toward base of wing. Antenna long, densely covered with long scales (Fig. 51) ....***Lepidophora*** Westwood
   3 spp.; widespread; Paramonov 1949



Figs. 45.2–10. Heads: lateral view of (2) *Villa lateralis* (Say), (3) *Bombylius major* Linnaeus, (4) *Heterostylum robustum* (Osten Sacken), (5) *Thyridanthrax fenestratoides* (Coquillett), (6) *Systoechus candidulus* Loew, and (7) *Anastoechus barbatus* Osten Sacken; posterior view of (8) *Paracosmus morrisoni* Osten Sacken and (9) *Bombylius major*; (10) anterior view of *Pantarbes pusio* Osten Sacken.



Figs. 45.11–22. Wings: (11) *Amphicosmus elegans* Coquillett; (12) *Paracosmus morrisoni* Osten Sacken; (13) *Lepidophora lutea* Painter; (14) *Toxophora virgata* Osten Sacken; (15) *Dolichomyia* sp.; (16) *Systropus macer* Loew; (17) *Aldrichia ehrmanii* Coquillett; (18) *Triploechus novum* (Williston); (19) *Heterostylum robustum* (Osten Sacken); (20) *Bombylius major* Linnaeus; (21) *Anastoechus barbatus* Osten Sacken; (22) *Conophorus fenestratus* (Osten Sacken) (*continued*).

Abbreviation: an lb, anal lobe.

M_2 absent (Fig. 14); R_{2+3} and R_4 sometimes connected by crossvein; scales lacking. Antenna long, but not densely covered with long scales .... ***Toxophora*** Meigen

7 spp.; widespread; Coquillett 1891

7. Metasternum elongate, widely separating mid and hind coxae. Abdomen long, slender, usually apically swollen. Body without bristles .... SYSTROPINAE....8

Metasternum normal, not widely separating mid and hind coxae. Abdomen short, round or cylindrical. Body with at least small bristles or setae 9

8. Pedicel about as wide as long; first flagellomere long, conical. Abdomen cylindrical or tapering. Anal lobe much reduced (Fig. 15). Metepimeron only a little enlarged .... ***Dolichomyia*** Wiedemann

1 sp., *gracilis* Williston; Arizona and Colorado; Painter and Painter 1963

Pedicel much longer than wide; first flagellomere flattened. Abdomen enlarged apically. Anal lobe only slightly reduced (Fig. 16). Metepimeron greatly enlarged (Fig. 50) .... ***Systropus*** Wiedemann

4 spp.; widespread; Painter and Painter 1963

9. At least mid and hind tibiae with bristles other than preapical or apical bristles. Proboscis usually elongate; palpus one- or two-segmented. Thorax with or without strong bristles 10

Bristles on legs other than apical tibial bristles lacking. If bristles present, then palpus two-segmented; proboscis short or elongate. Thorax without strong bristles 23

10. Abdomen broad or ovate, at least not elongate. Antennae approximate at base .... BOMBYLIINAE....11

Abdomen elongate, cylindrical, sometimes expanded apically, at least not ovoid or round. Antennae approximate or separated at base 21

11. R_{2+3} arising from R_{4+5} at a right angle and close to crossvein r-m (Fig. 17); R_4 straight or nearly so. Pulvilli large .... ***Aldrichia*** Coquillett

2 spp.; eastern U.S.A.

R_{2+3} arising from R_{4+5} at an acute angle (Fig. 18); R_4 often curved forward or recurved apically. Pulvilli normal 12

12. M_1 ending in R_{4+5} some distance from wing margin (Figs. 18–21) 13

M_1 ending in wing margin (Fig. 22), or in R_{4+5} close to wing margin (as in Fig. 36) 17

13. R_{2+3} curved upward apically to meet C at a right angle or less (Fig. 18); R_{2+3} and R_3 sometimes connected by a crossvein .... ***Triploechus*** Edwards

4 spp.; southwestern U.S.A.; Hall 1975*a*

R_{2+3} not strongly curved apically, and meeting C at an angle greater than 90°; no crossvein connecting R_{2+3} and R_4 14

14. Crossvein r-m placed at or beyond middle of cell dm, making cell br much longer than cell bm (Figs. 19, 20) 15

Crossvein r-m placed near base of cell dm, making the two basal cells equal in length or nearly so (Fig. 21) 16

15. Posterior margin of eye deeply sinuate (Fig. 4). Head as wide as or wider than width of thorax .... ***Heterostylum*** Macquart

6 spp.; widespread; Painter 1930

Posterior margin of eye entire, not sinuate (Fig. 3). Head small, rarely if ever as wide as thorax .... ***Bombylius*** Linnaeus

35 spp.; widespread; Painter 1940, Johnson and Johnson 1975

16. Face prominent with outline distinct, loosely pilose (Fig. 6). Cell dm acute apically. Body pile usually more or less uniform .... ***Systoechus*** Loew

5 spp.; widespread; Painter 1962

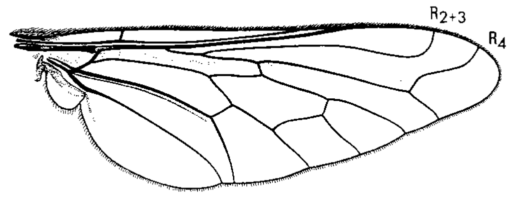
Face rounded, with outline obscured by long dense facial hair (Fig. 7). Cell dm obtuse apically (Fig. 21). Body pile shaggy in appearance .... ***Anastoechus*** Osten Sacken

3 spp.; widespread; Hall 1956

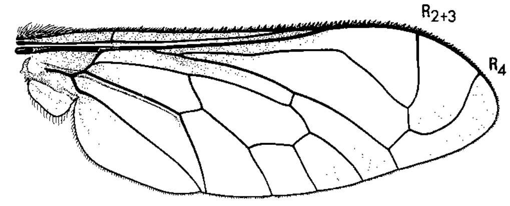
17. Scape greatly thickened; antenna as long as head .... ***Conophorus*** Meigen

19 spp.; western North America; Priddy 1958

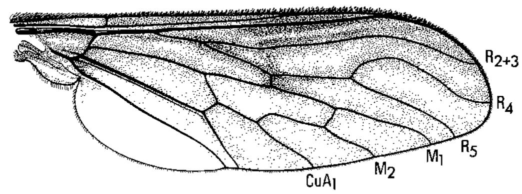
Scape linear, at most only slightly swollen; antenna longer than head 18



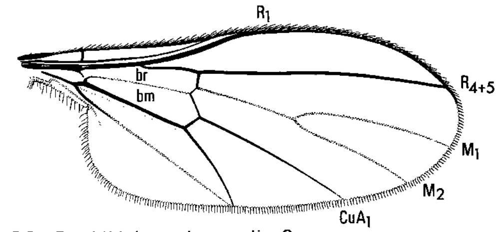
23 Sparnopolius lherminierii ♂



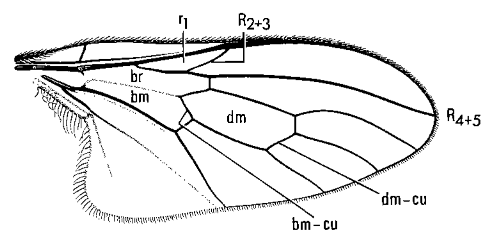
24 Lordotus striatus ♂



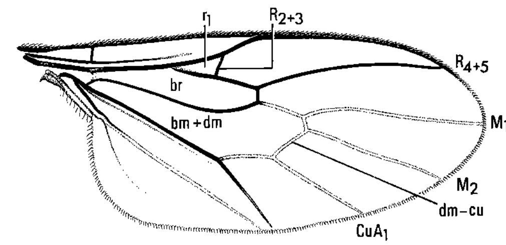
25 Thevenemyia celer ♂



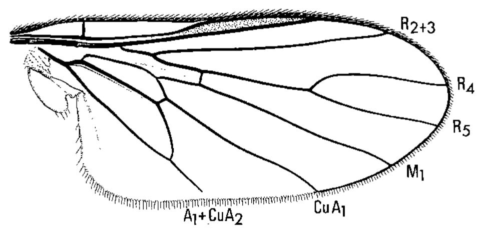
26 Empidideicus humeralis ♀



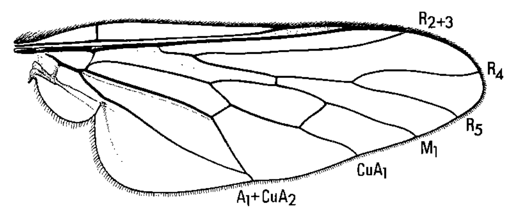
27 Mythicomyia rileyi ♂



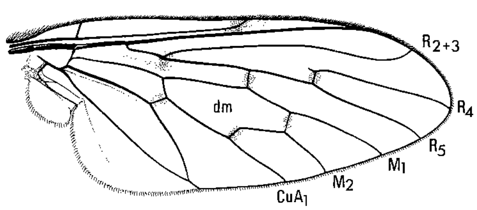
28 Glabellula crassicornis ♀



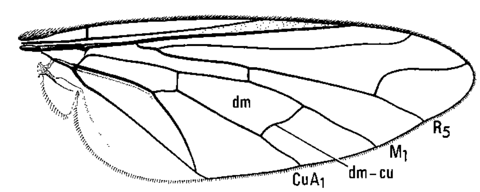
29 Apolysis timberlakei ♀



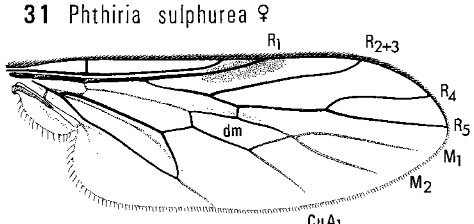
30 Oligodranes cincturus ♂



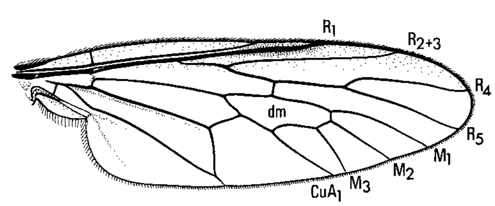
31 Phthiria sulphurea ♀



32 Geron albarius ♀

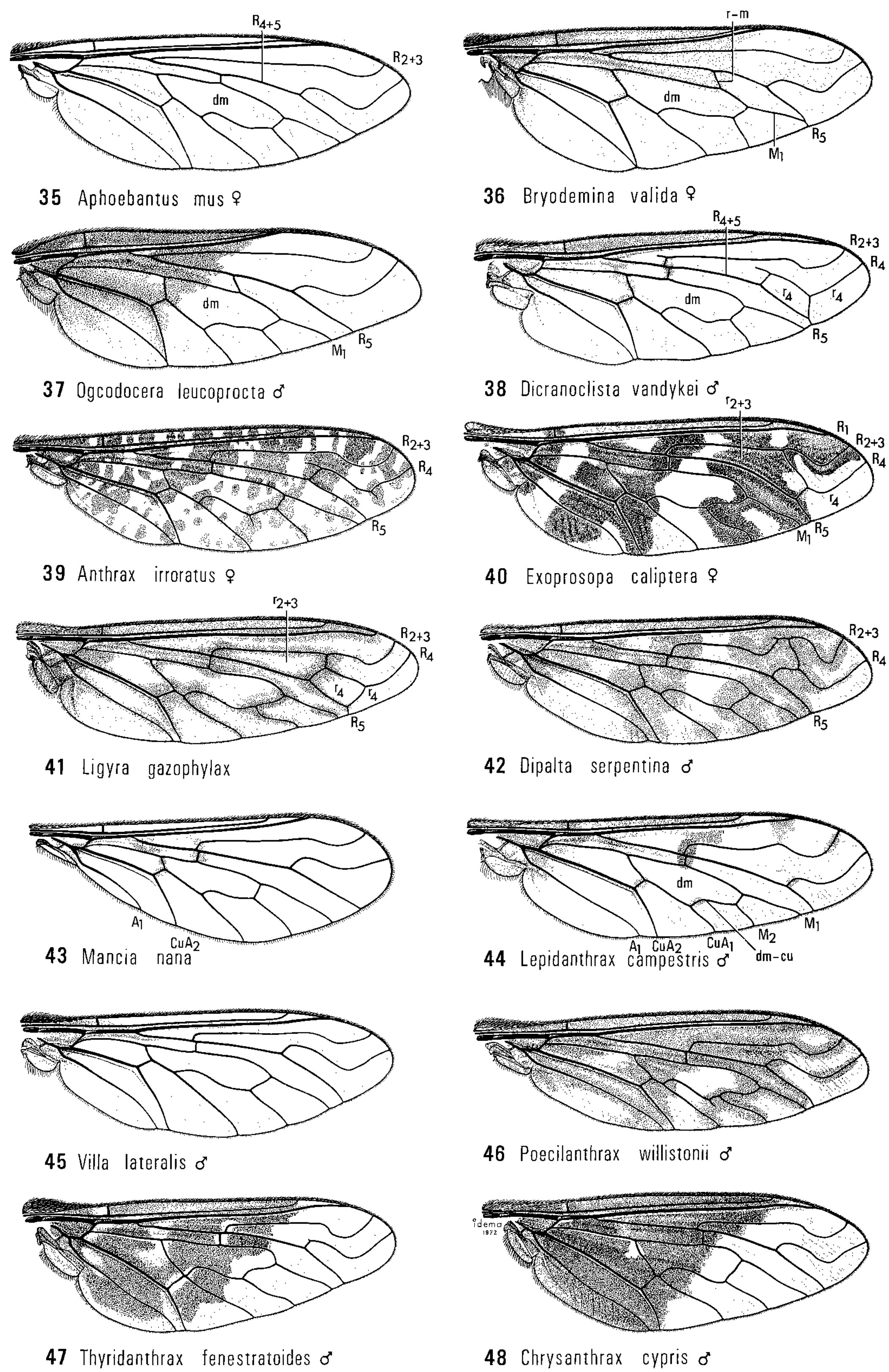


33 Prorates claripennis ♀



34 Caenotus inornatus ♀

Figs. 45.23–34. Wings (*continued*): (23) *Sparnopolius lherminierii* (Macquart); (24) *Lordotus striatus* Painter; (25) *Thevenemyia celer* (Cole); (26) *Empidideicus humeralis* Melander; (27) *Mythicomyia rileyi* Coquillett; (28) *Glabellula crassicornis* (Greene); (29)*Apolysis timberlakei* Melander; (30) *Oligodranes cincturus* (Coquillett); (31) *Phthiria sulphurea* Loew; (32) *Geron albarius* Painter; (33) *Prorates claripennis* Melander; (34) *Caenotus inornatus* Cole (*continued*).



Figs. 45.35–48. Wings (*concluded*): (35) *Aphoebantus mus* (Osten Sacken); (36) *Bryodemina valida* (Wiedemann); (37) *Ogcodocera leucoprocta* (Wiedemann); (38) *Dicranoclista vandykei* (Coquillett); (39) *Anthrax irroratus* Say; (40) *Exoprosopa caliptera* (Say); (41) *Ligyra gazophylax* (Loew); (42) *Dipalta serpentina* Osten Sacken; (43) *Mancia nana* Coquillett; (44) *Lepidanthrax campestris* (Coquillett); (45) *Villa lateralis* (Say); (46) *Poecilanthrax willistonii* (Coquillett); (47) *Thyridanthrax fenestratoides* (Coquillett); (48) *Chrysanthrax cypris* (Meigen).

18. R_{2+3} and R_4 not connected by a crossvein (Fig. 23); apical half of R_{2+3} at most only slightly curved forward 19

R_{2+3} connected to R_4 by a crossvein; apical half of R_{2+3} strongly curved forward (Fig. 24) 20

19. Face bare, at most with a few hairs present toward antennae. Scape sometimes slightly swollen. Hair on body strikingly uniform. No bristles on hind femur .... ***Sparnopolius*** Loew

5 spp.; widespread; Painter 1940

Face quite pilose. Scape long, narrow. Pile on body not uniform. Bristles present on hind femur .... ***Parabombylius*** Williston

9 spp.; southern and western U.S.A.; Curran 1930*a*

20. Scutellum sulcate in middle of posterior margin; sulcus covered with a spot of tomentum. Body loosely hairy .... ***Geminaria*** Coquillett

2 spp.; Arizona, California; Painter 1940

Scutellum not longitudinally sulcate, uniformly tomentose overall. Body more densely pilose .... ***Lordotus*** Loew

22 spp.; western U.S.A.; Hall 1954

21. M_1 ending in R_5 rather than at wing margin (as in Fig. 21). Abdomen short, broad. Antennae widely separated (Fig. 10). Head as wide as or wider than thorax .... CYTHEREINAE.... ***Pantarbes*** Osten Sacken

3 spp.; western U.S.A.; Painter 1940

M_1 ending in wing margin (Fig. 25). Abdomen long, slender. Antennae close together. Head narrower than thorax .... ECLIMINAE.... ***Thevenemyia*** Bigot.... 22

22. R_{2+3} and R_4 not connected by a crossvein (Fig. 25). Palpus elongate; apical palpal segment not greatly enlarged .... ***Thevenemyia*** (***Thevenemyia*** Bigot)

23 spp.; widespread; Hall 1969

R_{2+3} and R_4 connected by a crossvein (as in Figs. 14, 24). Terminal palpal segments greatly enlarged .... ***Thevenemyia*** (***Arthroneura*** Hull)

1 sp., *tridentata* (Hull); California; Hull 1966

23. R_{4+5} unbranched (Figs. 26–28) 24

R_{4+5} branched (Fig. 29) 27

24. R_{2+3} present, long, ending in C; cell br much longer than cell bm .... CYRTOSIINAE.... ***Platypygus*** Loew

1 sp., *americanus* Melander; southern California

R_{2+3} absent (Fig. 26) or short, ending in R_1, and forming small triangular cell r_1 (Figs. 27, 28); cells br and bm usually equal in length or nearly so .... MYTHICOMYIINAE.... 25

25. R_{2+3} vestigial, fused with R_1, or absent (Fig. 26); crossvein dm-cu absent.... ***Empidideicus*** Becker

5 spp.; southwestern U.S.A.; Melander 1946

R_{2+3} present, conspicuous, ending in R_1 (Figs. 27, 28); crossvein dm-cu present 26

26. Crossvein bm-cu present; cells bm and dm separate (Fig. 27). Eyes of male holoptic .... ***Mythicomyia*** Coquillett

130 spp.; western U.S.A.; Melander 1961

Crossvein bm-cu absent; cells bm and dm confluent (Fig. 28). Eyes of male dichoptic .... ***Glabellula*** Bezzi

6 spp.; widespread; Melander 1950*b*

27. First flagellomere stout, blunt, with a minute stylus arising from a small sulcus before apex (Fig. 52); if sulcus absent, then apex truncate or nearly so .... PHTHIRIINAE.... 28

First flagellomere slender, acutely pointed apically (Fig. 53); stylus if present terminal 32

28. Crossvein dm-cu absent; cell dm absent (Fig. 29) .... ***Apolysis*** Loew

8 spp.; Arizona, California; Melander 1946

Crossvein dm-cu present; cell dm thus complete 29

29. Three flagellomeres, with small subapical stylus (Fig. 54). Proboscis short, not projecting. M_2 present .... ***Desmàtomyia*** Williston

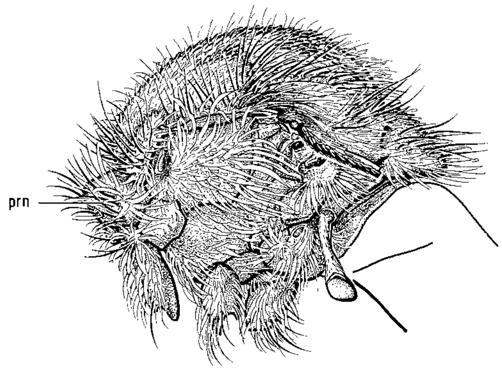
1 sp., *anomala* Williston; Arizona, Colorado; Painter and Painter 1968

One large basal flagellomere, with small subapical stylus (Fig. 52). Proboscis long, projecting. M_2 present or absent 30

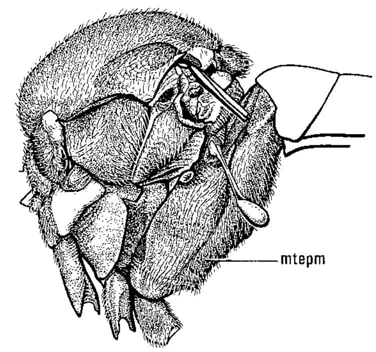
30. M_2 absent (as in Fig. 32). Proboscis short or long. Hair on gena not curving forward. Species usually black or gray .... ***Oligodranes*** Loew

52 spp.; widespread; Melander 1946

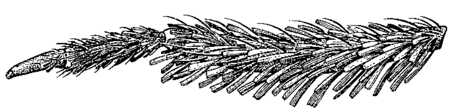
M_2 present (Fig. 31). Proboscis long, projecting. Hair on gena not as above. Species variously patterned with yellow and black, or entirely black or gray in male .... ***Phthiria*** Meigen.... 31



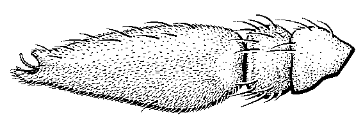
49 Lepidophora lutea ♀



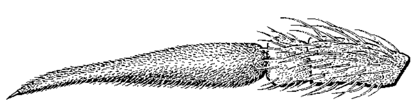
50 Systropus macer ♂



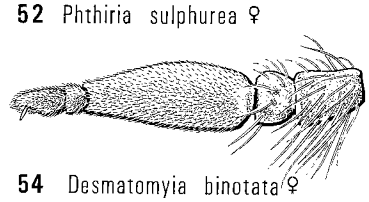
51 Lepidophora lutea ♀



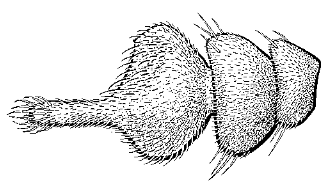
52 Phthiria sulphurea ♀



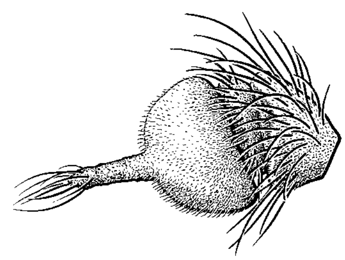
53 Geron albarius ♀



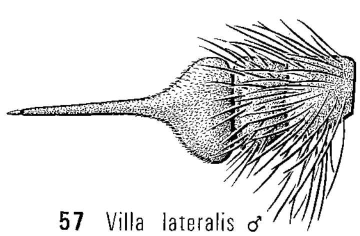
54 Desmatomyia binotata ♀



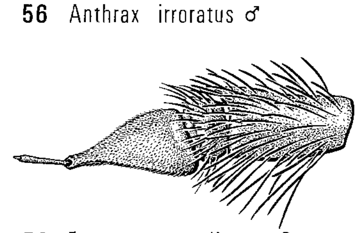
55 Caenotoides californica ♂



56 Anthrax irroratus ♂



57 Villa lateralis ♂



58 Exoprosopa caliptera ♀

Figs. 45.49–58. Thoraces and antennae: left lateral view of thorax and first abdominal segment of (49) *Lepidophora lutea* Painter and (50) *Systropus macer* Loew; left lateral view of antenna of (51) *Lepidophora lutea*, (52) *Phthiria sulphurea* Loew, (53) *Geron albarius* Painter, (54) *Desmatomyia binotata* Painter, (55) *Caenotoides californica* Hall, (56) *Anthrax irroratus* Say, (57) *Villa lateralis* (Say), and (58) *Exoprosopa caliptera* (Say).

Abbreviations: mtepm, metepimeron; prn, pronotum.

31. Palpus short, rarely exceeding subcranial margin. R_{2+3} usually originating proximal to base of cell dm. Last sternite in male with small median notch .... ***Phthiria*** **(*Phthiria*** Meigen)

10 spp.; western U.S.A.; Painter and Painter 1962

Palpus extending at least as far as antennae. R_{2+3} originating opposite or distal to base of cell dm (Fig. 31). Last sternite in male deeply concave on posterior margin .... ***Phthiria*** **(*Poecilognathus*** Jaennicke)

21 spp.; widespread

32. M_2 absent (Fig. 32). Hair of gena curving forward. Proboscis projecting .... GERONINAE .... ***Geron*** Meigen....33

M_2 present (Fig. 33). Hair of gena not curving forward. Proboscis long and projecting, or short .... HETEROTROPINAE....34

33. Frons with broad scales. Rs never more than two-thirds length of preceding section of R_{4+5} (Fig. 32) .... ***Geron*** **(*Geron*** Meigen)

16 spp.; widespread; Painter 1932

Frons without broad scales. R_5 about as long as preceding section of R_{4+5} .... ***Geron*** **(*Empidigeron*** Painter)

6 spp.; widespread; Painter 1932

34. Proboscis projecting well beyond subcranial margin 35

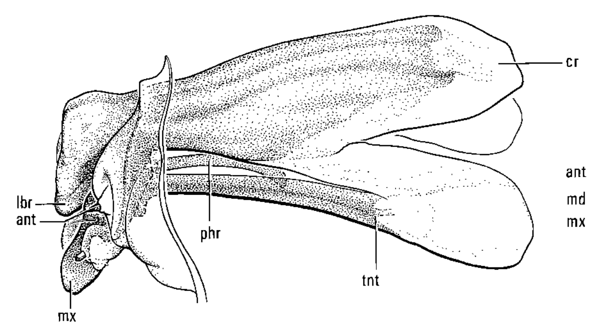
Proboscis short, not projecting or only barely projecting beyond subcranial margin 36

35. M_1 and M_2 united for a short distance beyond apex of cell dm (Fig. 33). First flagellomere conical; stylus microscopic .... ***Prorates*** Melander

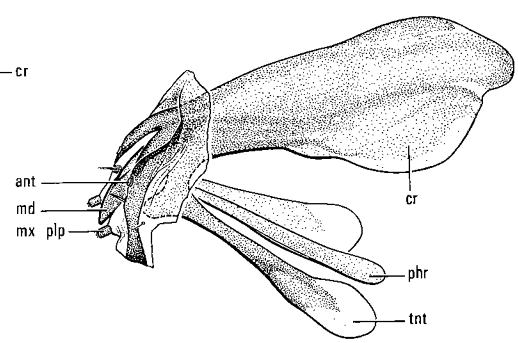
6 spp.; western U.S.A.; Hall 1972

M_1 and M_2 arising separately from apex of cell dm (as in Fig. 31). First flagellomere awl-shaped .... ***Heterotropus*** Loew

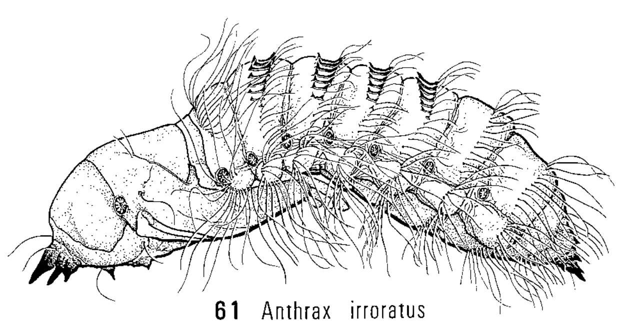
1 sp., *senex* Melander; Arizona; Melander 1950*b*



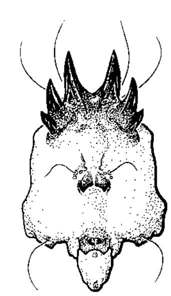
59 Sparnopolius sp.



60 genus unknown



61 Anthrax irroratus



62 Anthrax irroratus

Figs. 45.59–62. Immature stages: left lateral view of head skeleton of larva of (59) *Sparnopolius* sp. and (60) genus unknown; pupa of *Anthrax irroratus* Say showing (61) left lateral view and (62) anterior view of head.

Abbreviations: ant, antenna; cr, cranium; lbr, labrum; md, mandible; mx, maxilla; mx plp, maxillary palpus; phr, pharynx; tnt, tentorium.

36. M_1 and M_2 united beyond pointed apex of cell dm (as in Fig. 33); R_{4+5} branching near apex of wing .... ***Apystomyia*** Melander

1 sp., *elinguis* Melander; California; Melander 1950*b*

M_1 and M_2 arising separately from truncate apex of cell dm (as in Fig. 34); R_{4+5} branching near apex of cell dm (Fig. 34) 37

37. Apex of first flagellomere with a tuft of microscopic hair (Fig. 55). Palpus short. Body pile short, very sparse .... ***Caenotoides*** Hall

2 spp.; California, Idaho; Hall 1972

First flagellomere terminating in a small stylus; tuft of hair absent. Palpus longer than above. Body pile short, but more dense .... ***Caenotus*** Cole

4 spp.; western U.S.A.; Melander 1950*b*

38. R_{2+3} arising from R_{4+5} proximal to crossvein r-m, and typically at an acute angle (Figs. 35–37) .... LOMATIINAE....39

R_{2+3} arising from R_{4+5} near crossvein r-m, and usually at a right angle (Figs. 38–48) 45

39. Proboscis projecting well beyond subcranial margin; labella usually elongate, narrow, somewhat pointed .... ***Epacmus*** Osten Sacken

13 spp.; western U.S.A.; Melander 1950*a*

Proboscis short, not projecting or only barely projecting beyond subcranial margin 40

40. R_{2+3} arising from R_{4+5} at nearly a right angle distal to base of cell dm ....***Desmatoneura*** Williston

1 sp., *argentifrons* Williston; Utah, New Mexico

R_{2+3} arising from R_{4+5} at an acute angle proximal to base of cell dm (Figs. 35–37) 41

41. CuA_2 and A each terminating separately at wing margin (Fig. 35) 42

CuA_2 and A joining at or before wing margin (Figs. 36, 37) 44

42. R_{2+3} and R_4 connected by a crossvein (as in Figs. 11, 24). Body more or less pilose. First flagellomere twice as long as scape and pedicel combined .... ***Exepacmus*** Coquillett

1 sp., *johnsoni* Coquillett; southern California

R_{2+3} and R_4 not connected by a crossvein. Body short pilose; pile usually not dense. First flagellomere much longer than or scarcely longer than width at base 43

43. First flagellomere long, much longer than its width at base; base more or less bulbous, typically constricted into a slender styliform apical portion. Face usually pilose to antennae .... ***Aphoebantus*** Loew

54 spp.; primarily from western U.S.A.; Melander 1950*a*

First flagellomere scarcely longer than its width at base, not constricted into a styliform apical portion, somewhat broadly oval. Face bare between antennal base and subcranial margin .... ***Eucessia*** Coquillett

1 sp., *rubens* Coquillett; southern California

44. R_5 and M_1 joined apically (Fig. 36) or ending in wing margin close together; crossvein r-m at level of distal sixth of cell dm. First flagellomere long. Large robust species .... ***Bryodemina*** Hull[1]

2 spp.; southern Arizona into Mexico and South America

R_5 and M_1 ending in wing margin some distance apart (Fig. 37); crossvein r-m nearer middle of cell dm. Small species with broad abdomen .... ***Ogcodocera*** Macquart

2 spp.; eastern, southwestern

45. First flagellomere terminating in a tuft of hair (Fig. 56). Body with scales and hair .... ANTHRACINAE....46

First flagellomere with an apical stylus of one or two segments, without an apical tuft of hair. Body with hair, and with or without scales .... EXOPROSOPINAE....47

[1] The complete relationship of this genus with the Palaearctic genus *Anisotamia* Macquart has not been fully reconciled; ***Bryodemina*** and *Anisotamia* may be synonomous.

46. Cell r_4 subdivided by a crossvein between R_4 and R_5 (Fig. 38). Abdomen without bristles or bristle-like hair. Wing almost entirely hyaline .... ***Dicranoclista*** Bezzi

2 spp.; western U.S.A.; Johnson and Johnson 1960

Cell r_4 undivided (Fig. 39). Abdomen frequently with strong bristle-like hair. Wing typically spotted or half black .... ***Anthrax*** Scopoli

37 spp.; widespread; Marston 1963, 1970

47. Claws each with a small tooth at base. Stylus distinctly articulated with apex of first flagellomere (Fig. 58) 48

Claws simple, without a basal notch or tooth. Stylus usually not distinctly articulated with first flagellomere 49

48. Cell r_4 undivided by a crossvein; wing variously patterned to completely hyaline (Fig. 40) .... ***Exoprosopa*** Macquart

43 spp.; widespread; Curran 1930*b*

Cell r_4 subdivided by a crossvein; wing always patterned (Fig. 41) .... ***Ligyra*** Newman

2 spp.; western U.S.A., Mexico

49. CuA_2 and A joined apically (as in Fig. 37). Eyes of male contiguous at vertex .... ***Astrophanes*** Osten Sacken

1 sp., *adonis* Osten Sacken; western U.S.A., Mexico

CuA_2 and A ending separately in wing margin (Figs. 42–48). Eyes of male not contiguous 50

50. R_{2+3} apically strongly contorted, S-shaped, often connected to R_4 by a crossvein (Fig. 42) 51

R_{2+3} bent apically but not strongly contorted, usually not connected to R_4 by a crossvein (Figs. 43–48) 53

51. Face not produced conically. Wing brown with subhyaline areas; R_{2+3} and R_4 connected by a crossvein (Fig. 42) .... ***Dipalta*** Osten Sacken

2 spp.; 1 sp. eastern, other western

Face produced, conical or nearly so. Wing variously patterned; R_{2+3} and R_4 unconnected by a crossvein 52

52. Wing short, about one-half as broad as long, widened apically. Apical styliform portion of first flagellomere about equal in length to its conical base .... ***Paradiplocampta*** Hall

1 sp., *tabeti* Hall; southwestern U.S.A.; Hall 1975*b*

Wing longer, more than twice as long as broad, not widened apically. Styliform portion of first flagellomere much longer than conical basal portion .... ***Neodiplocampta*** Curran

4 spp.; western U.S.A., Mexico; Hull and Martin 1974

53. CuA_2 and A subparallel (Fig. 43) .... ***Mancia*** Coquillett

1 sp., *nana* Coquillett; southern California

CuA_2 and A converging toward wing margin (Figs. 44–48) 54

54. Proboscis strongly projecting beyond subcranial margin 55

Proboscis short, at most only with labella projecting beyond subcranial margin; or mouthparts vestigial 57

55. R_{2+3} and R_4 connected by a crossvein .... ***Stonyx*** Osten Sacken

1 sp., *clelia* Osten Sacken; Arizona, Mexico

R_{2+3} and R_4 unconnected by a crossvein (Fig. 44) 56

56. At least basal half of abdomen with broad scales; male usually with apex of abdomen silvery. Fore tibia with rows of short bristles. Crossvein dm-cu not much longer than middle portion of CuA_1 (Fig. 44) .... ***Lepidanthrax*** Osten Sacken

34 spp.; western U.S.A.; Curran 1930*a*, Hall 1976

No broad scales on abdomen. Fore tibia with strong bristles. Crossvein dm-cu much longer than middle portion of CuA_1 .... ***Rhynchanthrax*** Painter

4 spp.; widespread; Painter 1933

57. Mouthparts vestigial. Thoracic and scutellar bristles absent. Pulvilli absent .. ***Oestranthrax*** Bezzi

1 sp., *farinosus* Johnson & Maughan; Utah

Proboscis short but well-developed; palpus usually about half length of proboscis or more. Thoracic bristles well-developed. Pulvilli present or absent 58

58. Face projecting, without scales. Fore tibia without bristles .... ***Poecilanthrax*** Osten Sacken
33 spp.; widespread; Painter and Hall 1960
Face projecting or rounded, with scales present. Fore tibia with or without bristles 59
59. Face rounded, sometimes projecting slightly but not conically so 60
Face projecting conically or at least not rounded 61
60. Fore tibia almost always with easily seen dark bristles. Wing half black or more in both sexes .... ***Hemipenthes*** Loew
25 spp.; widespread; Coquillett 1894
Fore tibia without readily apparent bristles. Wing hyaline, at most with yellowish costal margin (Fig. 45) .... ***Villa*** Lioy, in part
30 spp.; widespread; Coquillett 1892
61. Wing hyaline, at most with yellowish costal cell. Fore tibia without bristles .... ***Villa*** Lioy, in part
7 spp.; widespread
Wing infuscated with various patterns, spotted or colored uniformly (Figs. 47, 48). Fore tibia with or without bristles 62
62. Fore tibia with darkened easily seen bristles; claws of foreleg as large as claws on other legs .... ***Paravilla*** Painter
24 spp.; widespread
Fore tibia smooth, without apparent dark bristles; claws of foreleg smaller than those of other legs 63
63. Femora without bristles. R_{2+3} and R_4 connected by a crossvein .... ***Diochanthrax*** Hall
1 sp., *morulus* Hall; California; Hall 1975*b*
Femora with bristles. R_{2+3} and R_4 unconnected by a crossvein (Figs. 47, 48) 64
64. Wing infuscated except for hyaline or subhyaline areas surrounding crossveins within infuscated portion (Fig. 47) .... ***Thyridanthrax*** Osten Sacken
7 spp.; widespread; Hall 1970
Wing infuscated, but without hyaline or subhyaline areas surrounding crossveins; crossveins frequently darker (Fig. 48) .... ***Chrysanthrax*** Osten Sacken
27 spp.; widespread but mainly southwestern U.S.A.

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HILARIMORPHIDAE 46

DONALD W. WEBB

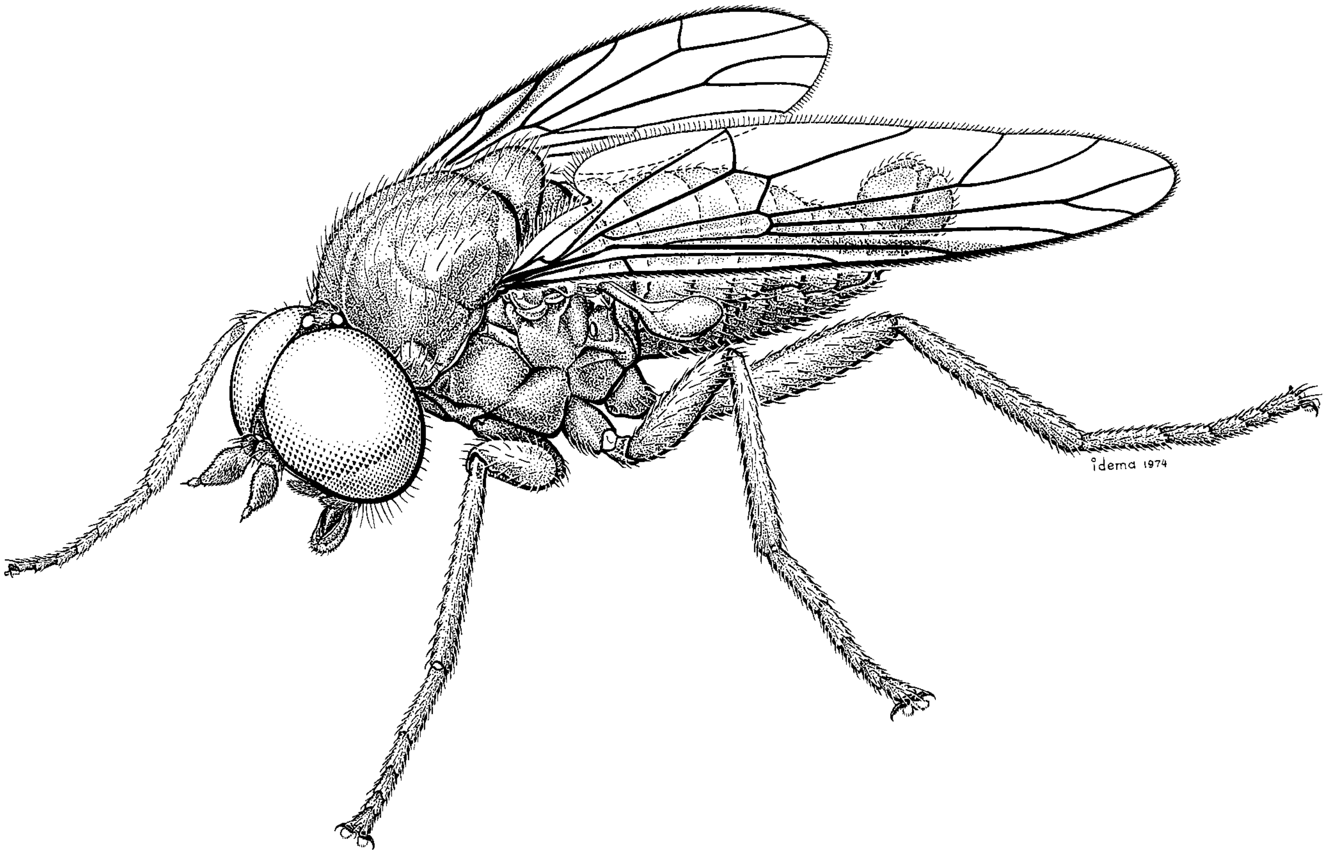


Fig. 46.1. Male of *Hilarimorpha ditissa* Webb.

Small dark robust flies (Fig. 1), 1.8–7.2 mm long. Wing hyaline to pale brown, usually with pterostigma.

Adult. Head: suboval, with concave occiput. Eye bare, not emarginate lateral to antenna; in male large, holoptic, contiguous from vertex to base of antenna, with facets in lower third smaller than those in upper area; in female small, dichoptic, with facets of uniform size. Ocelli prominent on vertex, clear, on subtriangular pad, usually with several short fine erect setae. Antenna (Fig. 3) with an apical two-segmented stylus; scape short, subconical, usually hidden by eyes in male; pedicel subglobose, with numerous long erect setae; first flagellomere fusiform or suboval, flattened laterally, occasionally with long fine erect setae; stylus short, with basal segment globose or cylindrical and usually longer than apical segment, and with apical segment narrow and linear. Palpus short, with one or two segments; apical segment lobate, fusiform, or clavate, generally with numerous erect setae. Proboscis short, acute apically. Prementum large, overlapping proboscis, with numerous long fine setae. Tentorial pit large, distinct. Parafacial setae abundant or absent; occipital setae numerous.

Thorax: postpronotal lobes small, widely separated medially when viewed from above, with several short fine erect setae. Scutum moderately arched dorsally; vittae usually indistinct; setae short, having no distinguishable pattern; macrotrichia absent. Scutellum short, subtriangular; setae short, arranged in a uniseriate row across apical margin.

Wing membrane (Fig. 2) hyaline to pale brown, covered with microtrichia. Calypter small, with complete fringe of long fine setae. Alula rounded. Anal angle oblique. Pterostigma, when present, pale to dark brown, usually covering apical half of R_1 and origin of R_{2+3}. Veins brown; crossvein h usually present; C circumambient, broader along anterior margin; Sc simple, reaching C well beyond crossvein r-m; R_1 simple, ending in C near middle of wing; Rs with three branches; R_{4+5} forked; R_5 ending at or near wing apex; M_{1+2} branched; M_3 absent; cell dm absent; petiole of R_{4+5} always longer than petiole of M_{1+2}; cell bm longer than cell br; cell cu*p* elongate, closing at or near wing margin, occasionally open, ending proximal to apex of cell bm. Posterior callus small, subtriangular, with several short fine erect postalar setae. Halter elongate, clavate, and pubescent with numerous fine setae.

Legs elongate; coxae short; femora fusiform; tibiae linear, lacking apical spurs. Tarsi linear, with third and fourth tarsomeres shorter than fifth tarsomere; pulvilli large, distinct; tarsal claws simple; empodia absent.

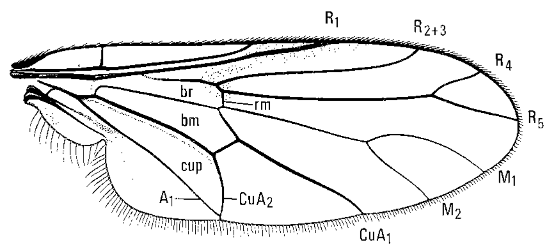
Abdomen: in male tapered posteriorly, ending in swollen globose terminalia curved dorsally; in female gradually tapered, then abruptly narrowed behind segment 7.

Terminalia of male (Fig. 4) with tergite 9 broadly rounded posteriorly, bearing semioval flattened cerci above a large apically rounded hypoproct. Sternite 9 indistinguishable; gonocoxites large, fused ventrally, with a deep narrow apicomedial notch, and with posterolateral tapered prolongations beyond articulation of simple tapered gonostyli; aedeagus slender, tapered or clavate apically, enclosed in an aedeagal sheath formed by the fused parameres; paramere also with an apically rounded lobe arising dorsolaterally at confluence of aedeagal sheath and base of gonocoxite.

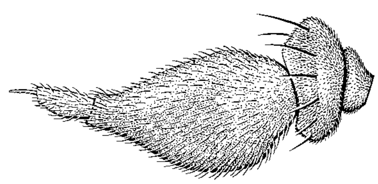
Terminalia of female (Fig. 5) with sternite 8 longer than wide, evenly rounded posteriorly, and about same size as combined tergites 8 and 9 above. Tergite 9 about twice as wide as long, much shorter than tergite 8; genital fork distinct. Cercus a simple compressed rounded lobe above the hypoproct.

Biology and behavior. Adults have been collected on species of *Salix* growing along narrow gravel-bottomed streams and on *Cryptotaenia canadensis*. Immature stages and fossil species are unknown. The fossil species *Palaeohilarimorpha bifurcata* Meunier from Baltic amber (Tertiary) is not a form of *Hilarimorpha* but rather agrees with the genus *Rhagio* Fabricius in the Rhagionidae (Hennig 1967).

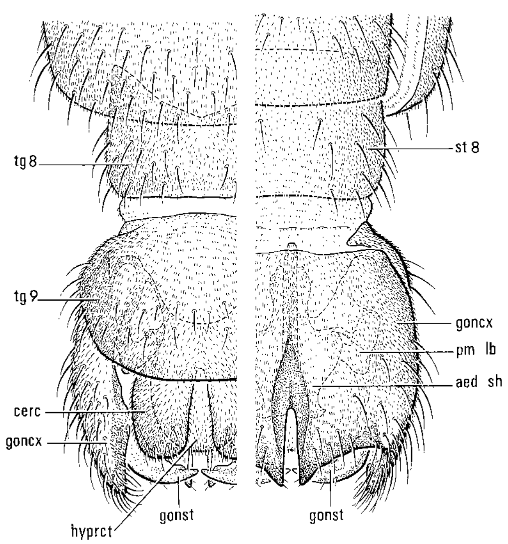
Classification and distribution. This family is represented by only one genus, *Hilarimorpha* Schiner, with



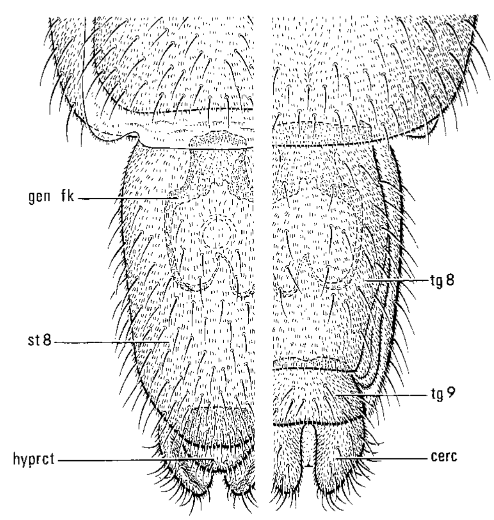
2 Hilarimorpha ditissa ♂



3 Hilarimorpha ditissa ♂



4 Hilarimorpha ditissa ♂



5 Hilarimorpha ditissa ♀

Figs. 46.2–5. *Hilarimorpha ditissa* Webb: (2) wing; (3) antenna; (4) male terminalia–dorsal *left*, ventral *right*; (5) female terminalia–ventral *left*, dorsal *right*.

Abbreviations: aed sh, aedeagal sheath; cerc, cercus; gen fk, genital fork; goncx, gonocoxite; gonst, gonostylus; hyprct, hypoproct; pm 1b, parameral lobe; st, sternite; tg, tergite.

33 recorded species. All species are north temperate in distribution; two species occur in Central Europe, one species occurs in Japan, and the remaining 30 species occur in Canada and the United States, excluding Hawaii. A revision of the genus was published by Webb (1974), who later described additional species (Webb 1975).

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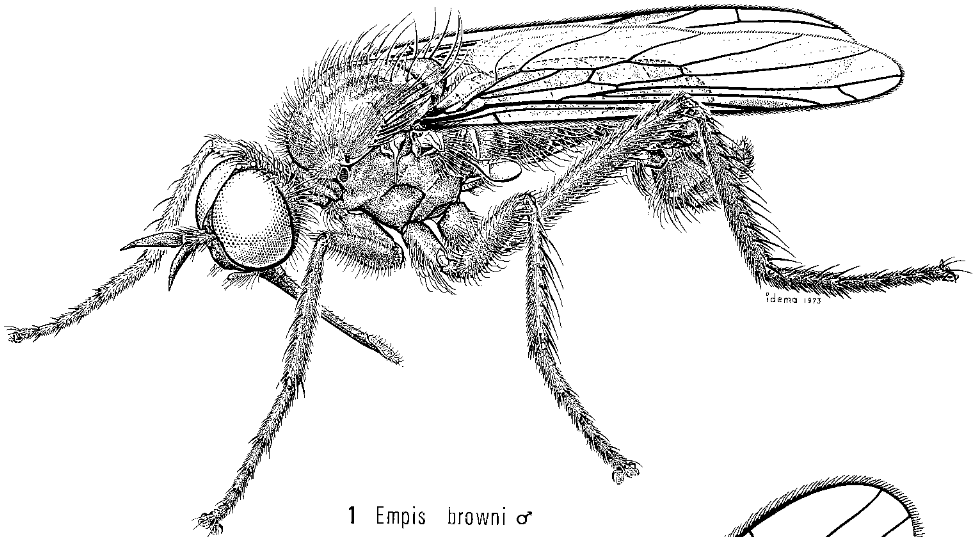
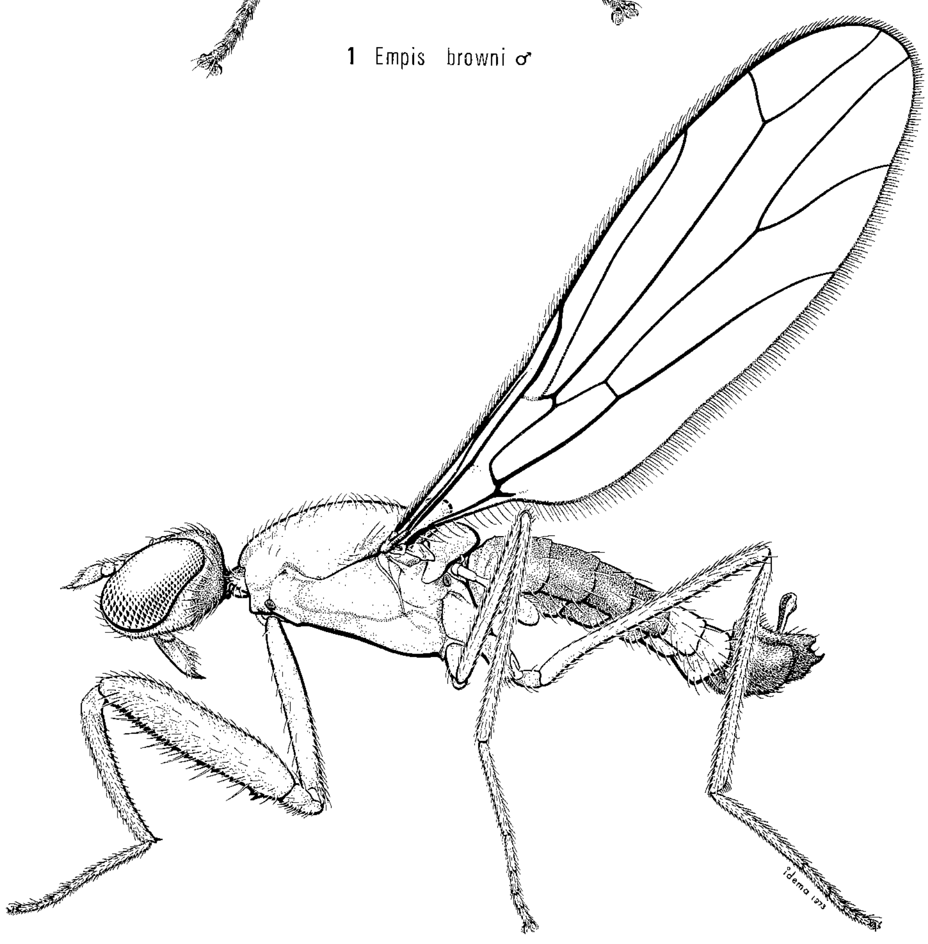
EMPIDIDAE 47

GEORGE C. STEYSKAL AND LLOYD V. KNUTSON[1]



1 Empis browni ♂



2 Hemerodromia rogatoris ♂

Figs. 47.1–2. Males: (1) *Empis browni* Curran; (2) *Hemerodromia rogatoris* Coquillett.

[1] Steyskal contributed the material dealing with the adult forms and the classification, and Knutson prepared that dealing with the immature stages and the biology. This account is dedicated to the memory of James G. Chillcott, whose excellent work contributed much to the knowledge of this family.

Predacious flies, small to medium in size, 1.5–12 mm long, usually rather elongate (Fig. 1). Legs slender, sometimes thickened and otherwise modified for raptorial use (Fig. 2). Color usually dark, sometimes black, but also sometimes yellowish or light brown, not metallic in North American species.

Adult. Head: of various shape and structure (Figs. 11, 12, 21, 26–29, 38–40, 45, 47), often with large eyes and elongated proboscis. Ptilinal fissure absent. Antenna with three or fewer segments, and usually with a stylus or arista (Figs. 9, 16, 35, 36, 48–50). Chaetotaxy of head very limited; true vertical bristles rarely developed, evident chiefly in Tachydromiinae.

Thorax: usually somewhat rectangular in dorsal outline, but anterior part sometimes considerably extended in Hemerodromiinae and Tachydromiinae (Fig. 2), and in Hybotinae sometimes greatly arched upward into a dome-like structure. Chaetotaxy often limited to notopleural and scutellar bristles, but other dorsal bristles sometimes present. A group of setae on laterotergite present in a group of Empidinae, distinguishing this group from other Empididae with bare laterotergite (Fig. 37). Wing of greatly varied shape and size (Figs. 3–7, 13–20, 22–25, 30–34, 41–44), occasionally reduced, sometimes greatly broadened; alula and anal lobe often lacking, with wing tapering to its base; venation of reduced brachycerous type (Figs. 22–25, 30–34); C sometimes circumambient (extending completely around wing margin); cell dm sometimes lacking or incomplete (Fig. 41); cell cu*p* never attaining wing margin, and often very short or sometimes completely lacking; a distinct bristle usually present at base of C. Legs varying remarkably in length, strength, structure, and armature, but usually rather long, and often exhibiting marked sexual dimorphism; rows of flattened setae arming legs of female of some species giving legs a feathered appearance; basal segments of one or more tarsi enlarged in male of some species, or conformation and armature differing in male and female of some species; in a few genera foreleg, midleg, or hindleg strongly developed and spinose in both sexes; tibia never having true apical spurs that are characteristic of some other brachycerous families, but tip of each tibia sometimes produced into a fixed spur (Fig. 8); empodia usually setiform, pulvilliform only in Clinocerinae.

Abdomen: usually more or less elongate and cylindrical, but sometimes (*Drapetis* Meigen) quite short. Terminalia of male variable, symmetric or asymmetric, much larger than preceding abdominal segments, or turned forward over these segments (Figs. 51–53); aedeagus sometimes extremely lengthened; other parts sometimes greatly enlarged at expense of others. Ovipositor soft, inconspicuous, and normally withdrawn (Fig. 54), or tip of female abdomen more or less flattened (*Leptopeza* Macquart) to form a sclerotized ovipositor (Fig. 55).

Larva. Terrestrial larva with amphipneustic respiratory system, and with a single median lobe below posterior spiracles; terminal segment frequently with lateral furrows; abdominal prolegs lacking (Figs. 57, 63); metacephalic rods not expanded apically (Fig. 58). For comparison, larva of Dolichopodidae (except that of *Neurigona* Rondani) with amphipneustic respiratory system, and with one or two pairs of odontoid lobes around posterior spiracles or with an evenly rounded terminal segment, at most with one pair of abdominal prolegs, six or seven abdominal creeping welts with regularly arranged spinules, and apically expanded metacephalic rods. Larvae of Dolichopodidae and terrestrial Empididae with two sclerites connecting the two apical sclerites of the mandibular complex (Dyte 1967).

Aquatic empidid larva more distinctive than terrestrial form, with apneustic respiratory system (except in *Oreogeton* Schiner and *Roederiodes* Coquillett), and with elongate caudal lobes or small tubercles ending in one or more pairs of fine bristles (Figs. 56, 59, 60), with seven or eight pairs of abdominal prolegs (Fig. 56) (eight creeping welts with irregularly arranged spinules in *Dolichocephala* Macquart), and with four sclerites connecting the two apical sclerites of the mandibular complex.

Biology and behavior. Apart from studies of mating behavior and swarming, little is known about the habits of Empididae. Some scattered information was summarized by Knutson and Flint (1971). Adults are most often found in vegetation in moist locations, on tree trunks, or even on the surface of the water. Larval habitats range from aquatic to strictly terrestrial mediums such as soil, leaf-litter, and rotten wood. Various intermediate situations are also represented, such as those of some species of the Clinocerinae; larvae of *Clinocera* Meigen, for example, live on surfaces covered by a thin film of flowing water or in water to a depth of 1 m. Whereas most females probably oviposit, females of the Holarctic *Ocydromia glabricula* (Fallén) larviposit on dung. Larvae of a few genera have been reared from cow dung, and there are records of *Drapetis* spp. reared from an owl's nest, roots, and myxomycetes fungi, but all larvae of Empididae are likely predacious. *Empis tessellata* Fabricius has been reared through the life cycle in the laboratory. The egg incubation period is 12–16 days, and the pupal period is 12–14 days; these larvae killed and ate larvae of *Drosophila* Fallén. Larvae of *Roederiodes* and *Wiedemannia* Zetterstedt prey on pupae of Simuliidae; larvae of *Oreogeton* kill and feed on simuliid larvae; larvae of some species of *Hemerodromia* Meigen live among mosses in flowing water where they prey on simuliid larvae; and larvae of some species of *Neoplasta* Coquillett attack pupae of Trichoptera (caddisflies).

Feeding habits of adult Empididae have been reviewed by Downes and Smith (1969) and Downes

(1970). Both sexes of most genera take a proteinaceous meal and also feed on nectar. Living insects, particularly swarming or emerging Diptera (including many Empididae), are the source of protein for most species. However, *Anthalia* Zetterstedt (and possibly *Euthyneura* Macquart) eat pollen; *Microphorus* Macquart feed on dead insects trapped in spider webs; and certain Clinocerinae feed on dead insects at the water's edge, or on mosquitoes and other aquatic Diptera emerging from the pupal skin at the water surface, as well as on living insects including larvae and pupae of Simuliidae. Many adult empidids have restricted feeding zones, such as among swarming Diptera, on tree trunks, on the ground, or on plant surfaces.

Feeding and mating are intimately related and highly specialized in many Empidinae, and in this group hunting and feeding are sexually differentiated. In most species of *Empis* Linnaeus, *Hilara* Meigen, and *Rhamphomyia* Meigen the male captures other insects (mainly small, swarming or emerging Nematocera) that he presents uneaten to the female when mating. The female has not been observed hunting, and her only source of proteinaceous food is apparently that given her by the male during repeated matings. Courtship with food transfer is highly ritualized and reaches its greatest development in species of *Hilara* and *Empis* (Kessel 1959, Downes 1970, Newkirk 1970). The male of these genera makes a light-reflecting, frothy or silken balloon that he carries into the swarm to attract a female. The balloon, which sometimes contains a small prey, is offered to the female as a mating stimulus; the balloon probably distracts her from attacking the male. Various stages in the evolution of this mating behavior have been suggested by Kessel (1955, 1959).

The significance of the swarming, mating, and feeding habits of Empididae in the evolution of the family was reviewed by Chvala (1976). He regarded the swarm flight as an original mode of meeting of the sexes and one that is preserved in most of the phylogenetically older groups. Predation is regarded as a primary habit of Mesozoic Empididae, representing a selectionally advantageous habit even in recent species. Nectar feeding appeared only later, coincident with the development of angiosperms.

The Empididae are probably important in natural control of some pest insects. The adult Tachydromiinae, for example, are known to control agromyzids, coccids, and mites (Kovalev 1966). Adults of several genera prey on emerging or swarming mosquitoes and black flies; larvae and adults of some species prey on black fly larvae and pupae; and some adult *Rhamphomyia* species take mosquitoes.

The immature stages of only seven species of North American Empididae have been described. Of the world fauna, only 16 genera representing five subfamilies are known in any immature stage. Larvae and pupae fall into two groups according to their life-form and ecology. The two groups, which are not entirely concordant with taxonomic categories, are: aquatic and semiaquatic, and terrestrial. The aquatic and semiaquatic group comprises *Clinocera*, *Dolichocephala*, *Roederiodes*, and *Wiedemannia* of the subfamily Clinocerinae; *Chelifera* Macquart, *Hemerodromia*, and *Neoplasta* of the Hemerodromiinae; and *Oreogeton* of the Empidinae. The terrestrial group comprises *Empis*, *Hilara*, *Microphorus*, and *Rhamphomyia* of the subfamily Empidinae; *Phyllodromia* Zetterstedt of the Hemerodromiinae; *Ocydromia* Meigen of the Ocydromiinae; and *Drapetis* and *Platypalpus* Macquart of the Tachydromiinae.

Classification and distribution. The seven subfamilies recognized here are those of Melander (1928). In Collin's monograph of the British Empididae (1961), only four subfamilies are recognized; the Brachystomatinae and the Clinocerinae are included with the Hemerodromiinae, and the Ocydromiinae are grouped with the Hybotinae.

Tuomikoski (1966), followed by Hennig (1970), placed the primary division of the Empididae between a group of subfamilies called the Ocydromiinea (Ocydromioinea of Hennig) and a group called the Empidinea (Empidoinea of Hennig). The Ocydromiinea comprise the Ocydromiinae, the Hybotinae, and the Tachydromiinae; to these Hennig adds the Microphorinae and the Atelestinae. The remainder of the subfamilies are in the Empidinea. The use of this classification is not yet feasible in a key, but the Ocydromiinea, according to Hennig, are characterized as follows: R_5 not separated from R_4; Sc ending free in membrane or running indistinctly alongside apical part of R_1, not attaining C; C ending at end of M_1 or R_5; precoxal bridge reduced; lacinia of maxilla lacking or reduced; palpus removed from stipes and joined to a special sclerite (palpifer); mouthparts movable into anteriorly directed position; fore tibia with a gland near base opening posteroventrally; abdominal spiracles with tubiform opening, without microtrichia; terminalia of male twisted to right; female without sclerotized spermathecae.

Studies of the male terminalia by Bährmann (1960) and of the mouthparts by Krystoph (1966) are available.

The taxonomy of the North American species has been neglected; keys to the species of most genera are no more recent than those of Melander (1928), and some genera have never been keyed. Smith (1969) recognized eight subfamilies, as well as a '*Microphorus*-group'. Recent work, such as on the genera *Syneches* Walker (Wilder 1974) and *Hilara* (unpublished), as well as specimens and data left by Melander and now deposited in the U.S. National Museum, indicates that there are many undescribed North American species.

An important paper by Smith (1969) on the southern African fauna may be profitably consulted for its extensive data and bibliography on many aspects of Empididae.

Keys to genera

Adult

1. Cell dm absent; neither R_{4+5} nor M_{1+2} obviously forked; all veins appearing to run without branching to wing margin; cell cu*p* usually lacking, but when present shorter than cells bm and br, and A_1 weak and faint (Figs. 3–7) ....................................TACHYDROMIINAE....2

   Cell dm present (Figs. 13–15, 17–20, 22–25, 30–34, 42–44) or absent (Fig. 41); when this cell absent, R_{4+5} or M_{1+2} or both forked (M_{1+2} evanescent in *Bicellaria* and Ocydromiinae), or cell cu*p* longer than cell bm, or foreleg raptorial..13

2. Thorax slender; scutum much longer than broad; postpronotal lobe large, strongly constricted (Fig. 10). Proboscis straight, vertical, slender; palpus usually narrow. Fore femur thickened 3

   Thorax broader; scutum as long as broad; postpronotal lobe rarely large. Proboscis usually curved backward and stronger at base; palpus usually quite broad. Fore femur usually not thickened 5

3. CuA_2 present (Fig. 3). Proboscis longer than palpus. Frons narrow, nearly parallel-sided. Scutum tomentose..*Tachypeza* Meigen

   17 spp.; widespread; Melander 1928

   CuA_2 absent (as in Figs. 4, 5, 7). Proboscis often shorter than palpus. Frons narrow or V-shaped. Scutum often shining 4

4. Frons narrow, nearly parallel-sided (Fig. 11). Palpus narrow and elongate, usually shorter than proboscis, subshining, and usually with apical seta. Wing usually patterned with crossbands.. ....*Tachydromia* Meigen

   13 spp.; widespread; Melander 1928

   Frons fairly broad and V-shaped; sides bowed outwardly. Palpus usually oval, white, densely hairy, longer than very short proboscis. Wing hyaline or nearly so ....*Tachyempis* Melander

   6 spp.; widespread; Melander 1928

5. Cell br equal to or longer than cell bm. Eyes widely separated on face and frons. Two pairs each of ocellar and vertical bristles 6

   Cell br usually shorter than cell bm. If these cells subequal (Figs. 4, 5), then eyes close together above or below antenna and mid tibia spurred. One pair of diverging ocellar bristles and usually one pair of vertical bristles present 7

6. Arista apical. Legs not obviously bristly. Gena linear. Ocellar bristles diverging ....*Charadrodromia* Melander

   3 spp.; Pacific coast; Melander 1960

   Arista subapical or dorsal. Legs bristly. Gena at least one-quarter height of eye. Lower ocellar bristles converging ....*Chersodromia* Walker

   8 spp.; 2 spp. along Atlantic beaches, 6 spp. along Pacific beaches; Melander 1945, less *Coloboneura* and *Thinodromia*, synonyms

7. Cells br and bm of same or nearly same length (Figs. 4, 5). Legs slender and simple; neither mid nor hind tibia spurred or with strong bristles. Eyes nearly or quite contiguous on frons..........8

   Cell br usually shorter than cell bm. If these cells equal, then mid femur and mid tibia seriately setulose beneath; legs usually stout, with femur of at least one pair thickened and often with mid or hind tibia spurred or bristly (Fig. 8). Eyes separated on frons 10

8. Cell cu*p* absent; R_{2+3} ending much closer to end of R_1 than to end of R_{4+5} (Fig. 4). Basal flagellomere little longer than broad, with long dorsoapical arista ....*Micrempis* Melander

   4 spp.; rare, widespread

   A_1 and sometimes CuA_2 present; R_{2+3} ending closer to end of R_{4+5} than to end of R_1. Basal flagellomere lanceolate, with terminal stylus...9

9. Wing elliptical, less than three times as long as broad; A_1 closely following margin of anal lobe; cell cu*p* not formed because of absence of CuA_2 (Fig. 5) ....*Megagrapha* Melander

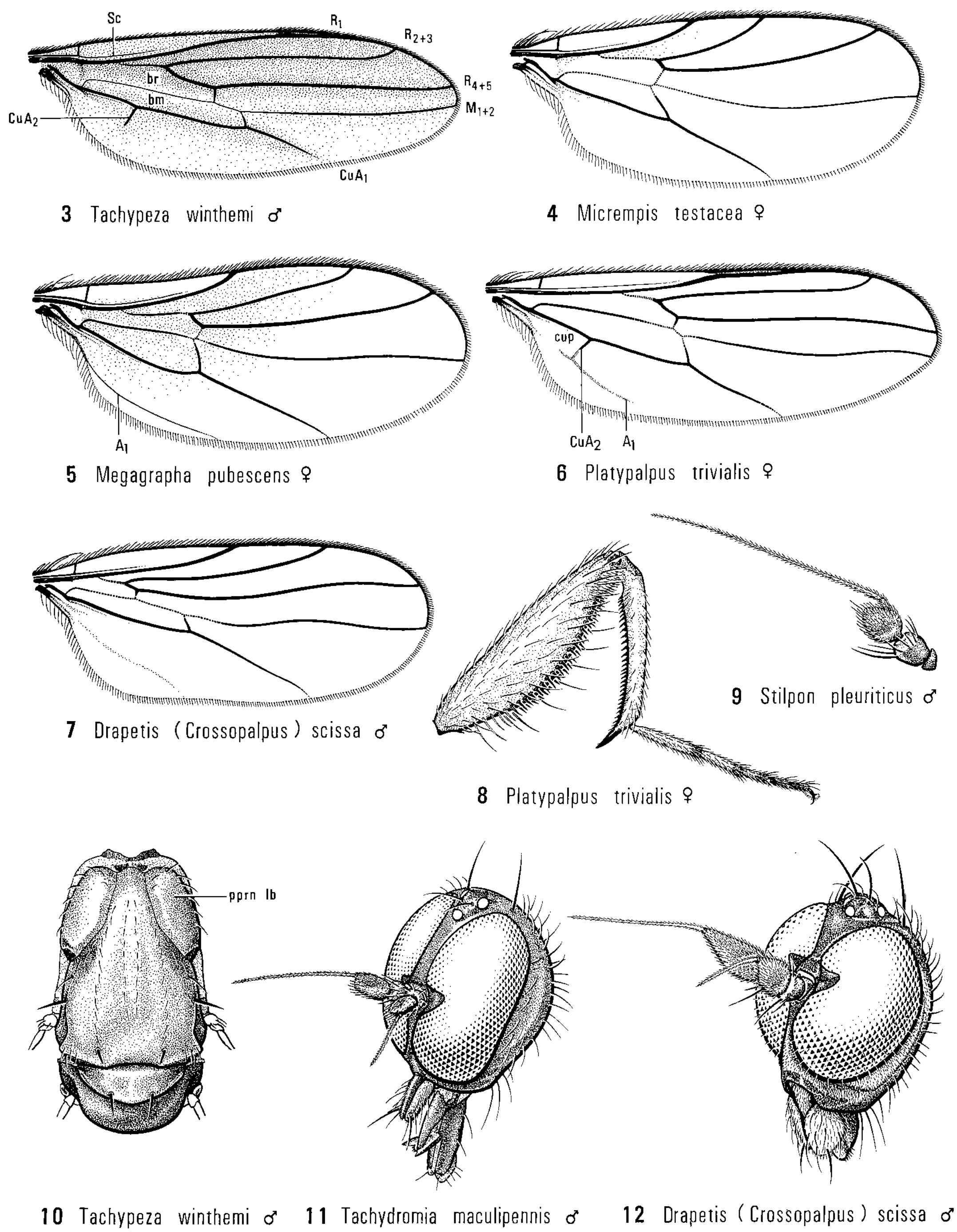
   2 spp.; Alberta to Georgia and northward; Chillcott 1958*a*

   Wing tapering to base, over three times as long as broad; A_1 nearly straight and not paralleling wing margin; cell cu*p* present...*Symballophthalmus* Becker

   1 sp., *masoni* Chillcott; Ontario, Michigan; Chillcott 1958*b*

10. Cell cu*p* more or less formed (Fig. 6). Mid femur thickest, with two rows of ventral denticles; mid tibia ending in sharp spur (Fig. 8). Scutum longer than broad ...... ***Platypalpus*** Macquart
over 100 spp.; widespread; Melander 1928, Chillcott 1962 (*juvenis* group)

Cell cu*p* absent (Fig. 7). Fore femur stronger than mid femur; mid femur rarely armed; mid tibia not spurred. Scutum not or scarcely longer than broad 11



Figs. 47.3–12. Tachydromiinae: wing of (3) *Tachypeza winthemi* Zetterstedt, (4) *Micrempis testacea* Melander, (5) *Megagrapha pubescens* (Loew), (6) *Platypalpus trivialis* Loew, and (7) *Drapetis* (*Crossopalpus*) *scissa* Melander; (8) midleg of *Platypalpus trivialis*; (9) antenna of *Stilpon pleuriticus* Melander; (10) thorax of *Tachypeza winthemi*, dorsal view; head of (11) *Tachydromia maculipennis* Walker and (12) *Drapetis* (*Crossopalpus*) *scissa*.

Abbreviation: pprn lb, postpronotal lobe.

11. Arista dorsal; basal flagellomere very short, round (Fig. 9). Eyes contiguous below antennae. Sides of frons usually parallel .... ***Stilpon*** Loew
6 spp.; eastern U.S.A. and west to Wisconsin; Melander 1928

Arista terminal or subterminal; basal flagellomere short–oval, lanceolate, or conical. Eyes more or less separated below antennae. Sides of frons usually diverging above (Fig. 12) .... ***Drapetis*** Meigen....12
about 40 spp.; widespread; Melander 1918

12. Gena distinctly developed below eye. Pedicel of antenna with distinct ventral bristle (Fig. 12) .... ***Drapetis*** (***Crossopalpus*** Bigot)[2]

Gena scarcely extended below eye. Pedicel without ventral bristle ..***Drapetis*** (***Drapetis*** Meigen)[2]

13. Foreleg raptorial, located near head, and distant from others; fore coxa greatly lengthened, at least twice as long as other coxae; fore femur more or less thickened and setose beneath (Fig. 2) .... HEMERODROMIINAE....14
Melander 1947 (revision), Harper 1974

Foreleg not raptorial; fore coxa short 20

14. Antenna with arista more than twice as long as basal flagellomere. Scutum with some discal macrotrichia; laterotergite with fine setulae. Male terminalia more or less reflexed over abdomen .... CHELIPODINI....15

Antenna with stylus shorter than basal flagellomere. Scutum without discal macrotrichia; laterotergite bare. Male terminalia erect or terminal; parts projecting backward (Fig. 2) .... HEMERODROMIINI....16

15. Cell dm closed, i.e. crossvein dm-cu present; M_{1+2} obtusely forked; CuA_2 usually arcuate .... ***Chelipoda*** Macquart
6 spp.; widespread, mostly northward

Cell dm open, i.e. crossvein dm-cu absent; M_{1+2} acutely forked; CuA_2 straight .... ***Phyllodromia*** Zetterstedt
1 sp., *americana* Melander; eastern

16. Crossvein h absent; Sc fused with C close to base of wing; R_1 ending before mid wing (Fig. 2). Eyes nearly or quite contiguous on face .... ***Hemerodromia*** Meigen
16 spp.; widespread

Crossvein h present, but sometimes vestigial; Sc free from C, evanescent apically; R_1 ending at or beyond mid wing. Eyes separated on face 17

17. Cell dm complete, separated from cell bm and emitting two veins apically; anterior one forked far from cell dm (Fig. 13) .... ***Chelifera*** Macquart
12 spp.; widespread

Cell dm either open apically (Fig. 14) or fused with cell bm (Fig. 15) 18

18. Cell dm separate from cell bm, but open apically (Fig. 14). Antennal stylus minute .... ***Thanategia*** Melander
3 spp.; 1 sp. in northeast, 2 spp. in northwest

Cell dm fused with cell bm (Fig. 15). Antennal stylus various 19

19. Fused cells bm and dm emitting two veins apically; anterior one forked. Fore femur strongly swollen and spinose beneath. Stylus one-third as long as basal flagellomere .... ***Metachela*** Coquillett
2 spp.; 1 sp. in northeast, other widespread in west

Fused cells bm and dm emitting three veins apically (Fig. 15). Fore femur relatively slender and not spinose. Stylus minute .... ***Neoplasta*** Coquillett
2 spp.; widespread

20. Anal lobe of wing not developed or only weakly developed (Figs. 22–25); alular sinus broadly arcuate; alula absent; C circumambient (continued around margin of wing). Empodia usually pulvilliform[3] 21

Anal lobe usually well-developed, alular sinus angular, and small alula usually present (Figs. 17–20, 30–34), but when not so, C not circumambient, or hind coxa well anterior to vertical line from tip of scutellum, or empodia setiform or vestigial 35

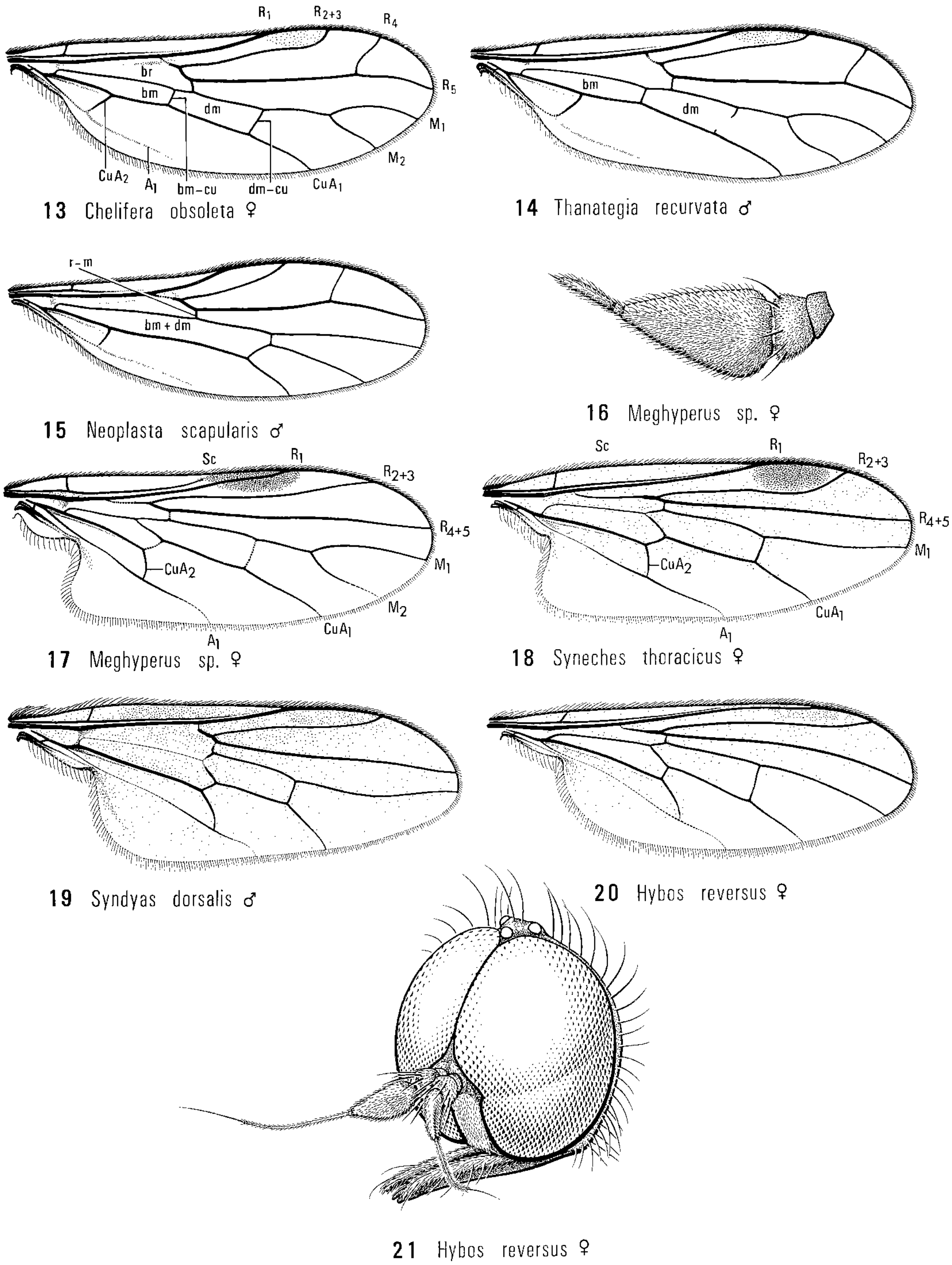
[2] Sometimes considered genera.

[3] H. J. Teskey has materially assisted in the construction of couplets 20–27.

21. Cell cu*p* at least a third the length of wing, and slightly longer than cell bm (Fig. 22) .... BRACHYSTOMATINAE....22

Cell cu*p* less than a quarter the length of wing, equal to or slightly shorter than cell bm (Figs. 23–25) .... CLINOCERINAE....23

22. R_{4+5} simple. Palpus slender, setose. Antenna with thick stylus .... ***Anomalempis*** Melander
2 spp.; northwestern



Figs. 47.13–21. Hemerodromiinae and Hybotinae: wing of (13) *Chelifera obsoleta* (Loew), (14) *Thanategia recurvata* Melander, and (15) *Neoplasta scapularis* (Loew); (16) antenna of *Meghyperus* sp.; wing of (17) *Meghyperus* sp., (18) *Syneches thoracicus* (Say), (19) *Syndyas dorsalis* Loew, and (20) *Hybos reversus* Walker; (21) head of *Hybos reversus*.

R_{4+5} forked (Fig. 22). Palpus short and broad, indistinctly setose. Antenna with slender stylus .... ***Brachystoma*** Meigen
4 spp.; widespread

23. Basal flagellomere greatly lengthened, without evident stylus, at most with tiny peg; antenna inserted above or below middle of head. R_{4+5} forked 24

Basal flagellomere not greatly lengthened, with stylus or arista; antenna inserted at or above middle of head. R_{4+5} forked or simple 25

24. Antenna inserted above middle of head; minute peg-like stylus present. Row of acrostichal bristles present .... ***Niphogenia*** Melander
1 sp., *eucera* Melander; Washington

Antenna inserted below middle of head, without trace of stylus. Acrostichal bristles absent .... ***Ceratempis*** Melander
1 sp., *longicornis* Melander; Washington

25. R_{4+5} forked (Figs. 23–25). Laterotergite usually haired (as in Fig. 37) 30

R_{4+5} simple. Laterotergite usually bare 26

26. Laterotergite haired (as in Fig. 37) .... ***Oreothalia*** Melander
2 spp.; 1 sp. in east, other in west

Laterotergite bare 27

27. A_1 not projecting beyond cell cu*p*; cell cu*p* shorter than cell bm .... ***Boreodromia*** Coquillett
1 sp., *bicolor* (Loew); northwestern

A_1 projecting beyond cell cu*p*; cell cu*p* as long as cell bm 28

28. Crossvein bm-cu complete. Face narrow, with eyes almost contiguous at lower margin; eye bare .... ***Heleodromia*** Haliday
1 sp., *pullata* (Melander); New Mexico

Crossvein bm-cu incomplete anteriorly. Face relatively broad resulting in eyes being widely separated at lower margin; eye usually pubescent (two genera of doubtful relationship, placed by Melander in Empidinae) 29

29. Scutum, abdomen, and legs with prominent white suberect hairs. CuA_2 straight. Four to six scutellar bristles .... ***Parathalassius*** Mik
3 spp.; Pacific coast

Body hairs relatively inconspicuous and dark. CuA_2 arcuate. Two scutellar bristles .... ***Microphorella*** Becker
5 spp.; western; Melander 1928

30. Sc evanescent apically; M arising close to base of cell cu*p*. Eye bare .... ***Proclinopyga*** Melander
5 spp.; widespread; Melander 1928

Sc ending in C; M usually arising nearer basal one-third of cell cu*p* (Figs. 23–25). Eye sometimes haired 31

31. Proboscis as long as head, slender, pointed, without labella; lower head rostrate (Fig. 29). Brownish species, with yellow legs .... ***Roederiodes*** Coquillett
7 spp.; widespread; Chillcott 1961, 1966

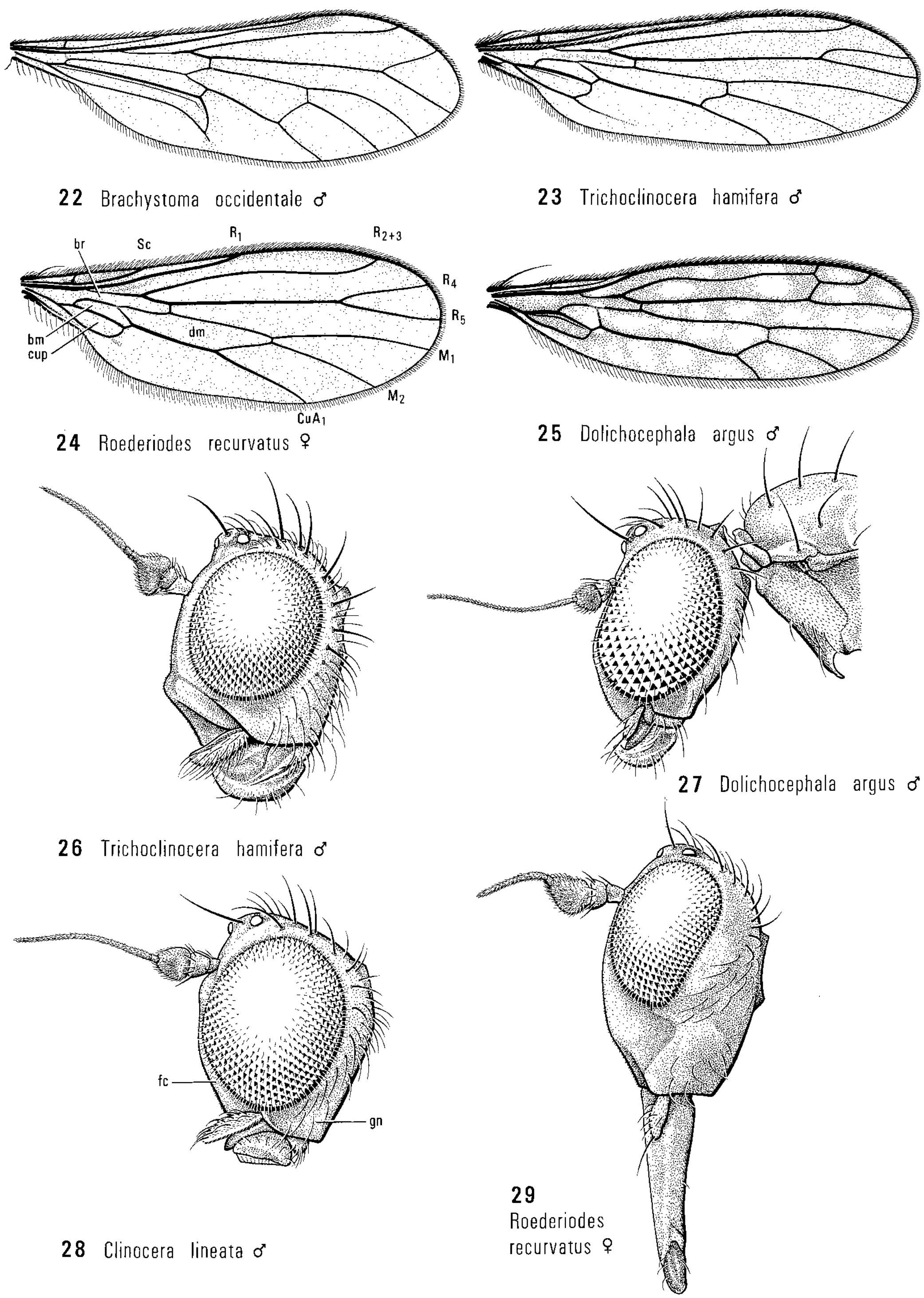
Proboscis short, thick, fleshy; lower head not rostrate; gena usually narrow (Figs. 26–28). Coloration various 32

32. Neck high on occiput; head extending obliquely forward (Fig. 27). Prosternum as long as mesosternum. Small species, not over 2.5 mm long. Wing with light spots on darker ground (Fig. 25) .... ***Dolichocephala*** Macquart
2 spp.; boreal

Neck near center of occiput; head vertical. Prosternum shorter than mesosternum. Species usually larger than 2.5 mm. Wing either hyaline or with dark spots on light ground 33

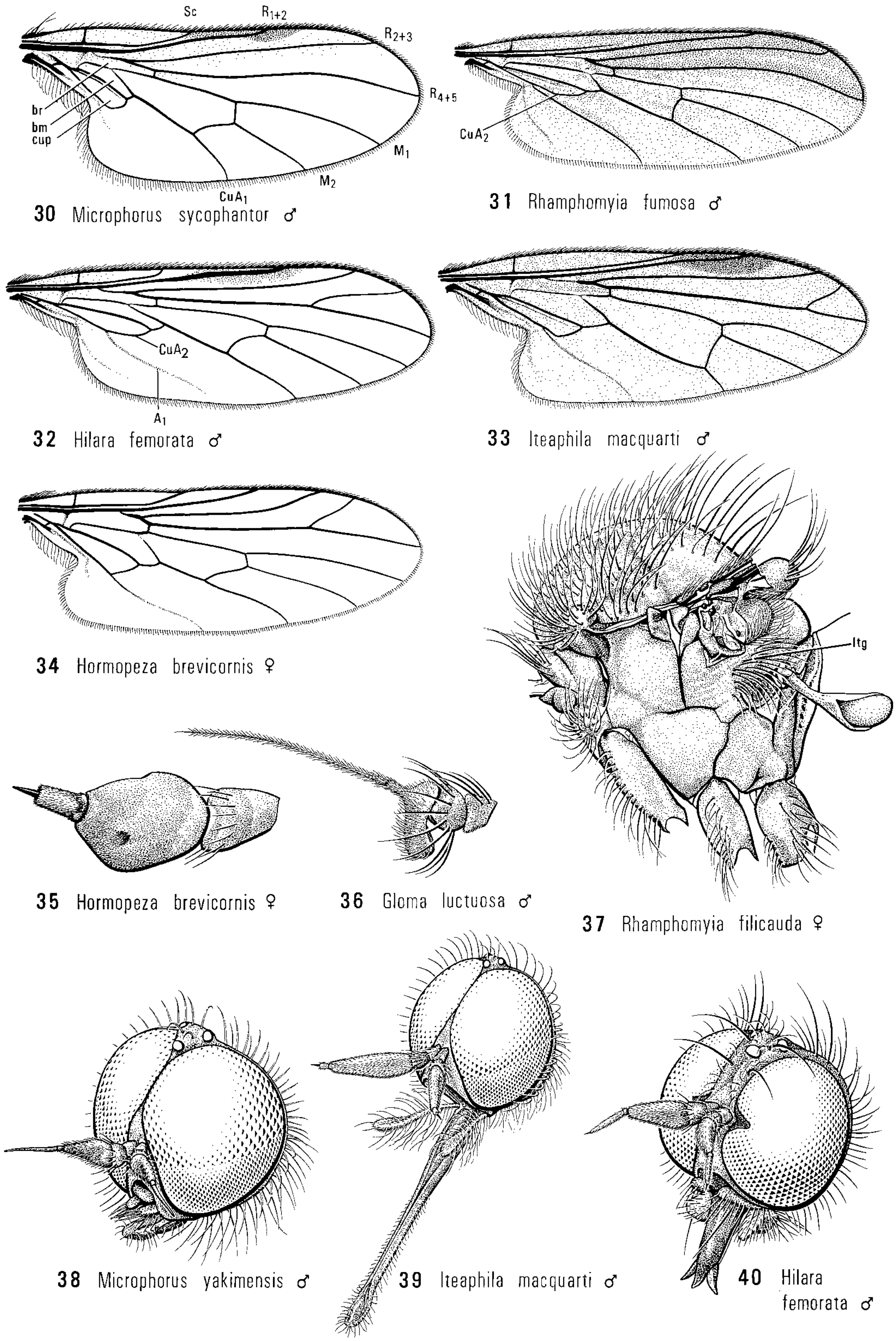
33. Face in lateral view extending well below eye, fused with gena (as in Fig. 29). Acrostichal setulae usually abundant .... ***Wiedemannia*** Zetterstedt
6 spp.; northern

Face in lateral view seldom much extended below eye, usually with division or groove extending to eye separating it from gena (Figs. 26, 28). Acrostichal setulae lacking 34



Figs. 47.22–29. Brachystomatinae and Clinocerinae: wing of (22) *Brachystoma occidentale* Melander, (23) *Trichoclinocera hamifera* (Melander), (24) *Roederiodes recurvatus* Chillcott, and (25) *Dolichocephala argus* Melander; head of (26) *Trichoclinocera hamifera*, (27) *Dolichocephala argus*, (28) *Clinocera lineata* Loew, and (29) *Roederiodes recurvatus*.

Abbreviations: fc, face; gn, gena.



Figs. 47.30–40. Empidinae: wing of (30) *Microphorus sycophantor* (Melander), (31) *Rhamphomyia fumosa* Loew, (32) *Hilara femorata* Loew, (33) *Iteaphila macquarti* Zetterstedt, and (34) *Hormopeza brevicornis* Loew; antenna of (35) *Hormopeza brevicornis* and (36) *Gloma luctuosa* Melander; (37) lateral view of thorax of *Rhamphomyia filicauda* Henriksen & Lundbeck; head of (38) *Microphorus yakimensis* Melander, (39) *Iteaphila macquarti*, and (40) *Hilara femorata*.

Abbreviation: ltg, laterotergite.

34. R_1 bare. Face and gena well-separated; base of palpus usually visible nearly to eye margin (Fig. 28) .... ***Clinocera*** Meigen

16 spp.; widespread, mostly well northward; Melander 1928

R_1 setose (Fig. 23). Face extending well below eye, usually divided from gena by a narrow groove; base of palpus hidden (Fig. 26) .... ***Trichoclinocera*** Collin

6 spp.; northern; Melander 1928 (with *Clinocera*)

35. CuA_2 recurved and confluent with underside of cell cu*p* (Figs. 30–33); in doubtful cases, R_{4+5} forked (Fig. 34), or bristles present on laterotergite (Fig. 37), or palpus long and bearing numerous bristles or hairs .... EMPIDINAE....36

CuA_2 forming distinct angle with basal part of A_1 (Figs. 41–44). Laterotergite never setose. Palpus short, at most with a few setae near tip 50

36. Basal cells (br and bm) and cell cu*p* very short; R_{4+5} simple (Fig. 30). Thorax usually longer than abdomen, robust, and gibbous. Eyes of male broadly contiguous on frons; upper ommatidia enlarged (Fig. 38). Male terminalia large, turned forward over preceding abdominal segments, and twisted to right .... ***Microphorus*** Macquart

15 spp.; mostly western; Melander 1940

Cells br, bm, and cu*p* never markedly short; R_{4+5} simple or forked (Figs. 31–34). Thorax not longer than abdomen. Eyes of male contiguous above or not; ommatidia various. Male terminalia not turned forward over preceding abdominal segments, nor twisted to right......37

37. Laterotergite with group of setae (Fig. 37) 38

Laterotergite bare........ 41

38. Sc attaining C; C circumambient, but weak posteriorly. Antenna with indistinctly four-segmented arista-like stylus .... ***Oreogeton*** Schiner

8 spp.; mostly in western mountains; Melander 1928

Sc evanescent apically (Fig. 31); C circumambient or lacking posteriorly. Antenna without or with two-segmented stylus 39

39. Face broad, very short; labrum long, slender, and straight, nearly attaining antennal bases in acute point. C circumambient. Antenna lacking stylus .... ***Brochella*** Melander

1 sp., *monticola* Melander; Washington

Face comparatively narrow; labrum well-separated from antennae. C extending only to tip of wing. Antenna with two-segmented stylus 40

40. R_{4+5} forked .... ***Empis*** Linnaeus

over 80 spp.; widespread; Melander 1902 and 1946*b*, Steyskal 1969

R_{4+5} simple .... ***Rhamphomyia*** Meigen

about 150 spp.; widespread; Coquillett 1895, Chillcott 1959, Steyskal 1964

41. Sc incomplete, not attaining C; R_{4+5} forked. Antenna well above subcranial cavity. Eyes of both sexes widely separated. Proboscis twice as long as head; palpus porrect .... ***Toreus*** Melander

1 sp., *neomexicanus* (Melander); New Mexico

Sc attaining C. Other characters various 42

42. Face narrow; subcranial cavity distant from antennal bases. Eyes of male usually well-separated; ommatidia usually uniform (Fig. 40) 43

Face broad and arched; subcranial cavity reaching closely to antennal bases. Eyes of male contiguous above; upper ommatidia enlarged (Fig. 39) 45

43. Sc bent forward to meet C; CuA_2 reaching nearly halfway to base of cell cu*p*; A_1 distinct (Fig. 32) .... ***Hilara*** Meigen

about 50 spp.; widespread; Melander 1902, Steyskal 1969 (*mutabilis* group)

Sc nearly straight, meeting C acutely; CuA_2 short; A_1 distinct or obsolete 44

44. Dorsocentral, lateral scutal, and scutellar bristles present. Ocelli anterior to vertex. Antenna below middle of head. Eyes of both sexes widely separated .... ***Philetus*** Melander

2 spp.; far western; Melander 1928

Thorax entirely without bristles. Ocelli at vertex. Antenna at middle of head. Eyes of male narrowly separated just below antennae .... ***Hesperempis*** Melander

2 spp.; far western

45. Proboscis stout, downcurved. Scape minute; basal flagellomere with stout bristle-tipped stylus .... ***Ragas*** Walker
 1 sp., *primigenia* Melander; California

 Proboscis directed horizontally or obliquely forward. Antenna various 46

46. Antenna with scape and pedicel apparently fused; basal flagellomere broadly orbicular to ovate, with short thick two-segmented stylus (Fig. 35). CuA_2 little reflexed; cell cu*p* as broad as cell bm (Fig. 34) .... ***Hormopeza*** Zetterstedt
 7 spp.; smoke flies, widespread; Kessel 1955, Steyskal 1969

 Antenna with scape and pedicel separate; basal flagellomere more or less elongate, and bearing arista-like stylus. CuA_2 abruptly reflexed; cell cu*p* narrower than cell bm (Fig. 33) 47

47. R_{4+5} simple. Proboscis long, extending obliquely forward .... ***Anthepiscopus*** Becker
 7 spp.; far western; Melander 1928

 R_{4+5} forked. Proboscis long or short 48

48. Proboscis long, extending obliquely forward (Fig. 39). Basal flagellomere two to five times as long as wide; stylus terminal short, thick .... ***Iteaphila*** Zetterstedt
 12 spp.; western and northern; Melander 1946*a*

 Proboscis short, scarcely protruding beyond face. Basal flagellomere oval or reniform, with elongate arista 49

49. Arista terminal; basal flagellomere globular .... ***Apalocnemis*** Philippi
 2 spp.; Pacific coast; Melander 1946*a*

 Arista dorsobasal; basal flagellomere reniform (Fig. 36) .... ***Gloma*** Meigen
 3 spp.; northwestern; Melander 1945

50. Cell cu*p* shorter than or about as long as cell bm, with its outer angle obtuse or right (Figs. 41–44). Proboscis short .... OCYDROMIINAE.... 51
 Melander 1928

 Cell cu*p* as long as cell bm, or longer, with its outer angle acute (Figs. 17–20). Proboscis various .... HYBOTINAE.... 59

51. Cell dm absent; branches of M evanescent near mid wing; CuA_2 strongly reflexed (Fig. 41). Face narrow (Fig. 47) 52

 Cell dm present, or rarely open by lack of crossvein dm-cu; branches of M not evanescent; CuA_2 not usually strongly reflexed. Face various 53

52. Hindleg raptorial; hind femur thickened; hind tibia strongly bent near base .... ***Hoplocyrtoma*** Melander
 2 spp.; 1 sp. northwestern, other eastern

 Hindleg slender, not raptorial .... ***Bicellaria*** Macquart
 11 spp.; widespread

53. Cell dm emitting two veins; M_2 thus absent (Fig. 42). Eyes of both sexes contiguous on face and frons. Antenna with long arista. Proboscis and palpus very small. Hind femur not thickened 54

 Cell dm emitting three veins (Figs. 43), rarely open by lack of crossvein dm-cu in which case M_{1+2} forked. Other characters various 55

54. Basal flagellomere conical; arista terminal. Mid tibia with several bristles. Ovipositor ensiform (Fig. 55) .... ***Leptopeza*** Macquart
 5 spp.; widespread

 Basal flagellomere oval; arista dorsoapical (Fig. 50). Mid tibia with only short apical bristles. Ovipositor not extruded .... ***Ocydromia*** Meigen
 1 sp., *glabricula* (Fallén); widespread, Holarctic

55. Basal flagellomere elongated, blunt at apex, more or less strap-shaped, with short stylus (Fig. 49); scape complete. Hind femur clavate, with strong spines below near tip (Fig. 46) .... ***Oedalea*** Meigen
 4 spp.; widespread

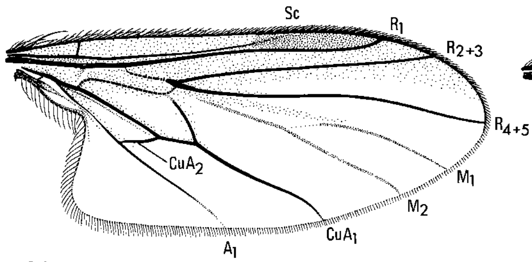
 Basal flagellomere globose to conical, pointed, usually with rather long stylus; scape incomplete. Hind femur usually slender, seldom with well-developed spines 56

56. Scape well-developed; flagellum with short terminal stylus. Cell bm very broad, with crossvein bm-cu nearly perpendicular (Fig. 43) .... ***Euthyneura*** Macquart
6 spp.; west, northeast

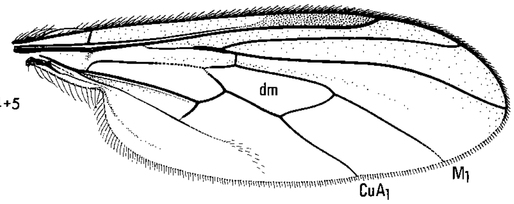
Scape quite vestigial; flagellum with or without stylus. Cell bm not greatly widened; crossvein bm-cu oblique (Fig. 44) 57

57. Antenna without stylus. Proboscis retracted within wide subcranial cavity; palpus bulbous. Eyes of both sexes widely separated; upper ommatidia not enlarged (Fig. 45) .... ***Allanthalia*** Melander
1 sp., *pallida* (Zetterstedt); east, Holarctic

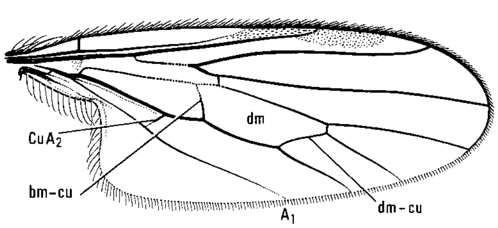
Antenna with stylus (Fig. 48). Proboscis more or less projecting. Male eyes broadly contiguous above antennae; upper ommatidia enlarged 58



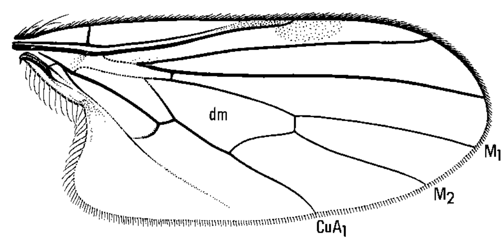
41 Bicellaria uvens ♀



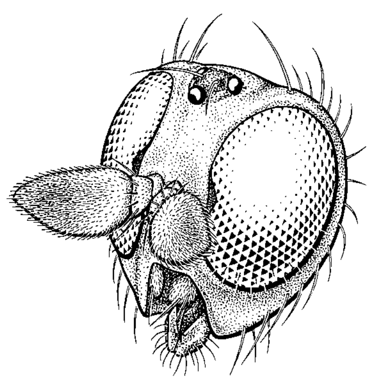
42 Leptopeza disparilis ♂

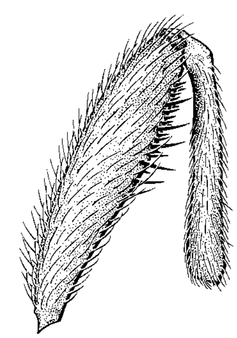


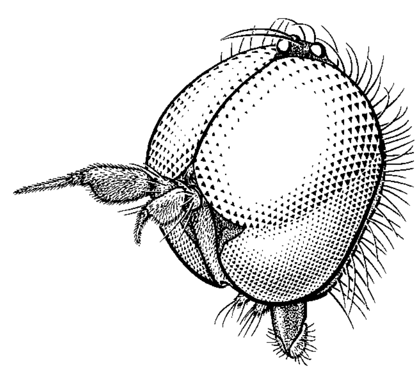
43 Euthyneura bucinator ♀

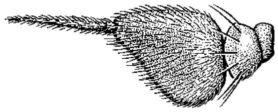


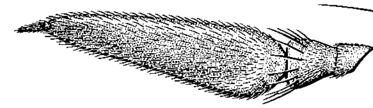
44 Anthalia lacteipennis ♀


45 Allanthalia pallida ♀


46 Oedalea ohioensis ♀

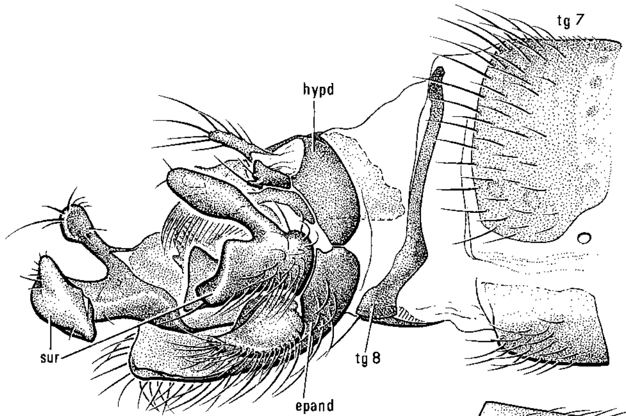

47 Bicellaria uvens ♀


48 Anthalia lacteipennis ♀

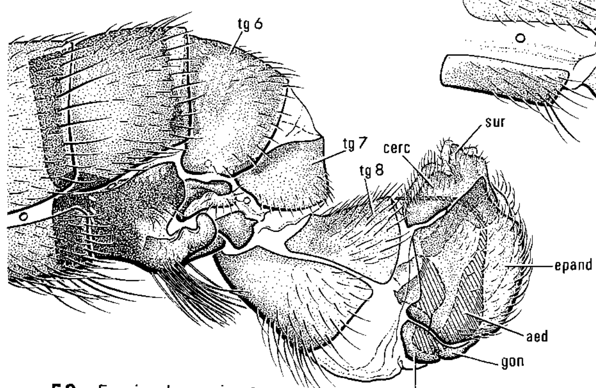

49 Oedalea ohioensis ♀


50 Ocydromia glabricula ♂

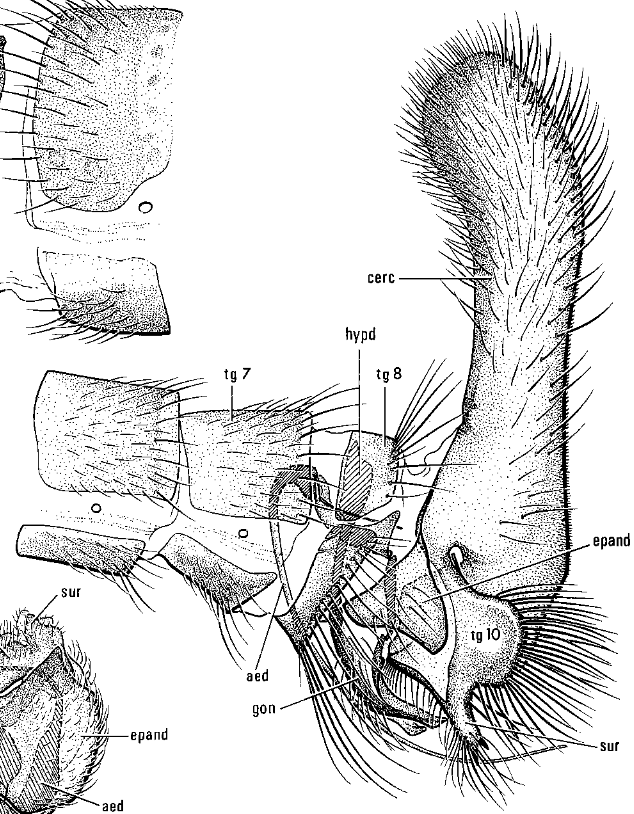
Figs. 47.41–50. Ocydromiinae: wing of (41) *Bicellaria uvens* Melander, (42) *Leptopeza disparilis* Melander, (43) *Euthyneura bucinator* Melander, and (44) *Anthalia lacteipennis* Melander; (45) head of *Allanthalia pallida* (Zetterstedt); (46) femur and tibia of *Oedalea ohioensis* Melander; (47) head of *Bicellaria uvens;* antenna of (48) *Anthalia lacteipennis,* (49) *Oedalea ohioensis,* and (50) *Ocydromia glabricula* (Fallén).



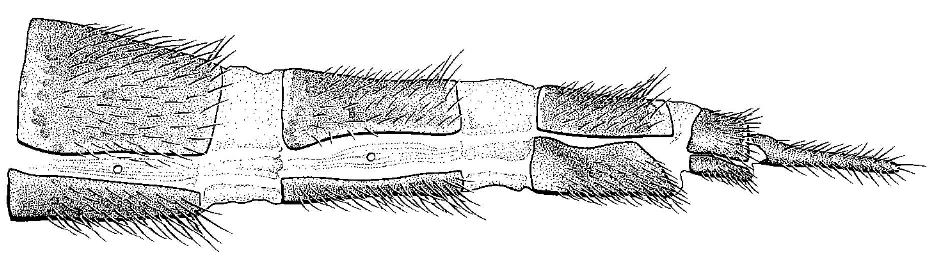
51 Drapetis armata ♂



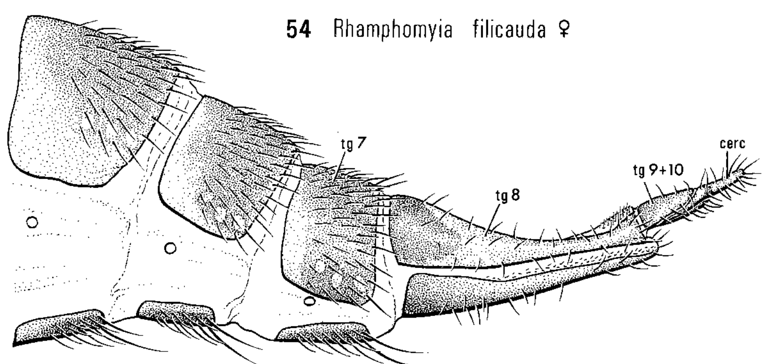
52 Empis browni ♂



53 Rhamphomyia fumosa ♂



54 Rhamphomyia filicauda ♀



55 Leptopeza disparilis ♀

Figs. 47.51–55. Terminalia: lateral view of male terminalia of (51) *Drapetis armata* Melander, (52) *Empis browni* Curran, and (53) *Rhamphomyia fumosa* Loew; lateral view of female terminalia of (54) *Rhamphomyia filicauda* Henriksen & Lundbeck and (55) *Leptopeza disparilis* Melander.

Abbreviations: aed, aedeagus; cerc, cercus; epand, epandrium; gon, gonopod; hypd, hypandrium; st, sternite; sur, surstylus; tg, tergite.

58. Antenna inserted below middle of head; basal flagellomere short and very broad (Fig. 48). Female frons broad; face usually emarginate up to antennae .... ***Anthalia*** Zetterstedt
11 spp.; west, northeast

Antenna inserted near middle of head; basal flagellomere elongate. Female frons narrow; face not emarginate up to antennae .... ***Trichina*** Meigen
7 spp.; widespread but uncommon

59. Antenna with stylus (Fig. 16). Eyes of male contiguous on frons, in female broadly separated. M_{1+2} forked; Sc distinctly separated from R_1; alula developed (Fig. 17) ...... ***Meghyperus*** Loew
2 spp.; far west

Antenna with long thin arista. Eyes contiguous above antennae in both sexes. M_{1+2} simple; Sc very close to R_1; alula lacking (Figs. 18–20) 60

60. Rs arising before middle of basal cells (br and bm) (Fig. 18). Scutellum with several marginal bristles or hairs. Hind femur more or less swollen .... ***Syneches*** Walker
14 spp.; widespread; Wilder 1974

Rs arising beyond middle of basal cells (Figs. 19, 20). Scutellum with two or only a few marginal bristles. Hind femur swollen or not 61

61. Basal section of M very weak; cell br broader than cell bm; cell dm much shorter than last section of M_1 (Fig. 19). Hind femur slender; hind tibia usually clavate .... ***Syndyas*** Loew
6 spp.; eastern North America westward to Texas and British Columbia; Teskey and Chillcott 1977

M strong basally; cell dm never much shorter than last section of M_1 (Fig. 20). Hind femur more or less thickened; hind tibia not clavate 62

62. R_{4+5} and M_1 parallel or diverging (Fig. 20). Eyes separated on face. Proboscis slender, projecting, about as long as head; palpus prominent (Fig. 21) .... ***Hybos*** Meigen
1 sp., *reversus* Walker; eastern

R_5 and M_1 somewhat convergent. Eyes contiguous or nearly so beneath antennae in both sexes. Proboscis and palpus short .... ***Euhybus*** Coquillett
12 spp.; eastern U.S.A. westward to Texas (*triplex* Walker also from California to British Columbia); Melander 1928

Larva

(modified in part from Smith 1969)

1. Respiratory system usually apneustic (posterior spiracles present in *Roederiodes*). Seven or eight pairs of abdominal prolegs present. Terminal segment with elongate lobes or short tubercles ending in long setae (Figs. 56, 59, 60), rarely ending in only a tuft of apical setae. Aquatic or semiaquatic 2

Respiratory system amphipneustic. Abdominal prolegs lacking. Terminal segment rounded, with a single midventral bare lobe (Figs. 57, 63). Usually terrestrial, found in soil, leaf litter, rotting wood 9

2. Terminal segment rounded posteriorly, at most with small dorsal and apical tubercles; each tubercle with one to three pairs of long setae (Fig. 60). Seven pairs of abdominal prolegs .... ***Chelifera***

Terminal segment with prominent caudal lobes (Figs. 56, 59). Seven or eight pairs of abdominal prolegs 3

3. Terminal segment with a single more or less medially divided setose caudal lobe (Fig. 56). Seven pairs of abdominal prolegs .... ***Hemerodromia***

Terminal segment with dorsal and apical caudal lobes. Eight pairs of abdominal prolegs 4

4. Terminal segment with two dorsolateral lobes and with one more or less divided apical lobe (Fig. 59) .... ***Clinocera*** (***Hydrodromia***)

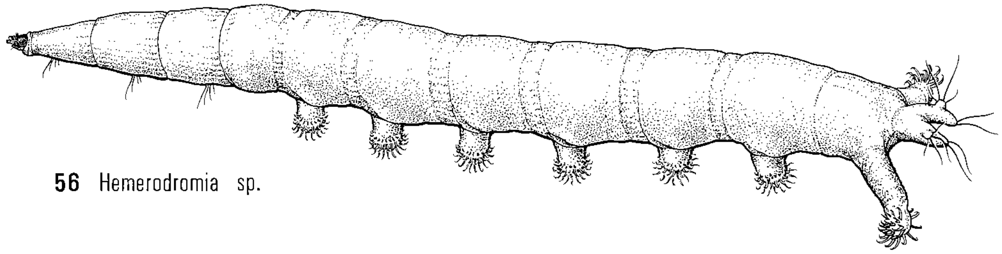
Terminal segment with two pairs of lobes 5

5. Prolegs and caudal lobes rounded, very short .... ***Dolichocephala***

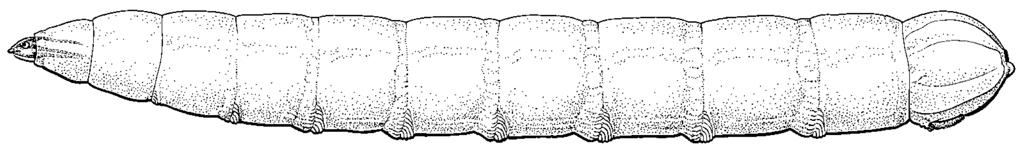
Prolegs and caudal lobes elongate, longer 6

6. Terminal segment with apical lobe short and with dorsolateral lobes long 7

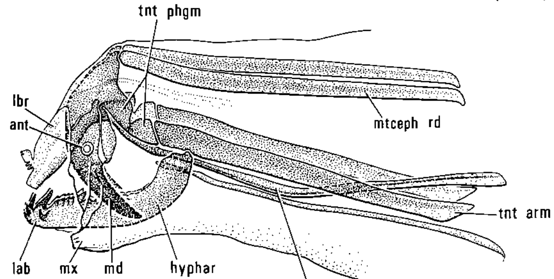
Terminal segment with lobes of equal length 8



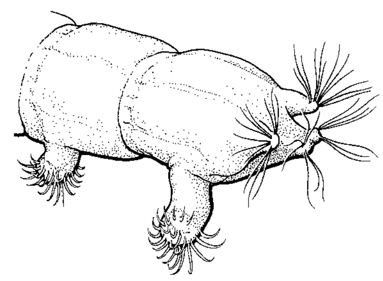
56 Hemerodromia sp.



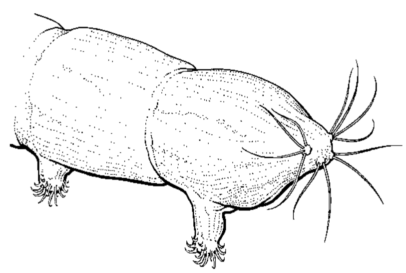
57 Rhamphomyia sp.



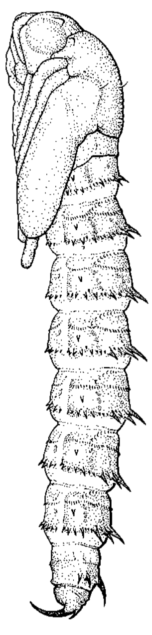
58 Empidinae

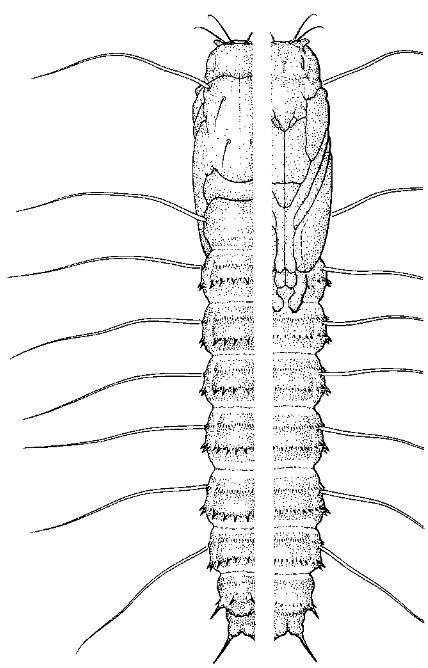


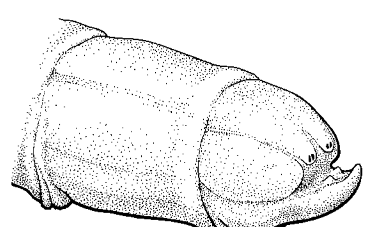
59 Clinocera sp.



60 Chelifera sp.







61 Clinocera stagnalis 62 Hemerodromia sp. 63 Phyllodromia sp.

Figs. 47.56–63. Immature stages: (56) dorsolateral view of larva of *Hemerodromia* sp.; (57) lateral view of larva of *Rhamphomyia* sp.; (58) head skeleton of larva of Empidinae; oblique posterolateral view of terminal segments of larva of (59) *Clinocera* sp. and (60) *Chelifera* sp.; (61) lateral view of pupa of *Clinocera stagnalis* (Haliday); (62) half dorsal and half ventral views of pupa of *Hemerodromia* sp.; (63) oblique posterolateral view of terminal segments of larva of *Phyllodromia* sp.

Abbreviations: ant, antenna; hyphar, hypopharynx; lab, labium; lbr, labrum; md, mandible; mtceph rd, metacephalic rod; mx, maxilla; phr, pharynx; tnt arm, tentorial arm; tnt phgm, tentorial phragmata.

7. Posterior spiracles present .... ***Roederiodes***
   Posterior spiracles absent .... ***Clinocera (Clinocera)***
8. Posterior spiracles present, on dorsolateral lobes. Abdominal segments 1–7 each with a group of six setae on either side. Last thoracic segment with row of brushy protuberances dorsally .... ***Oreogeton***
   Posterior spiracles absent. Abdominal segments without setae laterally. Last thoracic segment without brushy protuberances .... ***Wiedemannia***
9. Posterior spiracles subtended by a small lobe. Terminal segment without lateral furrows. Living in dung .... ***Ocydromia***
   Posterior spiracles subtended by a larger more obvious lobe. Terminal segment usually with lateral furrows (Fig. 57). Living in soil, leaf-litter, rotting wood 10
10. Caudal lobe very short, fairly broad, thick-based (Fig. 57); posterior spiracles yellowish brown, rather large, separated by one or two times their own diameter .... ***Drapetis***, ***Empis***, ***Rhamphomyia***
   Posterior lobe considerably longer than above, usually with apex curved dorsally (Fig. 63); posterior spiracles small, yellow or yellowish brown, separated from each other by about four to six times their diameter 11
11. Posterior spiracles with float hairs .... ***Hilara***
   Posterior spiracles without float hairs .... ***Phyllodromia***, possibly ***Microphorus***, possibly ***Platypalpus***

Pupa

1. Elongate lateral spiracular processes present (Fig. 62) 2
   Elongate lateral spiracular processes absent 3
2. Apical paired integumentary horns elongate and heavily sclerotized .... ***Neoplasta***
   These horns short and lightly sclerotized (Fig. 62) .... ***Chelifera***, ***Hemerodromia***
3. Prothorax with a pair of elongate respiratory horns extending above hind angle of head 4
   Prothorax without elongate respiratory horns 5
4. Abdominal segments with series of strong spines dorsally and weak hairs ventrally; terminal segment ending in two strong hooks .... ***Roederiodes***
   Abdominal segments with weak spines dorsally and without hairs ventrally; terminal segment not ending in hooks .... ***Drapetis***
5. Terminal segment ending in strongly sclerotized hooks; abdomen clothed mainly with strong spines 6
   Terminal segment ending in short bristles or processes; abdomen clothed mainly with bristles .... ***Empis***, ***Hilara***, ***Rhamphomyia***
6. Thorax in dorsal view more than one-third length of abdomen .... ***Phyllodromia***
   Thorax in dorsal view less than one-third length of abdomen (Fig. 61) .... ***Clinocera***, ***Oreogeton***, ***Wiedemannia***

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DOLICHOPODIDAE 48

H. Robinson and J. R. Vockeroth

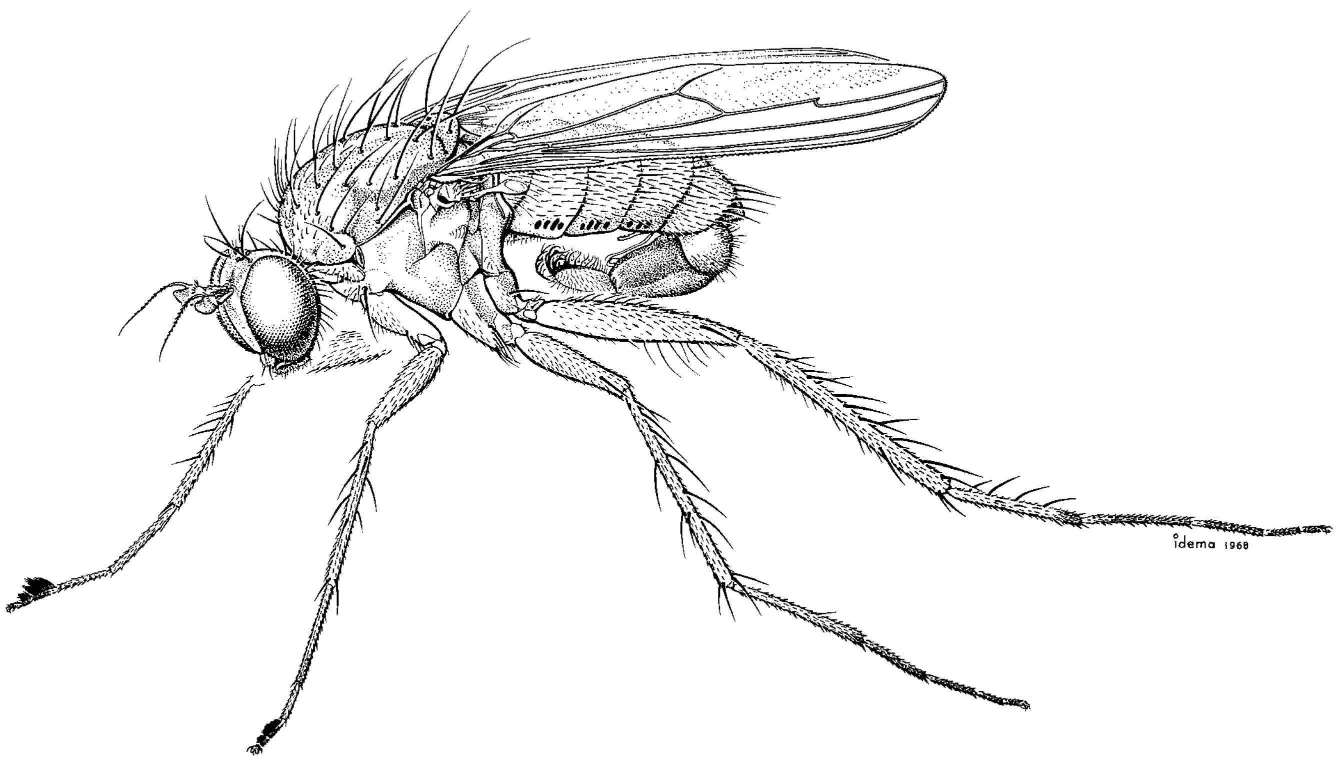


Fig. 48.1. Male of *Dolichopus cuprinus* Wiedemann.

Mostly slender flies, 0.8–9.0 mm long (Fig. 1); smaller forms often stout. Species usually green, sometimes yellow, more rarely brown or black, shining metallic to pruinose. Wing with cells dm and bm united; vein A_1 and cell cu*p* sometimes rudimentary or lacking (Figs. 21–35).

Adult. Head: frons usually broad, narrower anteriorly (Figs. 2–8, 11), obliterated by contiguous eyes in male of some species of *Diaphorus* Meigen and *Chrysotus* Meigen (Fig. 7), rarely bearing setae except along upper limit. Face sometimes broader than frons, usually narrow especially below, sometimes obliterated by contiguous eyes. Clypeus sometimes sharply demarcated, at other times indistinguishable, usually truncate below, sometimes projecting forward in roof-like form or projecting far downward in front of mouth. Eye usually haired, occupying entire lateral surface of head; subocular surface of head exposed slightly in female of some species. Complete series of postocular setae present, sometimes sparse or very fine; single pairs of ocellar and vertical bristles strong; postvertical bristles usually near vertical bristles, sometimes set far behind vertex, usually single, rarely with a series on each side; lower orbit usually with sparse hairs, sometimes with dense pubescence indistinguishable from lower postocular bristles; clypeus usually bare, or sometimes with weak to strong setae near lower margin; face and sometimes frons covered with many slender long hairs in some species of *Condylostylus* Bigot. Antenna variable (Figs. 10, 12–20); scape rarely wider than long, sometimes very elongate, with or without setae dorsally; pedicel usually slightly wider than scape, short truncate apically or overlapping first flagellomere dorsally or on inner surface, ringed by a series of sometimes very prominent setae; first flagellomere about as large as pedicel or very enlarged, sometimes strap-shaped, rarely bilobate, multilobate in *Cheirocerus* Parent (Neotropical), usually laterally compressed, bearing fine pubescence and rarely minute setulae; arista usually inserted on dorsal margin, sometimes apically, rarely below apex, two-segmented, bearing long or short hairs or essentially glabrous, with dorsal and ventral hairs or apical hairs sometimes unusually long; tip of arista sometimes enlarged into a plate, and with median node occasionally present; rarely entire arista swollen. Palpus flat, sometimes greatly enlarged into strap or palette form, bearing one to many distinct setae, or covered only with pollen that is often concolorous with face; complex epipharyngeal armature and usually a deltoid hypopharynx present (Fig. 2.51); labella usually flexible and spreading in repose, in *Melanderia* Aldrich highly sclerotized and mandibuliform (Fig. 11); usually six or more narrow pseudotracheae present on inside surface of labella, located in furrows, extending from base toward margin, and showing various patterns of sclerotization.

Thorax: scutum usually strongly bristled, rarely with all but hindmost setae reduced as in some Hydrophorinae; one postpronotal, two presutural supra-alar, and two notopleural bristles usually present; presence of presutural intra-alar bristle sometimes correlated with presence of acrostichal bristles; one postsutural intra-alar, two postsutural supra-alar, and one postalar bristle usually present; usually six pairs of large dorsocentral bristles present, namely two presutural and four postsutural, but sometimes one, two, or three anterior pairs reduced, and the fifth pair often displaced toward middle and sometimes lacking; rarely small dorsocentral bristles arranged in a series of 12–20 (*Enlinia* Aldrich); acrostichal setae usually very small, biserial, sometimes uniserial or lacking (a few usually present on anterior slope of scutum), but large in some Sciapodinae; scutellum haired or bare above, with two to six larger marginal bristles. Proepisternum with hairs or bristles above base of fore coxa, sometimes with one to many setae on upper half. Bristles absent from rest of lateral surface of thorax, but hairs sometimes present on some sclerites of mesopleuron and of metapleuron.

Wing (Figs. 21–35) usually oval, about as long as body, markedly reduced in only one Nearctic species, sometimes vestigial (in one species of *Acropsilus* Mik from Campbell Island wing and halter lacking); membrane usually clear, but sometimes marked with brown pigment and more rarely with white spots. C usually continuous to juncture with M, rarely vestigial beyond R_{4+5} (*Asyndetus* Loew); Sc ending in R_1 except in Hydrophorinae; Rs arising at or very near level of crossvein h; R_{4+5} unbranched; M often straight beyond crossvein dm-cu, sometimes forked or flexed near middle of last part; cells dm and bm united; crossvein r-m short, near wing base; vein A_1 and cell cu*p* sometimes rudimentary or absent.

Legs usually with large bristles on tibiae. All parts of legs in male subject to variation in shape and vestiture; legs of female rarely modified. Tarsi usually with bristle-like empodia and broad pulvilli; in some Hydrophorinae empodia pectinate below or deep and compressed; male of several genera with one or more tarsal claws absent or modified in form; first two tarsomeres of foreleg fused in *Neurigona lateralis* (Say).

Abdomen: five or seven pairs of spiracles present in male, and usually five pairs in female but seven pairs in at least *Xanthochlorus* Loew; spiracles situated in membrane below tergites. Sternite 1 vestigial or absent.

Male (Figs. 36–39, 2.127–129) with hind margin of tergite 5 sometimes modified; tergite 6 exposed or mostly retracted under tergite 5; tergite 7 exposed or partly or completely retracted, sometimes asymmetric; tergites 6 and 7 haired or bare. Sternites 2–5 usually well-developed, sometimes reduced in forms with large recessed terminalia; sternites 3 and 4 sometimes with projections in *Enlinia*; sternite 5 often enlarged, recessed, produced posteriorly or bearing projections which in *Scellus* Loew are very long and pale; sternites 6 and 7 rarely well-developed and haired, usually weak and bare or even lacking; sternite 7 sometimes asymmetric. Tergite 8 vestigial or absent; sternite 8 well-developed, lying laterally or dorsolaterally on left side of base of genital capsule, with weak to strong and sometimes long setae. Genital capsule apparently formed from fused elements of segment 9 (epandrium, hypandrium, and gonopods); segment 9 apparently rotated about 270° to the right in relation to segment 8, which in turn is rotated about 90° in relation to preceding segments; capsule then flexed downward and usually forward so that when at rest the cerci are ventral in position with the aedeagus projecting forward above them; ventroflexion usually involving also segments 6 and 7. Capsule small and enclosed in preceding segments (Fig. 36), large and exposed (Fig. 37), or greatly enlarged and reaching nearly to base of abdomen (Fig. 38). Aedeagus usually long, slender, and projecting from capsule, rarely short or broadened near apex, with its base in front of and slightly below bases of cerci from whence it curves forward, downward, and then backward; distal portion usually supported and sometimes partly enclosed by a slender or rather broad aedeagal guide; aedeagal guide, when distinct, projecting from ventromedial margin of capsule, weakly or firmly attached to capsule, apparently representing one or more processes of the hypandrium that project anterodorsally into the capsule and support the base of the aedeagus; ejaculatory apodeme distinct, lying in front of base of aedeagus. Posterolateral margin of capsule with one to three processes of varied form which may be articulated or partly or wholly fused with the margin of the capsule or with its inner surface; homologies of these structures uncertain but possibly representing a secondary lobe of the gonopod, a single or bifid gonostylus, a surstylus, a protruding apical portion of a paramere, or some combination of these [for figures and interpretations see Buchmann (1961), Negrobov and Stackelberg (1971, Lfg. 284), and Ulrich (1974)]. Cercus extremely varied in size, shape, texture, and vestiture. A median sclerite of varied form present below the bases of the cerci, sometimes projecting well beyond the posterior margin of the capsule, and perhaps representing sternite 10. Genital capsule strongly asymmetric at base, with anterior opening on left side; most structures associated with capsule symmetric but some, especially aedeagal sheath and hypandrium, slightly to strongly asymmetric.

Female (Figs. 2.102, 2.103) with tergites 1–5 and sternites 2–5 well-developed; rest of abdomen usually telescoped and retracted into segment 5. Tergites 6 and 7 and sternites 6 and 7 entire, if retracted then weaker than sclerites of segment 5 and each sclerite with a seta in each posterolateral corner or with an irregular row of setae along the posterior margin, and if partly or completely exposed then strongly sclerotized and usually with numerous hairs on the exposed portions; membrane behind segments 6 and 7 short or long, sometimes with elongate weakly sclerotized areas. Tergite 8 almost always retracted, posteriorly emarginate or divided, and bare, sometimes in the form of two elongate struts; sternite 8 entire or divided, sometimes much shorter than tergite 8; in *Lamprochromus* Mik tergite 8 entire and partly exposed and haired, and sternite 8 entire and with a pair of hairs; membrane behind sternite 8 usually deeply infolded and with many retrorse spicules. Proctiger formed of a dorsal epiproct, ventral hypoproct, and lateral cerci; anterolateral corner of hypoproct or base of cerci sometimes fused with anterolateral corner of epiproct. Epiproct usually broadly rounded apically or partly or completely divided medially, with weak setae, usually with one to six pairs of short strong erect spinose setae near apex, without spinose setae in *Neurigona* Rondani, in *Xanthochlorus*, and in some Sciapodinae; epiproct apparently absent in *Neurigona lateralis*. Hypoproct entire, broadly rounded apically, subtriangular or slender, usually with only weak setae, in *Neurigona lateralis* with a pair of rather long curved spinose setae. Cercus lateral in position, usually slender and partly or entirely divided into a longer dorsal and a shorter ventral lobe each of which bears one or several setae; in *Neurigona lateralis* cercus flat, broad, apically rounded, undivided. In *Thrypticus* Gerstäcker segment 8 and proctiger apparently fused to form a strongly sclerotized compressed lanceolate ovipositor. Spermatheca single, colorless, often coiled.

Egg. Short oval to elongate oval in dorsal view, flat below, convex above, white to brown when laid. Surface without obvious sculpturing, and sometimes polished.

Larva. Usually whitish, cylindrical, slightly tapered anteriorly (Figs. 40, 44). Head segment (Figs. 41, 43) usually short, unsclerotized externally, with four lobes; lateral pair of lobes bearing peg-like antennae; anterior pair considered maxillary palpi; sclerotized internal parts brown to black, including mandibular–maxillary sclerites, slender labrum extending anteriorly from anterior remnant of cranium, pharyngeal sclerite, pairs of tentorial arms and metacephalic rods, and pairs of hypopharyngeal and labial sclerites ventrally. Posterior surface of terminal segment crossed with a vertical and a horizontal furrow; four or more lobes so produced usually elongate giving a truncated appearance (Fig. 40), but sometimes very short with terminal segment rounded (Fig. 44) (*Neurigona* Rondani, *Medetera* Fischer von Waldheim); dorsal lobes each usually bearing a posterior spiracle, and fringed with a series of branched setae. Abdominal segments 1–7 each with a pair of creeping welts on anterior margin; in *Systenus* Loew those of segment 1 very large and resembling prolegs.

Pupa. Enclosed in a loose sometimes silky (*Medetera*) cocoon that usually has debris from the habitat incorporated or adherent. A pair of large respiratory horns arising from dorsal surface of cephalothorax just behind eyes (Fig. 42). A pair of frontofacial sutures running on ventral surface posteriorly from the apical cephalic tubercle, and diverging behind beyond posterior cephalic tubercles or behind antennae. Tergites of abdomen usually with a transverse row of spines. Anal segment bluntly rounded or ending in a pair of stout spines.

Biology and behavior. Adults and most larval forms, where known, are predacious; larvae of *Thrypticus* are phytophagous, adults of *Dolichopus* Latreille are notable as predators of larvae of Culicidae, and larvae of *Medetera aldrichii* Wheeler are predators of larvae of Scolytidae (bark beetles). The Dolichopodidae are very sensitive to cold and rarely appear after the first frost. A few species appear in mid spring, but most appear in late spring and early summer; farther north many species persist through the summer. In tropical regions most species appear during the rainy season, which usually lasts from October to March or from December to May. Few species walk or run; most remain still between flights. Some species hover close to rock, soil, or falling water. Most species occur along margins of streams or lakes on soil or vegetation. However, members of the Sciapodinae are often widely distributed on foliage in fields and gardens, and some species of *Medetera* occur in fairly dry sites. Several genera and species are restricted to maritime areas; some species (*Dolichopus*) rest and feed on the surface of water, and others (*Hydrophorus* Fallén) alight on water and are washed ashore. Most species prefer some direct sunlight, although some (*Sympycnus* Loew, *Calyxochaetus* Bigot) occur in deep shade. In some genera ecology seems related to mating. Often, females station themselves in specific habitats such as trunks of trees (*Neurigona*, *Medetera*), wet soil (*Enlinia ciliata* Robinson), wet rock (*Enlinia saxicola* Robinson), or fairly dry rock (*Microcyrtura* Robinson) where males of their species occur and scout for them. The normal habitats of males and females, however, occasionally differ slightly as to the amount of shade or water (*Harmstonia* Robinson). Males of some species, especially among the Dolichopodinae, perform complex mating dances. Males usually show little discrimination when mating, often attempting to copulate with females of other species or genera, by whom they are rejected. In *Gymnopternus* Loew, however, the female is sometimes specially marked, and the male apparently does discriminate.

Classification and distribution. The family occurs world wide and contains over 150 genera and nearly 6000 described species. The basic works on the family remain those of Becker (1917–1918, 1922*a*, 1922*b*). A comprehensive review of world subfamilies and genera is badly needed. More recent treatments of specific areas are those of Stackelberg (1930–1971) and Negrobov and Stackelberg (1971–1974) for the Palaearctic region, Parent (1938) for France, Robinson (1964) for the southeastern United States, Robinson (1975) for Dominica, and Fonseca (1978) for Great Britain. Robinson's (1964) paper is not referred to under the individual genera in the key unless all Nearctic species are treated. Lundbeck (1912) is a useful older reference for northern Europe. The study of the genus *Dolichopus* in North America by Van Duzee *et al.* (1921) remains a classic in spite of subsequent additions and corrections. Departures in the treatment here from that given by Foote *et al.* (1965) are clarified in the papers of Robinson (1964, 1970*a*, 1970*b*). Papers dealing with specialized aspects of the Dolichopodidae include those of Buchmann (1961) and Ulrich (1974) on terminalia, Cregan (1941) on mouthparts, and Dyte (1967) on larvae and pupae. Habitat preferences of many larvae are reviewed by Dyte (1959).

Species of Dolichopodidae occur from the high Arctic south to southern Chile and several subantarctic islands. They are well represented on oceanic islands, especially Hawaii, which has three endemic genera and about 200 endemic species, mostly in the genus *Campsicnemus* Haliday and the endemic genus *Eurynogaster* Van Duzee. Species with wings markedly reduced in one or both sexes occur in Hawaii, on subantarctic islands, in the Himalayas (Hardy and Delfinado 1974), and in eastern North America (female of an undescribed species of *Campsicnemus*).

Several Tertiary forms preserved in amber have been described by Meunier (1907). Most are assigned to recent genera.

Keys to genera

Adult

1. Vertex of head deeply excavated as seen from anterior view (Fig. 2). Scutum often as wide as long. M usually with a widely divergent fork (Fig. 21) 2

   Vertex of head not or only slightly excavated (Figs. 3–8). Scutum never as wide as long. M without well-developed widely divergent fork, although sometimes with a very short or faint fork (Figs. 22–35) 5

2. M unbranched, lacking posterior branch (Fig. 22) .... ***Mesorhaga*** Schiner

   11 spp.; widespread; Robinson 1964

   M distinctly branched (Fig. 21) 3

3. Frons with only black bristles. Setae of calypter usually pale, rarely black. Scutellum with one or two pairs of bristles .... ***Sciapus*** Zeller

   24 spp.; widespread; Van Duzee 1915*a*, Robinson 1964, Steyskal 1966 and 1973*a*

   Frons with pale and sometimes very short hairs among black bristles. Setae of calypter black. Scutellum with two pairs of bristles 4

4. Arista as long as head and thorax combined; tip often white or otherwise ornamented .... ***Chrysosoma*** Guérin-Méneville

   3 spp.; eastern; Robinson 1964 (as part of *Condylostylus* Bigot)

   Arista distinctly shorter than length of head and thorax combined; tip not ornamented .... ***Condylostylus*** Bigot

   40 spp.; widespread; Van Duzee 1915*a*, Parent 1929, Robinson 1964

5. C not distinct beyond tip of R_{4+5}; M weak, usually discontinuous in last part (Fig. 26) .... ***Asyndetus*** Loew

   21 spp.; widespread; Van Duzee 1919

   C continuous to tip of M; M not weak, and not discontinuous in last part 6

6. R_{4+5} and M distinctly diverging from base to tips (Figs. 25, 35); M usually ending far behind wing tip; in male of some species veins much distorted. Adult usually about 1 mm long 7

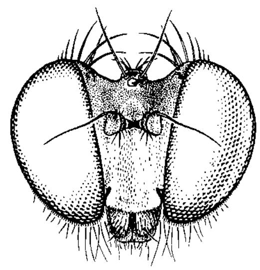
   R_{4+5} and M nearly parallel (Fig. 33) or converging (Figs. 27–32) beyond crossvein dm-cu; M ending at most slightly behind wing tip. Adult 1.3–9.0 mm long 9

7. Acrostichal setae absent. Face of female with small setulae below .... ***Harmstonia*** Robinson

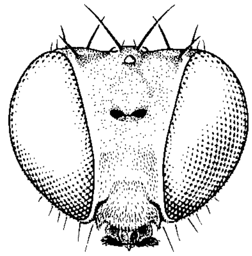
   2 spp.; eastern; Robinson 1967*b*

   Acrostichal setae present. Face of female without setulae 8

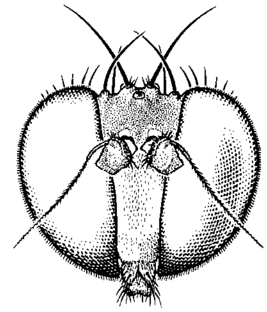
Figs. 48.2–20. Heads, hind tarsus, and antennae: head of (2) *Mesorhaga pallidicornis* Van Duzee, (3) *Psilopiella rutila* Van Duzee, (4) *Dolichopus cuprinus* Wiedemann, (5) *Nanomyina litorea* Robinson, (6) *Chrysotus pallipes* Loew, (7) *Chrysotus spectabilis* (Loew), and (8) *Tachytrechus vorax* Loew; (9) hind tarsus of *Dolichopus cuprinus*; (10) antenna of *Pelastoneurus vagans* Loew; (11) head of *Melanderia mandibulata* Aldrich; antenna of (12) *Rhaphium crassipes* (Meigen), (13) *Chrysotus pallipes*, (14) *Argyra currani* Van Duzee, (15) *Systenus albimanus* Wirth, (16) *Medetera aldrichii* Wheeler, (17) *Neurigonella nigricornis* (Van Duzee), (18) *Syntormon tricoloripes* Curran (inner surface of right antenna), (19) *Hypocharassus pruinosus* (Wheeler), and (20) *Hydrophorus intentus* Aldrich.



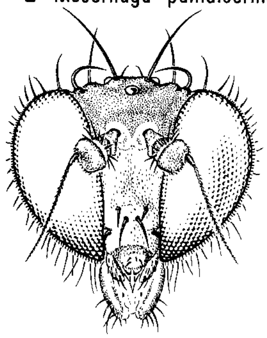
2 Mesorhaga pallidicornis ♀



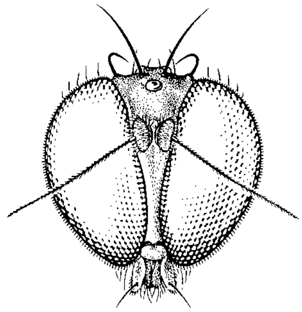
3 Psilopiella rutila ♀



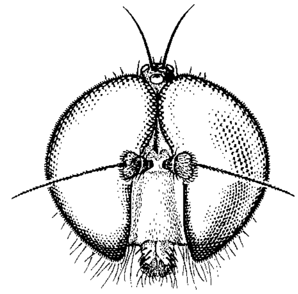
4 Dolichopus cuprinus ♂



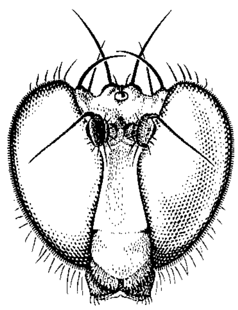
5 Nanomyina litorea ♂



6 Chrysotus pallipes ♂



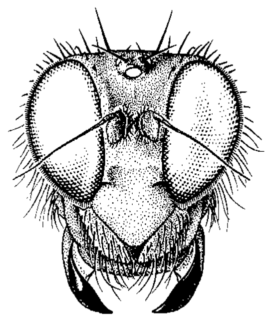
7 Chrysotus spectabilis ♂



8 Tachytrechus vorax ♂

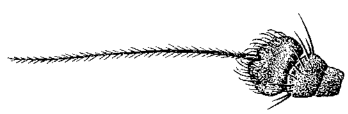
9 Dolichopus cuprinus ♂

10 Pelastoneurus vagans ♂



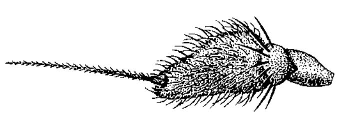
11 Melanderia mandibulata ♀

12 Rhaphium crassipes ♂



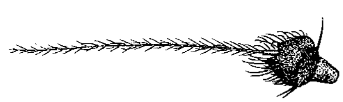
13 Chrysotus pallipes ♂

14 Argyra currani ♂

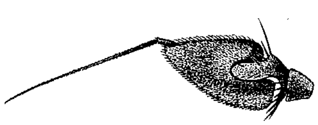


15 Systenus albimanus ♂

16 Medetera aldrichii ♂

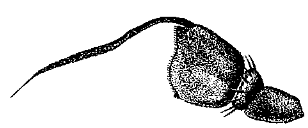


17 Neurigonella nigricornis ♂

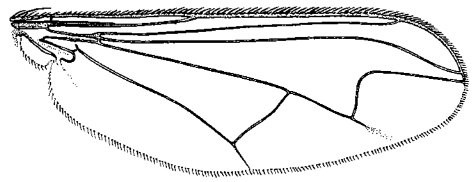


18 Syntormon tricoloripes ♂

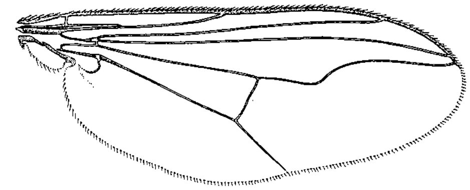
19 Hypocharassus pruinosus ♀



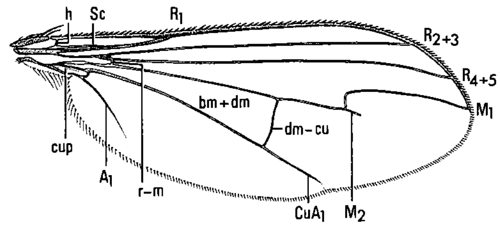
20 Hydrophorus intentus ♂



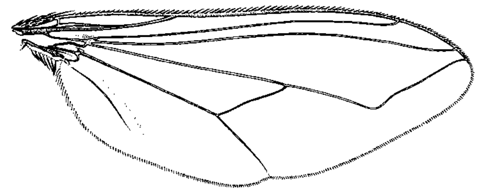
21 Sciapus scintillans ♂



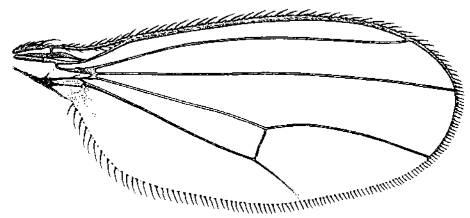
22 Mesorhaga pallidicornis ♀



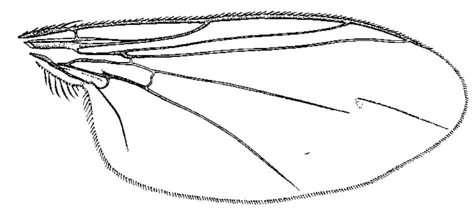
23 Dolichopus cuprinus ♂



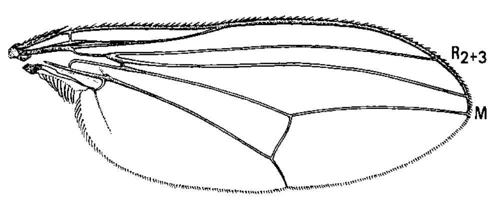
24 Plagioneurus univittatus ♂



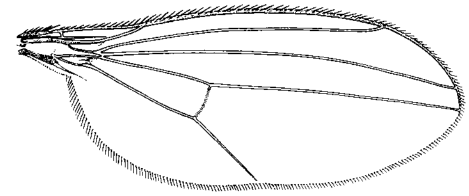
25 Enlinia magistri ♀



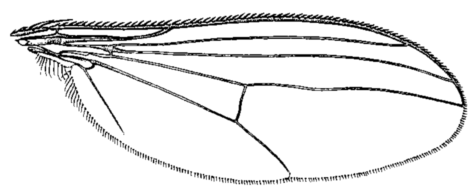
26 Asyndetus appendiculatus ♂



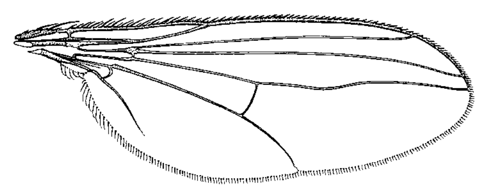
27 Medetera aldrichii ♂



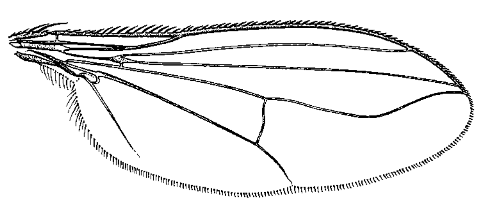
28 Thrypticus willistoni ♂



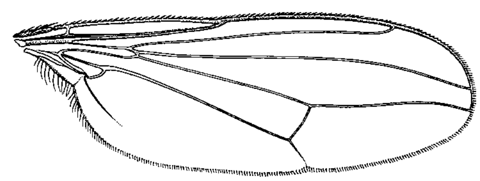
29 Gymnopternus spectabilis ♂



30 Hercostomus chetifer ♂



31 Paraclius minutus ♂



32 Hydrophorus intentus ♂

Figs. 48.21–32. Wings: (21) *Sciapus scintillans* (Loew); (22) *Mesorhaga pallidicornis* Van Duzee; (23) *Dolichopus cuprinus* Wiedemann; (24) *Plagioneurus univittatus* Loew; (25) *Enlinia magistri* (Aldrich); (26) *Asyndetus appendiculatus* Loew; (27) *Medetera aldrichii* Wheeler; (28) *Thrypticus willistoni* (Wheeler); (29) *Gymnopternus spectabilis* Loew; (30) *Hercostomus chetifer* (Walker); (31) *Paraclius minutus* Van Duzee; (32) *Hydrophorus intentus* Aldrich.

8. R_{4+5} and M ending about the same distance from wing tip (Fig. 35). Male with veins not distorted. Length 1.9 mm or more .... ***Achalcus*** Loew
2 spp.; western; Steyskal 1970

R_{4+5} ending in or near wing tip; M ending far beyond wing tip (Fig. 25). Male sometimes with veins distorted. Length 1.5 mm or less .... ***Enlinia*** Aldrich
6 spp.; widespread; Robinson and Arnaud 1970

9. Mid and hind femora without distinct preapical bristle on anterior to anterodorsal surface. Upper part of proepisternum bare or with few setae 10

Mid or hind femur with distinct preapical bristle on anterior to anterodorsal surface, or upper part of proepisternum densely covered with long pale setae 18

10. Disc of scutum with posterior one-third to one-half flattened 11

Disc of scutum evenly convex or at most slightly flattened immediately before scutellum 15

11. Acrostichal setae absent or present only at anterior end of scutum .... ***Xanthochlorus*** Loew
1 sp., *helvinus* Loew; eastern

Acrostichal setae extending at least to transverse suture 12

12. Distal part of M straight or very slightly and evenly curved (Figs. 27, 28). Upper part of proepisternum bare. Male terminalia elongate, projecting forward under abdomen; tergite 7 exposed and haired (Fig. 38) 13

Distal part of M with a slight to strong depression. Upper part of proepisternum with one to three pale setae. Male terminalia short or elongate; tergite 7 mostly hidden, bare 14

13. R_{2+3} and M nearly equidistant at level of crossvein dm-cu and at apices of veins; A_1 weak but distinct (Fig. 27). Hind coxa with one lateral bristle. Female terminalia short and broad .... ***Medetera*** Fisher von Waldheim
52 spp.; widespread; Van Duzee 1928

R_{2+3} and M divergent beyond level of crossvein dm-cu; A_1 nearly obsolete (Fig. 28). Hind coxa with two lateral bristles. Female terminalia elongate, lanceolate .... ***Thrypticus*** Gerstäcker
13 spp.; widespread; Van Duzee 1921

14. First flagellomere slightly to greatly enlarged, much larger than pedicel; arista nearly apical (Fig. 15). Male terminalia usually extending far forward under preceding abdominal segments; cercus usually long and slender; tergite 6 haired. Female terminalia with dorsal spine-like setae at apex .... ***Systenus*** Loew
6 spp.; widespread; Steyskal 1970

First flagellomere not much larger than pedicel; arista dorsal. Male terminalia borne on or under tip of preceding abdominal segments; cercus short and broad; tergite 6 bare (Fig. 37). Female terminalia without spine-like setae .... ***Neurigona*** Rondani
40 spp.; widespread; Van Duzee 1913

15. Upper part of proepisternum, in front of anterior spiracle, with one strong white seta; scutellum sometimes with fine hairs on disc. Scape often setose above (Fig. 14). Abdominal sternite 1 sometimes with fine hairs. Male with face and frons at least as wide as ocellar triangle, and with all tarsal claws present .... ***Argyra*** Macquart
46 spp.; widespread; Van Duzee 1925*a*

Upper part of proepisternum bare or with two to four fine setae; scutellum without hairs on disc. Scape bare (Fig. 13). Abdominal sternite 1 bare. Male sometimes with either face or frons narrower than ocellar triangle (Figs. 6, 7), and sometimes with one or both claws of fore tarsus lacking 16

16. Upper part of proepisternum with two to four fine setae. Setae of calypter black. Male with face parallel-sided (as in Fig. 7), without claws on fore tarsus, with tergite 6 bare, and with four to eight long strong setae on sternite 8 (Fig. 39). Female with narrowest part of face subequal in width to widest part of frons .... ***Diaphorus*** Meigen
about 15 spp.; widespread; Van Duzee 1915*b*, Harmston 1968

Upper part of proepisternum bare. Setae of calypter dark or pale. Male with face narrowed below or parallel-sided (Figs. 6, 7), with or without claws on fore tarsus, with tergite 6 bearing at least one seta near each lateral margin and usually with many setae and sometimes with strong marginal setae, and with setae on sternite 8 not longer nor stronger than those on tergite 6 (Fig. 36). Female with narrowest part of face slightly to very markedly narrower than widest part of frons 17

17. First flagellomere of male with slender apical projection bearing apical arista. Lower postocular surface of male with many rows of flattened pale hairs .... ***Achradocera*** Becker
2 spp.; widespread; Van Duzee 1924 (as part of *Chrysotus* Meigen)

First flagellomere of male with arista subapical in notch or to side of tip (Fig. 13). Lower postocular surface of male with only marginal and small central rows of hairs, or with many rows of fine pale hairs .... ***Chrysotus*** Meigen
about 120 spp.; widespread, including Arctic; Van Duzee 1924

18. Scape with one or more distinct setae on the dorsal surface, sometimes only with one or two at tip (Figs. 10, 19) 19
Scape without setae above (Figs. 18, 20) 26

19. First flagellomere with projection below; arista apical (Fig. 19). Abdomen distinctly flattened dorsoventrally .... ***Hypocharassus*** Mik
2 spp.; Massachusetts to Florida, marine shores; Becker 1922*a*

First flagellomere without a projection below; arista usually dorsal or subapical. Abdomen not flattened dorsoventrally 20

20. Acrostichal setae absent. Terminalia small, not projecting far forward under preceding abdominal segments .... ***Diostracus*** Loew
2 spp.; eastern or western; Aldrich 1911, Robinson 1964

Acrostichal setae present. Male terminalia enclosed in very large capsule, projecting forward under most preceding abdominal segments 21

21. First tarsomere of hindleg with distinct bristles above (Fig. 9) .... ***Dolichopus*** Latreille
311 spp.; widespread, including Arctic; Van Duzee *et al.* 1921, Van Duzee and Curran 1934*a* and 1934*b*, Steyskal 1973*b*

First tarsomere of hindleg without bristles above 22

22. Lower margin of face rounded, projecting downward (Fig. 8) .... ***Tachytrechus*** Haliday
33 spp.; widespread; Green 1922, Van Duzee 1927 (in part, as *Polymedon* Osten Sacken), Harmston and Knowlton 1940

Lower margin of face nearly straight or recessed 23

23. Upper and lower hairs of arista much longer than lateral hairs (Fig. 10) ...... ***Pelastoneurus*** Loew
29 spp.; widespread; Van Duzee 1923*a*

Upper and lower hairs of arista not longer than lateral hairs 24

24. R_{4+5} and M nearly parallel beyond crossvein dm-cu (Fig. 29). A group of fine setulae present before posterior spiracle .... ***Gymnopternus*** Loew
74 spp.; widespread; Curran 1933

R_{4+5} and M distinctly convergent beyond crossvein dm-cu (Figs. 30, 31). Pleural surface before posterior spiracle bare 25

25. M straight or slightly sinuous beyond crossvein dm-cu (Fig. 30). Hind femur with only one preapical bristle .... ***Hercostomus*** Loew
26 spp.; widespread

M distinctly bent beyond crossvein dm-cu (Fig. 31), or hind femur with a second smaller preapical bristle anteroventrally .... ***Paraclius*** Loew
17 spp.; widespread; Aldrich 1904

26. First flagellomere with a few scattered minute setulae in addition to velvety pubescence, and with apiculate and sometimes flexuous tip that bears an arista .... ***Paraphrosylus*** Becker
6 spp.; British Columbia to California, marine shores; Wheeler 1897

First flagellomere with only velvety pubescence, either not apiculate at tip or with dorsal arista 27

27. Crossvein dm-cu as long as or longer than last part of CuA_1 (Fig. 32) 28
Crossvein dm-cu not as long as last part of CuA_1 32

28. Anepimeron in front of posterior spiracle, and metepimeron, with fine hairs 29
Anepimeron and metepimeron bare 30

29. Labella mandibuliform (Fig. 11). Notopleuron with two bristles. Hairs of pleuron and of hind coxa black .... ***Melanderia*** Aldrich
3 spp.; Washington to California, marine shores; Arnaud 1958

Labella not mandibuliform. Notopleuron with one bristle. Hairs of pleuron and of hind coxa pale .... ***Hydrophorus*** Fallén, in part
54 spp.; widespread, including Arctic; Aldrich 1911, Van Duzee 1923*b*, Hurley 1965

30. Proepimeron with ventral finger-like projection behind base of fore coxa. Fore femur rather slender, without black setae below; hind coxa with strong black lateral bristle. Scutum with six long dorsocentral setae .... ***Liancalus*** Loew
5 spp.; widespread; Van Duzee 1917

Proepimeron without projection. Fore femur strongly swollen at base, usually with strong black ventral setae; hind coxa usually with only short pale hairs, rarely with one or two weak dark bristles near lower end. Dorsocentral setae short; the last one or two markedly longer than the others 31

31. Anepimeron with blunt or acute conical projection in front of halter, or scape longer than first flagellomere. Face two and a half to three times as high as wide. Notopleuron with one bristle. Male with long slender white filament (process of sternite 5) extending beyond apex of abdomen on either side .... ***Scellus*** Loew
12 spp.; widespread, including Arctic; Greene 1924, Harmston 1939

Anepimeron without projection. Scape shorter than first flagellomere (Fig. 20). Face usually not more than twice as high as wide. Notopleuron with one or two bristles. Male without processes extending beyond apex of abdomen .... ***Hydrophorus*** Fallén, in part
see couplet 29

32. Pedicel extending thumb-like into inner side of first flagellomere (Fig. 18) or at least with its apex distinctly convex 33
Pedicel truncate at tip on inner side, without projection 34

33. Anepimeron in front of posterior spiracle, and metepimeron, with fine pale hairs. Arista apical .... ***Syntormon*** Loew
20 spp.; widespread; Van Duzee 1925*b*

Anepimeron and metepimeron bare. Arista often distinctly dorsal .... ***Parasyntormon*** Wheeler
20 spp.; widespread; Van Duzee 1922

34. Notopleuron with one strong bristle 35
Notopleuron with two strong bristles 36

35. Acrostichal setae absent .... ***Thinophilus*** Wahlberg
24 spp.; widespread; Van Duzee 1926*c*

Acrostichal setae present .... ***Campsicnemus*** Haliday, in part
21 spp.; widespread; Curran 1933, Harmston and Knowlton 1942

36. Upper part of proepisternum in front of anterior spiracle with many long pale hairs 37
Upper part of proepisternum bare or with a few short hairs 41

37. Arista apical (Fig. 12) .... ***Rhaphium*** Meigen
79 spp.; widespread, including Arctic; Curran 1926, 1927

Arista subapical or dorsal 38

38. Face with a vertical median furrow. Abdominal sternites 3 and 4 with large submarginal bristles. Crossvein dm-cu very oblique, parallel to last part of M (Fig. 24) .... ***Plagioneurus*** Loew
1 sp., *univittatus* Loew; eastern

Face without vertical median furrow. Abdominal sternites 3 and 4 without obvious bristles. Crossvein dm-cu not parallel to last part of M 39

39. Proepimeron, and anepimeron in front of posterior spiracle, with fine pale hairs. Abdomen slightly to strongly flattened dorsoventrally .... ***Campsicnemus*** Haliday, in part
see couplet 35

Proepimeron and anepimeron bare. Abdomen cylindrical or nearly so 40

40. Setae of calypter and of lower orbit pale .... ***Nematoproctus*** Loew
7 spp.; eastern; Van Duzee 1930*a*, Robinson 1964

Setae of calypter and of lower orbit black .... ***Keirosoma*** Van Duzee
1 sp., *slossonae* Van Duzee; Florida

41. Scutum with three or four pairs of dorsocentral bristles 42
Scutum with five or six pairs of dorsocentral bristles 43

42. Acrostichal setae uniserial; scutum without velvety black or violet markings .... ***Telmaturgus*** Mik
1 sp., *parvus* (Van Duzee); eastern

Acrostichal setae biserial; scutum with a velvety black area over wing base, and with median violet stripe .... ***Lamprochromus*** Mik
3 spp.; widespread; Robinson 1964

43. M distinctly bent near basal third of last part, with trace of posterior fork; anterior branch of M ending very close to tip of R_{4+5} (Fig. 34) .... ***Psilopiella*** Van Duzee
1 sp., *rutila* Van Duzee; Florida

M straight or only slightly bent in last part, without trace of fork; anterior branch not ending very close to tip of R_{4+5} (Fig. 33) 44

44. Disc of postsutural scutum flattened. Male terminalia borne below and extending somewhat forward from tip of preceding abdominal segments 45
Disc of postsutural scutum not flattened. Male terminalia usually forming a cap on tip of preceding abdominal segments (as in Fig. 36) 49

45. Acrostichal setae absent .... ***Micromorphus*** Mik
7 spp.; widespread; Robinson 1967*a*

Acrostichal setae present 46

46. Face with strong setae near clypeus (Fig. 5) .... ***Nanomyina*** Robinson
1 sp., *litorea* Robinson; Massachusetts to North Carolina, marine shores

Face bare 47

47. All setae pale .... ***Chrysotimus*** Loew
9 spp.; widespread; Robinson 1964

Setae mostly black or brown 48

48. Acrostichal setae uniserial. Arista dorsal or, if apical, not inserted in a notch. Fore tarsus of male with a modified claw; first tarsomere of hindleg of male without a basal spur .... ***Peloropeodes*** Wheeler
8 spp.; widespread; Van Duzee 1926*b* (as *Kophosoma* Van Duzee)

Acrostichal setae biserial. Arista inserted in an apical notch. Fore tarsus of male without a modified claw; first tarsomere of hindleg of male with very small basal spur abutting apex of tibia .... ***Neurigonella*** Robinson
2 spp.; eastern

49. Abdomen broad, distinctly flattened dorsoventrally. Face narrowest near middle .... ***Campsicnemus*** Haliday, in part
see couplet 35

Abdomen cylindrical or conical. Face narrowest near mouth 50

50. Acrostichal setae biserial; five distinct pairs of dorsocentral bristles present, and an additional anterior pair greatly reduced. Hind tibia of male with a minute apical notch anterodorsally; second tarsomere of male foreleg shortened, with special hairs .... ***Sympycnidelphus*** Robinson
3 spp.; Harmston 1968

Acrostichal setae uniserial or lacking; usually six pairs of dorsocentral bristles present, with fifth pair often reduced or out of line. Hind tibia of male without apical notch; second tarsomere of male foreleg not particularly shortened nor setiferous 51

51. Scutellum with only one pair of stout bristles, without hairs 52
Scutellum with two or more hairs in addition to one pair of bristles 53

52. First tarsomere of male foreleg very short, shorter than fifth tarsomere. Male cercus very short .... ***Calyxochaetus*** Bigot
15 spp.; widespread; Van Duzee 1930*b*

First tarsomere of male foreleg not shortened, longer than second tarsomere. Male cercus filiform, almost as long as abdomen .... ***Neoparentia*** Robinson
1 sp., *caudata* (Van Duzee); California

53. Metepimeron with fine hairs. Male with C thickened (Fig. 33) or with spur on underside of hind tibia. Abdomen of male tapering .... ***Teuchophorus*** Loew
4 spp.; central and western; Harmston and Knowlton 1946

Metepimeron bare. Male with C normal and without spur on underside of hind tibia. Abdomen of male usually cylindrical .... ***Sympycnus*** Loew
32 spp.; widespread, including Arctic; Van Duzee 1930*b*, Parent 1932

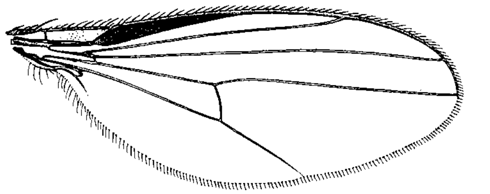
Larva

1. Terminal segment rounded, without lobes 2
   Terminal segment with two or more distinct lobes (Figs. 40, 44) 3
2. Mouthparts reduced. Species phytophagous, plant miners .... ***Thrypticus***
   Sclerified mouthparts large; median dorsal piece large and plate-like. Species predacious .... ***Neurigona***
3. Terminal segment appearing rounded with short lobes, sometimes with only two ventral lobes evident (Fig. 44). Known species living under bark, predacious on larvae of bark beetles .... ***Medetera***
   Terminal segment appearing truncate, with four prominent lobes forming a spiracular cup that is able to close, and sometimes with additional lobes or lobules (Fig. 40). Species not found in tunnels of bark beetles 4
4. First abdominal segment with prominent pair of prolegs. Species associated with oozing sap from tree wounds or with tree holes .... ***Systenus***
   Prolegs absent 5
5. Terminal segment with a distinct median dorsal lobule and a pair of distinct median lateral lobules in addition to the four lobes; the five lobules as long as wide or longer. Species intertidal .... ***Paraphrosylus***
   Terminal segment with lobules short or absent 6
6. Species forming sand cocoons with large pore at one end long before pupation; cocoons often washing up on beaches in large numbers .... ***Hypocharassus***
   Species not forming cocoons long before pupation 7
7. Posterior spiracles of third stage poorly developed; apical portion of each with only two inornate lobes. Mouth with labrum lacking dark projecting teeth above; metacephalic rods of mouthparts distinctly bent and diverging in posterior part; labrum with only one pair of teeth posteriorly .... ***Syntormon***[1]
   Posterior spiracles of third stage each with a distinct inner tube enclosed in an outer tube. Mouth with labrum bearing dark projecting teeth above; metacephalic rods of mouthparts not distinctly bent in posterior part; labrum with two pairs of teeth posteriorly (Fig. 41) 8
8. Posterior spiracles of third stage bilaterally symmetric 9
   Posterior spiracles of third stage radially symmetric 10
9. Posterior spiracles of third stage each with a pair of slender projections internally from upper surface; outer tube continuous around lower surface of inner tube. Creeping welts with highly differentiated spicules; large spicules arranged in one transverse series followed by minute spicules in numerous oblique rows .... ***Dolichopus***
   Posterior spiracles of third stage each without evident slender projections internally from upper surface; outer tube with many perforations, reaching outer surface as two or more separate lobes. Creeping welts with larger spicules intergrading with smaller spicules .... ***Hydrophorus***
10. Terminal segment of third stage without a lobule between dorsal lobes, with lateral lobule simple; subapical tuft of dorsal lobe very prominent, with about 40 setae .... ***Liancalus***
    Terminal segment of third stage with lobule above and between dorsal lobes, with lateral lobule bifid; subapical tuft of dorsal lobe with at most 20 setae (Fig. 40) 11
11. Subapical tuft of dorsal lobe with at most 10 setae .... ***Rhaphium***
    Subapical tuft of dorsal lobe with 15–20 setae .... ***Tachytrechus***

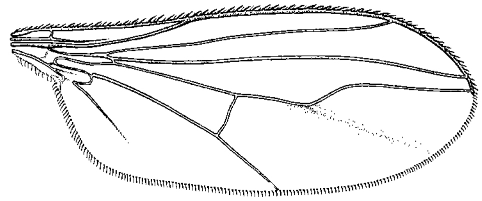
Pupa

1. Species with prominent pointed structures on abdominal segments 2–5 .... ***Thrypticus***
   Species without pointed structures on abdominal segments 2
2. Species with flat ventral profile. Last in series of eight abdominal tergites bearing a crest of larger or sometimes hooked hairs or spines; functional spiracles on only abdominal segments 1–5 .... ***Medetera***

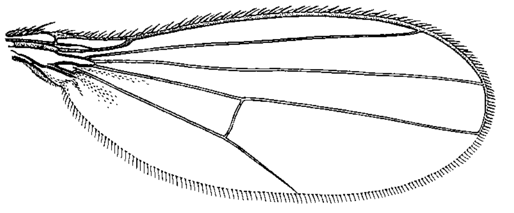
[1] *Argyra*, *Asyndetus*, *Campsicnemus*, and *Sciapus* run to couplet 7, but lack of information about their posterior spiracles makes it impossible to separate them from the following six genera.



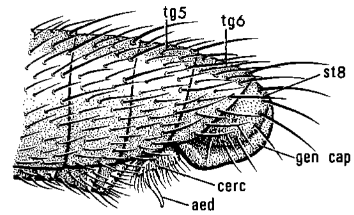
33 Teuchophorus signatus ♂



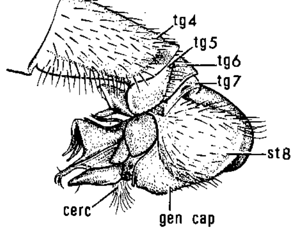
34 Psilopiella rutila ♀



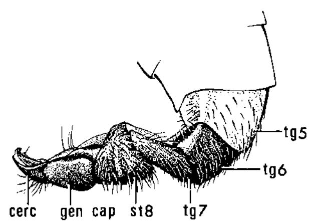
35 Achalcus utahensis ♂



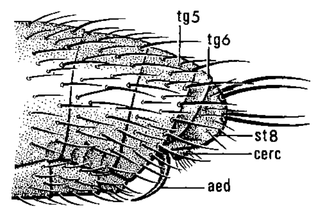
36 Chrysotus choricus ♂



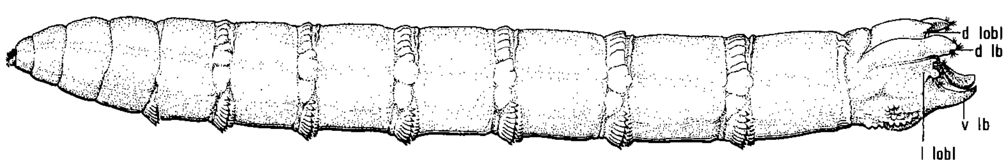
37 Neurigona disjuncta ♂



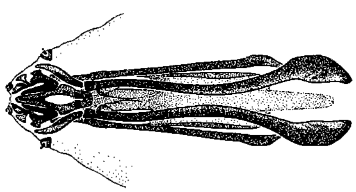
38 Medetera aldrichii ♂



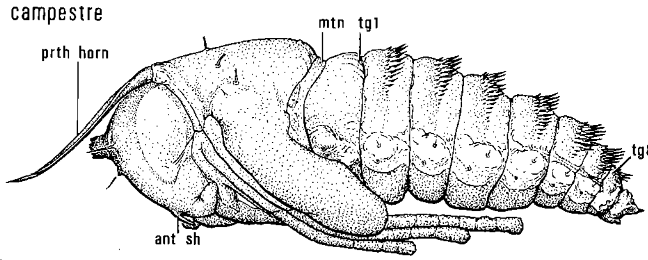
39 Diaphorus gibbosus ♂



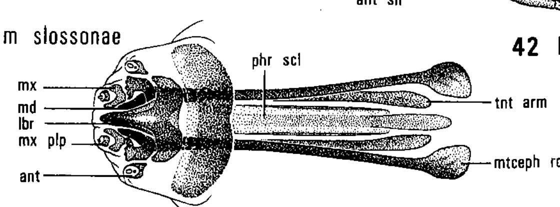
40 Rhaphium campestre



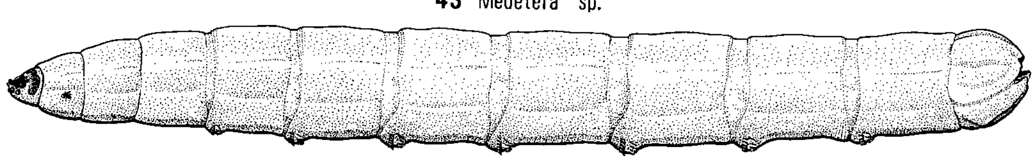
41 Rhaphium slossonae



42 Rhaphium slossonae



43 Medetera sp.



44 Medetera sp.

Species with ventral profile of head convex (Fig. 42). Last in series of setiferous abdominal tergites without larger hairs than those of other tergites; functional spiracles on abdominal segments 1–7 3

3. Abdomen cylindrical, elongate, with dorsal setae on only tergites 2, 3, 4, and 8. Species forming sand cocoon with a large pore at one end. Found on Atlantic coast .... ***Hypocharassus***
Abdomen tapering, stout, with dorsal setae on at least five tergites. Cocoon without large pore .. 4

4. Prothoracic horn very short, scarcely extending beyond head. Metanotum with numerous long erect setae; first eight abdominal tergites with long appressed setae .... ***Asyndetus***
Prothoracic horn elongate, extending at least half its length beyond head. Metanotum without long erect setae; tergites of abdomen with only short appressed or suberect setae (Fig. 42) .. 5

5. Thorax bearing sparse stiff hairs .... ***Neurigona***
Sciapus
Thorax with few or no hairs 6

6. Only six abdominal tergites bearing setiferous bands 7
Seven or eight abdominal tergites bearing setiferous bands (Fig. 42) 8

7. Prothoracic horn with free portion somewhat flattened except at base, broadest at middle. Apex of head with three pairs of tubercles .... ***Campsicnemus***
Prothoracic horn with free portion blade-like, broadest at or near base. Apex of head bearing two pairs of tubercles; upper tubercles with a ventral spine-like tooth .... ***Systenus***

8. Prothorax at base of horns extending forward over most of head. Species found among algae in intertidal areas .... ***Paraphrosylus***
Prothorax usually not extending forward over more than half of head. Species terrestrial or found in mud or sand along shores 9

9. Frontofacial sutures diverging and widely separated in posterior half 10
Frontofacial sutures close and nearly parallel along most of their length 11

10. Apex of head with group of tubercles appearing somewhat truncate in lateral view .. ***Hydrophorus***
Apex of head with simple pair of tubercles, appearing pointed in lateral view .... ***Liancalus***

11. Apex of head with tubercles closely appressed, in profile truncate with a crenulate margin (Fig. 42), in anterior view circular .... ***Rhaphium***
Apex of head with a pair of tubercles that are simple and pointed or transversely divided into four tubercles 12

12. Each tubercle of apex of head transversely divided, with the upper portion of the tubercle extending beyond the lower portion. Free portion of prothoracic horns sometimes shorter than thorax .... ***Dolichopus***
Tubercles at apex of head undivided 13

13. Antennal sheath elongate and tapering, obscuring clypeal region of head .... ***Syntormon***
Antennal sheath very short, abruptly constricted into a short tip 14

14. Abdomen with first tergite bearing setiferous band. Prothoracic horn with differentiated zone completely beyond middle of free portion .... ***Argyra***
Abdomen with only tergites 2–8 bearing a setiferous band. Prothoracic horn with differentiated zone extending to basal third of free portion .... ***Tachytrechus***

Figs. 48.33–44. Wings, abdomens, and immature stages: wing of (33) *Teuchophorus signatus* (Zetterstedt) (not Nearctic), (34) *Psilopiella rutila* Van Duzee, and (35) *Achalcus utahensis* (Harmston & Miller); (36) apical part of abdomen of *Chrysotus choricus* Wheeler; terminalia of (37) *Neurigona disjuncta* Van Duzee and (38) *Medetera aldrichii* Wheeler; (39) apical part of abdomen of *Diaphorus gibbosus* Van Duzee; (40) dorsolateral view of larva of *Rhaphium campestre* Curran; (41) dorsal view of larval head skeleton of *Rhaphium slossonae* (Johnson); (42) pupa of *R. slossonae*; (43) dorsal view of larval head skeleton of *Medetera* sp.; (44) dorsolateral view of larva of *Medetera* sp.

Abbreviations: aed, aedeagus; ant, antenna; ant sh, antennal sheath; cerc, cercus; d lb, dorsal lobe; d lobl, dorsal lobule; gen cap, genital capsule; lbr, labrum; l lobl, lateral lobule; md, mandible; mtceph rd, metacephalic rod; mtn, metanotum; mx, maxilla; mx plp, maxillary palpus; phr scl, pharyngeal sclerite; prth horn, prothoracic horn; st, sternite; tg, tergite; tnt arm, tentorial arm; v lb, ventral lobe.

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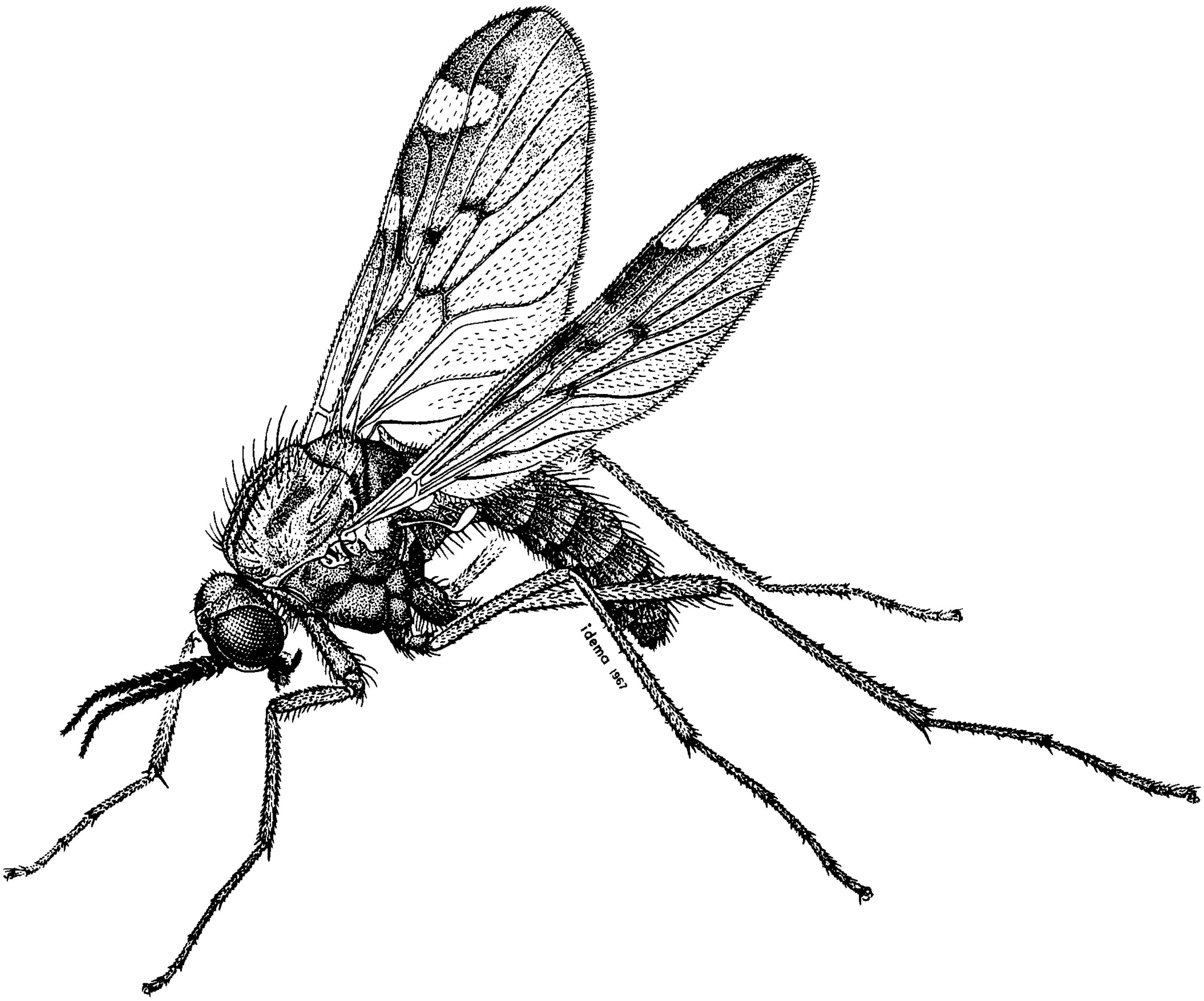

This index is restricted to the taxonomic names and morphological terms associated with Diptera that appear in Volume 1 of the Manual. Similar names and terms for plants and animals other than Diptera are excluded. Bibliographic references are not indexed.

Accepted taxonomic names for all categories (suborders, infraorders, superfamilies, families, subfamilies, tribes, genera, subgenera, species, and subspecies) are given in Roman type; synonyms are in italics. Every such citation throughout the Manual is listed. Authors' names are provided for species only, followed in parentheses by the names of the genera to which the species are assigned. Subgeneric names are indexed in the same way as generic names; subspecies are indexed in the same way as species. Boldface page numbers indicate family chapters or designate where taxa appear in keys to genera; italicized numbers indicate the location of illustrations of these taxa.

Preferred morphological terms for adults and larvae are given in Roman type; synonyms are in italics. The plural spelling follows the singular if it is formed irregularly. Terms that apply only to larvae are designated by a capital "L" in parentheses. For practical reasons, page references provided for each morphological term are restricted to those places in the text where the term is first mentioned, where an explanation of its usage is given, or where its relationship is explained. Most of these citations occur in Chapters 2 and 3. Boldface page numbers indicate principal discussions of the terms. Italicized page numbers indicate locations of illustrations of the morphological features involved. Terms enclosed in single quotes are accepted for use in certain families but are not morphologically correct.

The index for Volume 1 will be incorporated in the index for Volume 2, which will have a composite index for both volumes.