TREATISE ON THE ISOPTERA OF THE WORLD

1. INTRODUCTION

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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

KRISHNA ET AL.: ISOPTERA OF THE WORLD:
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AMNH BULLETIN 377 (1)

2013

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VOLUME 1

INTRODUCTION

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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
Number 377, 2704 pp., 70 figures, 14 tables
Issued April 25, 2013

ISSN 0003-0090

Alfred E. Emerson at the microscope surrounded by some of his termite collection at the University of Chicago. Oil on canvas by Edith Emerson.

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ABSTRACT

A comprehensive compendium on the taxonomy and biology of the 3106 living and fossil species of the world's termites is presented, along with reviews of Isoptera morphology and evolution, identification keys, the history of termite systematics, and summary of the world's 363 significant pest species. A complete bibliography is provided of nearly 5000 references covering virtually all aspects of termite taxonomy and biology through December 2011.

The morphology of Isoptera is thoroughly reviewed and illustrated with original scanning electron micrographs and photomicrographs, covering the cuticular anatomy and those internal organs that are taxonomically and phylogenetically significant, including several new character systems. Terminology is presented for the systems of tibial spines and spurs so as to establish homologs. Keys are presented to the nine living families of termites, and the world subfamilies and genera of Archotermopsidae, Hodotermitidae, Kalotermitidae, Mastotermitidae, Rhinotermitidae, Serritermitidae, Stolotermitidae, and Stylotermitidae. A key to subfamilies of the Termitidae is included. A detailed morphological diagnosis for each family and subfamily is provided, along with images of exemplar species. The history of isopteran research in taxonomy, systematics, morphology, paleontology, and biology is reviewed from 1758 to the present, with emphasis on transformative workers such as Holmgren, Silvestri, Emerson, Roonwal, Noirot, and Sands. Evolution of the Isoptera is reviewed, including the diversity and natural history of genera and species in all zoogeographic regions, major patterns in social biology, the phylogeny of Recent and fossil genera and families, and 135 million years of fossils preserved as compressions, mineralized replicas, and in amber. The definitive sister group to the Isoptera is the monogeneric family of wood roaches, Cryptocercidae (*Cryptocercus*), so the taxonomic ranks of the two groups are now **Infraorder Isoptera** and Infraorder Cryptocercoidea within Order Blattaria (roaches and termites).

The compendium summarizes the taxonomic history, nomenclature, distribution, type locality, and repository, and all significant aspects of natural history and biology for each species of the world, exclusive of pest control and colony inquilines (termitophiles). The classification of Recent and fossil lower termites (all those exclusive of family Termitidae) used in the compendium is from Engel et al. (2009), which is based on morphology and largely congruent with molecular studies. Rhinotermitidae s.s. (exclusive of Stylotermitidae) may be paraphyletic with respect to Termitidae, although the six traditional subfamilies of the former are used here. A separate section summarizes the nomenclatural changes made in the compendium, including new synonymies, new combinations, status novus, lectotype selection etc. A detailed list is provided of museums and other institutional collections that house type specimens. An index is included. The *Treatise* is intended to provide an authoritative foundation for taxonomic work on the Isoptera, present and future.

INTRODUCTION

When the Portuguese were colonizing South America in the 17th century, they called ants "the real conquerors of Brazil." Termites may lack the infamous aggressiveness of ants, but they share in the title of conquerors. They are no less pervasive than ants in the tropical ecosystems of the world, and in some regards have an even more profound impact and intriguing biology.

The primary ecological significance of ants is as predators of arthropods, although the Neotropical leaf-cutter (attine) ants can be serious defoliators. In contrast, termites have evolved to quietly exploit the most abundant terrestrial biomolecule, lignocellulose, and in a uniquely efficient way. Whereas many beetles, larval sawflies, and assorted larval flies and moths mine wood, these feed principally on the cambium layer or on fungus in the galleries. Termites actually ingest the wood, as well as grasses, humus, and ungulate dung (which form of cellulose depends on the species), and in startling amounts: in tropical dry forests, they consume 40%–100% of the dead wood, and in savannas up to 20% of the grass (Dettling, 1988). Eating so much biomass results in prodigious excretion, and it is estimated that termites contribute 2%–5% of the world's methane to the atmosphere (Sanderson, 1996; Sugimoto et al., 2000). Plant matter converted into tonnage of fecal pellets makes termites pivotal in the formation and mineralization of tropical soils. Indeed, some species are landscape architects. Near Lake Malawi in East Africa lies a geological formation created 10,000 to 100,000 years ago from the eroded mounds of the living species *Macrotermes falciger* Gerstäcker, covering over 8800 km^2, or some 44 million cubic meters of soil (Crossley, 1986).

It has been known for at least a century that the dietary exploitations by termites are made possible entirely by the symbiotic protists and bacteria inhabiting their gut (or in the case of the macrotermitines, the fungus they cultivate). Probably no eukaryotic organism is devoid of symbiotic microbes, and even ants host a plethora of symbiotic gut bacteria, but termites are again unique. Termites harbor protists of two orders (Parabasalia and Oxymonadida), comprising some 470 species found only in the "lower" termites (which include all families except Termitidae); hundreds of species ("phylotypes") of spirochetes and other bacteria *per termite*; and methane-producing archaeans, the methanogens (reviewed by Honigberg, 1970; Yamin, 1979; Ohkuma and Brune, 2011). Among the bacteria in termite guts, in fact, are major lineages, or phyla, found nowhere else. In the few cases that have been intensively studied (e.g., *Pseudotrichonympha* and Rhinotermitidae [Noda et al., 2007]), the phylogenies of protist and termite correspond in a nearly perfect example of coevolution. Probably all the endosymbiotic protists are themselves hosts to bacteria. In the case of *Mixotricha paradoxa,* living in the gut of *Mastotermes darwiniensis* Froggatt, the protist propels itself with synchronous waves of what appear to be cilia, but which actually are ectosymbiotic spirochetes (Wenzel et al., 2003). The termite gut, obscure as it sounds, is actually a microcosm of microbial diversity and symbiosis, with a great deal to teach about the evolution of eukaryote cells.

This symbiosis between termite and its intestinal microbiota may have been the driving force behind the evolution of eusociality of termites, with their polymorphic caste system and intricate social life (Wilson, 1971; Grimaldi and Engel, 2005). When an insect molts, it sheds even the fine cuticular lining of its hind gut, where termite endosymbionts reside. To reinoculate themselves, first instar and newly molted lower termites must engage in the very intimate social act of anal trophallaxis, a feature inherited from their closest living relatives, *Cryptocercus* wood roaches (Seelinger and Seelinger, 1983; Nalepa, 1984). As in ants, all species of termites are eusocial, although basal ants do not have the degree of caste differentiation found in all termites. The repeated origin of eusociality in ants and other Hymenoptera is explained in part by their haplodiploid sex determination and the close genetic relatedness of nestmates, conditions that are ideal for kin selection (Hamilton, 1964). It is hardly coincidental that social aphids, thrips, and even a scolytine beetle also have some form of parthenogenesis or inbreeding that renders nest mates very closely related (reviewed in Grimaldi and Engel, 2005). But termites are completely diploid, so their sociality may be uniquely explained by their physiology and ecology.

True, eusocial termites probably appeared in the Late Jurassic 150 Mya (Engel et al., 2009; Martínez-Delclòs and Martinell, 1995), preceding ants by some 30 million years and making termites the oldest-known eusocial organisms. Like ants, termites exploded in diversity and abundance in the Late Paleocene and Eocene with the global spread of tropical forests and climates. This marked the beginning of their New Kingdom dynasties and ecological rule.

Despite the ecological dominance of termites, the Isoptera is a group of relatively modest species diversity compared to most orders and suborders of insects; as of April 2012, it consists of 3105 living and fossil species classified into 12 families and 330 living and fossil genera. Literature on the termites, however, is immense—excluding control literature, some 8500 titles according to *The Zoological Record* and other sources, which clearly reflects the significance of the group. By comparison, there are 14,711 living species and subspecies in the family Formicidae (ants), classified into 283 genera and 21 subfamilies. The superb online database of ants, AntWeb (www.antweb.org) provides photomicrographs of most genera and thousands of species, distribution maps, and a bibliography of approximately 10,500 references (many of them with links to PDFs of the original publications). AntWeb is the effort of dozens of myrmecologists and web techs, and is a model to emulate, but it all began with the world catalog of ants by Barry Bolton (1995). Perhaps this *Treatise* will inspire a TermiWeb.

According to a Chinese proverb, “the first part of wisdom is getting the names right.” Indeed, a stable, accurate, and informative taxonomy is essential to all aspects of biology. The last comprehensive catalog of termite species was T.E. Snyder’s *Catalogue of the Termites* (*Isoptera*) *of the World,* published in 1949. It has been a fundamental reference for decades, but over the past 60 years more than 1500 species, 160 genera, five families, and six subfamilies have been added to the Isoptera, and there has been a plethora of synonymies and revised placements. Since Snyder, catalogs have been produced for the New World (Araujo, 1970; Constantino, 1998a), Australia (Watson et al., 1996), Africa (Bouillon and Mathot, 1965, 1966, 1971), the Indian region (Roonwal and Chhotani, 1989, 1997), and China (Huang et al., 2000). But these regional treatments contain limited references, and some of them propagate long-standing taxonomic errors, as well as outdated and incomplete classifications. Moreover, the species of some regions have not been cataloged, notably Eurasia, southern Asia, Papua New Guinea, and the Pacific Islands. We wanted the *Treatise* to be fully global and truly comprehensive for each species, which is why we prefer to call the "catalog" section a *compendium*. Besides the typical taxonomic information (e.g., original citations, synonyms, type localities), for each species in the compendium there is information on the type repository, a summary of its distribution, castes, ecology, and biology. Thus, the citations are a condensed history of the research on each taxon, exclusive of control literature.

The compendium of world species in the *Treatise* is drawn from approximately 5000 references published from the time of the 10th edition of *Systema naturae* (1758) to 2012. All of these sources are listed in the References, with full journal titles cited, which should facilitate finding original documents and obscure publications. Virtually all the references were personally examined, including early and rare classical works of natural history and esoteric journals. Unlike some modern catalogs that simply add new items to older versions, the *Treatise* was created de novo, so that numerous errors in Snyder (1949a) and other catalogs could be corrected.

The family classification used here follows that of Engel et al. (2009). Various thorny nomenclatural problems and errors overlooked for many years have been resolved by a strict application of the International Code of Zoological Nomenclature, fourth edition (1999). Seven petitions were made to the commission of the ICZN for resolution (for case numbers see Engel and Krishna, 2001a, 2001b, 2002, 2004b, 2005a, 2007b, 2011; for opinions see ICZN in the References). Nomenclatural changes made by the authors are separated into a special section, so as to make them more easily seen. Although manuscript names and other nomina nuda have no standing under ICZN rules and are not available names, we have included them simply for the historical record as well as to clarify questions about their status.

Various review volumes thoroughly cover the fascinating biology of termites (Grassé, 1949; Krishna and Weesner, 1969, 1970; Wilson, 1971; Grassé, 1982b, 1984, 1985; Abe et al., 2000; Bignell et al., 2011), so we did not attempt to duplicate that effort here. We did, however, include a Morphology chapter, entirely illustrated with original figures, since morphology is the basis for taxonomy. To facilitate identification, keys are also included to the families, subfamilies, and genera of lower termites, but only to the subfamilies of Termitidae as there are 235 genera. A chapter on general Evolution was provided as a means of summarizing and synthesizing myriad aspects of termite biology, and provides us with an opportunity to explain and update aspects on relationships and classification.

Acknowledgments

Many people and sources of support have made this work possible. Initial funding was provided by the U.S. National Science Foundation (grant no. 9870097 to Kumar Krishna and David Grimaldi). Robert G. Goelet, trustee and Chairman Emeritus of the American Museum of Natural History, generously funded acquisition of amber specimens and other aspects of work associated with this project. A Guggenheim Fellowship awarded to Michael S. Engel funded his stay at the AMNH for a year, during which time he worked on the species compendium and history, and researched the fossil record and phylogeny of termites.

The *Treatise* could not have been done anywhere except the American Museum of Natural History, from its unique collections of specimens and references to the many talented staff members who assisted us over many years. The ultimate archive, of course, has been the magnificent collection of termites built by Alfred E. Emerson, which contains approximately 80% of the world's species and nearly half of the world's types. Additions to the collection were made through fieldwork and exchanges with other institutions. The AMNH is also fortunate to have the massive slide collections of termite endosymbiont protists made by H. Kirby and L.R. Cleveland between 1920 and 1950. Accompanying the specimen collection was Emerson's card catalog, in its time the most comprehensive bibliography of work on the Isoptera. The card catalog was updated by Krishna for many years until it was replaced by the present *Treatise.* The AMNH library, particularly impressive for rare and old natural history works, made this work possible. Library staff members Priscilla Watson, Tom Baione, Mary DeJong, Ingrid Lennon, Annette Springer, and Mai Qaraman helped chase down references and interlibrary loans of obscure works. Andrew Johnston assisted with indexing. Our special thanks to our wonderful and learned editor, Mary Knight, for bringing these volumes to fruition.

Gratitude is also expressed to the staff of the General Library, the Entomology Library, and the Palaeontology Library at the Natural History Museum, London (NHML). Paul Eggleton of the Department of Entomology, NHML, generously provided unlimited access to the termite collections and library there, and Andrew Ross, formerly of the Department of Palaeontology at the NHML (now at the National Museums of Scotland) provided access to study fossils in that collection.

The original database platform for the *Treatise* was Platypus, developed by Keith Houston at CSIRO, Canberra; Keith patiently guided us through the program in the early stages of this work. Christopher Boyko, then at the AMNH, did painstaking work on the interpretation and entry of information into the database. The assistance of Tam Nguyen (former Senior Scientific Assistant) and Steve Thurston (graphic artist), both of them at the AMNH, was instrumental in production of the lovely images. Tam provided the electron micrographs and Steve did all of the graphics. We are also grateful to Lou Sorkin, Senior Scientific Assistant at the AMNH, for helping us sort out knotty programming problems with his boundless patience, expertise, and good nature. We are particularly indebted to our close colleague Lee Herman, Curator of Coleoptera at the AMNH, who shared with us his encyclopedic knowledge of the International Code of Zoological Nomenclature and intricacies of rule applications. Lee fielded hundreds of queries, often on a daily basis, and helped in unraveling some particularly difficult nomenclatural and taxonomic tangles. His masterful *Catalogue of the Staphylinidae* (Herman, 2001) is and has been a model.

We are also grateful to Kara A. Salazar and the Dr. Laura Hare Charitable Trust for information and the image reproduced herein, Dick R. Nässel of the Department of Zoology, Stockholm University for information on and images of Nils Holmgren, Jean Deligne of the Free University of Brussels for information on Jules Desneux, and Holger H. Dathe and the Senckenberg Deutsches Entomologisches Institut for various images of early termite workers.

This book is dedicated to the memory of Alfred E. Emerson, great naturalist, field biologist, philosopher, and teacher, whose lifetime of devotion to termite research stands behind and inspires the present volume.

A BRIEF HISTORY OF TERMITE SYSTEMATICS

Linnaeus and His Followers

The classification of termites begins, as does all binomial nomenclature, with the founder of taxonomy, **Carl Linnaeus** (1707–1778), a botanist and professor of medicine at Uppsala University, who was ennobled as Carl von Linné in 1762 (fig. 1A). In the 10th edition of Linnaeus's *Systema naturae* (1758) termites appear in two disparate parts of the classification. *Termes* was placed in the Aptera, between *Podura* (now the type genus of the springtail family Poduridae: Collembola) and *Pediculus* (now the type genus of the lice family Pediculidae), with *Termes fatale* the only true termite included therein (Linnaeus, 1758). Two alates were also described, but under the generic name *Hemerobius* and within Linnaeus's heterogeneous order Neuroptera. *Hemerobius testaceus* Linnaeus and *H. marginalis* Linnaeus were based on accounts received from his student **Daniel Rolander** (1725–1793), who collected in Suriname and noted the destructive power of insects, presumably including termites, writing to his teacher in 1755 that insects were "the only [creatures] that seem to be able to devastate these extensive forests. . . ." While Linnaeus indicated his *T. fatale* was from "Indiæ," this material was actually in Rolander's collections from Suriname. Students of Linnaeus, young, enthusiastic, and adventurous—referred to as his "apostles"—were afforded opportunities to explore throughout the world, but some did not fare well. Of the 17 who were sent on expeditions to the far ends of the Earth, many succumbed to disease and only 10 returned. Rolander himself suffered from ill health, ultimately had a falling out with Linnaeus, and died in obscurity. His 700-page *Diarium Surinamicum,* virtually ignored for 240 years, was translated and finally published in 2008 by the IK Foundation as *Daniel Rolander's Journal.*

Another student, who chose to specialize in insects, was **Johann C. Fabricius** (1745–1808; fig. 1D). Fabricius began his work under Linnaeus's direction in 1762 and traveled throughout Europe collecting insects and examining collections. He fared better than many other Linnaean disciples, perhaps because his travels were within the relatively safe confines of Europe. By 1769 Fabricius was a professor himself, with a position at the University of Copenhagen, relocating to a new appointment at the University of Kiel in 1771. Fabricius devoted his energies toward reclassifying and documenting insects, with his famous *Systema entomologicae* first appearing in 1775 (Fabricius, 1775b). His perspective on insect classification differed significantly from that of his mentor, and Fabricius had more knowledge of termites as a result of his visits to London, where he examined the collections made by the famous aristocratic British explorer and a founder of the Royal Society of London, Sir Joseph Banks (1743–1820). Linnaeus apparently never saw a termite until 1772 (when Anders Sparrman, one of his "apostles," sent him a queen), basing his earlier accounts on drawings and information supplied by others like Rolander. Nonetheless, though Fabricius had seen termite specimens he classified *Termes* alongside the ants until later considering them near *Hemerobius, Myrmeleon* Linnaeus, and *Psocus* Latreille.

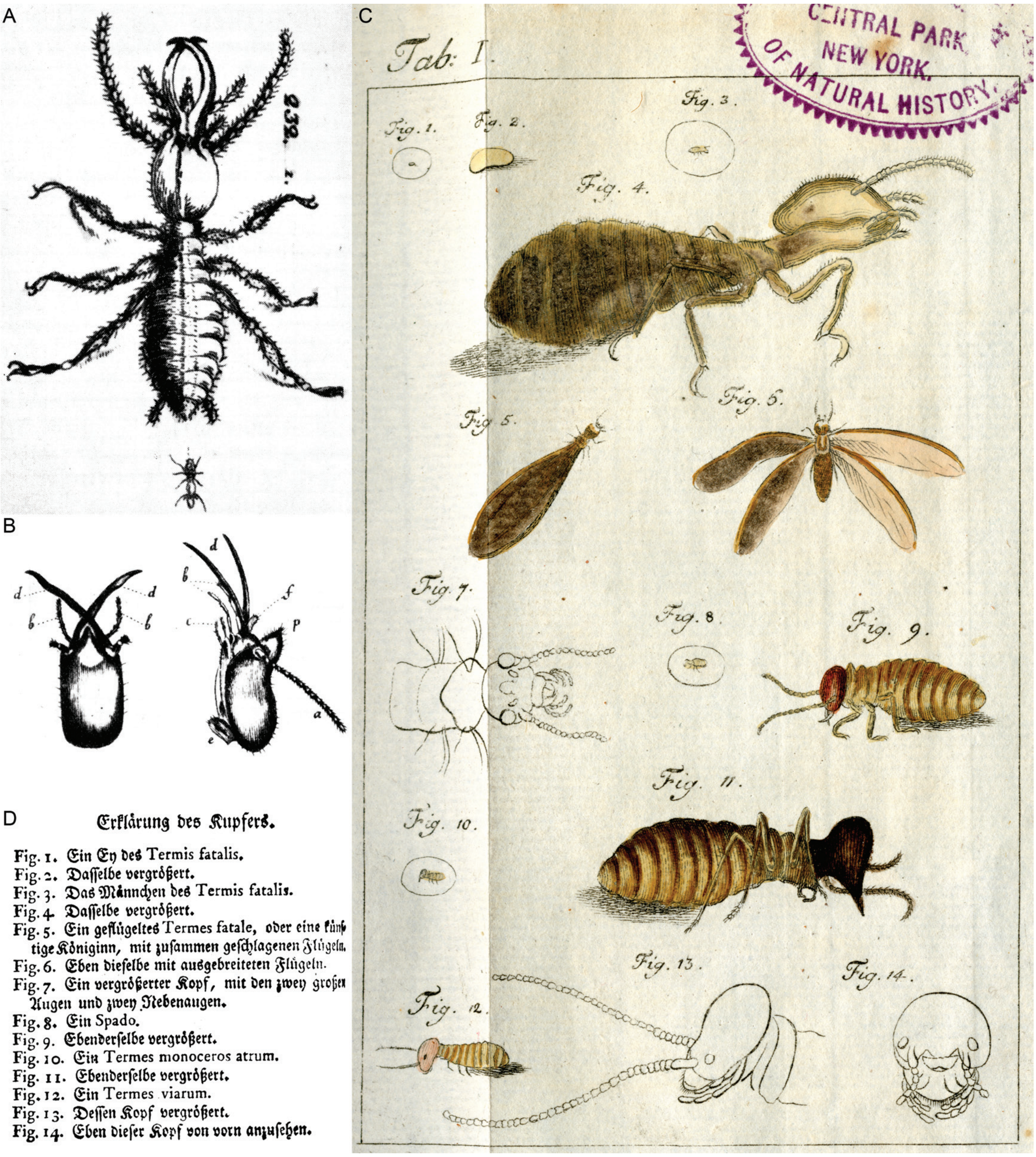
In what only can be considered one of the most eloquent accounts of termite natural history, **Henry Smeathman** (1750–1787) presented his observations on termites in western Africa

FIGURE 1. **A.** Carl Linnaeus (Carl von Linné), the founder of taxonomy; **B.** Pierre A. Latreille, author of the family Termitidae; **C.** Charles De Geer, French naturalist; **D.** Johann C. Fabricius, Danish entomologist and one of the more successful "apostles" of Linnaeus.

in a 53-page letter to Banks (23 January 1781), which was read before the Royal Society on February 15, 1781. With detailed and precise observations, Smeathman elaborated upon the remarkable mound nests of African termites and their biology (most notably, *Macrotermes bellicosus* and *Cubitermes atrox*), with spectacular plates of nests and the various castes (Smeathman, 1781; figs. 4, 5). Though Smeathman was awed by the depredations inflicted by these insects, he was also sensitive to their role in clearing away dead wood and setting the stage for new growth. His accounts remained for decades the only accurate and thorough summaries on termite biology. **Daniel C. Solander** (1733–1782; fig. 2), another student of Linnaeus, who exasperated his mentor with his repeated failure to send material from his journeys with Banks aboard the H.M.S. *Endeavour,* provided Smeathman with an account of the specific differences among termites and the names of the various species he had observed. Despite Smeathman's forthright claim that "it is possible the accounts I have here communicated would not appear credible to many, without such vouchers and such corroborating testimony as I am fortunately able to produce, and are now before you," many subsequent authors tried to challenge his accuracy until **Thomas S. Savage** published a new set of supporting observations (Savage, 1849, 1850). While Smeathman is rightfully credited for accurately detailing termite biology in the 18th century, he was not the only early author to do so. **Johann G. König** (1728–1785), a student of Linnaeus, was sent to India by the king of Denmark as physician to the Danish settlement at Tranquebar, where he threw himself energetically into the collection and study of botanical specimens, as well as insects. König published his *Naturgeschichte der sogenannten Weissen Ameisen* in 1779 in the usually overlooked serial, *Beschäftigungen der Berlinischen Gesellschaft Naturforschender Freunde* (König, 1779: translated and reprinted by Fletcher, 1921). Smeathman briefly alluded to König's article in his letter, but noted that he was able to obtain only a translated *précis,* and the two gentleman made and published their observations independently, those of the latter undertaken in southern India. Life in the tropics ultimately took its toll on König's health, and he died in India in 1785. Like Smeathman, König faithfully documented the natural history of those termites known to him, correctly detailing their nests, social life, and complete life history (fig. 3C, D). Together these two works represented the definitive knowledge on termites for nearly 75 years after their publication.

Various authors made modest contributions to the taxonomy of termites, largely by describing species or providing revised accounts of species elaborated on by others during these early days of the new binomial nomenclature. Most notable were **Carl De Geer** (1720–1778; fig. 1C), whose *Mémoires pour servir à l'histoire des insectes* includes descriptions of some early termite taxa and whose 1778 figure is the first known recognizable taxonomic illustration of a termite—*Termes fatale*—which he described under the name *Termes destructor* (fig. 3B) (the image of *fatale* by Rydbeck in the 1758 *Pandora insectorum* by Linnaeus is too stylized to be positively identified as a termite; fig. 3A); **Vincenz Kollar** (1797–1860), who was the first to describe *Reticulitermes flavipes,* a native of the United States and a notorious pest introduced into Europe and first discovered in the greenhouses of Schönbrunn Palace, near Vienna; and **Pierre A. Latreille** (1762–1833; fig. 1B) who established the first family-group name for termites, Termitidae (Latreille, 1802), in addition to having the distinction of saving his neck from the guillotine by discovering a new beetle species while incarcerated during the French

FIGURE 2. Captain James Cook, Sir Joseph Banks, Lord Sandwich, Daniel Solander, one of Linnaeus's "apostles," and John Hawkesworth: 1771 oil on canvas by John Hamilton Mortimer, 1740–1779. Image courtesy of the National Library of Australia.



Erklärung des Kupfers.

Fig. 1. Ein Ey des Termis fatalis.
Fig. 2. Daſſelbe vergrößert.
Fig. 3. Das Männchen des Termis fatalis.
Fig. 4. Daſſelbe vergrößert.
Fig. 5. Ein geflügeltes Termes fatale, oder eine künftige Königinn, mit zuſammen geſchlagenen Flügeln.
Fig. 6. Eben dieſelbe mit ausgebreiteten Flügeln.
Fig. 7. Ein vergrößerter Kopf, mit den zwey großen Augen und zwey Nebenaugen.
Fig. 8. Ein Spado.
Fig. 9. Ebenderſelbe vergrößert.
Fig. 10. Ein Termes monoceros atrum.
Fig. 11. Ebenderſelbe vergrößert.
Fig. 12. Ein Termes viarum.
Fig. 13. Deſſen Kopf vergrößert.
Fig. 14. Eben dieſer Kopf von vorn anzuſehen.

FIGURE 3. **A.** Figure of *Termes fatale* from *Pandora insectorum,* Linnaeus, 1758; **B.** figures of *Termes destructor* (= *Termes fatale* Linnaeus) from De Geer, 1778; **C.** hand-colored copperplate engraving, one of the earliest known taxonomic illustrations of termites showing castes, from J.G. König, 1779; **D.** König's legends for figure 3C.

FIGURE 4. Hand-colored copperplate engraving of a mound of *Macrotermes bellicosus* (Smeathman), from H. Smeathman, 1781.

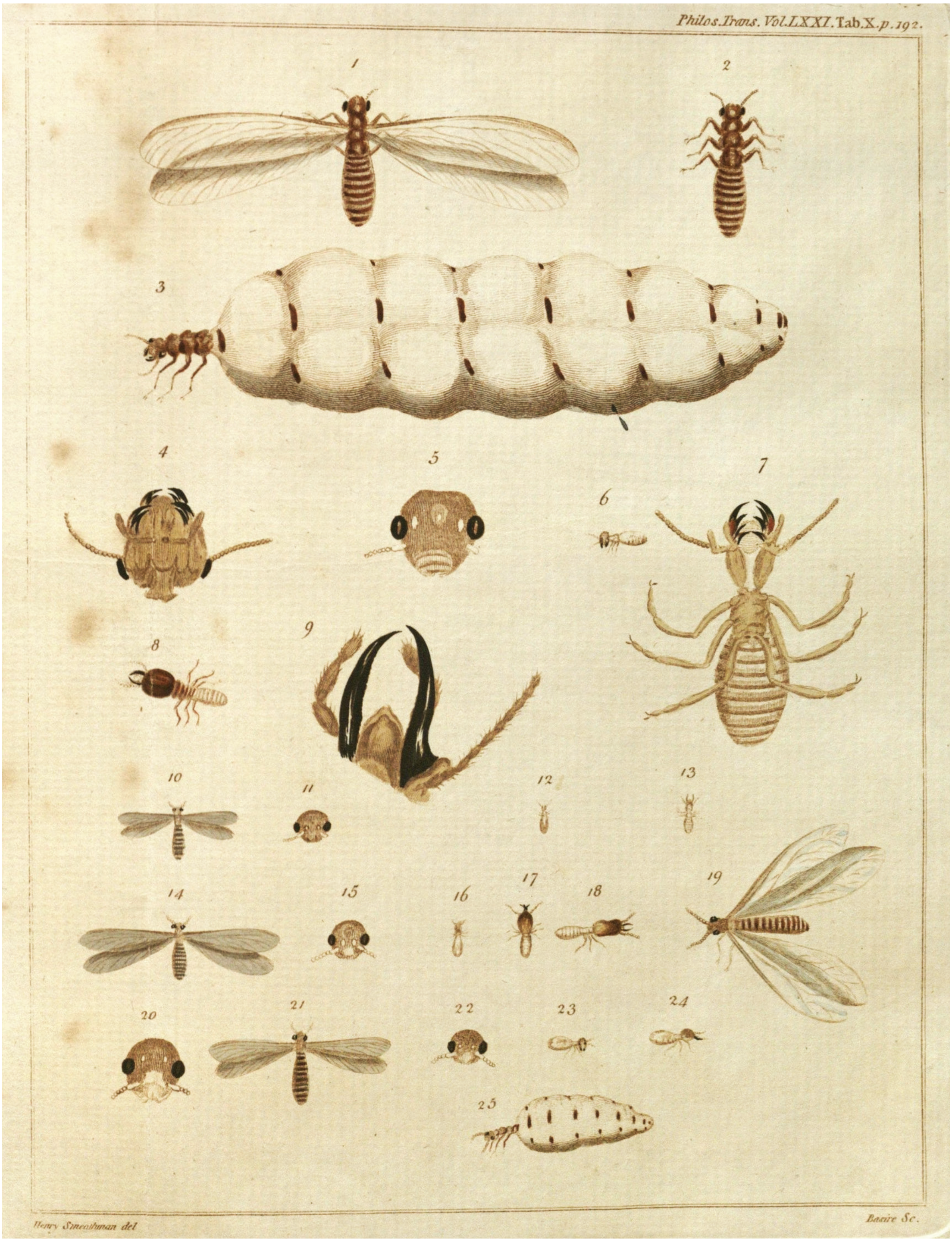


FIGURE 5. Engraving from Smeathman's 1781 paper, showing kings, queens, soldiers, and "labourers" of *Macrotermes bellicosus* (Smeathman) and *Cubitermes atrox* (Smeathman).

Revolution (Grimaldi and Engel, 2005). The next generation of investigators made similar advances, largely providing a few new species or updated information on more widespread and well-documented taxa. Indeed, while much descriptive work was under way during these decades, relatively few new termites were accumulated, such that by the close of the 19th century scarcely more than 100 valid species were known. Among the early contributors, those most notable were **John O. Westwood** (1805–1893), the first Hope Professor of Entomology at Oxford, and **Francis Walker** (1809–1874), today known for his thousands of superficial descriptions of species in the Diptera. In 1832 **Gaspard A. Brullé** (1809–1873) coined the name "Isoptères" (Gk., "equal wings") for an order of insects distinguished from the Orthoptera and Hemiptera of his day, including therein the termites and, later in the same publication, the webspinners (species of *Embia* of the day) (Brullé, 1832). Some authors adopted the more finely split ordinal classification, while many continued to recognize a heterogeneous Neuroptera, Orthoptera, or Dictyoptera, classifying termites only as a family therein. Regardless, Brullé's simple act created the name Isoptera with which we are so familiar today.

Early Paleontologists

The paleontology of termites was in its beginning stages at about this same time. Early paleoentomologists made contributions to a geological perspective of termite classification. Of note were **Ernst F. Germar** (1786–1853) and **Christoph G.A. Giebel** (1820–1881). But more accomplished than either of these men was **Oswald Heer** (1809–1883; fig. 6A, C), the famous Swiss naturalist and geologist, who, after taking holy orders and completing work in philosophy and medicine, launched into a lifetime of study in entomology and eventually botany, becoming a noted pioneer in paleoentomology and paleobotany. Heer's (1849a, 1849b) work on the Tertiary insects from Radoboj, Croatia, and Oeningen, Germany, was the beginning of serious inquiry into the ancient history of termites. He also described various termites in "amber" (much of Heer's material is now understood to have been East African copal) and compression-fossilized termites and established such widely employed names as *Termopsis* and *Eutermes.*

Founders of Modern Isopteran Taxonomy

The first comprehensive account of termite classification was undertaken by **Hermann A. Hagen** (1817–1893; fig. 6B), who in three parts revised the world fauna and provided a comprehensive historical synthesis. Hagen's *Monographie der Termiten* (1855, 1858c, 1860a), a classic of Isoptera research, represented a significant leap forward in the study of termites, recognizing four principal lineages—*Termopsis, Hodotermes, Kalotermes,* and *Termes.* Hagen was a surgeon by training but, like many educated men of the day, was equally versed in natural history and selected insects as his specialty, particularly the Linnaean "Neuroptera," a group that in that period comprised everything from lacewings to dragonflies, with termites just one family among these. His initial interest in natural history and dragonflies was influenced by the efforts of his father and grandfather, purportedly because the first insect he collected as a young man was a new species. Hagen also took a considerable interest in fossil insects,

FIGURE 6. **A.** Oswald Heer, pioneer paleoentomologist; **B.** Hermann A. Hagen, founder of modern termite taxonomy; **C.** imago of *Reticulitermes antiquus* (Germar) in Baltic amber.

particularly those preserved in Baltic amber, so not surprisingly he provided the first cogent treatment of Baltic amber termites, partially in collaboration with his colleague **François J. de la Rive Pictet-Baraban** (1809–1872). This interest was perhaps understandable, given that Hagen's native city of Königsberg sits on the Samland Peninsula, where some of the most productive outcrops of succinite are known and where there resided the single greatest collection of biological inclusions in this resin. (Portions of the collection were tragically destroyed by fire during World War II; other portions eventually resided at the University of Göttingen). Hagen emigrated from Königsberg to the United States in 1867 and took over as the head of the Department of Entomology at Harvard's Museum of Comparative Zoology. Unfortunately, after his relocation to Cambridge, Massachusetts, Hagen undertook only smaller projects on termites, largely focusing his attention elsewhere. Hagen died in November 1893 after lingering largely paralyzed for three years.

George D. Haviland (1857–1901), curator of the Kuching Museum and contributor to the Kew Herbarium, was famed for his early work in Malaya and Borneo, producing meticulous descriptions and observations, as well as exquisite illustrations of termites and their nests (figs. 7, 8). He followed Hagen's classification, but was the first to recognize that *Termes* was a heterogeneous group and divided it into subgroups such as "Section with *Termes bellicosus* for Type." His collection of termites was regarded in its day as "the finest ever brought to Europe" and is now preserved along with his diaries in the Cambridge University Museum of Zoology. Haviland spent his later years in Natal, rode out on his bicycle into the jungle one morning, and disappeared mysteriously. **Erich Wasmann** (1859–1931; fig. 10C) was a Jesuit priest and keen observer of the insect associates of ants and termites, contributing significantly to the natural history of myrmecophilous and termitophilous beetles in his numerous papers on the systematics and biology of the ant and termite hosts. Wasmann set the stage for the later work by Charles Seevers, David Kistner, and others.

Walter W. Froggatt (1858–1937), born in Melbourne, Australia, was the son of an architect turned miner. A frail child, he was encouraged to spend his time in natural history pursuits, and on his sixth birthday was given his first insect-collecting materials. In 1885, the young Froggatt accompanied an expedition to New Guinea as an assistant zoologist and, upon his return, he was employed by the prominent Australian statesman and naturalist **William J. Macleay** (1820–1891) to collect insects and eventually work in Macleay's private museum until 1892. Following this, Froggatt worked as a geological collector before being appointed entomologist for the Department of Mines and Agriculture in 1896. It was during this period that Froggatt developed his interests in termites, particularly their systematics and life history, becoming most famous for his description of *Mastotermes darwiniensis,* the most primitive species and genus of living Isoptera (Froggatt, 1897a). Froggatt, while retaining the historical classification of termites as a single family (Termitidae), inaugurated the modern era of subdividing the group into finer and finer suprageneric categories bearing formalized names. Froggatt recognized four subfamilies among the termites, attempting to make the classification more reflective of putative relationships, as originally articulated by Hagen, i.e., that some groups were more "primitive" in nature relative to "higher" forms such as *Termes* s.l. (table 1) (Froggatt, 1896, 1897a, 1898). All subsequent students of the Isoptera would similarly

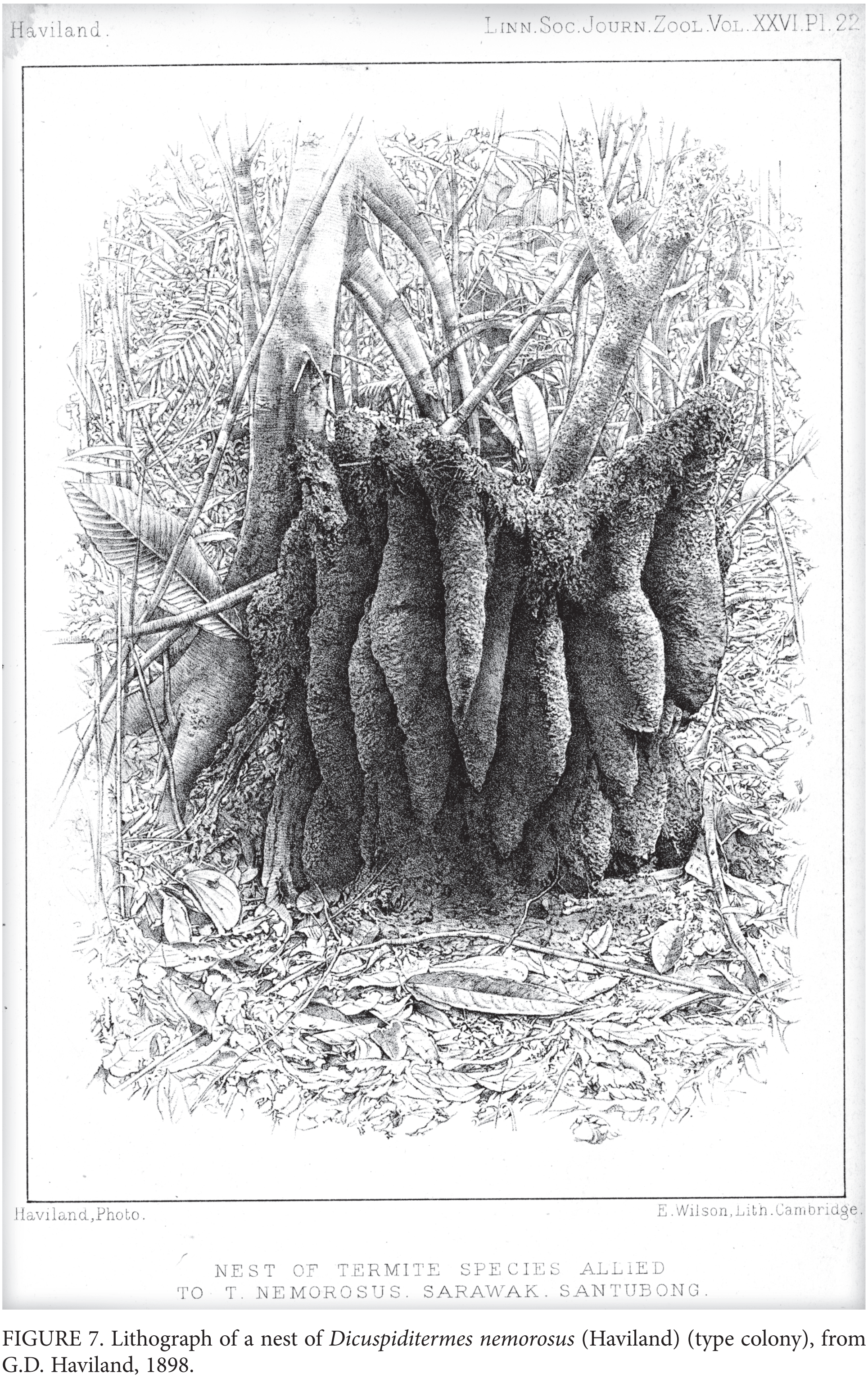


FIGURE 7. Lithograph of a nest of *Dicuspiditermes nemorosus* (Haviland) (type colony), from G.D. Haviland, 1898.

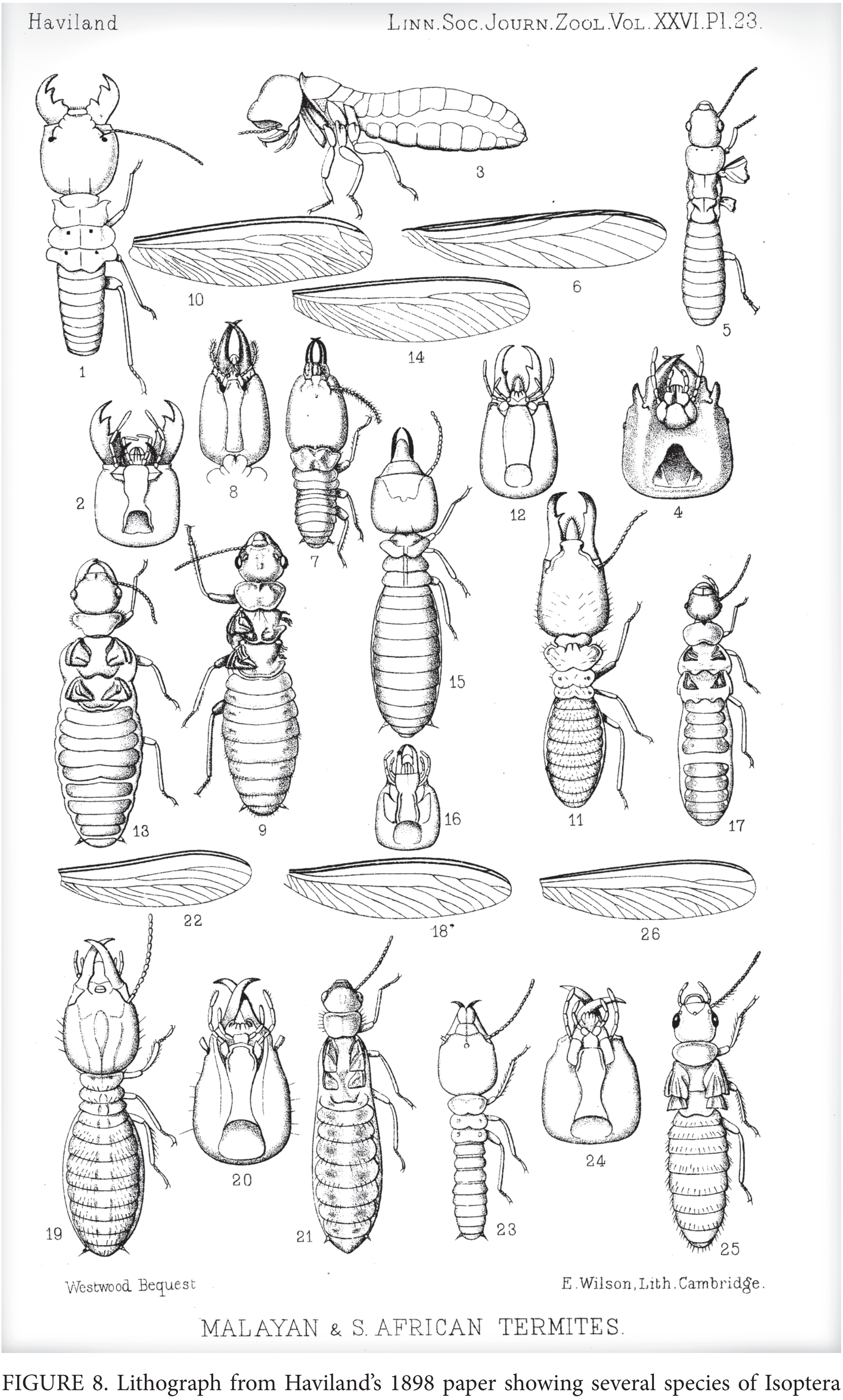


FIGURE 8. Lithograph from Haviland's 1898 paper showing several species of Isoptera from Malaya and Africa.

TABLE 1. Froggatt's (1897a) Classification of Isoptera

- Family Termitidae Latreille
  - Subfamily Calotermitinae Froggatt
    - Genus *Mastotermes* Froggatt
    - Genus *Calotermes* Hagen
    - Genus *Termopsis* Heer
    - Genus †*Parotermes* Scudder
    - Genus *Hodotermes* Hagen
    - Genus *Porotermes* Hagen
    - Genus *Stolotermes* Hagen
    - Genus †*Mixotermes* Sterzel [now known to not be a termite]
  - Subfamily Rhinotermitinae Froggatt
    - Genus *Rhinotermes* Hagen
  - Subfamily Glyptotermitinae Froggatt
    - Genus *Glyptotermes* Froggatt
  - Subfamily Heterotermitinae Froggatt [initially placed in Glyptotermitinae]
    - Genus *Heterotermes* Froggatt
  - Subfamily Termitinae Latreille
    - Genus *Termes* Linnaeus
    - Genus *Eutermes* Heer
    - Genus *Anoplotermes* Müller

segregate the group into a gradually increasing number of families and subfamilies, each further refining an understanding of isopteran relationships.

As mentioned earlier, termites were frequently classified as a family among the Neuroptera up till this time, and usually considered allied to the Embiidae and Blattidae in the sense of many 19th-century workers. Comstock and Comstock (1895), in their influential textbook on entomology, revived the ordinal status of Brullé's "Isoptères" and generally from that time onward, the term "Isoptera" has been employed for the termite lineage, although its formal taxonomic rank, either as order, suborder, or otherwise, has been debated. Some important near contemporaries of Froggatt were quick to adopt the ordinal status of Isoptera, most noteworthy being **Jules Desneux** (1885–1962) of Belgium and the colorful **Bror Yngve Sjöstedt** (1866–1948; fig. 9B) of Sweden.

Desneux, a medical doctor, numismatist, and art critic, classified the termites as a single family, Termitidae, within the order Isoptera. Noteworthy for his system was the recognition of the uniquely primitive features of Froggatt's *M. darwiniensis,* removing this genus to its own subfamily, Mastotermitinae, and of the unique biology and anatomy of *Hodotermes, Stolotermes,* and *Porotermes* relative to the kalotermitids, characterizing these for the first time as a separate tribe, Hodotermitini (Desneux, 1904c, 1904e; table 2). Desneux was also the first to compile a catalog of the world's termites with his contribution to the *Genera insectorum* (1904b), and while he is perhaps most remembered for these early papers, he continued to publish on the nest structure of *Apicotermes* into the 1950s, representing an amazingly long and robust career. Following up on the work of Desneux, **Augustus D. Imms** (1880–1949), Forest Entomologist, Dehradun, Government of India, later reader in entomology at Cambridge University, and famed for his 1925 *General Textbook of Entomology,* was the first to write a monograph on

FIGURE 9. **A.** One of the greatest isopterists of all time, Nils F. Holmgren; **B.** Bror Ingve Sjöstedt, explorer, collector, and authority on African termites; **C.** Holmgren lecturing on comparative anatomy to a roomful of students.

TABLE 2. Desneux's (1904c) Classification of Isoptera

- Order Isoptera Brullé
  - Family Termitidae Latreille
    - Subfamily Mastotermitinae Desneux
      - Genus *Mastotermes* Froggatt
    - Subfamily Calotermitinae Froggatt
      - Tribe Hodotermitini Desneux
        - Genus *Hodotermes* Hagen
        - Genus *Porotermes* Hagen
        - Genus *Stolotermes* Hagen
        - Genus *Termopsis* Heer
      - Tribe Calotermitini Froggatt
        - Genus *Calotermes* Hagen
    - Subfamily Termitinae Latreille
      - Tribe Rhinotermitini Froggatt
        - Genus *Rhinotermes* Hagen
        - Genus *Arrhinotermes* Wasmann
      - Tribe Termitini Latreille
        - Genus *Termes* Linnaeus

the primitive species, *Archotermopsis wroughtoni* Desneux (Imms, 1919), detailing and illustrating its morphology and its protists (fig. 13).

Sjöstedt explored West Africa from 1890–1892 and led an expedition to Mt. Kilimanjaro and other areas in East Africa in 1905–1906, publishing numerous papers on a variety of zoological subjects, including tomes on the termites. He was pompous, publicizing his expeditions to the extent of minting medals to commemorate his travels, and authoring self-congratulatory reviews decades later (e.g., Sjöstedt, 1925, *Geografiska Annaler,* 7: 1–8). He was also territorial and intolerant of others intruding into what he perceived to be "his" field. Despite his overbearing ego, Sjöstedt contributed significantly to our knowledge of the isopteran fauna of Africa in his *Revision der Termiten Afrikas.* Sjöstedt received his doctorate in 1896 in Uppsala and eventually became professor and head of the entomological collections at the Rijksmuseum in Stockholm.

The Holmgren Era

Alongside Sjöstedt was **Nils F. Holmgren** (1877–1954; figs. 9A, C), working in the University of Stockholm. Holmgren started his career as an entomologist and traveled in Bolivia and Peru during 1904–1905 to study ants and termites, eventually publishing 23 papers on the systematics and anatomy of Isoptera and completing his doctoral work in 1906 at the University of Stockholm. Eventually he became full professor and chair of zoology at the University of Stockholm in 1919. Holmgren was an obsessive researcher. A typical working day began at 9 A.M. and finished at 9:30 P.M., with hour-long breaks for lunch and supper. This grueling schedule was relaxed a bit on Saturday and Sunday although he carried on some research during the weekend as well. Indeed, it was remarked that Holmgren had largely no interests in life outside of zoological research. Aside from his obviously intensive work schedule, this was perhaps manifest

TABLE 3. Holmgren's Early (1910b) Classification of Isoptera

- Family Protermitidae Holmgren
  - Subfamily Mastotermitinae Desneux
  - Subfamily Hodotermitinae Desneux
  - Subfamily Stolotermitinae Holmgren
  - Subfamily Calotermitinae Froggatt
- Family Mesotermitidae Holmgren
  - Subfamily Leucotermitinae Holmgren
  - Subfamily Coptotermitinae Holmgren
  - Subfamily Rhinotermitinae Froggatt
  - Subfamily Serritermitinae Holmgren
  - Subfamily Termitogetoninae Holmgren
- Family Metatermitidae Holmgren
  - Subfamily Termitinae Latreille

in the recollections of his students who noted that his lectures were dull and uninspired. Nonetheless, while not a stellar lecturer he was considered a good one-on-one mentor with students interested in serious zoological study, and he trained 16 doctoral students during his career.

Although he did not consider himself an isopterist he was easily the greatest contributor to the subject during his brief time in the field. Indeed, it can be said that Holmgren was one of the most influential of all termite investigators, paving the path for the later studies of Nils Kemner, Alfred Emerson, Muzaffer Ahmad, William Sands, and Kumar Krishna. The systems developed by subsequent authors were largely refinements of the foundation established by Holmgren. What is perhaps most remarkable about Holmgren's work is that he appears to have presciently recognized nearly all of the major lineages supported today, complete with their genealogical relationships and in large part their accurate generic composition (though many fewer genera were known at that time). Keeping in mind that he came from an era in which paraphyletic groups were an accepted classificatory convention, his 1911 and 1912 classifications and phylogenies for the most part parallel our modern understanding of termite relationships (Holmgren, 1910b, 1911a, 1912a; tables 3, 4). He considered Mastotermitidae as the most basal lineage of living termites; his Protermitidae comprised a grade of basal families leading up to what we today consider the Euisoptera; his composition of groups in Protermitidae (Termopsinae, Hodotermitinae, Stolotermitinae, and Kalotermitinae) largely correspond to the grade of families in place today; and he considered the Mesotermitidae (= Rhinotermitidae) intermediate between Protermitidae and the Metatermitidae (= Termitidae) (i.e., he recognized what we today call the Euisoptera). His Mesotermitidae corresponds to our modern Rhinotermitidae, with the exception that he also included Serritermitidae and Stylotermitidae, but his subfamilies within Rhinotermitidae have stood the test of time and additional data. Holmgren's Metatermitidae corresponds to the Termitidae and several of his "Reihe" have similarly held up to scrutiny (e.g., Syntermitinae, Foraminitermitinae). What also characterized Holmgren's work was his detailed consideration of the anatomical structures that supported his conclusions regarding relationship. While earlier authors tended to rely on superficial similarity or vague statements concerning the character of particular lineages, Holmgren explicitly backed his findings with voluminous and detailed accounts of everything

TABLE 4. Hierarchical Classification of Termites as Proposed by Holmgren (1911a, 1912a). In addition to recognizing each of these groups, Holmgren provided a hypothesis of phylogenetic relationship among the families, subfamilies, and genera, the first ever for termites

- Family Mastotermitidae Desneux
- Family Protermitidae Holmgren
  - Subfamily Termopsinae Holmgren
  - Subfamily Hodotermitinae Desneux
  - Subfamily Stolotermitinae Holmgren
  - Subfamily Calotermitinae Froggatt
- Family Mesotermitidae Holmgren
  - Subfamily Psammotermitinae Holmgren
  - Subfamily Leucotermitinae Holmgren
  - Subfamily Coptotermitinae Holmgren
  - Subfamily Termitogetoninae Holmgren
  - Subfamily Rhinotermitinae Froggatt
  - Subfamily Serritermitinae Holmgren
- Family Metatermitidae Holmgren
  - *Termes*-Reihe (Subfamily Termitinae Latreille)
  - *Microcerotermes*-Reihe (Subfamily Microcerotermitinae Holmgren)
  - *Pseudomicrotermes*-Reihe (Subfamily Pseudomicrotermitinae Holmgren)
  - *Foraminitermes*-Reihe (Subfamily Foraminitermitinae Holmgren)
  - *Syntermes*-Reihe
  - *Hamitermes*-Reihe
  - *Mirocapritermes*-Reihe

from external morphology to soft-tissue anatomy and biology (e.g., Holmgren, 1909b). Today it is well recognized that the imago-worker mandibles are conservative and useful features for reconstructing relationships among termite lineages, but this seemingly small detail was not made known until Holmgren identified it in his monographs, just one of the innumerable steps forward that he made in clarifying termite systematics.

Considering that this singular individual undertook all of this careful and groundbreaking work early in his career, much as part of his doctoral studies, it is staggering to conjecture what advances he might have made had he continued to focus on termites. Instead, largely owing to pressure from the overbearing Sjöstedt, Holmgren moved along to other areas of inquiry shortly after the publication of his four major volumes on termite anatomy and systematics, abandoning the field of isopterology entirely. In 1916 he launched wholeheartedly into the comparative anatomy of the nervous system, first examining the brains of polychaetes, onychophorans, and arthropods, eventually migrating into the vertebrates (pineal and parietal organs and eventually the brain itself). In addition, he became fascinated by the comparative anatomy of tetrapod limbs and cranial structure. During World War II he published his comprehensive four-part series on the head of fishes, finally retiring in 1944 and passing away in September of 1954 from prostate cancer.

While not influencing the larger classification of Isoptera, numerous authors undertook important faunal treatments and revisionary syntheses of particular lineages during this same period. Of significance was another Swede, **Nils V.A. Kemner** (1887–1948; fig. 10A), who between 1925 and 1936 produced numerous fine papers principally on the termites of Southeast Asia. In addition, the famous insect biologist and systematist, **Filippo Silvestri** (1873–1949;

fig. 10B), based in Portici, Italy, within sight of Mt. Vesuvius, worked on the South American, Australian, and central African faunas. Silvestri was widely known to the entomological world for his travels, extensive work on many arthropod lineages, and his descriptions of the obscure hexapod orders Protura and Zoraptera. Most of his publications were meticulously illustrated with elegant and minutely detailed figures (fig. 11). In Australia, **Gerald Freer Hill** (1880–1954; fig. 14B), expanding massively upon the early compilation of Froggatt, provided the first truly comprehensive account of the Australian and New Guinean termite fauna, bringing Froggatt's count of 37 species to 217 (Hill, 1942). After retirement, Hill conveyed his entire collection of termites to the American Museum of Natural History, where it has been incorporated into the main termite collection. The tradition founded by Hill was continued into our modern era by the efforts of **Frank J. Gay**, **Leigh D. Miller**, and **Tony Watson**, who eventually compiled revisions and an annotated catalog of the Australian Isoptera with 348 species (Watson and Gay, 1983, 1991; Watson et al., 1998).

Meanwhile in eastern Asia, **Masamitsu Oshima** (1884–1965) and **Sanji Hozawa** (1885–1947), both Japanese, made similar advances into the diversity of termites of their native country and Taiwan (Formosa), where Oshima was entomologist at the Institute of Science (e.g., Oshima, 1909, 1911b, 1912, 1914c, 1915, 1917b; Hozawa, 1915). These same authors also opened doors into the broader Asiatic fauna as a whole (e.g., Oshima on fishes and snakes and Hozawa on calcareous sponges), for better or, in some cases, for worse. In China, a flood of literature has been produced in the last half century, with descriptions of over 480 new species, many for which the validity will need to be critically evaluated—a significant challenge to future generations of termite investigators.

Expanding on the work of **Claude W. Fuller** (1872–1928) on the termites of South Africa, **William G.H. Coaton** (1911–1983; fig. 14A) led several expeditions, collecting extensively in South Africa and Namibia, documenting in detail in the National Survey Series, the distribution of termites in the area (1972–1980) the most complete survey to date, and amassing an outstanding collection, which is housed in the insect collection, Pretoria. Following Coaton, **Jean E. Ruelle** expounded upon the biology and systematics of the South African fauna. **W. [William] Victor Harris** (fig. 17C) who moved to the British Museum (Natural History) from Kenya, and who documented the pest species in *Termites: Their Recognition and Control* (1961) and his colleagues **R. Michael C. Williams** and **William A. Sands**, worked extensively on the Ethiopian fauna. Sands' revisionary work was detailed and comprehensive, and explored, for example, the diverse intricacy of the enteric valve in the Termitidae—work that involves meticulous dissection and long hours at the microscope. He integrated detailed studies of gut anatomy with that of external morphology to produce invaluable revisionary studies of African termites, as well as work on the associations of termites and fungi (e.g., Sands, 1969, 1972, 1998; see table 8 herein). The South American fauna received similar attention after Silvestri's studies, particularly as a new generation of isopterists revived faunistic studies of the continent. Study of the diverse Neotropical fauna was eventually inherited by **Renato L. Araujo** (1912–1978), who compiled the first catalog of Neotropical termites (Araujo, 1977c; fig. 17D). **Herbert A. Weidner** (1911–2009; fig. 14C) investigated the termites of southern Europe, Africa, Central Asia, and the Middle East, while also producing works on Tertiary fossil species.

FIGURE 10. **A.** Nils Kemner, authority on the termites of Southeast Asia; **B.** Filippo Silvestri, Italian systematist and meticulous illustrator; **C.** Father Erich Wasmann, early investigator into the termites as hosts of termitophilous beetles.

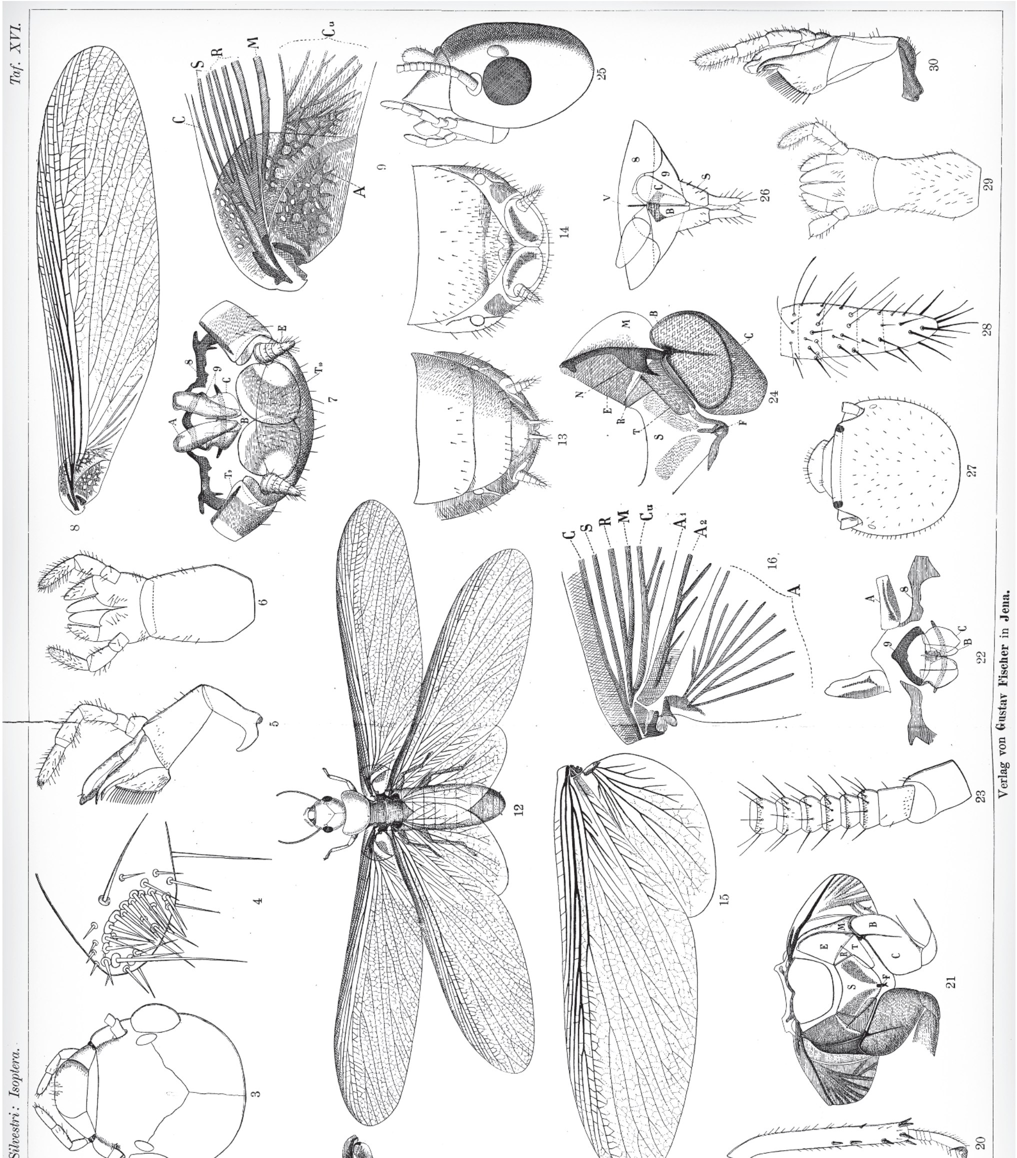


FIGURE 11. Illustrations of *Mastotermes darwiniensis* Froggatt, from Silvestri, 1909b.

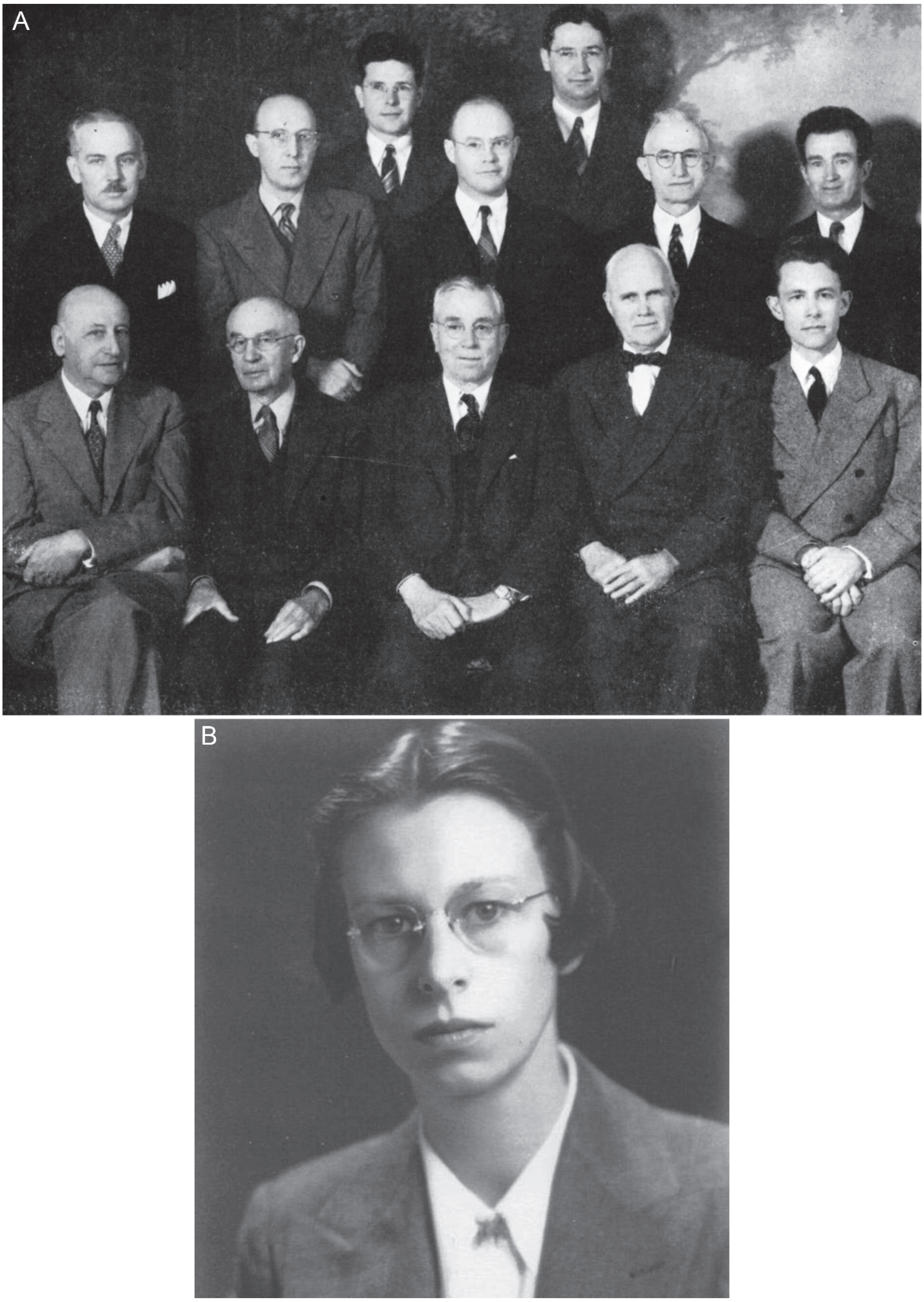


FIGURE 12. **A.** The University of California, Berkeley's Faculty of Zoology in 1944, with three illustrious contributors to termite systematics, biology, and evolution among its staff: Charles A. Kofoid, Harold Kirby, and Sol F. Light. Front row (left to right): Richard Goldschmidt, S.J. Holmes, Kofoid, H.B. Torrey, and Kirby. Second row: E. Raymond Hall, J.E. Gullberg, Alden H. Miller, Light, and S. C. Brooks. Third row: Ray L. Watterson and Richard M. Eakin. **B.** Laura Hare, author of the Nasutitermitinae, the largest subfamily of termites.

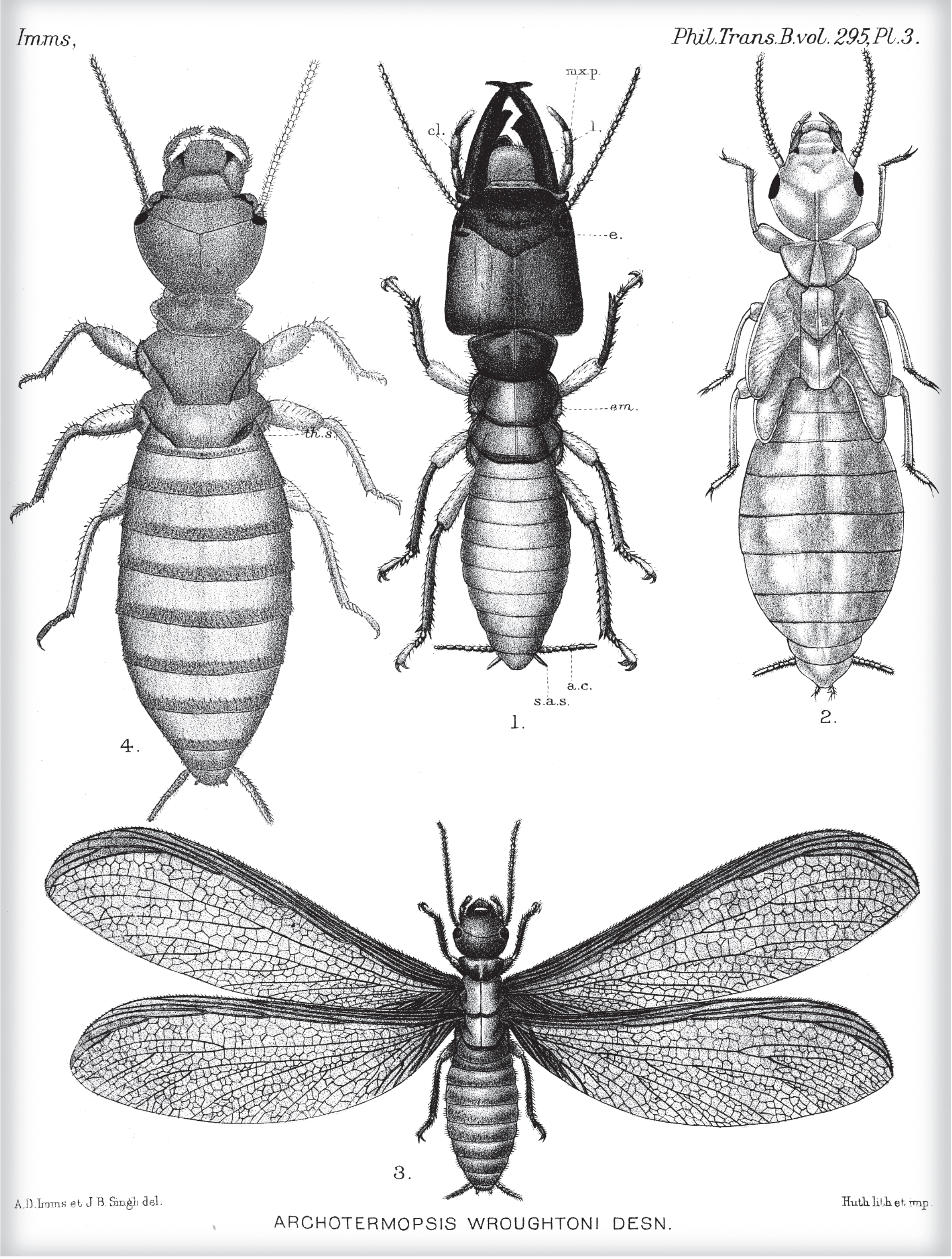
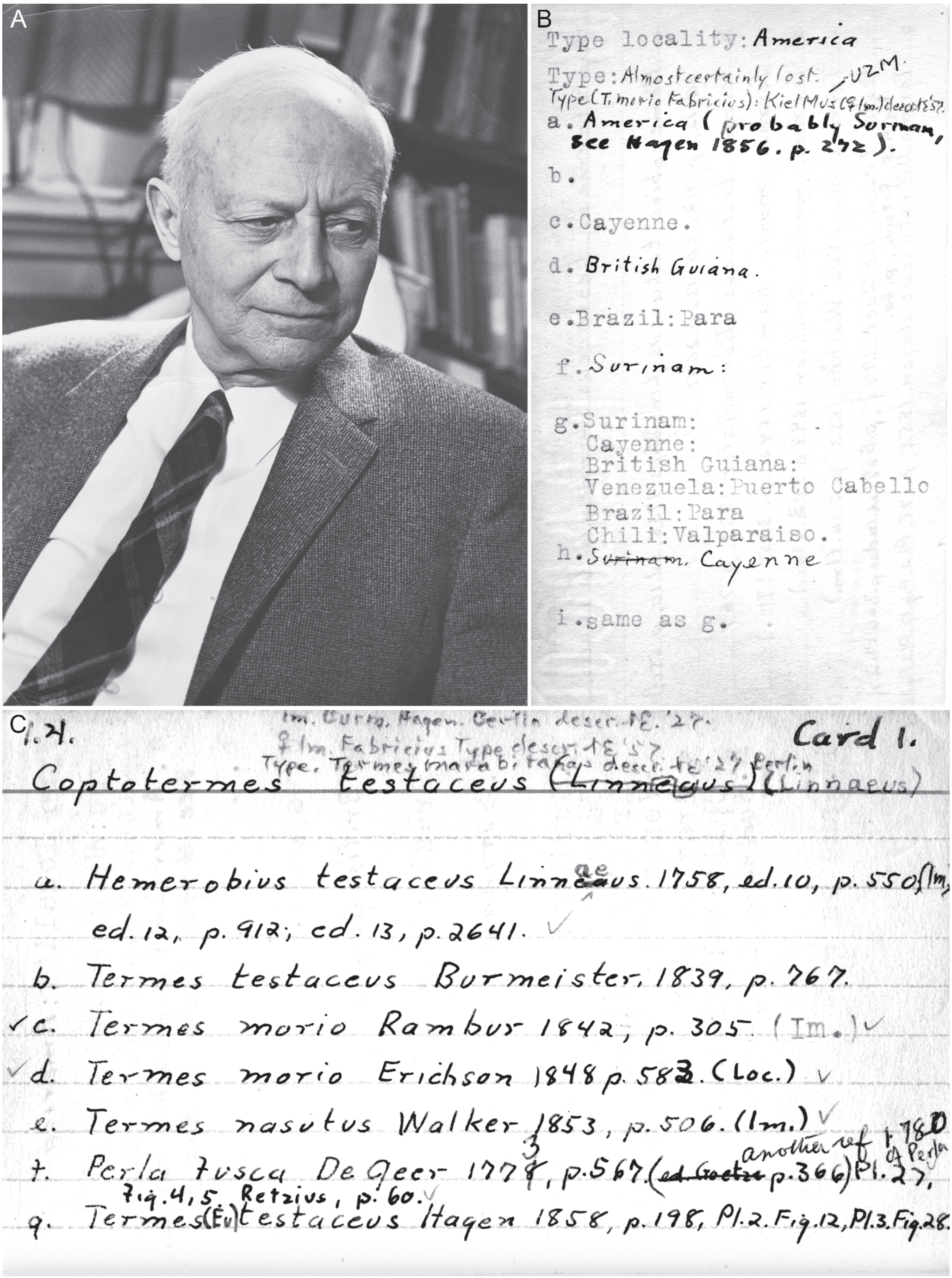


FIGURE 13. Lithograph of *Archotermopsis wroughtoni* (Desneux), from A.D. Imms, 1919.

FIGURE 14. **A.** William G.H. Coaton, authority on South African termites; **B.** Gerald Freer Hill, specialist on the termites of Australia and New Guinea; **C.** Herbert A. Weidner, German termite scholar who studied both fossil and living species; **D.** Thomas E. Snyder, termite specialist for the USDA, who, in addition to control work, produced numerous systematic and biological studies of termites and is most famed as compiler of the first worldwide catalog of the Isoptera.

The Emerson Era

In regard to the broader classification of the order, following Holmgren the mantle of termite systematics was picked up by an adventurous young entomologist, **Alfred E. Emerson** (1896–1976; figs. 15). However, unlike many naturalists, Emerson did not embark on entomology as a child. Emerson's father was a professor of classical archaeology and his mother a concert pianist and specialist in music history. Not surprisingly, the young Emerson pursued the humanities and arts, briefly considering a career in music. As a student at the Interlaken School in Indiana he established and operated the school's poultry farm, developing an intense desire to work in biology. In 1914 he went to Cornell University with the intention of becoming a poultry scientist but soon found the coursework not to his liking. In order to resolve the dilemma surrounding his career development, Emerson enrolled in the introductory course of each science department in the hope of identifying a new passion, eventually selecting entomology as his major. Under the tutelage of Cornell professors John H. Comstock (1849–1931) and James G. Needham (1868–1957), Emerson was broadly trained in insects and detailed observations of their biology and, after a nine-month service in the army in 1918, he embarked on a trip to Kartabo, British Guiana, where he was encouraged to investigate the termites (Emerson, 1925) by the then-director of the New York Zoological Station, William L. Beebe (1877–1962). From this time onward, Emerson was devoted to the Isoptera. It was because of his expertise and encyclopedic knowledge of their biology that he was able to later develop broad-reaching theories in ecology, behavioral biology, and philosophy ultimately becoming a member of such prestigious organizations as the American Academy of Arts and Sciences and the National Academy of Sciences. Of particular significance were Emerson's contributions to the superorganism theory (Emerson, 1939a, 1952c, 1954b), one that is regaining its influence in modern biology (e.g., Hölldobler and Wilson, 2009), and to the application of ethological data (e.g., nest architecture in *Apicotermes*) to phylogeny reconstruction and species circumscription (Emerson, 1938, 1956b). After completing his studies at Cornell and several return trips to Kartabo and later Barro Colorado Island in Panama, Emerson occupied various smaller appointments including one of the first Guggenheim fellowships in 1925–1926. He finally settled at the University of Chicago, where he remained until his retirement, and developed his worldwide and comprehensive collection, now at the American Museum of Natural History, which at one time comprised no less than 95% of the world's species, at least 80% represented by primary type specimens. In addition, he developed a library and catalog for everything known about termites, materials which served as the foundation and stimulus for Snyder's famous catalog of world species (Snyder, 1949a; table 5), as well as for the present work. Emerson contributed more than anyone of his time to the systematics, phylogeny, biology, biogeography, and paleontology of termites (e.g., Emerson, 1929, 1933b, 1936, 1942, 1952a, 1954a, 1955, 1961, 1965, 1968a, 1968b, 1971; Emerson and Krishna, 1975). He was a great field naturalist and aside from his time in French Guiana and Panama, he also traveled throughout the Congo and made treks to India. Given that entire colonies could be collected, Emerson was generous in sharing material from his collection, including paratypes, and freely exchanged with researchers and collections throughout the world. In no small part, contributions from Emerson's collection launched the serious inquiry of termites in many parts of the world,



Type locality: America

Type: Almost certainly lost. ; UZM.
Type (T. morio Fabricius): Kiel Mus (♀ Im.) descr. 1857.
a. America (probably Surinam, see Hagen 1856. p. 272).
b.
c. Cayenne.
d. British Guiana.
e. Brazil: Para
f. Surinam:
g. Surinam:
Cayenne:
British Guiana:
Venezuela: Puerto Cabello
Brazil: Para
Chili: Valparaiso.
h. ~~Surinam.~~ Cayenne
i. same as g.

1.71. Card 1.

Im. Burm. Hagen. Berlin descr. 1827.
♀ Im. Fabricius Type descr. 1857
Type. Termes marabitanas descr. 1827 Berlin

Coptotermes testaceus ~~(Linneaus)~~ (Linnaeus)

a. Hemerobius testaceus Linnaeus. 1758, ed. 10, p. 550 (Im; ed. 12, p. 912; ed. 13, p. 2641. ✓
b. Termes testaceus Burmeister, 1839, p. 767.
✓c. Termes morio Rambur 1842, p. 305. (Im.) ✓
✓d. Termes morio Erichson 1848 p. 583. (Loc.) ✓
e. Termes nasutus Walker 1853, p. 506. (Im.) ✓
f. Perla fusca De Geer 1773, p. 567. (~~ed. Goetze~~ another ref. of Perla p. 366) Pl. 27, Fig. 4, 5. Retzius, p. 60. ✓ 1780
g. Termes (Eu) testaceus Hagen 1858, p. 198, Pl. 2. Fig. 12, Pl. 3. Fig. 28.

FIGURE 15. **A.** Alfred E. Emerson, giant of 20th-century Isopteran studies, who amassed the world's preeminent collection of termites through his travels, fieldwork, and exchanges, whose encyclopedic knowledge of the Isoptera was unparalleled, and whose monumental card catalog was the inspiration for the present work; **B, C.** front and back of one card of the tens of thousands in the Emerson card catalog.

TABLE 5. Snyder's and Emerson's Classification of Isoptera
(Snyder, 1949a; Emerson, 1955, 1968a and 1968b; Krishna, 1970)

- Family †Uralotermitidae Zalessky [now known to not be a termite]
- Family Mastotermitidae Desneux
- Family Kalotermitidae Froggatt
  - Subfamily †Electrotermitinae Emerson [treated as a synonym in Krishna 1961, 1970]
  - Subfamily Kalotermitinae Froggatt
- Family Hodotermitidae Desneux
  - Subfamily Termopsinae Holmgren
  - Subfamily Stolotermitinae Holmgren
  - Subfamily Porotermitinae Emerson
  - Subfamily Hodotermitinae Desneux
  - Subfamily †Cretatermitinae Emerson [added in 1968a]
- Family Rhinotermitidae Froggatt
  - Subfamily Psammotermitinae Holmgren
  - Subfamily Heterotermitinae Froggatt
  - Subfamily Stylotermitinae Holmgren and Holmgren
  - Subfamily Coptotermitinae Holmgren
  - Subfamily Termitogetoninae Holmgren
  - Subfamily Rhinotermitinae Froggatt
- Family Termitidae Latreille
  - Subfamily Serritermitinae Holmgren [raised to family rank by Emerson, 1965]
  - Subfamily Amitermitinae Kemner
  - Subfamily Termitinae Latreille
  - Subfamily Macrotermitinae Kemner
  - Subfamily Nasutitermitinae Hare

particularly in Brazil, India, Pakistan, and even at such honored institutions as the Natural History Museum in London. Emerson died suddenly of a heart attack on 3 October 1976, leaving the Isoptera so more richly understood than he first found them.

Numerous contemporaries of Emerson were also making important strides in the systematics of Isoptera. **Thomas E. Snyder** (1885–1970; fig. 14D) was the resident specialist on termites in the U.S. Department of Agriculture's Bureau of Entomology's Division of Forest Insects, who produced a significant body of work on termite biology and control (e.g., Snyder, 1916, 1926h, 1931a, 1935, 1954a, 1954b; Snyder and Zetek, 1924). Snyder's interests and expertise were not constrained by the management and pest aspects of termite life, despite his appointment within the USDA. Indeed, Snyder also worked on the systematics of living and fossil termites throughout his career. For example, Snyder collaborated early on with **Nathan Banks** (1868–1953) of Harvard University, who had been publishing minor works on New World termites for a couple of decades, to produce a revision as well as biological and biogeographical overview of Nearctic Isoptera (Banks and Snyder, 1920). From about this time onward, Snyder consistently made excellent contributions to termite taxonomy. In particular, utilizing the extensive library of Emerson, he produced the first major catalog of living and fossil termites (Snyder, 1949a) as well as a bibliography on the order through 1965 (Snyder, 1956a, 1961, 1968). Snyder never fully recovered from the death of his wife in 1967 and, although he continued to work in his office at least a few hours most days, he suffered a stroke in 1970 and died shortly thereafter.

In terms of termite paleontology, **Kurt Freiherr von Rosen** (1889–1946) made the next major leap in understanding the Tertiary fauna of Isoptera. While he produced relatively few papers on termites, of particular note is Rosen's 1913 overview of fossil termites (Rosen, 1913a). In this work Rosen reviewed the then-known fauna, and documented many important taxa from Baltic amber as well as demonstrating the presence of *Mastotermes* in the geological record outside of Australia. Other contributors during this era were **Theodore D.A. Cockerell** (1866–1948) and **Sándor Pongrácz** (1887–1945), who was tragically killed during bombing raids in World War II. Emerson, who took a truly holistic perspective to termite systematics, also delved into the fossil record of Isoptera, and over the course of his career provided the most critical revisions and descriptions of fossil termites, revising most of the known fauna between the 1930s and early 1970s, work picked up and continued by **André Nel** and the authors of the present volume, among others.

The isopterological students of Emerson were also among his fine contributions to the field. **Laura Hare** (1906–2006; fig. 12B) and **Muzaffer Ahmad** (fig. 17b), both building on Holmgren's use of mandibular structure, constructed detailed phylogenetic hypotheses for termites based on the soldier (Hare, 1937) and imago-worker (Ahmad, 1950) mandibles. Hare worked on termites under Emerson's guidance, completing a M.S. in 1931, and later became a medical doctor. Hare's work corroborated much of Holmgren's phylogeny, and she is the author of the Nasutitermitinae, the largest subfamily of termites. Ahmad, still working today as editor-in-chief of the *Pakistan Journal of Zoology,* produced valuable species-level treatments, largely of the Pakistani fauna. His 1950 consideration of termite phylogeny, however, remains as one of the most highly cited and classic works on the Isoptera.

During the 20th century great progress was made on understanding the symbiotic association of termites with their intestinal bacteria and protozoa, as well as the diversity of inquilines hosted in their colonies. In particular, the work of **Lemuel R. Cleveland** (1892–1969), of Harvard Medical School's Department of Tropical Medicine, launched the critical investigation of symbionts in roaches and termites, identifying related protozoans in the hindguts of *Cryptocercus* and lower termites and demonstrated for the first time how the ability of termites to live on lignocellulose was dependent on the digestion of their associated flagellates (fig. 16). Cleveland's work on the flagellates of these two taxa was a real tour de force that established *Cryptocercus* as the sister group to termites.

Similarly, **Harold Kirby** (1900–1952; fig. 12A), who died relatively early from a heart attack suffered on a boy scout trip into the Sierras, made advances into the study of termite protozoans. Cleveland and Kirby's massive slide collections of termite protist symbionts, along with their termite voucher specimens as well as diaries and notes, are now housed in the American Museum of Natural History alongside the termite collection. Kirby was influenced early on by Cleveland and his professor, Charles A. Kofoid. Meanwhile, revisionary studies by **Charles H. Seevers** (1907–1965), of Roosevelt University and the Field Museum, and more recently by **David H. Kistner**, of Chico State University, have made the termitophilous Staphylinidae one of the better-documented lineages of termite associates and revealed a diversity Wasmann could only have dreamt of.

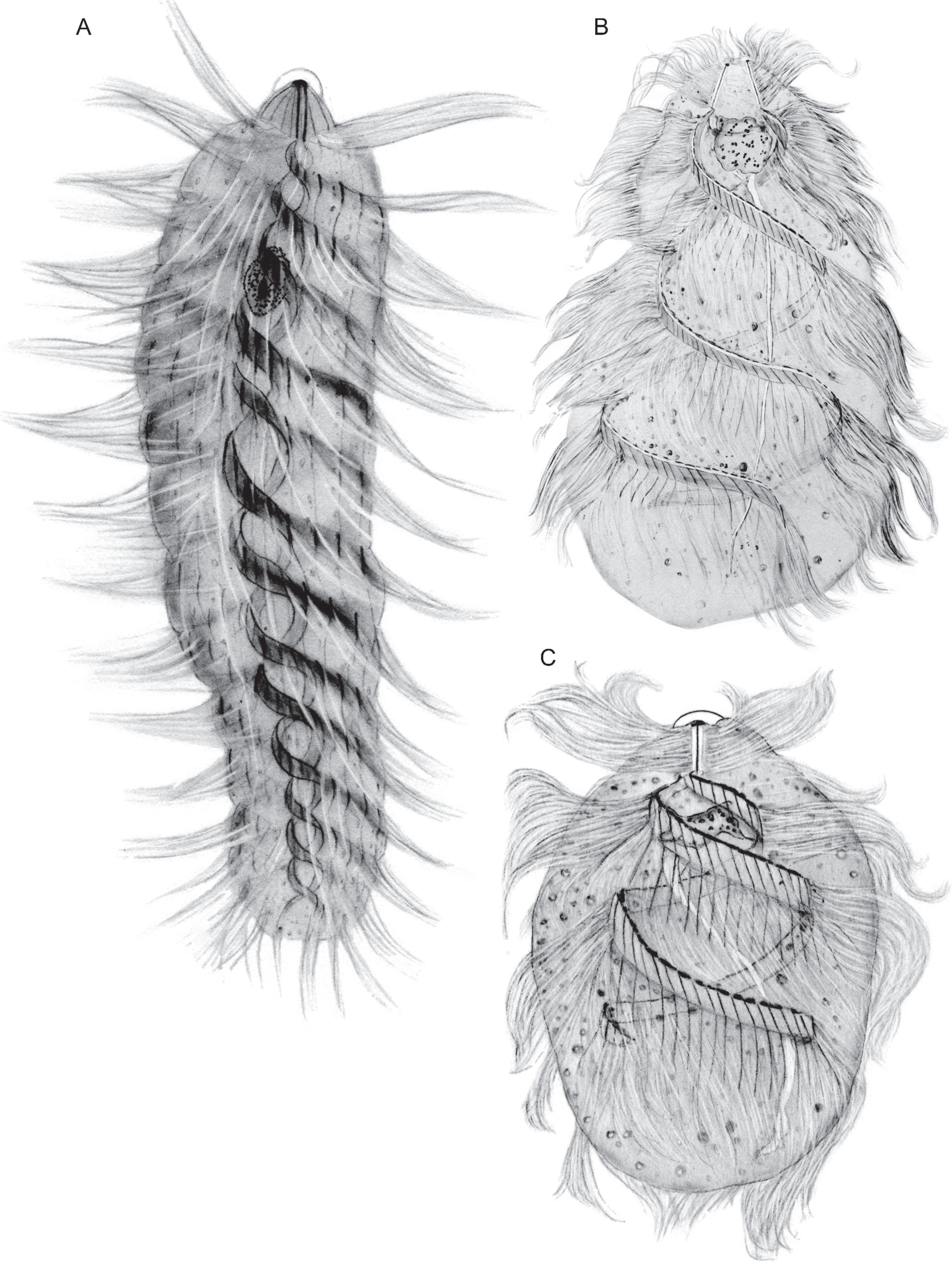


FIGURE 16. Illustrations of the three species of the endosymbiotic protist genus *Leptospironympha,* in *Cryptocercus* wood roaches. From Lemuel R. Cleveland's seminal (1934) monograph on this protist fauna.

This same period saw an explosion in the number of investigators working both on various aspects of basic termite biology and on systematics. One of the first synthetic reviews was that of **Charles A. Kofoid** (1865–1947; fig. 12A) and **Sol F. Light** (1886–1947; fig. 12A) and their collaborators (Kofoid, 1934a), *Termites and Termite Control.* This volume also focused on the application of termite biology and natural history to their effective control; in it Light delved deeply into the classification and distribution of various groups in North and Central America and into the termite fauna of the Pacific islands and the Philippines. In his later years Light did experimental work on "ectohormonal" control of caste development in *Zootermopsis.* He was a member of the Department of Zoology at the University of California from 1925 until his untimely death by drowning in 1947. After his death the major portion of his collection, along with his field notes and diaries, was presented to the American Museum of Natural History.

Throughout the world different labs were examining with new tools and fresh minds novel suites of characters ranging from microreticulation of the wings to detailed gut anatomy, sociochemicals, and eventually genetic materials such as allozymes and DNA sequences. In particular, **Mitthan L. Roonwal** (1908–1990; fig. 17A), of the Forest Research Institute in Dehra Dun, India, and later of the Zoological Survey of India, spearheaded an entire school of Indian researchers working on the phenomenal diversity in that country as well as numerous comparative studies of morphological characters among the Isoptera. Roonwal and his numerous disciples, such as **Parimal K. Sen-Sarma** (1929–2002) and **Om B. Chhotani** (1931–1997) studied everything from the papillae on spurs and spines and microsculpturing of wings, to the morphometric details of eggs, often with the power of scanning electron microscopy, representing some of the first applications of this technology. Of particular note was their two-volume *Fauna of India,* which reviewed the entire Indian subregion and summarized their perspective on isopteran classification (Roonwal and Chhotani, 1989; Chhotani 1997; table 6). Meanwhile, **Charles Noirot** (1922–2010; figs. 18C, D), a student of the great French entomologist **Pierre-Paul Grassé** (1895–1985; figs. 18A, B), developed the use of termite gut morphology for the investigation of fundamental elements of isopteran biology and patterns of relationship, sometimes in collaboration with his wife **Cécile Noirot-Timothée**. Furthermore, he contributed significantly to our understanding of caste development and the evolutionary history of the Isoptera, all the while maintaining a phylogenetic perspective in his approach. Grassé himself provided valuable contributions to the biology and classification of Isoptera, most notably his reviews, such as the *Traité de Zoologie* (1949) volumes on Isoptera and his *Termitologia* (1982b, 1984, 1985; table 7), as well as a voluminous literature on ethology and basic biology covering nearly six decades of dedicated investigation. Beginning in the early 1960s **Jean Deligne** of Belgium produced important works on the biology and defensive mechanisms of termites, particularly of head glands, as well as on mandibular and integumental morphology, and with **André Quennedey** he utilized such characters to recognize the distinctiveness of *Prorhinotermes* as a separate subfamily among the Rhinotermitidae. This same era saw the publication of a two-volume set, *Biology of Termites,* edited by the senior author of the present work and **Frances M. Weesner**, which synthesized all aspects of termite systematics, biology,

FIGURE 17. **A.** Mithan L. Roonwal, leader of termite studies in India and originator the study of wing microsculpturing as a taxonomic character; **B.** Muzaffer Ahmad, dean of termite studies in Pakistan and authority on imago-worker mandibles; **C.** W. Victor Harris, expert on termite control; **D.** Renato L. Araujo, prominent Brazilian termite specialist, who compiled the first catalog of Neotropical termites.

FIGURE 18. **A.** Pierre-Paul Grassé, towering figure among European entomologists and general editor of the *Traité de Zoologie,* an encyclopedic work covering the entire animal kingdom; **B.** Grassé with a mound of *Macrotermes bellicosus* (Smeathman); **C.** Charles Noirot, student of Grassé, expert on caste development, and pioneer in the use of gut anatomy in taxonomic studies; **D.** Noirot with a mound of *Macrotermes natalensis* (Haviland).

TABLE 6. Roonwal and Chhotani's (1989) Classification of Isoptera

- Family Mastotermitidae Desneux
- Family Termopsidae Holmgren
- Family Hodotermitidae Desneux
  - Subfamily Stolotermitinae Holmgren
  - Subfamily Porotermitinae Emerson
  - Subfamily Hodotermitinae Desneux
  - Subfamily †Cretatermitinae Emerson
- Family Kalotermitidae Froggatt
- Family Stylotermitidae Holmgren and Holmgren
- Family Rhinotermitidae Froggatt
  - Subfamily Psammotermitinae Holmgren
  - Subfamily Coptotermitinae Holmgren
  - Subfamily Termitogetoninae Holmgren
  - Subfamily Rhinotermitinae Froggatt
  - Subfamily Heterotermitinae Froggatt
- Family Serritermitidae Holmgren
- Family Indotermitidae Roonwal and Sen Sarma
- Family Termitidae Latreille
  - Subfamily Amitermitinae Kemner
  - Subfamily Termitinae Latreille
  - Subfamily Macrotermitinae Kemner
  - Subfamily Nasutitermitinae Hare

TABLE 7. Grassé's Classification of Isoptera (1949, 1982b, 1984, 1985)

- Family Mastotermitidae Desneux
- Family Calotermitidae Froggatt [as Kalotermitidae in *Termitologia*]
  - Subfamily †Electrotermitinae Emerson [removed in *Termitologia*]
  - Subfamily Calotermitinae Froggatt [as Kalotermitinae in *Termitologia*]
- Family Termopsidae Holmgren
  - Subfamily Termopsinae Holmgren
  - Subfamily Porotermitinae Emerson
  - Subfamily Stolotermitinae Holmgren
  - Subfamily †Cretatermitinae Emerson [added in *Termitologia*]
- Family Hodotermitidae Desneux
- Family Rhinotermitidae Froggatt
  - Subfamily Psammotermitinae Holmgren
  - Subfamily Heterotermitinae Froggatt
  - Subfamily Coptotermitinae Holmgren
  - Subfamily Arrhinotermitinae Sjöstedt [removed in *Termitologia*]
  - Subfamily Prorhinotermitinae Quennedey and Deligne [added in *Termitologia*]
  - Subfamily Stylotermitinae Holmgren and Holmgren [added in *Termitologia*]
  - Subfamily Termitogetoninae Holmgren
  - Subfamily Rhinotermitinae Froggatt
- Family Serritermitidae Holmgren [as a subfamily in *Traité de Zoologie*]
- Family Termitidae Latreille
  - Subfamily Macrotermitinae Kemner
  - Subfamily Nasutitermitinae Hare
  - Subfamily Termitinae Latreille [added in *Termitologia*]
  - Subfamily Apicotermitinae Grassé and Noirot [added in *Termitologia*]
  - Subfamily Amitermitinae Kemner [removed in *Termitologia*]
  - Subfamily Mirocapritermitinae Kemner [removed in *Termitologia*]
  - Subfamily Microcerotermitinae Holmgren [removed in *Termitologia*]

TABLE 8. Sands' Classification of Termitidae (1972)

Subfamily Macrotermitinae Kemner
Subfamily Nasutitermitinae Hare
Subfamily Termitinae Latreille
Subfamily Apicotermitinae Grassé and Noirot
Subfamily Amitermitinae Kemner [synonymized with Termitinae, with some genera placed in Apicotermitinae and others in Termitinae]

and control through 1969 (Krishna and Weesner, 1969, 1970), serving as an English precursor to Grassé's *Termitologia*. These works are foundational resources for any investigation of the Isoptera, and although some newer volumes have been produced (e.g., Abe et al., 2000; Bignell et al., 2010), *Biology of Termites* remains a most valuable reference.

Contemporary Investigators

One of the first developments in the application of chemical data sources was the examination of cuticular hydrocarbons for species distinction, which permitted recognition of clusters of populations based on the chemical blend expressed (e.g., Howard et al., 1978, 1982; Howard and Blomquist, 1982). This technique continues to provide insights into problematic taxa and cryptic species (e.g., Nelson et al., 2008), and fully realizes its potential when united with data from other sources. The modern era of molecular systematics has also fueled research into termite systematics, with innumerable studies investigating higher- or lower-level relationships among lineages and species, and either in isolation or combination with other forms of data like morphology (e.g., Lo et al., 2000, 2004, 2006; Inward et al., 2007b; Legendre et al., 2008; Lo and Eggleton, 2010; Ware et al., 2010b). With the addition of these new methods, the suites of potential data have grown dramatically and the impact on the field shall be profound, particularly for the Termitidae.

Today there are researchers contributing to a synthetic approach to termite classification, systematics, and evolution. Every element of termite biology, anatomy, physiology, ecology, and paleontology is brought to bear on questions surrounding this uniquely dominant group of recyclers and social architects. Among the more notable specialists in the field are Paul Eggleton and David Jones in the United Kingdom; André Nel of France; the Brazilian researchers Eliana Cancello and Reginaldo Constantino; Yves Roisin in Belgium; F.-S. Huang of China; and Barbara L. Thorne, Rudolf Scheffrahn, and Christine A. Nalepa in the United States. No longer need specialists sit in relative isolation contemplating the subject as was largely the case for early giants such as Hagen or Holmgren. Instead, integration, cooperation, and multidisciplinary approaches synergized collaboratively from teams with diverse expertise and all regions of our shrinking world are the standard for this era. It shall be exciting to see what new revelations arise in the years to come from this fresh crop of isopteran investigators.

MORPHOLOGY

Introduction

The morphology of termites is essentially a generalized one typical of Dictyoptera and other polyneopterous insects, the major exceptions being of course the specializations of termite castes, but also a progressive reduction of structures from the earliest to most recently evolved termite lineages. The most anatomically specialized caste is the soldier, which typically possesses a much larger head and mandibles than the imago (reproductive adult) and worker, as well as a smaller pronotum and eyes that are vestigial or entirely lost. Imagoes are the most anatomically generalized, possessing wings that dehisce (when lost they are *dealates,* vs. *alates*), and having proportions of the tagmata most typical of polyneopterans. Imagoes have the largest eyes among the castes, and a generalized mandible structure as well. Our discussion here is limited to exoskeletal characters and those internal characters (e.g., apodemes, glands) that are intimately associated with the skeletal characters or that are important systematically (e.g., structure of the digestive system). Major references on insect morphology or specifically that of termites are the following: Donovan et al. (2000), Emerson (1965), Grassé (1949, 1982, 1986), Holmgren (1909), Klass (1995, 1998), Roonwal and Chhotani (1989), Snodgrass (1935), Weidner (1955f, 1970c), Weesner (1969), and various specialized papers on particular organ systems as cited throughout the text below.

Head

The head of termites, like those of all insects, is a composite tagma composed of approximately six segments, manifest by *sutures* and the serial nature of appendages like antennae, mandibles, maxillae, and the labium. It possesses the structures specialized for sensory perception (eyes, antennae, maxillary and labial palps), integration (brain, subesophageal ganglion), and ingestion (mandibles, laciniae, hypopharynx, esophagus). The termite head is generally *prognathous,* such that the cervical connection is at the posterior end and the mouthparts are held anteriorly, in contrast to the other dictyopterans: mantises with a *hypognathous* head and roaches with an *opisthognathous* head. The shape of the head capsule varies dramatically between soldiers and the imago-worker. Soldiers have a longer, often rectangular-shaped head (figs. 31–36, figs. 45–49, figs. 51–52), except for the bulbous head of nasute soldiers (Termitidae: Nasutitermitinae: fig. 57); the imago-worker head is rounded to slightly elliptical. The soldiers of some Kalotermitidae have plug-shaped (*phragmotic*) heads (figs. 45–48), which are employed to close the openings to the nest tunnels.

The following account refers largely to the sutures of the termite imago-worker head. The sutures of the head capsule are significantly reduced from those of more generalized dictyopterans such as roaches. There is an inverted Y-shaped groove on the occiput, the stem of which is the coronal ecdysial cleavage line, or *coronal sulcus* (also called the "epicranial suture" [e.g., Weesner, 1969]), while the arms of the Y (the *frontal sulci*) diverge to the ocelli or slightly anterior or posterior to the ocelli (fig. 19A). The coronal and frontal sulci are best developed

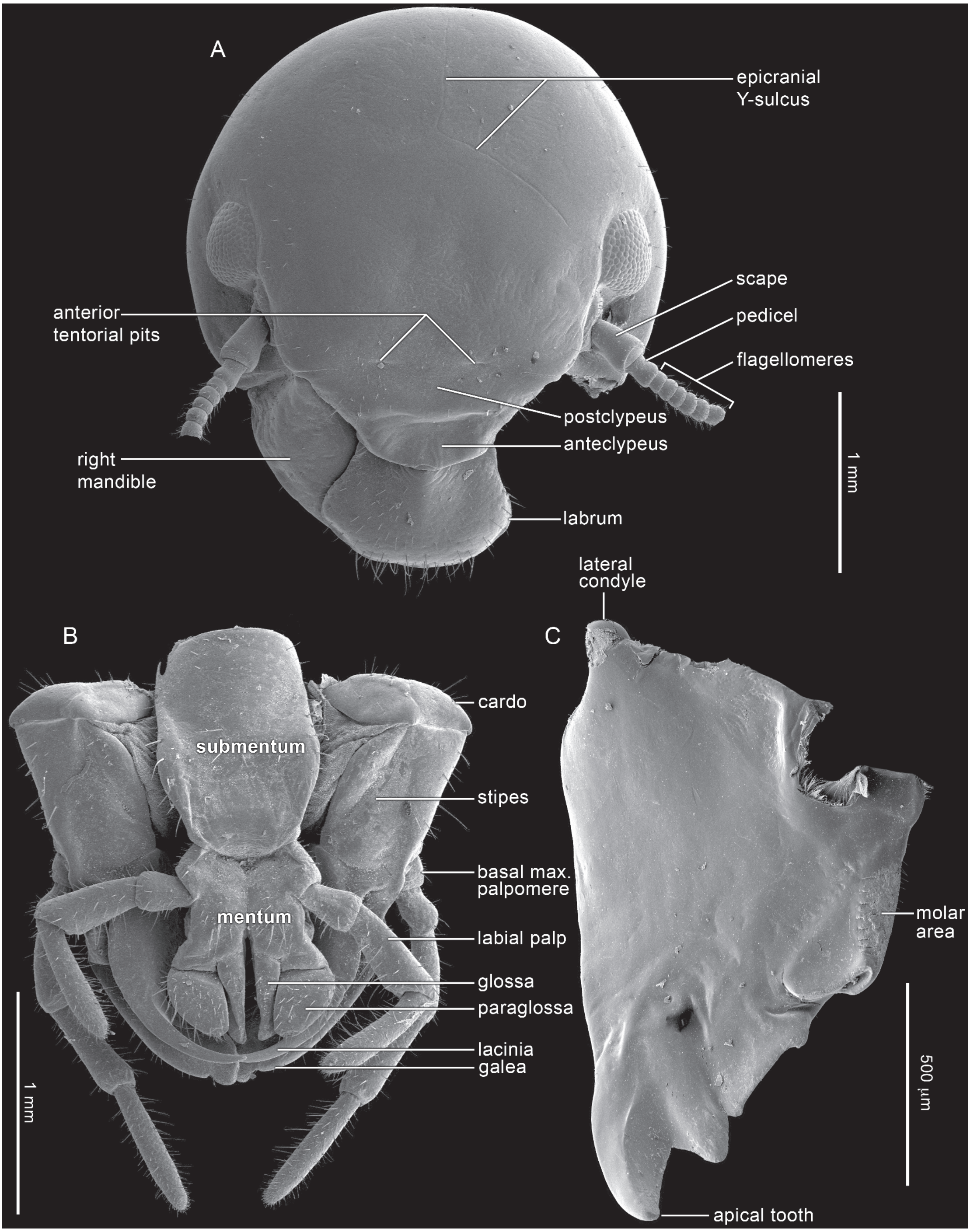


FIGURE 19. The head and appendages of an alate of the basal termite, *Microhodotermes viator* (Latreille) (Hodotermitidae) (scanning electron micrographs). **A.** Full frontal view of head, with left mandible removed. **B.** Labium and maxillae, removed from head capsule and shown in ventral view. **C.** Left mandible, view of inner surface.

in basal taxa, including Mastotermitidae, Hodotermitidae s.s., Archotermopsidae, Stolotermitidae, and Kalotermitidae, and are poorly developed to lost in Rhinotermitidae and Termitidae. Another significant suture is the *occipital suture* on the *postgena,* which runs from the occipital foramen parallel to the length of the head, to just shy of the maxilla. The occipital suture is well developed in polyneopterans and in basal termites like *Mastotermes,* but becomes progressively weaker to completely lost in Rhinotermitidae and Termitidae. This suture is frequently referred to as the postoccipital suture, but that suture surrounds the occipital foramen. The *subantennal sulcus,* which is present in most roaches and other polyneopterans and lies beneath the antennal socket, is lost in *Cryptocercus* and in termites (Klass and Eulitz, 2007). Termites and *Cryptocercus* do possess a *subgenal sulcus,* which connects to the epistomal sulcus and then turns obliquely ventrad.

Along the posterior edge of the cardo (base of the maxilla) in the imago-worker is a pair of *posterior tentorial pits,* which are invaginations where the *posterior arms of the tentorium* attach to the inner wall of the head. In soldiers where the head is greatly enlarged, the postmentum (of the labium) is an elongate sclerite (also called the "gula," but not homologous with the true gula in some neuropterids and adephagan beetles). In these soldiers the posterior tentorial pits are elongate sulci that border the lateral margins of the postmentum. The *anterior tentorial pits* in termites are deep slits within the epistomal suture on the face, just below the bases of the antennae. The tentorium itself is an internal sclerotized strut in the head to which are attached muscles that control the mouthparts, head movements, and even the spray from the frontal gland. Typical of Dictyoptera (indeed, a defining feature), termites have a central hole, or *tentorial perforation,* in the middle of the anterior transverse bridge. The ventral margin of the tentorial perforation has a pronged structure in roaches, except in *Cryptocercus,* further evidence for the close relationship of this roach to termites (Klass and Eulitz, 2007). There is modest variation in the structure of the termite tentorium (Hudson, 1947; Grimaldi, unpubl.). A pair of *anterior tentorial arms* flare into flanges that connect to the inner wall of the head, and there is a pair of thin, straplike *dorsal tentorial arms* that have free endings, along with a short pair of posterior tentorial arms that also connect internally to the head capsule.

With the exception of some reductions in the eyes, ocelli, and sometimes the mandibles, termites have the full complement of head structures. Antennae of termites have distinctive *moniliform* segments (fig. 20), varying in number from the primitive state of 25–33 antennomeres in *Mastotermes* and Hodotermitidae s.s., to as few as 11 in some Termitidae (nymphs have fewer flagellomeres than alates). Roaches typically have many more than 40 antennomeres. The scape is the longest antennomere, being generally several times the length of other antennomeres; the pedicel is shorter. The third antennomere (basal flagellomere) has significant variation in shape and size. The basal flagellomeres (segments distal to the scape and pedicel) of termites are shorter than those of roaches, the apical ones longer, and there is a ring of fine, stiff setae on each antennomere, along with a covering of minute setulae (fig. 20). The more distal flagellomeres in particular are goblet shaped, with a narrow, bare stem that fits into the swollen section of the preceding segment, whereas most roach antennomeres are *filiform,* being elongate cylinders (fig. 20). With the exception of the primitive mastotermitid *Garmitermes* in Baltic amber (fig. 65A–C), the apex of the termite antenna barely tapers (unlike the

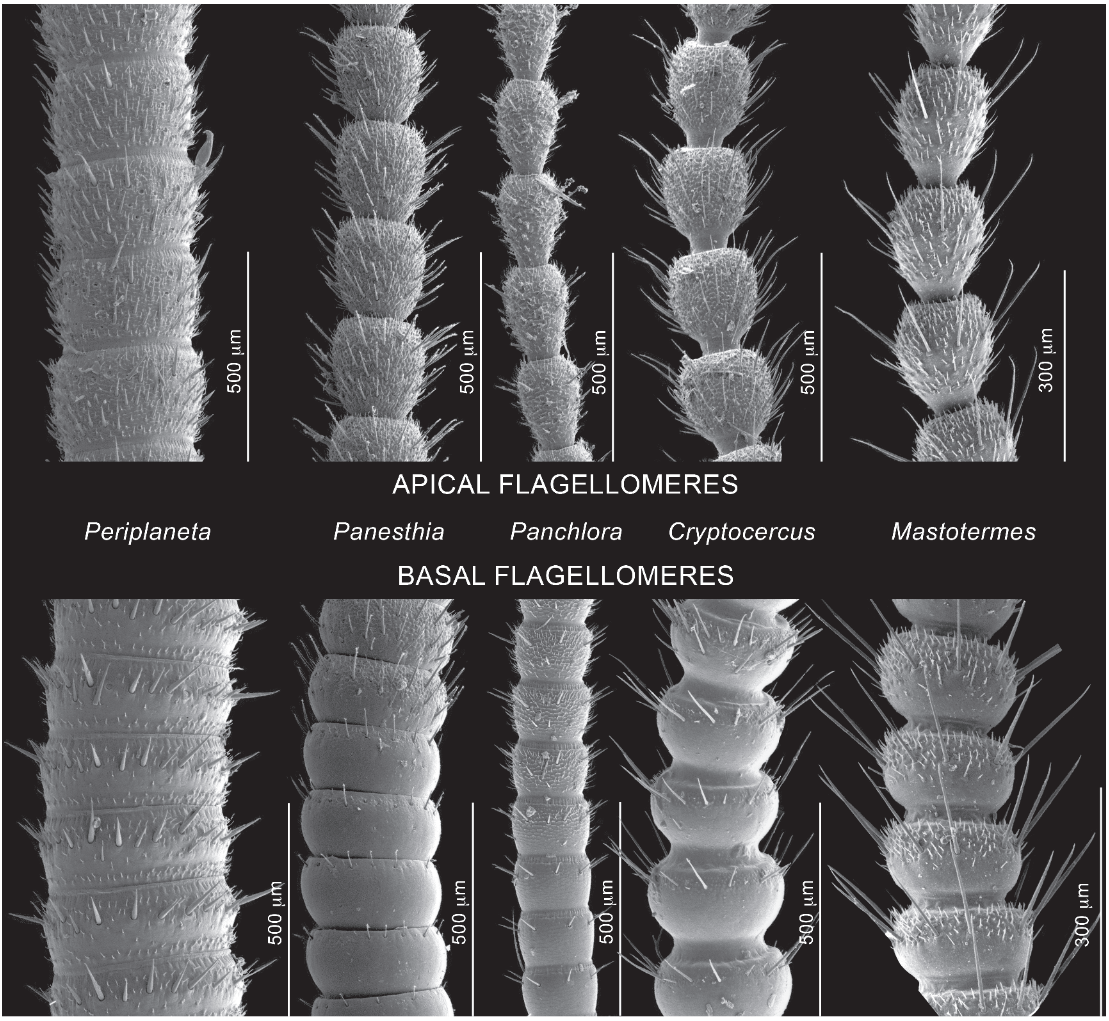


FIGURE 20. Flagellomeres from apical and basal sections of the antennae of representative roaches (Blattodea), and the basal termite *Mastotermes darwiniensis* Froggatt (scanning electron micrographs). The distinctive moniliform shape of termite flagellomeres also occurs in *Cryptocercus* (Blattodea: Cryptocercidae), a genus of wood roaches and the living sister group to Isoptera.

flagellate antennae of roaches and mantises). Interestingly, the antennal shape and the antennomere structure and number of *Cryptocercus* are very similar to that of *Mastotermes* (fig. 20). The antennae of termites are maneuvered by extrinsic muscles, whose insertions are within the antenna and origins in the head capsule, as in all pterygote insects.

The *compound eyes* in termites are simple, with no differentiation of facets within an eye and few if any setulae between the facets. The size and shape of the eye in lateral view are important taxonomic characters for the imago-worker (generally larger in the imago), as is the distance beyond the curvature of the head capsule from which the eye protrudes. The eye of soldiers is highly reduced to a few facets in Hodotermitidae s.s. or completely lost in all Rhinotermitidae and Termitidae. Most termite imagoes possess a pair of distinctive, large *lateral* *ocelli* that are close to the inner margins of the eyes; the third, *median ocellus* typical of other insects is lost in termites (in roaches all ocelli are vestigial, but mantises retain three well-developed ocelli in the typical position in the center of the frons). The imagoes in some groups of termites have lost all ocelli, notably the species of Hodotermitidae s.s., Termopsidae, and Archotermopsidae, and the workers and soldiers of all species. Taxonomically important variations of the ocelli are size, distance from the mesal margin of the eyes, and shape (round, oval, elliptical, crescentic, and reniform).

The *fontanelle* is a highly significant structure in termite systematics and biology; it is the opening to the *frontal gland,* which produces defensive secretions and is therefore most highly developed in soldiers. Its function in imagoes is unknown. The structure of the fontanelle is itself hardly just a hole; preliminary observations using scanning electron microscopy reveal significant variation (fig. 22). The fontanelle can be slit shaped, drop shaped, rounded, Y-shaped, or with a bifid anterior end, and it can lie in a depression or be raised on a plate. It can also be ringed with fine setae (as in many nasutes), and even consist of a cluster of fine pores. There is also some sexual dimorphism in structure of the fontanelle in the imagoes of some nasutitermitines (Sands, 1957b). Only the Rhinotermitidae, Termitidae, the small families Stylotermitidae and Serritermitidae, and the stem-group Cretaceous *Archeorhinotermes* possess a fontanelle, which is the defining feature of the Neoisoptera. The fontanelle occurs on the frons, with its position varying from above, between, and below the eyes. The structure is very large and partially produced into a short nasus in some rhinotermitid soldiers, notably *Coptotermes.* Perhaps the best-known soldiers in termites are the *nasutes,* of the subfamily Nasutitermitinae (Termitidae), which have a bulbous head with the fontanelle (also called the "frontal pore") situated at the tip of a long, pointed nasus, through which a defensive secretion is squirted. (Zoraptera also have a fontanelle, though it is structurally different than in termites).

Like the fontanelle, the *frontal gland,* first studied in detail by Holmgren (1909b), has no known homolog in other insects. This gland consists of invaginated epidermis lined with glandular cells, often with a reservoir connected to the fontanelle by a narrow duct. In basal termites that do not possess a fontanelle, there is merely swelling of the epidermis beneath the cuticle where the coronal and frontal sulci meet, which corresponds to the "mid-dorsal spot" of Roonwal and Sen-Sarma (1960). However, all termites that have been examined have a pair of minute muscles, the *tentorial-fontanellar muscles,* that connect the tentorium to the frontal gland area; in those with a frontal gland, the muscles connect to the neck of the gland near the fontanellar opening (Noirot, 1969). Presumably, these muscles control the release of frontal gland secretions, though explosive discharge in nasutes is presumably achieved by contractions of the *mandibular muscles* (even though the mandibles themselves may be vestigial). In the Rhinotermitidae the soldier frontal glands can be huge, extending from the head, through the thorax, and occupying much of the abdomen (Noirot, 1969a). This feature has been observed, specifically, in *Coptotermes,* in major and minor soldiers of *Schedorhinotermes,* and in minor soldiers of *Rhinotermes* (Noirot, 1969a). Noirot described the frontal gland secretion of *Coptotermes* as becoming viscous and sticky when ejected, entangling both attacker and soldier. Not all Neoisoptera have well-developed frontal glands. The soldiers of many Macrotermitinae have them weakly developed, defense provided instead by salivary secretions (much in the way of some stingless bees). Likewise, termitid genera with snapping mandibles (e.g., fig. 57) in the soldiers also have weakly developed frontal glands. Not surprisingly, the frontal glands are very well developed in the nasute soldiers of the Nasutitermitinae, which typically possess a reservoir of the gland in the posterior half of the head bulb, with a long, thin channel that connects to the fontanelle. Interestingly, nasutes eject their secretions with remarkably good aim, even though they are blind. The gross morphology and histology of the termite frontal gland deserve comprehensive study. The nature of the secretions is discussed by Prestwich (1979b, 1984a).

The *clypeus* is an area of the face ventral to the *epistomal suture*; muscles are attached to its inside wall that dilate the *cibarium,* or *preoral cavity.* The clypeus in termites is typically divided by a well-defined to weak transverse groove into an anterior, somewhat flexible *anteclypeus* and a stiff, posterior or proximal *postclypeus* (fig. 19A). Taxonomically significant variation in the clypeus, particularly in Rhinotermitidae and Termitidae, includes relative depth of the anteclypeus and postclypeus, whether or not they are bulging, the shape of the ventral margins, and the development of a median longitudinal furrow. The *labrum* is a sclerotized flap that hangs over the mouthparts and is attached to the ventral margin of the clypeus. In imago-workers the labrum is typical of other polyneopterans: roughly hemispherical in shape, sometimes with the ventral margin slightly pointed. Soldiers show great variation in the shape of the labrum, which is commonly a short to elongate triangle with a pointed apex. The labrum is elongate in some Rhinotermitidae, particularly in minor soldiers, with a median furrow on the clypeus that extends from the fontanelle to the tip of the labrum; in this situation the soldiers are called *nasutoids.* Soldiers of Termitidae have diverse labral structures, with the apical margin being flat to concave and having lateral points (e.g., *Cubitermes, Cavitermes,* and other genera with long swordlike manidibles), with a hyaline tip (e.g., *Macrotermes, Pseudacanthotermes, Syntermes*), and even asymmetrical (in those genera with snapping mandibles, e.g., *Dicuspiditermes*). In many of the more specialized nasute soldiers the labrum is minute.

Mandibles are the anteriormost pair of feeding appendages and are always heavily sclerotized; those of the imago-worker are most similar among species and are generalized chewing mandibles, typically being trapezoidal or triangular in shape with one or more teeth (figs. 19C, 21A–D), while soldier mandibles are usually much larger and specialized, gaff or sickle shaped, are often toothless, and can even be minute and functionless. Typical of the dicondylic insects, there are two *condyles* at the base of each mandible. Mandibles are closed by large adductor muscles that attach to the base of the mesal surface and to the ventral tentorial arms within the head capsule; they are opened by smaller abductor muscles that insert at the lateroproximal corner of the mandible. The classic study of Ahmad (1950) surveyed the imago-worker dentition of 137 genera, with many other authors making subsequent observations (Sands, 1972, 1998). Though differences in imago-worker dentition can be subtle, these are generally consistent and have been reliably used in higher classification, so terminology of the dentition is important (fig. 31D). The *apical tooth* is the distalmost one; the *marginal teeth* lie along the mesal edge just proximal to the apical tooth, designated as the first, second, and third marginal tooth. Proximal to the third marginal tooth is a flattened, filelike edge with fine, transverse grooves, the *molar plate* (figs. 21A–D, 32–36, 38, 56, 58–59). On the underside of the molar plate is a small, toothlike process usually not visible from above, which is referred to as the *subsidiary marginal, 4th marginal tooth* (Sands, 1998), or *molar tooth* (Krishna, 1968). The mandibles in the termite imago-worker are asymmetrical, and it is crucial to distinguish between the two when referring to dentition. The left mandible is typically narrower, has a slightly smaller molar plate, and often a long, flat gap between marginals. In many higher termites the left mandible has a distinct *molar prominence*. Important features of mandible dentition include the following: size of the apical tooth; distance between the apical tooth and first marginal (as in some genera of Termitidae); the number and shapes of marginal teeth; presence/absence of a small subsidiary tooth on the first marginal tooth of the right mandible; size, shape, and number of ridges along the molar plate of the right mandible. At the base of the mandible on the mesal margin is a tuft of spiculelike setulae, the prostheca, which is found in basal genera like *Masotermes* and whose function is unknown.

Several authors (e.g., Ahmad, 1950; Emerson, 1961, 1962) have considered the dentition of the imago-worker mandible to be a relatively conservative structure, variations in which are nonadaptive and not correlated with diet and therefore considered reliable in deducing phylogenetic relationships. This view, however, has been challenged by Sands (1965c, 1998), who interprets significant variation in mandible structure with diet. The apical tooth, for example, is longer than the first marginal tooth in most soil feeders, shorter in grass feeders, and generally subequal in wood feeders. Also, the molar plate is convergently reduced in genera that are humus feeders among some members of the subfamilies Apicotermitinae, Nasutitermitinae, and Termitinae (family Termitidae) (Sands, 1965c; figs. 58–59).

Soldier mandibles are far more specialized and elaborate than those of imagoes and workers (figs. 31–36, 44–49, 51–52, 56–57). Oddly, with the exception of a few early studies (e.g., Hare, 1937), there has not been a comprehensive comparative study of the mandibles in soldiers. The mandibles of soldiers typically project far in front of the insect and can be half the length of the head capsule (most basal families) or longer than the capsule (some Termitidae), which thus serve well in colony defense. The plesiomorphic condition is a long, flattened pair of mandibles with large teeth on the mesal surface, as seen in basal genera like *Mastotermes, Archotermopsis,* etc. As in the imago-worker, the dentition of these plesiomorphic mandibles is asymmetrical. Slightly more specialized mandibles are gaff shaped, being linear with the tip curved inward. If teeth are present they are at the base of the mesal margin, occurring as a single tooth and/or as serrations. The most specialized mandibles are in the Termitidae, and include sickle-shaped mandibles (e.g., *Armitermes, Rhynchotermes*), long lance-shaped ones that scissor (e.g., *Cavitermes*), and the peculiar snapping mandibles of some Termitidae (e.g., *Dicuspiditermes*) (fig. 57). Snapping mandibles are grossly distorted blades, the left with a fold in the middle, and when the mandibles are scissored there is a sudden release of energy. If the mandibles are scissored underneath an attacker, the attacker is launched into the air, or the termite itself launched away from an attacker. Snapping mandibles can be relatively symmetrical or distinctly asymmetrical. The snapping action of a species of *Termes* is reported to be the fastest known animal movement (Seid et al., 2008). The mandibles of nasute soldiers (Nasutitermitinae: Termitidae) vary from large, sickle-shaped structures (*mandibulate nasutes* of the Syntermitinae) to vestigial, nonfunctional lobes in the very diverse *Nasutitermes* group of genera. Termite soldiers cannot feed themselves, so they rely on *trophallaxis* with workers.

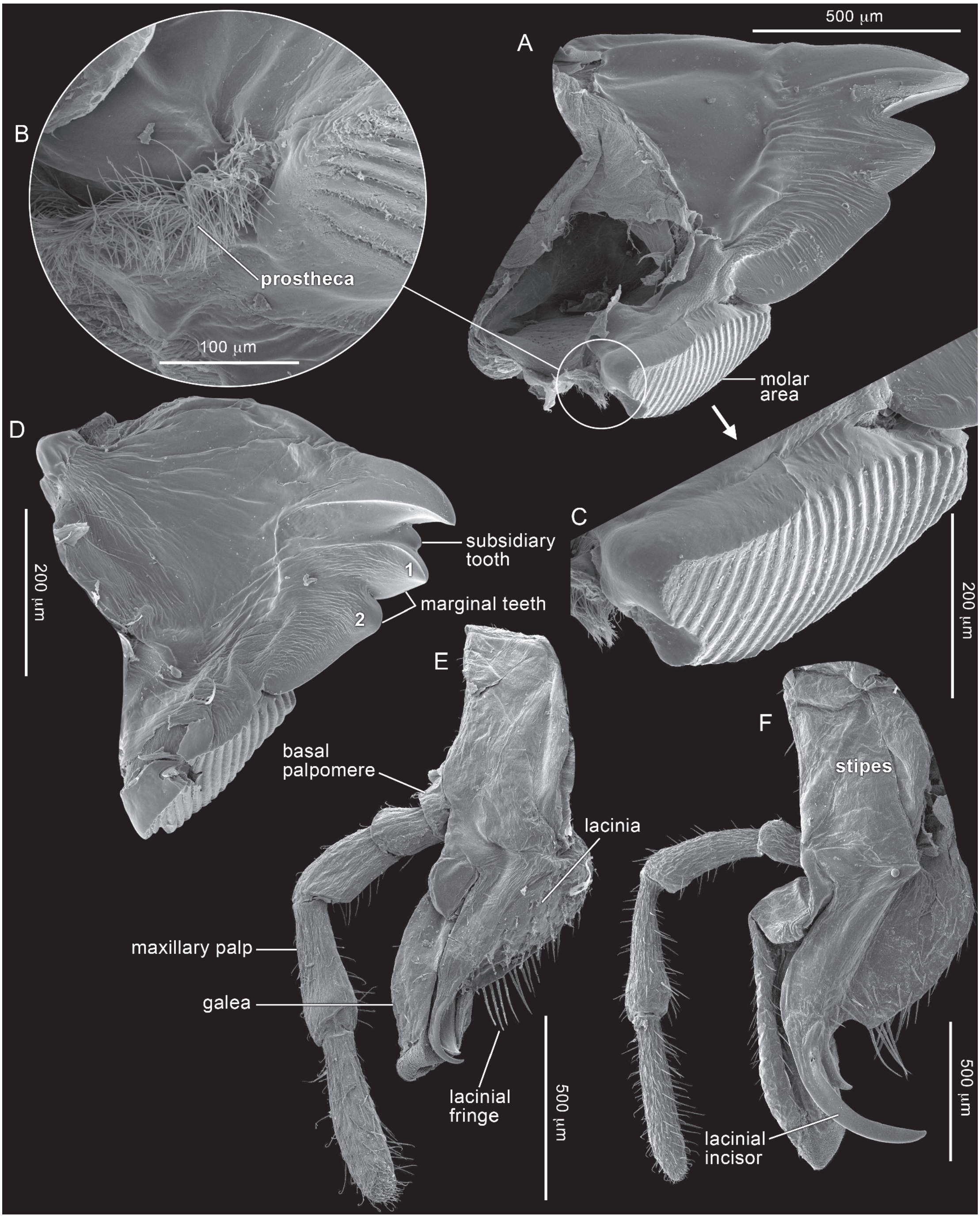


FIGURE 21. Mouthparts (alates) of exemplar basal Isoptera (scanning electron micrographs). **A–C.** *Mastotermes darwiniensis* Froggatt. **A.** Right mandible, inner surface. **B.** Detail of setose structure at base of mandible, the prostheca. **C.** Detail of the molar plate. **D.** *Hodotermopsis* sp. right mandible, outer surface. **E.** *Zootermopsis angusticollis* (Hagen) right maxilla, ventral view. **F.** *Hodotermes mossambicus* (Hagen) right maxilla, ventral view.

Other than salivary glands, basal termites retain only two kinds of exocrine glands on the head: the *mandibular glands* and *hypopharyngeal glands* (only the former of these occur in Rhinotermitidae and Termitidae). This contrasts with a total of seven types of exocrine glands in roaches (Brossut, 1973). Interestingly, *Cryptocercus* uniquely possesses just a pair of lower hypostomal glands. Mandibular glands are small, paired exocrine structures that lie at the base of the mandibles. These glands probably occur in all termites, and their gross structure shows some variation: it is one- or two-branched in Mastotermitidae, a narrow and unbranched tube in Kalotermitidae and Rhinotermitidae, and saclike with a tubular neck in *Stolotermes* (Miller, 1989). The fine structure of these glands shows little variation among termites (Noirot, 1969a; Brossut, 1973), even in nasute soldiers with vestigial mandibles, and the composition and function of the secretions are unknown. Interestingly, mandibular glands harbor symbiotic nematodes, the effect on termites of which appears to be insignificant (Miller, 1989b).

The *maxilla* lies just posterior to the mandibles, and consists of paired appendages: the galeae, laciniae, and maxillary palps (fig. 21E, F). Its structure in termites is generalized as in most polyneopterans, with the base of each half being the broadly joined basal *cardo* and distal *stipes.* The stipes is generally much broader than the cardo in termites, and its long axis aligned at a right angle to the long axis of the cardo. Joined to the lateral surface of the stipes is the maxillary palp, which has the primitive neopteran segmentation of five palpomeres in termites. The apex of the stipes bears two lobes: the mesal *lacinia* and the outer *galea.* The apex of the lacinia is sclerotized and has two teeth, being serially homologous with the mandibles (fig. 21E, F). With the exception of two basal genera, termites possess the primitive lacinial dentition of two apical teeth commonly seen in roaches; one of these teeth is preapical in *Hodotermes* and *Anacanthotermes.* The swollen base of the lacinia has a comb of stiff setae on the mesal margin. The galea is membranous and has similar stiff setae on the mesal surface; the apex of the galea is covered by minute spicules (fig. 21E, F).

The *labium* is posterior to the maxilla and is a rudimentary homolog of the maxilla, a significant difference being that the labial palps are three segmented instead of five, typical of pterygotes. *Mastotermes* retains a vesitigial *palpiger,* or small lobe at the base of the palps as seen in many polyneopterans, but which in *Mastotermes* is a tiny sclerite just posterior to the base of the palps. The apical pair of fleshy lobes, the *paraglossae* and between them the *glossae* (collectively: the *ligula*) are homologous to the maxillary galeae and laciniae (figs. 21E, F; 23). In the labium the *prementum* is a fused homolog of the maxillary stipes. The *postmentum* is the basal plate of the labium that is attached to the ventral surface of the head and is homologous to the fused cardines of the maxillae; it is elongate in many soldiers. The prementum and attached appendages are the free, movable parts of the labium. There is little variation among taxa in the labial anatomy of termites. The maxillary and labial palps, the ligula, and galeae serve a primarily gustatory function; the mandibles and laciniae are masticatory.

The *hypopharynx* is a soft, fleshy lobe under the labrum, lying between the cibarium (preoral cavity) and the labium. The salivary duct opens at the base of the hypopharynx on the ventral surface. The surface of the hypopharynx is covered with sensilla and internally it is muscular, so the structure probably functions like a tongue in tasting and manipulating food

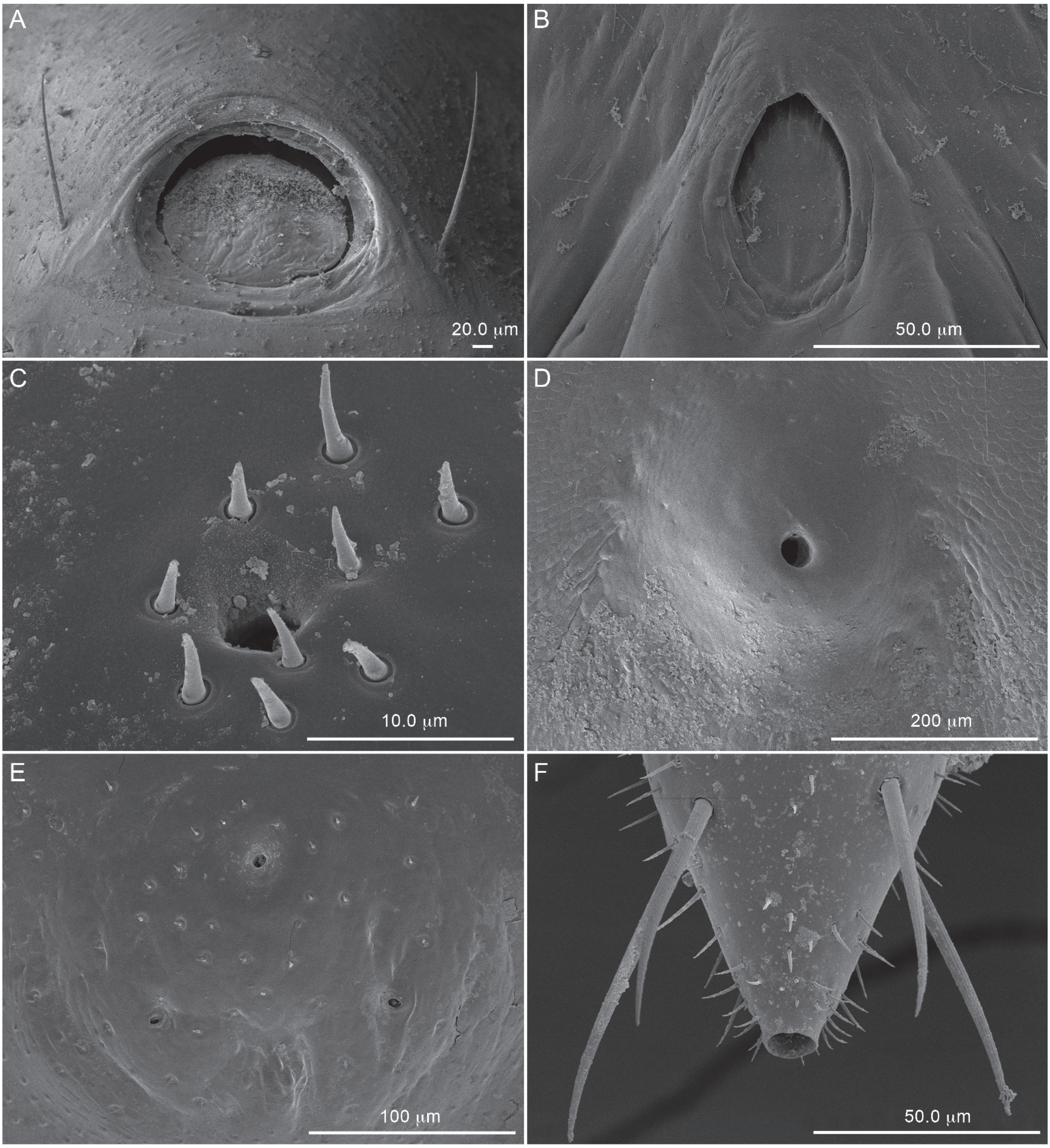


FIGURE 22. The fontanelle, or frontal pore, in exemplar species and castes. Presence of the fontanelle is a defining feature of the Neoisoptera, which includes the living families Rhinotermitidae, Serritermitidae, Stylotermitidae, and Termitidae. The fontanelle is the external opening to the frontal gland, and its structure can vary among species and even among castes of the same species. **A.** *Coptotermes vastator* Light, soldier. **B.** *Dolichorhinotermes longilabus* (Emerson) alate. **C.** *Heterotermes platycephalus* Froggatt. **D.** *Macrotermes natalensis* (Haviland) soldier. **E.** *Foraminitermes coatoni* Krishna, soldier. **F.** *Nasutitermes* sp., soldier. Scanning electron micrographs courtesy of Philip Barden.

in the preoral cavity. The *salivary glands* are paired structures consisting of secretory lobes (acini) that empty into a salivary duct; their histology has been described in detail by Noirot (1969a). These glands are presumably highly developed in those termites that use salivary secretions in building the nest, but they have also been coopted for defense in some termites. The soldiers of some Amitermitinae and Macrotermitinae have salivary reservoirs that occupy most of the abdomen, and instead of dousing attackers with frontal gland secretions, they use salivary secretions that become viscid and sticky when emitted. Chemistry of the diverse salivary secretions has not been studied in detail.

Finally, the *occipital foramen* is an opening at the posterior end of the head that is connected via membranes and muscles to the anterior end of the thorax, and through which pass the ventral nerve cord, esophagus, some tracheae, and sometimes the frontal and salivary glands. Shape of the occipital foramen varies slightly, with *Mastotermes* having a rounded foramen, and all other termites having ones that are trapezoidal to triangular in shape.

Thorax

This region is the muscular, locomotory tagma of all hexapods, since it bears the legs and the muscles that power them, as well as the wings and flight muscles in the pterygotes. There has been little comparative study of the thoracic sclerites in termites, even though there is significant reduction in the higher termites. Sclerotization of the termite thorax overall is substantially reduced compared to other dictyopterans, with extensive membranous areas occurring among the ventral sclerites (fig. 23).

The thorax is connected to the head via the *neck* or *cervix,* which is largely membranous but braced by *cervical sclerites.* These sclerites were studied in detail by Weiland (2006) for Dictyoptera, including some termites. Almost all living termites have lost the *median cervical sclerite,* which lies isolated in the cervical membrane in other Dictyoptera and often occurs as two narrow, transverse strips. The median cervical sclerite is lost in many basal mantises as well, but oddly a vestige of it occurs in *Stolotermes,* and it is well developed in some extinct termites such as *Mylacrotermes* in Burmese amber. There is a pair of large, somewhat parallel *lateral cervical sclerites,* which articulate posteriorly with the *intercervical sclerites* (ICSs). The ICSs lie transversely in a line but are separated medially by a large gap (in many mantises the ICSs meet medially or are even fused). Longitudinal grooves in the lateral and intercervical sclerites are poorly defined in termites and roaches, but well developed in mantises. Just posterior to the ICS is a thin, straplike, transverse sclerite with a short lateral arm, which Wieland (2006) defines as the "detached posterior part of the intercervical sclerite," but which Grassé (1949) defined as the *proepisternum,* a designation that we are following here.

Ventrally on the prothorax, the proepisternum articulates with the protrochantin, or *trochantin*1, a similarly small strip of sclerite, which lies just anterior to the forecoxa. Lateral to the basal arm of the proepisternum is a small, lightly sclerotized *episternum,* which is separated from the pronotum in *Mastotermes* but attached to it in *Anacanthotermes.* Trochantins2, 3 are much larger than pair 1, and are roughly shaped into a long triangle that articulates with

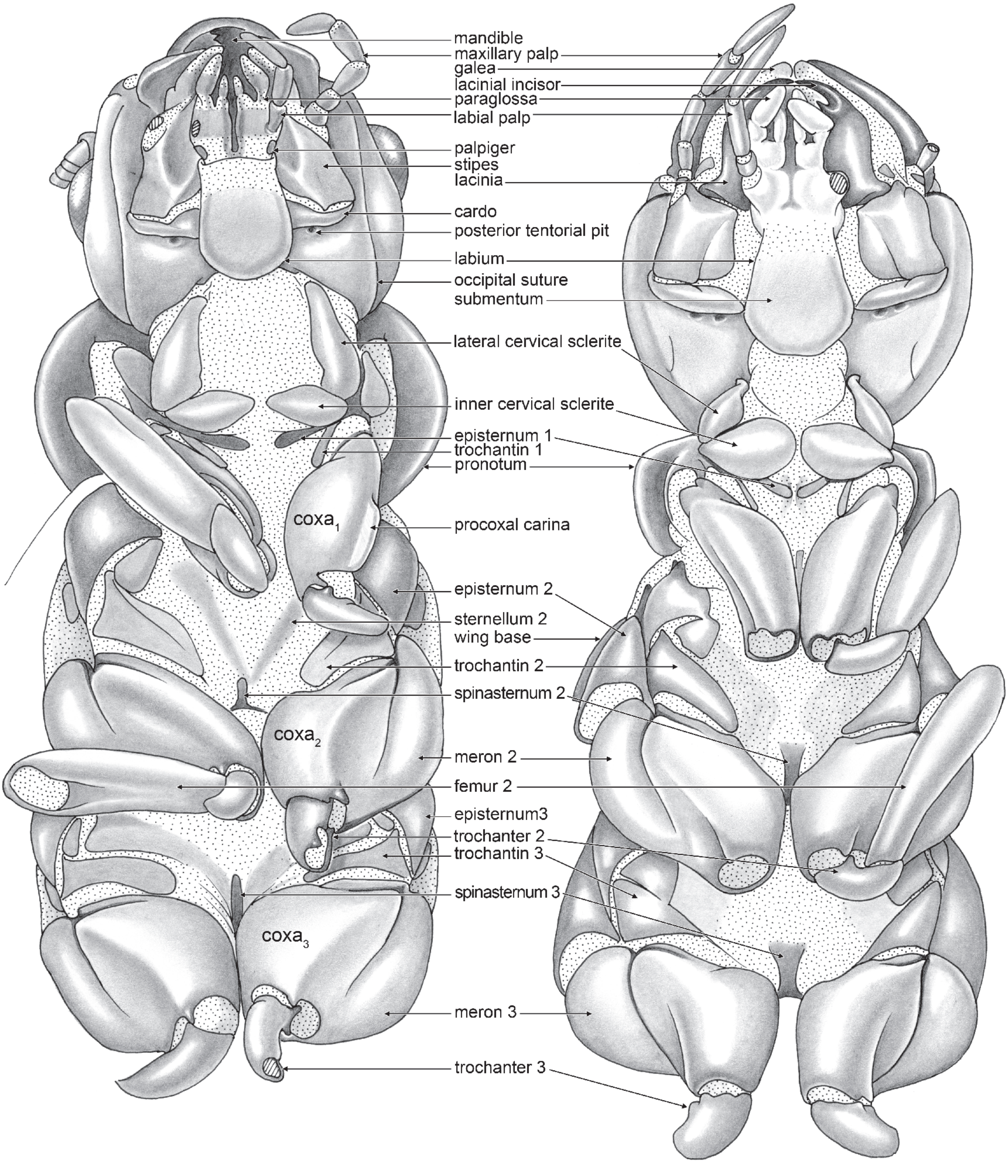


FIGURE 23. Ventral surfaces of the head and thorax of alates of two representative basal termites, *Mastotermes darwiniensis* Froggatt (left) and *Anacanthotermes viarum* (König) (right). Coxae and pleural sclerites are more reduced in more derived families of termites.

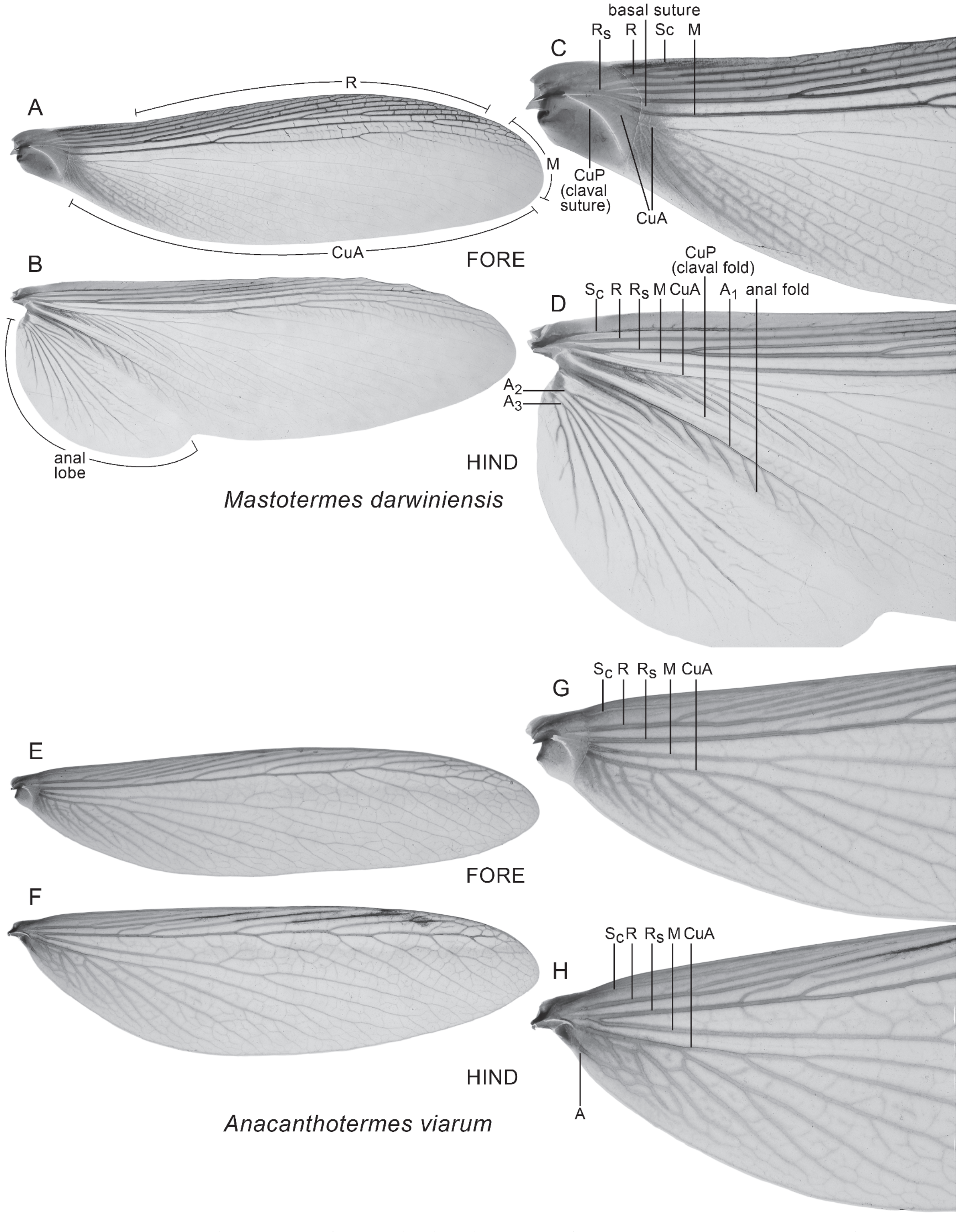


FIGURE 24. Wings and venation of exemplar basal species of termites. **A–D.** *Mastotermes darwiniensis* Froggatt (Mastotermitidae). **E–H.** *Anacanthotermes viarum* (König) (Hodotermitidae). Venation follows the Comstock-Needham system. A, B, G, H: details of fore- and hind wings, showing bases of major veins and structure of basal scale.

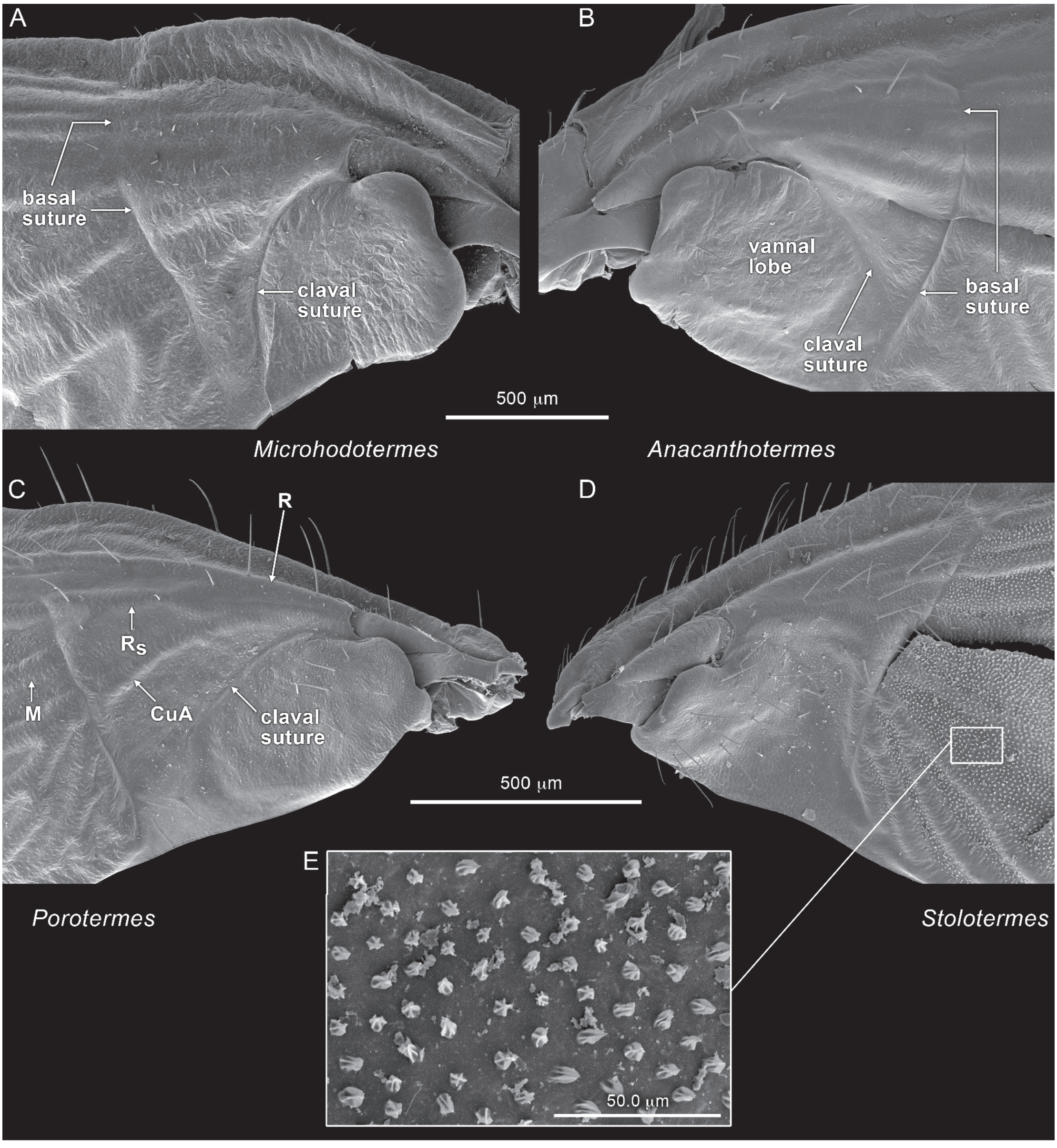


FIGURE 25. Detailed structure of forewing bases of representative basal genera of termites (scanning electron micrographs). **A.** *Microhodotermes viator* (Latreille) (Hodotermitidae). **B.** *Anacanthotermes viarum* (König) (Hodotermitidae). **C.** *Porotermes adamsoni* (Froggatt) (Stolotermitidae). **D.** *Stolotermes brunneicornis* (Hagen) (Stolotermitidae), with detailed structure of stellate nodules on wing membrane (inset).

the anterior margins of the mid- and hind coxae, respectively. The trochantins are larger in alates of basal termites. Anterior to the pair of trochantins lies a pair of small, free sclerites, the *laterosternites.* Dorsolateral to the laterosternites are the *epimeron* and (anteriorly) the *episternum,* both of which are much larger in the pterothoracic segments. The *sternites* are very lightly sclerotized, barely distinguishable from the surrounding membrane. Sternites are generally V-shaped, with both arms converging on a median, deep, sclerotized pit, the *spina* (or *spinasterna*). The spina lies near the posterior margin of each thoracic segment and is an invagination of the furca, which is an internal, sclerotized fork to which muscles attach.

Dorsally, the thoracic tergites are dominated by the *pronotum, mesonotum,* and *metanotum,* with the first of these the only thoracic tergum that is visible when the wings are closed. The pronotum in roaches is usually a large shield that covers the head; in many mantises it is a long, necklike sclerite. In termites the pronotum is reduced in size, but quite variable, and so size and shape are taxonomically extremely important for the group. The termite pronotum is largest in the most basal termites, such as the Mastotermitidae (living and extinct) and *Cratomastotermes,* and it is significantly narrower than the head in more derived lineages (cf. figs. 11, 31, 32, 62, 65 vs. figs. 49, 52, 56). The shapes of the anterior, lateral, and posterior margins are taxonomically significant, especially at the species level. Among the three castes soldiers have the smallest pronotum relative to body size, particularly in Termitidae. The soldiers of some Termitidae have a pronotum with spines and the lateral margins produced into narrow points (in which case, so are the lateral margins of the meso- and metanota, e.g., *Acanthotermes*). In nasutes the pronotum is very small and saddle shaped. The meso- and metanota are slightly larger than the pronotum (typical of pterygotes), but with their lateral edges emarginate in order to accomodate the axillary sclerites and musculature at the base of the wings.

The legs of termites are relatively simple and generalized, but possess phylogenetically significant variation in tarsomere number and size, presence/absence of the arolium, and number, position, and fine structure of spines and spurs on the tibiae (figs. 26, 27, 37). Compared to roaches and especially mantises, the legs of termites are relatively short, though the legs of some termitid soldiers (e.g., *Acanthotermes, Longipeditermes*) are long and slender. In termites the *coxae* articulate ventrally on the thorax, with the trochanter articulation on the posteromedial margin, as in roaches. The forecoxa, or coxa1, is the smallest of the three coxal pairs since it does not have the laterally expansive *meron* found in coxa2 and coxa3. The meron in these two coxal pairs is demarcated by an incomplete sulcus running anteroventrally along the coxa. In basal taxa—notably Mastotermitidae and some extinct genera like *Carinatermes*—coxa1 retains a distinctive ventral, keel-like carina in all castes that runs longitudinally (fig. 23). This carina is barely developed in other basal taxa and completely absent in higher termites. There is little differentiation of the *trochanters* among legs or taxa; the *femur* is always the stoutest podomere.

On the *tibia,* the most significant variation concerns the number and fine structure of spines and spurs, which are actually just thick, heavily sclerotized, socketed setae (figs. 26, 27). Those that occur along the shaft of the tibia are called *spines,* and those at the apex of the tibia are *spurs.* The number of tibial spurs is typically denoted by the following notation, e.g., 3:4:4 for the fore-, mid-, and hind tibiae, respectively, as is found in many basal termite genera.

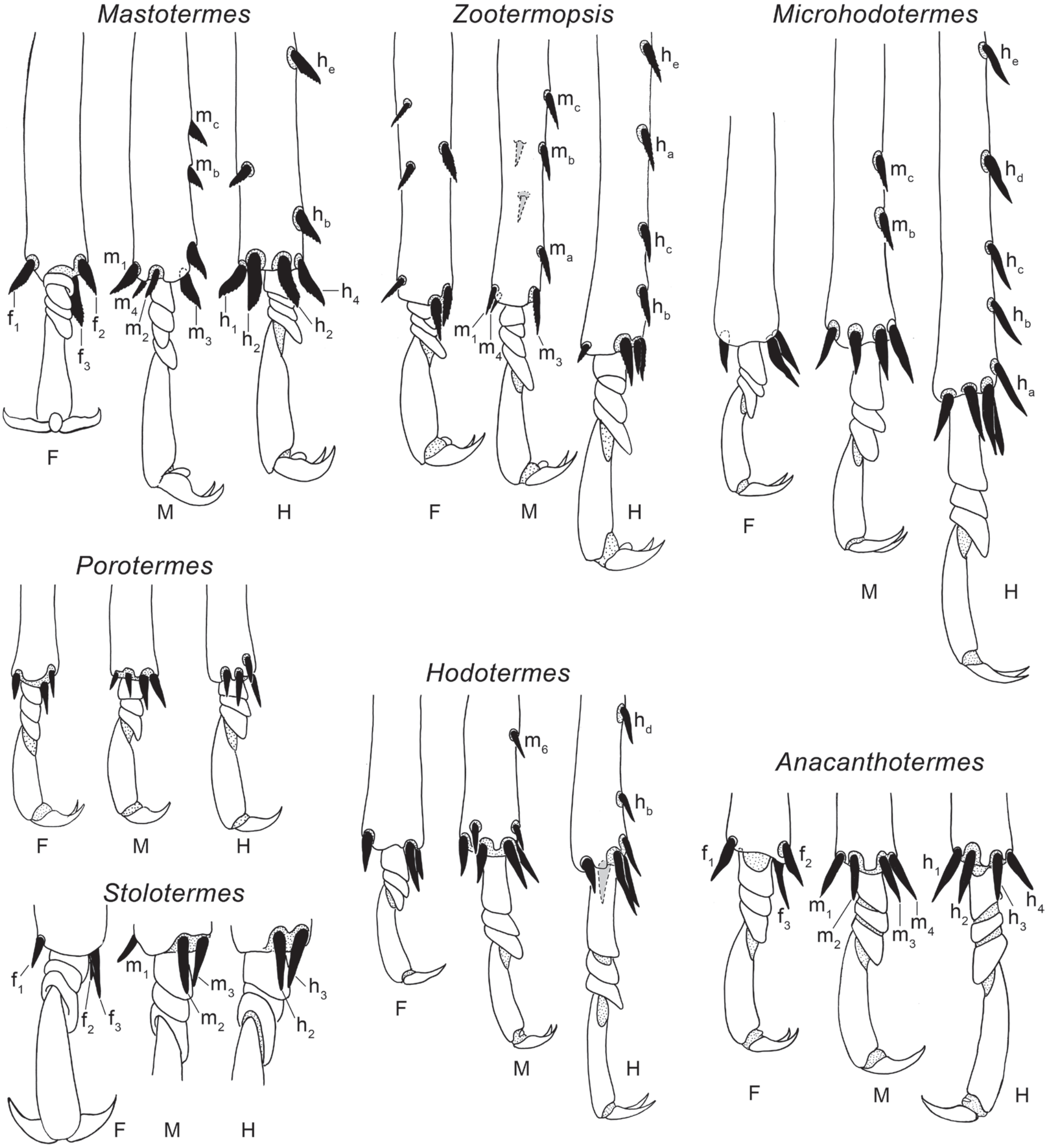


FIGURE 26. Tibial spurs (labelled with numbers) and spines (labelled with letters) of the fore (F), mid- (M), and hind (H) legs of alates of representative basal genera of termites. The system is for identifying homologous spurs and spines.

Kalotermitidae, Rhinotermitidae, and Termitidae typically have 2–3 tibial spurs on the mid- and hind legs. Ideally, tibial spur number should be better defined on the basis of individual, homologous spurs. Tibial *spines* occur preapically and along the shaft of the tibia. As for the spurs, there is significant variation in the number and arrangement of the spines. To homologize individual spurs and spines in termites, illustrations of the genera and complementary terminology are presented in figure 26. Spurs and spines on the fore-, mid-, and hind leg are denoted by an F, M, and H, respectively. Individual spurs are denoted by numbers (F1, M1, H1, F2, etc.); individual spines are denoted by letters (Fa, Ma, Ha, Ma, etc.) Basal genera like *Mastotermes, Microhodotermes,* and *Zootermopsis* have a row of 3–5 spines on the hind tibia (fewer on the midtibia, and often none on the foretibia). Most Kalotermitidae and all higher termites lack tibial spines. Interesting details of the spines and spurs of termites that have traditionally been neglected taxonomically concern their fine structure. In basal termites the spines and spurs are typically asymmetrical and slightly bent in the middle, as seen in *Cryptocercus* and many roaches. The distal surfaces of such spines and spurs are usually flattened, even slightly concave, making them trowel shaped (fig. 27B, D, E, G). In certain basal genera (e.g., *Mastotermes, Zootermopsis,* many extinct genera), these spines and spurs are heavily scaled, which makes the margins of the trowel-shaped portion serrated (fig. 27B, E). The tibial spines and spurs of all other termites are smooth, and in higher termites, they are symmetrical.

The *tarsomeres* of termites are primitively and fully 5-segmented, the groundplan condition of pterygotes. This feature is found in *Mastotermes darwiniensis* and various extinct genera (figs. 11, 27D). In the extant genera *Zootermopsis* and *Archotermopsis,* tarsomere 2 is reduced in size, such that it is visible only laterally and ventrally, but not dorsally (fig. 27A). This reduction is what leads to the conclusion that it is the loss of tarsomere 2 that results in the 4-tarsomere condition, which all other termites possess save for *Stylotermes, Parastylotermes, Indotermes,* and *Speculitermes* (which have 3 tarsomeres). The *basitarsomere* (tarsomere 1) is generally slightly longer than tarsomeres 3 and 4, but in *Hodotermes* and *Microhodotermes* the hind basitarsomere is several times the length of the other tarsomeres. The tarsomeres of *Garmitermes* in Baltic amber are very interesting: they retain *plantular pads* on the ventral surface, as seen in roaches (fig. 65B). The *pretarsus* always possesses a pair of sclerotized, simple claws, which have little or no obvious variation among taxa. In contrast, the arolium is present in various basal taxa, like *Mastotermes, Zootermopsis, Archotermopsis,* many Kalotermitidae, and various extinct genera (*Garmitermes, Melqartitermes, Proelectrotermes, Tanytermes, Termopsis*) (fig. 27C, F); it is absent in all other termites (fig. 27H). The *arolium* is a small, membranous, saclike structure lying between the claws, which presumably assists in adhesion while walking.

Wings in termites are unique, making the identification of even isolated fossilized wings immediately recognizable as isopteran. Both roaches and termites are adapted to live in tight spaces among leaf litter, under bark, or in galleries, a life style that requires either protection or loss of the wings. Roaches have adapted to this lifestyle by being flattened and having forewings that are *tegminous* (leathery and sclerotized) with the flight (hind) wings folded and protected beneath the forewings, whereas termite alates have *dehiscent* wings. Alates generally shed their wings when they have descended to the ground after nuptial flights, becoming *dealates.*

Indeed, the most specialized feature of termite wings is their dehiscence, made possible by the *basal scale,* which is a small, sclerotized lobe at the base of the wing that remains attached to the axillary region of the pterothorax after most of the wing dehisces (figs. 24, 25). The wing dehisces along the *basal suture,* which is a transverse, membranous line at the distal margin of

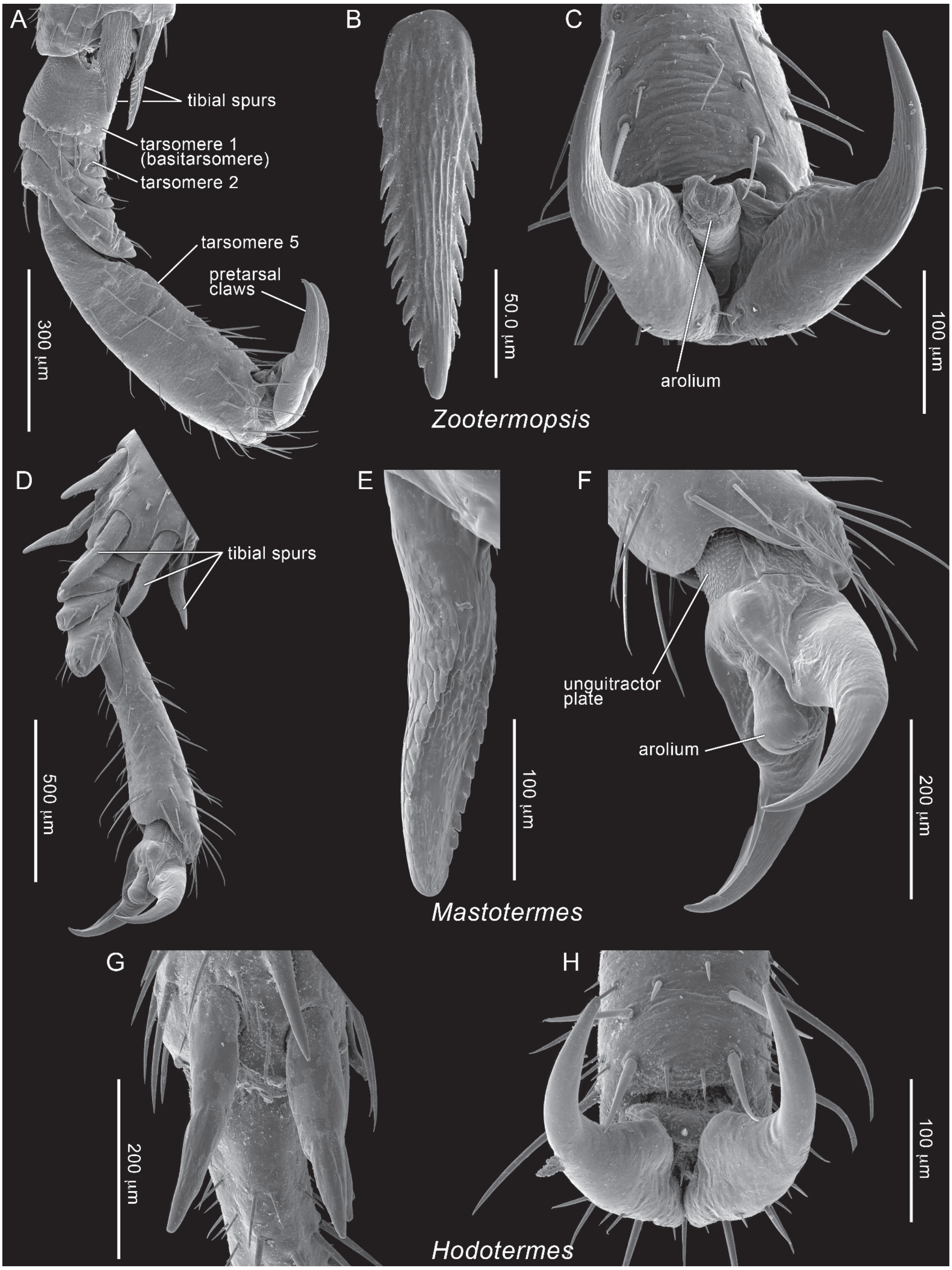


FIGURE 27. Details of the tarsal and tibial structures of representative basal termites (scanning electron micrographs). **A–C.** *Zootermopsis angusticollis* (Hagen). **A.** Foretarsus, mesal view, showing small second tarsomere. **B.** Detail of tibial spine, showing highly developed serrations. **C.** Pretarsus, with well-developed arolium. **D–F.** *Mastotermes darwiniensis* Froggatt, **D.** Foretarsus, lateral view. **E.** Detail of tibial spur, showing flattened surface and two rows of serrated edges. **F.** Pretarsus. **G, H.** *Hodotermes mossambicus* (Hagen). **G.** Tibial spurs. **H.** Pretarsus, showing loss of the arolium.

the scale. The basal suture is well developed in the forewings of all species, but is poorly developed in the hind wings of lower termites like the Hodotermitidae s.s., Archotermopsidae, and Stolotermitidae, but particularly in the Mastotermitidae (fig. 24B). In all species, the forewing basal scale is larger than the hind wing scale. The basal suture is generally slightly convex in shape in lower termites, but is straight and oblique in Stolotermitidae, or straight and transverse in Rhinotermitidae and Termitidae. Within the basal scale are the bases of veins R, M, and Cu. In Mastotermitidae (figs. 24, 25), the first branches of the forewing Rs are within the scale, but the branches are outside the scale in most other termites. Most Kalotermitidae have a distinctive swelling on the humeral margin of the basal scale in the forewing. *Vein CuP* in the termite basal scale is very distinctive as a desclerotized fracture that runs from the base of R-M to the posterior margin of the scale. It is convex in the forewings of lower termites but typically straight or even concave in shape in the Rhinotermitidae and Termitidae. Also in lower termites, CuP terminates in the basal suture, whereas in Rhinotermitidae and Termitidae it terminates at the scale margin proximal to the basal suture. Vein CuP in the hind wing of lower termites is a small, convex fracture bordering the base of vein A. Recent and fossil Mastotermitidae possess a small, distinctive *radial fracture* in the forewing basal scale. Vestiges of vein reticulation are retained between CuP and the margin of the scale in Mastotermitidae and some extinct termites.

Except for Mastotermitidae, there is little difference in shape between the fore- and hind wings in termites, which is typical of those pterygotes with a fluttering type of flight, like lacewings (Neuroptera: Chrysopidae) and male webspinners (Embiodea). Mastotermitidae retain a large anal lobe or fan at the base of the hind wing, typical of polyneopterous insects (fig. 24B). Termites have no wing coupling mechanism that joins the fore- and hind wings as is found in many other groups of insects.

There is a consistent trend in the structure of termite wings from basal taxa to the most recently derived ones, by which the forewings lose tegminization, and both pairs of wings lose reticulations along with some of their longitudinal veins and branches. Reticulations are short, anastomosing veins between the straight longitudinal veins, which are vestiges of the archedictyon of lower pterygotes. Reticulations are lightly sclerotized, and the ends of the short, interconnecting branches rarely connect to the longitudinal veins (except in the most basal termite, the Cretaceous *Cratomastotermes*) (e.g., fig. 24). Reticulations are well developed in the fore- and hind wings of Mastotermitidae, Hodotermitidae s.s., the extinct family Termopsidae s.s., Archotermoposidae, Stolotermitidae, Stylotermitidae, Serritermitidae, and some Rhinotermitidae.

Forwing veins we use here the classic Comstock-Needham system of vein nomenclature (Grimaldi and Engel, 2005; Emerson, 1965; figs. 24, 40–43, 53–56). Dietz et al. (2003: 74) gave a detailed comparison of several vein nomenclatural systems, employing a system most similar to that of Kukalová-Peck (1991). Again with the exception of Mastotermitidae, there is little difference between fore- and hind wings in venation. There is typically a slightly larger field of Cu veins in the hind wing of lower termites, which is larger in the forewings of Rhinotermitidae and Termitidae. In some genera (e.g., *Psammotermes, Prorhinotermes*), vein M is lost in the forewing but is present (albeit sometimes as a vestige) in the hind wing. Vein Sc is generally simple (unbranched), though it has very short anterior branches in some lower termites. Veins

R and Rs have multiple anterior branches at the base of the wing in Mastotermitidae, but these branches are more distal in other lower termites and lost entirely in *Serritermes,* Rhinotermitidae, and Termitidae. In these last two families vein Sc+R runs along the anterior edge of the wing and lying very close and parallel to it is vein Rs. These two veins are the only thick, sclerotized veins in Rhinotermitidae and Termitidae. In Hodotermitidae s.s. there are a parallel series of oblique ventral branches of Rs. Branching off the base of Rs (within or outside the scale) is vein M, which generally runs longitudinally along the midline of the wing; it can have 2–6 branches, and is often simple in higher termites (even lost in some genera, above). Vein Cu is usually pectinate, with a series of parallel ventral branches, at least at the base of the wing. In the higher termites the Cu field of veins can occupy the entire posterior half of the wing. The anal veins of termites are typically absent or highly vestigial, the most exceptional situation being Mastotermitidae, which has retained a large anal lobe in the hind wing. Posterior to vein CuP in *Mastotermes* (which is a straight, unbranched, foldlike vein) is a pectinate vein A1 (with many short, ventral, parallel branches), then the anal fold (along which the anal lobe folds beneath the rest of the wing), and then posterior to the fold are multiply branched veins A2 and A3. Vein A is essentially lost in the forewing of all termites, but small vestiges of it remain in the hind wing of lower termites as a small basal sclerite with a tapered tail.

Abdomen

The termite abdomen, like that of most adult insects, consists of 10 segments (the vestigial 11th segment has been retained in only a few insects). The abdomen contains not only the reproductive system, but the excretory and most of the digestive system as well. Dorsally the abdomen is covered by a series of sclerites, the *tergites*; ventrally by *sternites,* of which sternite I (sI) is greatly reduced or absent in termites. All the sternites are reduced in size in many Termitidae. Termites have genitalia that are extremely vestigial to entirely lost, but sexes can be distinguished by sVII. In females, sVII is enlarged (the subgenital plate) and covers sVIII and sIX, these latter two sternites of which are divided in some Termitidae. Sternite VII in males is not enlarged, nor are the more posterior sternites reduced or divided.

Invaginated within the intersegmental membrane between certain sternites is the *sternal gland,* which lies along the midline. This gland occurs in all castes and consists of specialized epidermal cells and also contains several campaniform sensilla. Cellular differentiation of the gland is least specialized in some basal genera like *Mastotermes* and *Porotermes,* but other basal genera (e.g., *Zootermopsis, Kalotermes*) and all higher termites that have been examined have specialized lipid vacuoles and intercalary cells, the latter with long microvilli (Noirot, 1969a; Noirot and Noirot-Timothée, 1965c; Quennedey, 1978). The sternal gland produces secretions that are important in laying the trails used in foraging and recruitment. In all termites except *Mastotermes darwiniensis* there is just one sternal gland; this gland occurs on segment IV in Hodotermitidae s.s. and Archotermopsidae, but on segment V in Kalotermitidae, Rhinotermitidae, and Termitidae. *Mastotermes* has a sternal gland on each of segments III, IV, and V. There are two scenarios, both equally parsimonious, for this distribution of glands: either there were 3–4 independent origins of sternal glands or the ancestral condition was the presence of the glands on segments III, IV, and V, loss of the gland on segment III in all termites except *Mastotermes,* and the subsequent losses of the glands on segment V in Hodotermitidae and Archotermopsidae and on segment IV in Kalotermitidae and higher termites. Biologically, the latter scenario seems to make more sense (Noirot, 1995a).

The digestive system, or gut/digestive "tube" to termitologists, consists of the typical three divisions found in insects: *foregut, midgut,* and *hind gut* (fig. 29A–C, E). The foregut consists of the *esophagus,* the *crop,* and the *proventriculus* (or "gizzard"). Food passes down the narrow, tubelike esophagus, which extends from the mouth and through the thorax, opening in a dilated, nearly symmetrical crop that lies at the anterior end of the abdomen. The crop is visible in dorsal view and extends into a muscular, grinding proventriculus, where the food is masticated. The epithelium of the proventriculus has a cuticular armature consisting of 48 folds in two groups—anteriorly the columns have a sclerotized cuticle and a median tooth and posteriorly they have *pulvilli* with a soft, unsclerotized cuticle. In some Termitidae the musculature and cuticular armature of the proventriculus are greatly reduced; in other groups of Termitidae and in other families of termites the number and arrangement of proventricular spines are taxonomically significant. The narrow end of the proventriculus (the *stomodeal valve*) invaginates into the midgut, or the *mesenteron.* The midgut is a tube of uniform diameter, seen in dorsal view as a loop from left to right, joining the hind gut as a simple, straight junction. In lower termites the midgut has fingerlike projections, or *caecae,* near the midgut–hind gut junction, that are absent in higher termites. In higher termites, the mesenteron extends over the first proctodeal segment of the hind gut, forming a mixed segment that varies in its structure. The *Malpighian tubules* vary from two to 16 and are attached in varying ways to the straight junction or near the mixed segment. These tubules are long, narrow, uniform in diameter (though swollen at the base in higher termites), and anastomose around the midgut, in some higher termites forming a tangled cluster over the midgut (the *Malpighian knot*), in rare cases (e.g., in Foraminitermitinae) wrapped around the first proctodeal segment and known as the *pseudo-Malpighian knot.* The hind gut, or *proctodeum,* is divided into five segments: *first proctodeal segment* (P1), *enteric valve* (P2), *paunch* (P3), *colon* (P4), and *rectum* (P5). P1 is tubular, of varying lengths (though always short in lower termites), its epithelium forming six longitudinal thickenings or cushions; P2, generally funnel shaped, invaginates into P3, whose development of internal cuticular armature provides important taxonomic features, particularly since the enteric valve can be intricate and elaborate (Sands, 1972; figs. 29D, F; 30). P3 is dilated, voluminous, and harbors the well-known symbiotic protists in lower termites, or the symbiotic bacteria in the Termitidae; P3 tapers posteriorly into P4, and at the P3–P4 junction a small diverticulum is present in some genera. P4 is narrower than P3 and passes through the mesenteric loop to the right and downward, terminating in P5, the junction of which is controlled by a muscular sheath, the *rectal valve.* Variation in gut structure is phylogenetically very significant (e.g., Bitsch and Noirot, 2002). For details and comparisons of families and subfamilies, see Noirot and Noirot-Timothée (1969), Noirot (1995b, 2001), and the descriptions of families and subfamilies in the present volume.

Externally, the terminal two segments of the termite abdomen in many species bear two pairs of small appendages, the cerci and styli (fig. 28). *Styli* are unsegmented appendages on

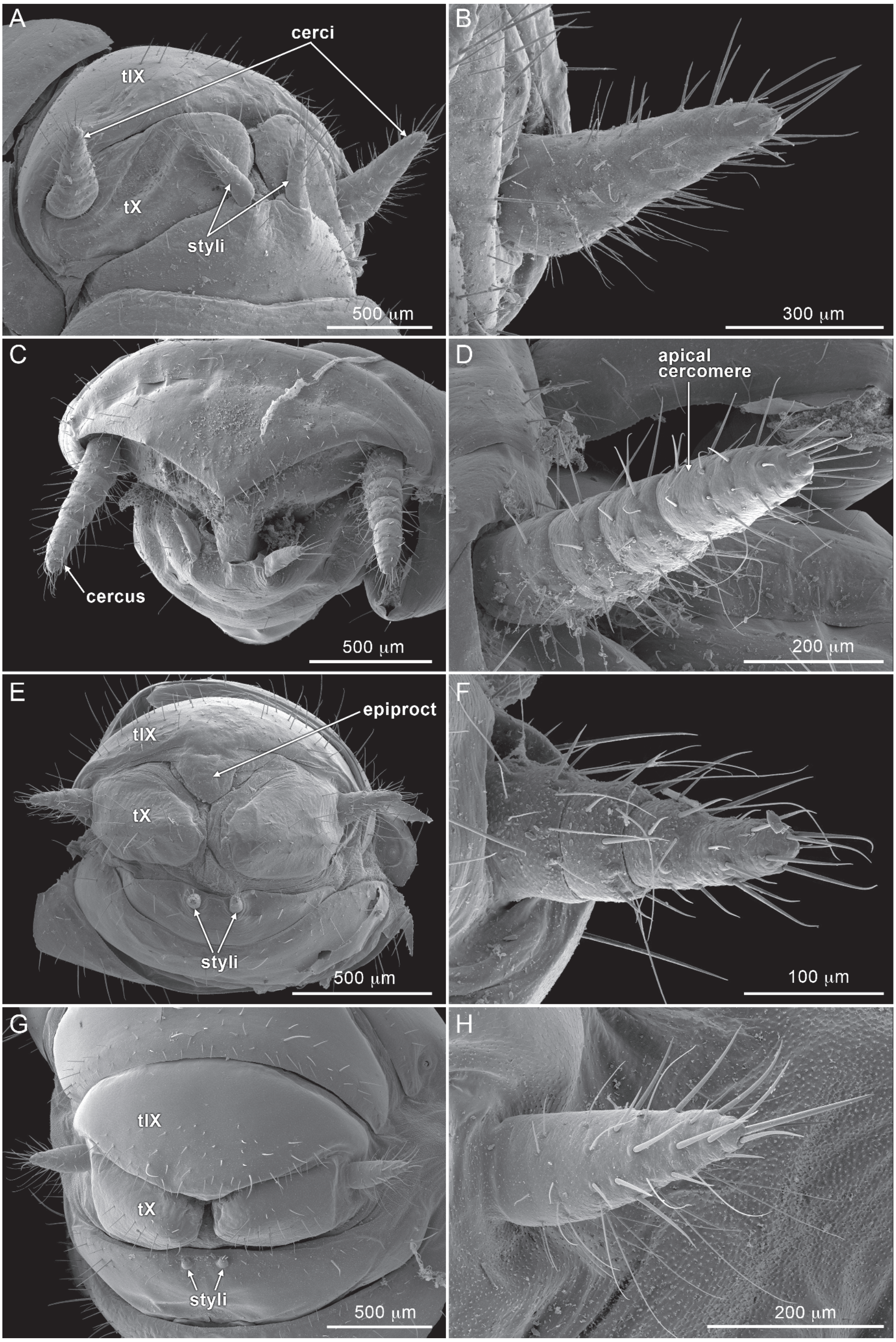


FIGURE 28. Alate terminalia of representative species of basal termites (scanning electron micrographs, not to the same scale), showing positions of cerci and styli and reduction in segmentation of cercus (B, H). **A, B.** *Mastotermes darwiniensis* Froggatt. **C, D.** *Zootermopsis angusticollis* (Hagen). **E, F.** *Porotermes adamsoni* (Froggatt). **G, H.** *Anacanthotermes viarum* (König).

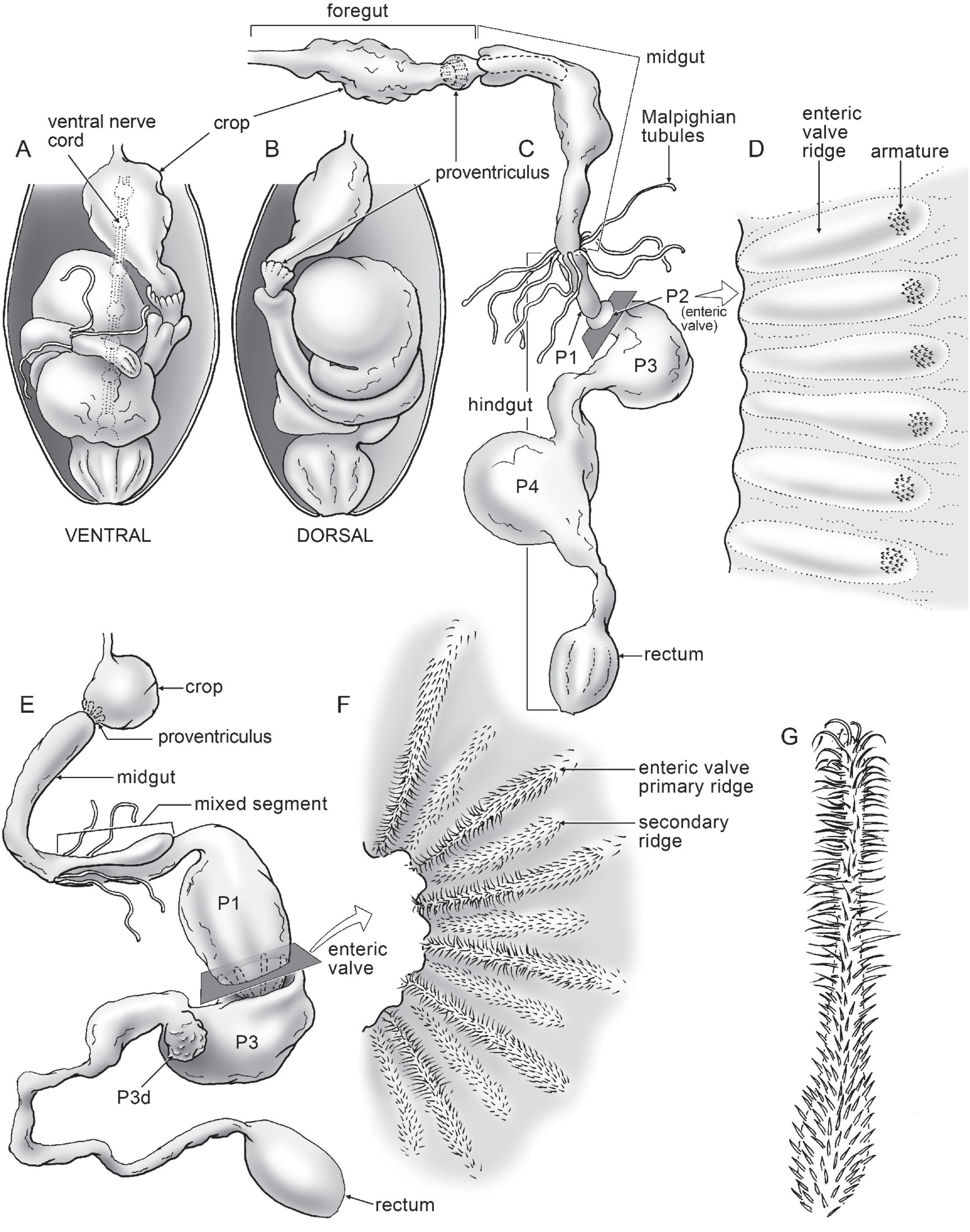


FIGURE 29. Worker digestive system structure of two exemplar species of termites, including position and detailed structure of the enteric valves (D, F, G). **A–D.** *Hodotermes* sp. (Hodotermitidae). **E–G.** *Euchilotermes umbraticolla* (Williams) (Termitidae). **G.** Detail of enteric valve ridge with armature. Not to the same scale. Redrawn from Sands (1998).

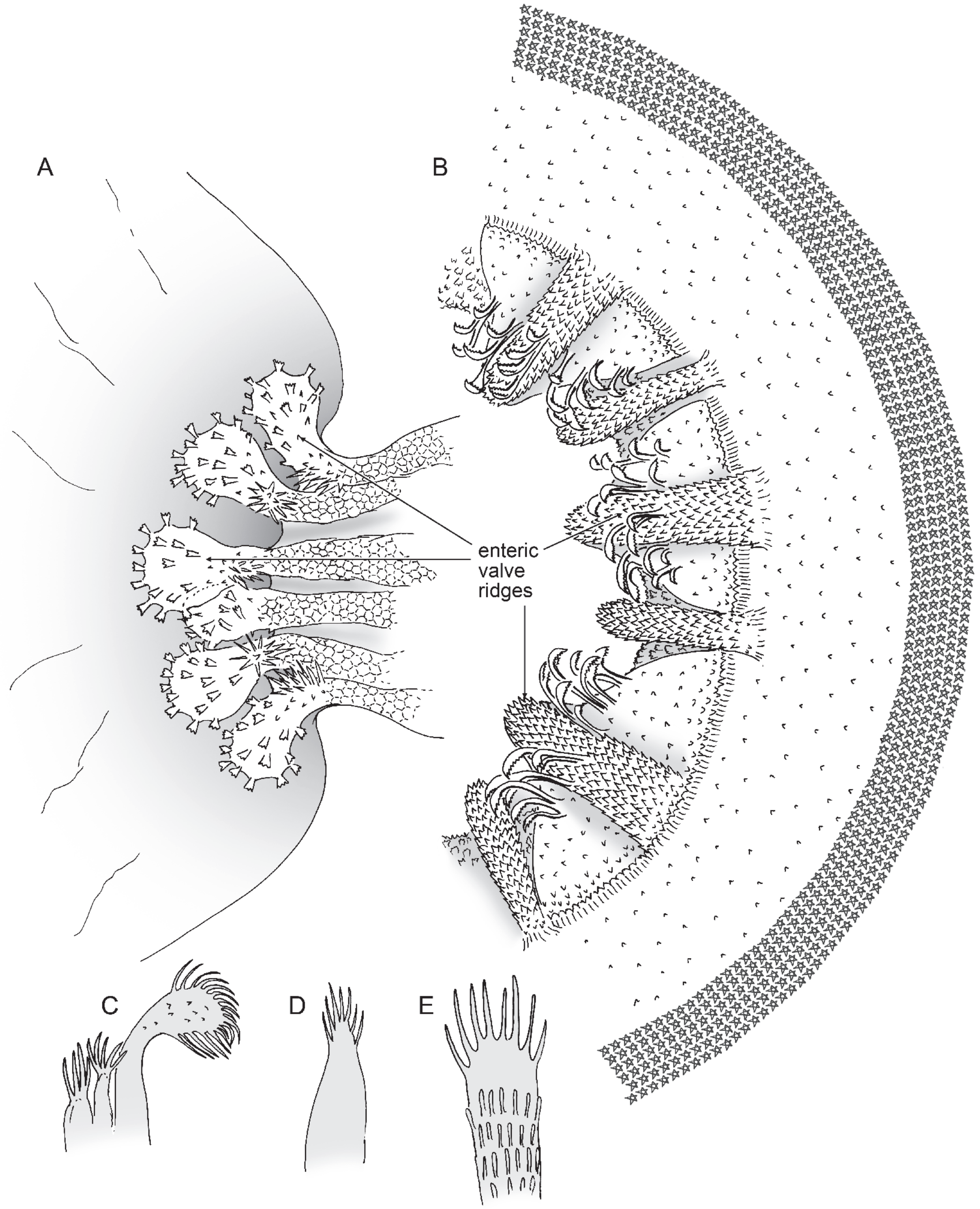


FIGURE 30. Complex enteric valves and armature in the workers of exemplar species of Termitidae (not to the same scale). **A, B.** Whole enteric valves shown split open longitudinally and spread out. **A.** *Phoxotermes* sp. **B.** *Heimitermes* sp. **C–E.** Details of enteric valve armature. **C.** *Ateuchitermes pectinatus* Sands. **D.** *Amicotermes* sp. **E.** *Apagotermes stolidus* Sands.

the posterior margin of sIX in immature females and mature male imagoes. They are conspicuous in lower termites and small to absent in the more derived lineages. Styli occur on sIX in the males of some paleopterous insects (Ephemeroptera) and polyneopterans (Mantodea, Blattodea, Grylloblattodea, and some Orthoptera), which are considered homologous with the series of abdominal styli seen in apterygote hexapods. Thus, retention of styli in some termites is unquestionably a primitive condition. Though they have a locomotory function in apterygotes, the terminal styli of pterygote insects (including termites) probably have little or no function. The other pair of small abdominal appendages are the *cerci,* whose bases articulate with the laterobasal corners of sX (the paraproct) in male and female termites; sX is typically divided in termites. Systematically significant variation occurs in the segmentation of the cerci (fig. 28B, D, F, H), with the more basal termites like Mastotermitidae and Hodotermitidae possessing 5–8 cercomeres; Kalotermitidae, Rhinotermitidae, and Termitidae possess two cercomeres. Cerci are found throughout hexapods and are often lost; they are presumably homologous to the uropods of malacostracan crustaceans according to Snodgrass (1935), and not to abdominal styli. Detailed study of the cercus in Blattodea has revealed it to have exceptional sensitivity and to play a primary role in escape responses; no doubt this sensory role has been retained in the termite cercus, albeit reduced.

The genitalia of termites are extremely reduced, particularly when compared to the other dictyopterans. Female *Mastotermes darwiniensis* have retained unsclerotized vestiges of the *ovipositor valvulae,* on the dorsal wall of an internal pouch (Crampton, 1920; McKittrick, 1964; Klass, 1998). All other termites have lost these valvulae. Interestingly, *Mastotermes* has also retained a vestigial *ootheca,* or egg pod, homologous with that of the roaches but much smaller and with a very thin, barely sclerotized shell. The male genitalia of the related dictyopterans, mantises and roaches, are highly complex, with various large, sclerotized, asymmetrical lobes (*phallomeres*); those of termites, however, are extremely reduced and mostly to entirely unsclerotized (McKittrick, 1964; Roonwal, 1970a; Klass, 1997, 2000). Even in the most basal termite, *Mastotermes darwiniensis,* the male genitalia are reduced to a minute, symmetrical, papillalike phallomere that has a pair of barely developed ventral sclerites (Klass, 2000). The basal species *Stolotermes inopinus* Gay from New Zealand has male genitalia that are uniquely developed in Isoptera, possessing a larger, symmetrical *phallic lobe* (= genital papilla) that is largely sclerotized (Klass et al., 2000). In both species the gonopore is located on the ventral surface near the apex of the lobe or papilla. According to Klass et al. (2000), genital papillae may exist in a wide array of termites, but the question still remains as to the mechanics of copulation in insects with such vestigial genitalia.

KEY TO THE EXTANT FAMILIES OF ISOPTERA

Based on the Characters of the Imago

1. Hind wing with anal lobe; tarsi distinctly 5-segmented; antenna with 29–32 articles; left mandible with two marginal teeth .... **Mastotermitidae** (*Mastotermes*)
- Hind wing without anal lobe; tarsi imperfectly 5-segmented or 4-segmented; antenna with 11–32 articles; left mandible with two or three marginal teeth........... 2

2. Fontanelle absent 3
- Fontanelle present 6

3. Ocelli present; cerci 2-segmented; antenna with 11–24 articles; left mandible with two marginal teeth; right mandible without subsidiary tooth; tarsi 4-segmented .... **Kalotermitidae** (see key to genera, page 75)
- Ocelli absent; cerci 1–8 segmented; antenna with 13–32 articles; left mandible with three marginal teeth; tarsi 4–5-segmented.. 4

4. Tarsi 4-segmented 5
- Tarsi 5-segmented, sometimes cryptically......................... **Archotermopsidae**
  - a. Nearctic; styli short, not extending beyond abdomen; eyes small to medium sized; forewing suture strongly arched; left mandible with apical tooth long, same size as first marginal tooth, second marginal tooth reduced, its tip projecting half the length of first marginal tooth (fig. 32C); cerci 4–6-segmented; antenna with 24–27 articles ....*Zootermopsis*
  - – Oriental .... b
  - b. Styli long, extending beyond abdomen; eyes large; forewing suture weakly arched; left mandible with apical, first marginal and second marginal tooth equally developed (fig. 31D); cerci 6–8-segmented; antenna with 19–25 articles .... *Archotermopsis*
  - – Styli short, not extending beyond abdomen; eyes small forewing suture moderately arched; apical tooth short, subequal and close to first marginal tooth, second marginal tooth reduced, its tip projecting the full length of first marginal tooth (fig. 32D); cerci 3–7-segmented; antenna with 23–26 articles .... *Hodotermopsis*

5. Cerci 1–5-segmented; antenna with 23–32 articles; right mandible without subsidiary tooth .... **Hodotermitidae**
  - a. Tibia without spines .... *Anacanthotermes*
  - – Tibia with spines .... b
  - b. Sc in forewing with branches to costal margin; styli at tip of abdomen atrophied or lacking; antenna with 26–32 articles ....*Hodotermes*
  - – Sc in forewing without branches to costal margin; styli at tip of abdomen well developed; antenna with 25–29 articles.................... *Microhodotermes*

– Cerci 4–5-segmented; antenna with 13–19 articles; right mandible with subsidiary tooth . . . . **Stolotermitidae**

  a. Cerci 4–5-segmented; antenna with 13–18 articles; left mandible with second marginal tooth reduced; tibial spurs 3:3:2 or 2:2:2; femur swollen . . . . Stolotermitinae (*Stolotermes*)
  – Cerci 5-segmented; antenna with 15–19 articles; left mandible with second marginal tooth well developed; tibial spurs 3:3:3 or 3:3:4; femur not swollen . . . . Porotermitinae (*Porotermes*)

6. Forewing scale distinctly overlapping hind wing scale; wings reticulate; pronotum flat. 7
– Forewing scale not overlapping hind wing scale; wings not reticulate; pronotum saddle shaped . . . . **Termitidae** (see key to subfamilies, page 74)

7. Tarsi 4-segmented 8
– Tarsi 3-segmented . . . . **Stylotermitidae** (*Stylotermes*)

8. Each mandible with a long apical tooth, left with 1–2 marginal teeth, right without a subsidiary tooth . . . . **Serritermitidae**

  a. Antenna with 13–14 articles; left mandible with one marginal tooth. . . . *Serritermes*
  – Antenna with 11–13 articles; left mandible with two marginal teeth . . . *Glossotermes*

– Each mandible with a short apical tooth, left with 3 marginal teeth, right with a subsidiary tooth . . . . **Rhinotermitidae**

  a. Forewing scale about same size as hind wing scale, not overlapping hind wing scale . . . . Psammotermitinae (*Psammotermes*)
  – Forewing scale distinctly overlapping hind-wing scale, almost reaching tip of hind-wing scale . . . . b

  b. Postclypeus with noselike projection, narrow groove from fontanelle to tip of labrum. . . . . .Rhinotermitinae

    a¹. Neotropical only . . . . b¹
    – Indomalayan, Australian, Papuan, Ethiopian only . . . . c¹

    b¹. Antenna with third article distinctly shorter than first . . . . *Dolichorhinotermes/Acorhinotermes*
    – Antenna with third article same length or longer than first . . . . . *Rhinotermes*

    c¹. Antenna with 20 articles . . . . d¹
    – Antenna with 16–17 articles . . . . *Parrhinotermes*

    d¹. Larger species; head and pronotum large; postclypeus seen from above not triangularly swollen, medially not longer than sides . . . . *Macrorhinotermes*
    – Smaller species; head and pronotum relatively small; postclypeus seen from above triangularly swollen, medially longer than sides . . . . *Schedorhinotermes*

- Postclypeus without noselike projection, without groove from fontanelle to tip of labrum c

c. Head flat, subtriangular, with posterior margin sinuate; pronotum with anterior margin with median projection . . . . Termitogetoninae (*Termitogeton*)

– Head not flat, roundish or ovalish, with posterior margin even; pronotum with anterior margin without median projection . . . . d

d. Head narrow, with sides parallel . . . . Heterotermitinae

  a¹. Left mandible with second marginal tooth as long as first marginal tooth . . . . *Reticulitermes*

  – Left mandible with second marginal tooth longer than first marginal tooth . . . . *Heterotermes*

– Head wide, with sides rounded . . . . e

e. M present or absent; when present, branching from a common stem with Cu outside wing scale in middle of wing; wing membrane with few setae . . . . Prorhinotermitinae (*Prorhinotermes*)

– M always present, branching from Rs inside wing scale; wing membrane with dense setae . . . . Coptotermitinae (*Coptotermes*)

Based on the Characters of the Soldier

1\. Tarsi 5-segmented 2

– Tarsi 3- or 4-segmented 3

2\. Pronotum large, as wide as head, saddle shaped; cerci 4-segmented; antenna with 20–26 articles. . . . . **Mastotermitidae** (*Mastotermes*)

– Pronotum small, narrower than head, flat; cerci 4–8-segmented; antenna with 19–27 articles. . . . . **Archotermopsidae**

  a. All tibia with lateral spines. . . . . b

  – Only hind tibia with lateral spines; head with posterior margin evenly curved; cerci 4–6-segmented; antenna with 24–25 articles; Oriental . . . . *Hodotermopsis*

  b. Head with posterior margin bilobed; cerci 6–7-segmented; antenna with 22–27 articles; Oriental . . . . *Archotermopsis*

  – Head with posterior margin evenly curved; cerci 4–6-segmented; antenna with 9–27 articles; Nearctic. . . . . *Zootermopsis*

3\. Head without fontanelle 4

– Head with fontanelle 6

4\. Cerci short, 2-segmented; antenna with 10–21 articles . . . . **Kalotermitidae** (see key to genera, page 75)

– Cerci long, 1–8-segmented; antenna with 19–33 articles 5

5. Pronotum flat; head nearly flat; hind femur swollen; cerci 4–5-segmented; antenna with 13–19 articles . . . . **Stolotermitidae**

   a. Mandible short, stout; head somewhat flat; tibial spurs 3:2–4:2–3 . . . . Porotermitinae (*Porotermes*)

   – Mandible longish, not stout; head distinctly flat; tibial spurs 3:3:2 or 2:2:2 . . . . Stolotermitinae (*Stolotermes*)

– Pronotum weakly saddle shaped (anterior lobe slightly raised); head not flat; hind femur not swollen; cerci 1–5-segmented; antenna with 22–33 articles . . . . **Hodotermitidae**

   a. Right mandible with anterior edge of first marginal tooth straight or evenly convex from tip to junction with inner edge of apical tooth (figs. 33B, 34B) . . . . b

   – Right mandible with anterior edge of first marginal tooth distinctly humped at junction with inner edge of apical tooth (fig. 35B) . . . . *Microhodotermes*

   b. Antenna with 23–31 articles; tibial spurs 3:2–5:3–5; Ethiopian only . . . . *Hodotermes*

   – Antenna with 23–33 articles; tibial spurs 3:4:4; Ethiopian (Yemen and Sudan with a single species), Oriental, Palaearctic . . . . *Anacanthotermes*

6. Pronotum flat 7

– Pronotum saddle shaped . . . . **Termitidae** (see key to subfamilies, page 74)

7. Mandible with serrations along entire inner margins . . . . **Serritermitidae**

   a. Mandible long, left with entire length of inner margin with serrations; right with serrations only in upper half; labrum narrow, pointed at tip; anterior and posterior margins of pronotum deeply indented in middle (fig. 56A) . . . . *Serritermes*

   – Mandible short, left with inner margin with fine serrations in upper half, coarse in lower half, right without serrations; labrum large and wide, blunt at tip; pronotum with anterior margin moderately or slightly indented, posterior margin almost even (fig. 56B) . . . . *Glossotermes*

– Mandible without serrations along inner margins, except a few at base 8

8. Tarsi 3-segmented . . . . **Stylotermitidae** (*Stylotermes*)

– Tarsi 4-segmented . . . . **Rhinotermitidae**

   a. Head with large, rounded fontanelle at base of clypeus . . . . Coptotermitinae (*Coptotermes*)

   – Head with small fontanelle, away from base of clypeus . . . . b

   b. Groove present, extending from fontanelle to base of clypeus c

   – Groove absent from fontanelle to base of clypeus . . . . d

   c. Tip of labrum with a brush; mandibles with prominent marginal teeth . . . . Rhinotermitinae

a^1. Neotropical . . . . b^1
– Oriental, Papuan, Ethiopian . . . . d^1

b^1. Soldier dimorphic; minor soldier with sides of head almost straight or rounded, frontal pore at base of labrum . . . . c^1
– Soldier monomorphic; minor soldier only; head with sides broad anteriorly, narrowing posteriorly; frontal pore at projection of head, one-third length of labrum (fig. 51C) . . . . *Acorhinotermes*

c^1. Major soldier: labrum elongate; head narrow, width less than 1.20 mm; minor soldier: labrum short; head length with labrum less than 1.20 mm (fig. 51A, B) . . . . *Dolichorhinotermes*
– Major soldier: labrum oval or quadrate; head wide, with more than 1.50 mm labrum long; minor soldier: head length with labrum more than 1.20 mm (fig. 52A) . . . . *Rhinotermes*

d^1. Soldier monomorphic; mandibles with inner margins with fine serrations at base . . . . *Parrhinotermes*
– Soldier dimorphic; mandibles with inner margins without serrations at base. . . . . *Schedorhinotermes*

– Tip of labrum without brush; mandibles without prominent marginal teeth . . . . Prorhinotermitinae (*Prorhinotermes*)

d. Head with sides rounded . . . . e

– Head with sides subparallel . . . . Heterotermitinae

a^1. Mandible distinctly hooked at tip; labrum tongue shaped. . . . . . . *Reticulitermes*
– Mandible faintly curved at tip; labrum with pointed hyaline tip . . . . *Heterotermes*

e. Head triangular, flat, posterior margin sinuate; mandibles without prominent teeth, except for a basal tooth and a few crenulations; pronotum with anterior medial projection. . . . . . . Termitogetoninae (*Termitogeton*)
– Head subrectangular, posterior margin even; mandibles with prominent marginal teeth; pronotum without anterior medial projection . . . . Psammotermitinae (*Psammotermes*)

Key to the Subfamilies of Termitidae

Based on the Characters of the Imago, Worker, and Soldier

1. Imago/worker: labrum with dark, sclerotized transverse band; worker gut: mesentero-proctodeal junction with four lobes. Fungus growers .... Macrotermitinae
– Imago/worker: labrum without dark, sclerotized transverse band; worker gut: mesentero-proctodeal junction without four lobes. Non–fungus-growers 2

2. Imago/worker: right mandible with subsidiary tooth at base of apical tooth; left mandible with anterior margin of third marginal tooth twice or more length of posterior margin; worker gut: conspicuous backward oriented bristles at P3–P4 (paunch-colon) junction .... Sphaerotermitinae
– Imago/worker: right mandible without subsidiary tooth at base of apical tooth; left mandible with anterior margin of third marginal tooth less than twice length of posterior margin; worker gut: without conspicuous backward oriented bristles at P3–P4 (paunch-colon) junction 3

3. Imago/worker: left mandible with third marginal tooth with distinct notch or indentation between third and fused first plus second marginal tooth (fig. 58A, B); imago: fontanelle not slitlike, obscure, oval or round; worker gut: mixed segment usually absent, if present, on inner surface of mesenteron. Soldier generally absent .... Apicotermitinae
– Imago/worker: left mandible with third marginal tooth without distinct notch or indentation between third and fused first plus second marginal tooth (fig. 58C, D); imago: fontanelle slitlike, oval or round; worker gut: mixed segment present. Soldier always present 4

4. Worker gut: P3 (paunch) with a blind diverticula or caecum .... Cubitermitinae
– Worker gut: P3 (paunch) without a blind diverticula or caecum 5

5. Worker gut: pseudo-Malpighian knot present; Malpighian tubules not paired .... Foraminitermitinae
– Worker gut: pseudo-Malpighian knot absent; Malpighian tubules paired 6

6. Soldier: nasus absent, short frontal projection sometimes present; fontanelle (frontal pore) at front of head or base of frontal projection; mandibles well developed, long, biting, symmetrical or asymmetrical .... Termitinae
– Soldier: long or short nasus present; fontanelle (frontal pore) at tip of nasus; mandibles reduced or vestigial 7

7. Soldier: head with vestigial mandibles; frontal pore narrow; tibial spurs 2:2:2. Worker gut: double mixed segment absent .... Nasutitermitinae
– Soldier: head with functional biting mandibles; frontal pore wide and conspicuous; tibial spurs 3:2:2. Worker gut: double mixed segment present .... Syntermitinae

KEY TO THE GENERA OF THE FAMILY KALOTERMITIDAE
(from Krishna, 1961)

Based on the Characters of the Imago

1. Forewing with M and Cu arising from a common stem outside wing scale; arolium absent (fig. 43B) 2
– Forewing with M and Cu arising from inside wing scale; arolium present or absent (fig. 41B) 3

2. Left imago/pseudergate mandible with anterior margin of third marginal tooth long than 1.5 times length of posterior margin of first plus second marginal tooth (fig. 38I) . . . . *Epicalotermes*
– Left imago/pseudergate mandible with anterior margin of third marginal tooth clearly longer but usually not more than 1.5 times longer than posterior margin of first plus second marginal tooth (figs. 38E, F) . . . . *Bifiditermes, Bicornitermes*

3. Middle tibia with three apical spurs and additional spines (figs. 37A, B, C) 4
– Middle tibia with three apical spurs only, additional spines absent 6

4. Middle tibia with two outer spines and one inner spine; fossil only (fig. 37A) . . . . †*Proelectrotermes*
– Middle tibia with one or two outer spines, inner spine absent 5

5. Middle tibia with two outer spines; fossil only (fig. 37B) . . . . †*Electrotermes*
– Middle tibia with one outer spine; living (fig. 37C) . . . . *Postelectrotermes*

6. Left imago/pseudergate mandible with anterior margin of third marginal tooth equal to posterior margin of first plus second marginal tooth (fig. 38A) 7
– Left imago/pseudergate mandible with anterior margin of third marginal tooth clearly longer than posterior margin of first plus second marginal tooth (fig. 38D) 16

7. Forewing with M unsclerotized, weak, and running midway between Rs and Cu to tip of wing (fig. 41B) 8
– Forewing with M sclerotized (figs. 39C, 40A, B, C, 41C) 9

8. Wings dark, with pimplelike nodules (fig. 41B); arolium present . . . . *Kalotermes*
– Wings hyaline, with no nodules (fig. 42B); arolium absent . . . . *Pterotermes*

9. Forewing with M sclerotized, but not so strongly as Rs (figs. 39C, 41C) 10
– Forewing with M as strongly sclerotized as Rs (figs. 40B, C, 41A, 42A) 12

10. Head and pronotum densely covered with very long and wavy hairs (fig. 39A) . . . . *Comatermes*
– Head and pronotum covered with short bristles; long hairs absent 11

11. Left imago/pseudergate mandible with distinct apical dent in posterior margin of first plus second marginal tooth; posterior margin of first plus second marginal tooth slightly larger than anterior margin of third marginal tooth (fig. 38B) . . . . *Paraneotermes*

– Left imago/pseudergate mandible with no apical dent in posterior margin of first plus second marginal tooth, evenly rounded; posterior margin of first plus second marginal tooth equal to anterior margin of third marginal tooth (fig. 38C) . . . . *Ceratokalotermes*

12. Rs without branches; M running close to Rs to tip of wing (fig. 42A) 13
– Rs with branches 14

13. Left imago/pseudergate mandible with distinct angular notch at junction of posterior margin of first plus second marginal tooth and anterior margin of third marginal tooth (fig. 38G) . . . . *Glyptotermes*
– Left imago/pseudergate mandible without distinct angular notch at junction of posterior margin of first plus second marginal tooth and anterior margin of third marginal tooth (fig. 38H) . . . . *Calcaritermes*

14. M very small, coalescing with Rs very close to suture (fig. 40C) . . . . *Rugitermes*
– M running close and parallel to Rs to tip of wing (figs. 40B, 41A) 15

15. Anterior margin of forewing scale convex (fig. 40B); eye diameter 0.46–0.78 mm . . . . *Neotermes*
– Anterior margin of forewing scale almost straight (fig. 41A); eye diameter 0.43 mm . . . . *Eucryptotermes*

16. M slightly sclerotized and running closer to Rs than to Cu (fig. 43A) . . . . *Proneotermes*
– M not sclerotized and running midway between Rs and Cu (figs. 39D, 42C, 43C) 17

17. M bending up and joining Rs in middle or beyond middle of wing (fig. 43C, D) . . . . *Procryptotermes, Cryptotermes*
– M running to tip of wing (figs. 39D, 42C) 18

18. Arolium always absent . . . . *Marginitermes, Allotermes*
– Arolium usually present; occasionally absent . . . . *Incisitermes, Tauritermes*

Based on the Characters of the Soldier

1. Middle tibia with one outer spine . . . . *Postelectrotermes*
– Middle tibia with no spine 2

2. Foretibia with a thick, conspicuous spur near apex of outer side, much larger than two apical spurs (fig. 37D) . . . . *Calcaritermes*
– Foretibia with apical spur not enlarged 3

3. Head short and highly phragmotic (figs. 44G, 47A, D, I) 4
– Head long or short, not phragmotic, sloping in front at approximate angle of 20°–45°; with or without anterolateral prominences (figs. 44A, B, D, E, J, L, 45A, C, D, E, G, H, 46A, B, D, E, G, H, J, K, 47F, G) 8

4. Anterior margin of pronotum serrated (figs. 44G, 47A, I) 5
– Anterior margin of pronotum even, not serrated (fig. 47D) 7

5. Anterior margin of pronotum sharply serrated; head bilobed, with region between lobes depressed; ridge between vertex and frons absent (fig. 47A) . . . . *Bicornitermes*
– Anterior margin of pronotum wavy, weakly or finely serrated; ridge between vertex and frons present (figs. 44G, 47I) 6

6. Head in front strongly scooped out; antennal socket at one-third to one-half the length of head from front (fig. 44G) . . . .*Eucryptotermes*
– Head in front vertical, not so strongly scooped out; antennal socket close to side base of mandibles (fig. 47I, J) . . . .*Cryptotermes*

7. Ridge between vertex and frons distinct; head in front not vertical; third article of antenna large and club shaped (fig. 47D) . . . . *Procryptotermes*
– Ridge between vertex and frons absent; head in front vertical; third article of antenna not large . . . . *Glyptotermes* (some spp.), *Kalotermes* (some spp.)

8. Anterior margin of pronotum not deeply concave or incised 9
– Anterior margin of pronotum deeply concave or incised. 13

9. Head with a prominent ridge in front, formed by a continuation of dorsal antennal margin medially (fig. 44D) . . . . *Rugitermes*
– Head without a prominent ridge 10

10. Head usually with distinct anterolateral prominences, sometimes phragmotic (fig. 46A, B). . . . .*Glyptotermes*
– Head long, without distinct anterolateral prominences (figs. 45A, B, 47F, G) 11

11. Mandibles short in proportion to rest of head capsule (figs. 45A, 47F). 12
– Mandibles long, not short in proportion to rest of head capsule (figs. 44A, J) . . . . *Kalotermes, Neotermes*

12. Postmentum very broad in front (fig. 45C); pseudergate mandible as in figure 38B . . . . *Paraneotermes*
– Postmentum not very broad in front; head slope in front concave (fig. 47H) . . . . *Comatermes*

13. Sides of head distinctly and clearly rounded (fig. 48A, B, C); sclerotized swelling at base of postmentum . . . . *Pterotermes*
– Sides of head almost straight; no swelling at base of postmentum 14

14. Third segment of antenna very large, as long as next 5–7 segments together; head with a ridge between vertex and frons (fig. 46D) . . . .*Marginitermes*
– Third segment of antenna not so long as next 5–7 segments together. 15

15. Head dorsoventrally flat (figs. 45H, 48K) 16
– Head thick (figs. 45E, 46H, 48E, H) 17

16. Head sloping anteriorly from near middle; mandibles long in proportion to rest of head capsule and strongly curved (figs. 48J, K); femur not swollen. . . *Epicalotermes*
– Head not sloping anteriorly from near middle; mandibles short in proportion to rest of head capsule (figs. 45G, H); femur strongly swollen . . . . *Incisitermes*

17. Head with a hornlike projection below and in front of antennal socket . . . . . .
    (fig. 48G, H) . . . . *Allotermes*
- – Head without a hornlike projection 18

18. Head with distinct anterolateral prominences (figs. 45D, E, 48D, E) 19
- – Head with indistinct anterolateral prominences 20

19. Third segment of antenna modified, longer and darker than fourth; anterior
    margin of pronotum distinctly wavy (fig. 48D, E) . . . . *Tauritermes*
- – Third segment of antenna not modified, equal to fourth; anterior margin of
    pronotum faintly wavy (fig. 45D, E) . . . . *Ceratokalotermes*

20. Femur swollen; head in front dark; faint ridge between vertex and frons
    (fig. 46G, H) . . . . *Proneotermes*
- – Femur not swollen; ridge between vertex and frons absent (fig. 46J, K) . . . . . . *Bifiditermes*

DIAGNOSES OF FAMILIES AND SUBFAMILIES

INFRAORDER ISOPTERA

Cellulose-eating eusocial insects living in integrated and highly organized colonies, with morphologically distinct castes: reproductives and sterile soldiers and workers. Wings membranous, of almost equal size, shed at flight along basal suture, anterior veins strongly sclerotized, regular cross veins absent, network of irregular veinlets between veins (archidictyon) in some lower taxa. Cerci short, with 2–11 segments. Tarsi with 3–5 segments. Genitalia absent or rudimentary. Development hemimetabolous.

BASAL FAMILIES
(alphabetical by family)

Family Archotermopsidae

Figures 31, 32

Imago: Fontanelle absent; Y-suture present; eyes medium sized to large (in *Archotermopsis* not protruding beyond border of head, anterior margin notched); ocelli absent; antennae with 22–27 articles; postclypeus flat in profile, short relative to width; pronotum faintly arched, narrower than head; imago-worker mandibles: left with an apical tooth and three marginal teeth; right with an apical tooth and two marginal teeth, subsidiary tooth present at base of apical and first marginal tooth. Legs: tarsi with five articles; tibial spurs 4:3–4:2 (*Archotermopsis*), 3–4:2–4:1–3 (*Zootermopsis*); fore-, middle, and hind tibia with additional spines, spurs, and spines with papillae; arolium present. Cerci with 3–8 articles; styli long, extending beyond abdomen (*Archotermopsis*). Sternal gland one, on fourth abdominal sternite. Forewing: scale overlapping hind wing scale (in *Archotermopsis* forewing scale short and not overlapping), costal margin flat to faintly arched; humeral suture well defined, almost straight (*Archotermopsis*) to arched (*Zootermopsis*); subcosta (Sc), R1, R2, R3, Rs sclerotized, Rs with the main branch bending to apex of wing, 5–6 secondary branches and additional tertiary branches joining costal margin; median (M) weak, closer to cubitus (Cu) than to radial sector (Rs), with secondary branches terminating at lower margin; Cu with primary and secondary branches extending to lower margin; anal vein absent. Hind wing: humeral suture weak, barely visible; anal vein present.

Soldier: Head large, flat, Y-suture visible; mandibles long and stout: left with three marginal teeth, right with two marginal teeth; eyes rudimentary; antennae with 19–27 articles; pronotum flat, narrower than head. Legs: tarsi with five articles; tibial spurs 3–4:2–3:2 (*Archotermopsis*), 3–5:2–4:2 (*Zootermopsis*); fore-, middle, and hind tibia with additional spines; arolium absent. Cerci with 5–8 articles (*Archotermopsis*), 4–6 (*Zootermopsis*); styli long, extending beyond abdomen, present in both sexes, 1-segmented.

Pseudergate: Gut: esophagus not separated from crop; crop elongated, voluminous, slightly asymmetrical, muscle sheath reduced, cuticular surface with pectinated scales; gizzard

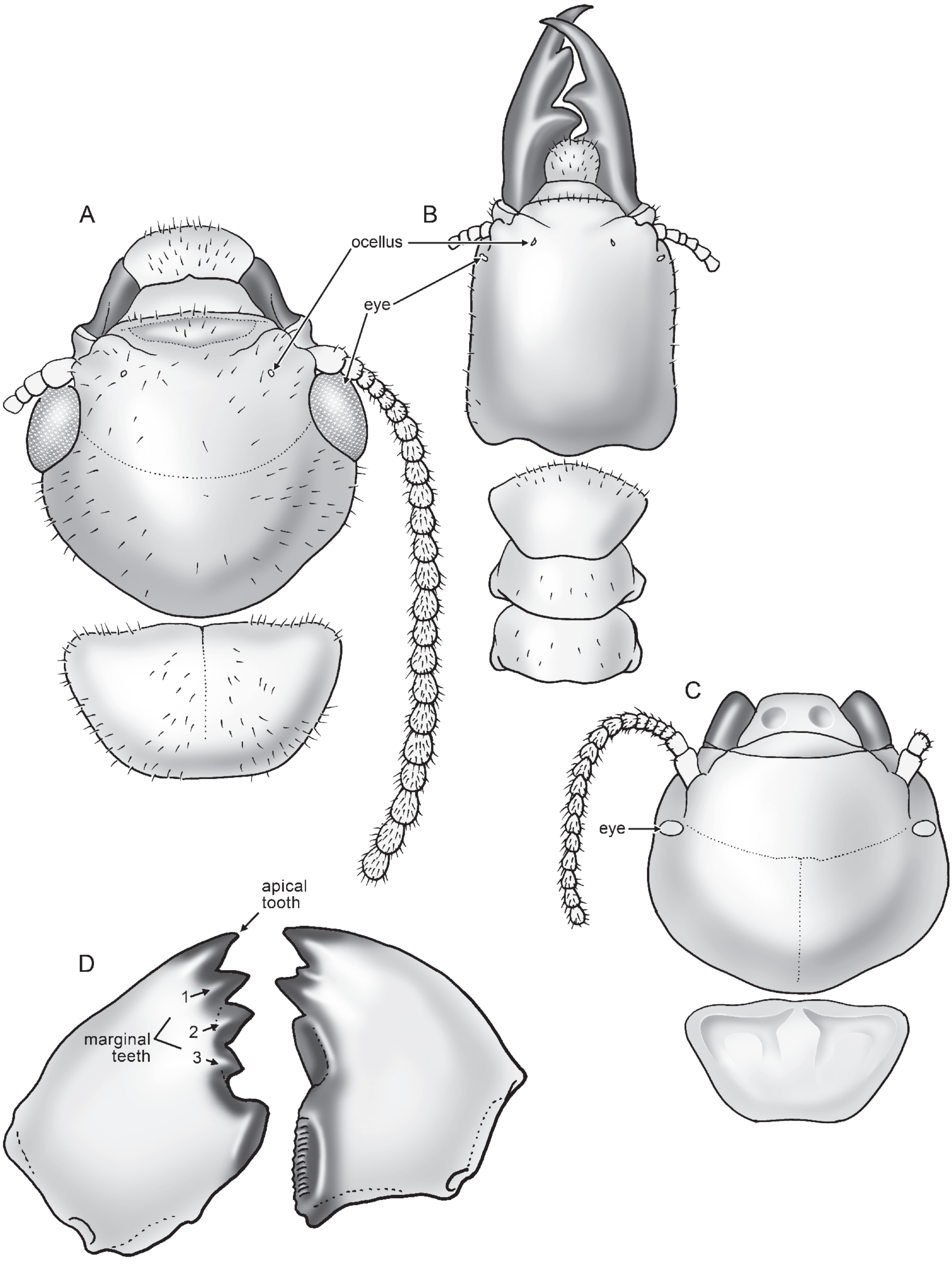


FIGURE 31. Heads, pronota, and mandibles of *Archotermopsis wroughtoni* castes (Archotermopsidae). **A.** Imago. **B.** Soldier. **C.** Pseudoworker. **D.** Imago mandibles. Not to the same scale.

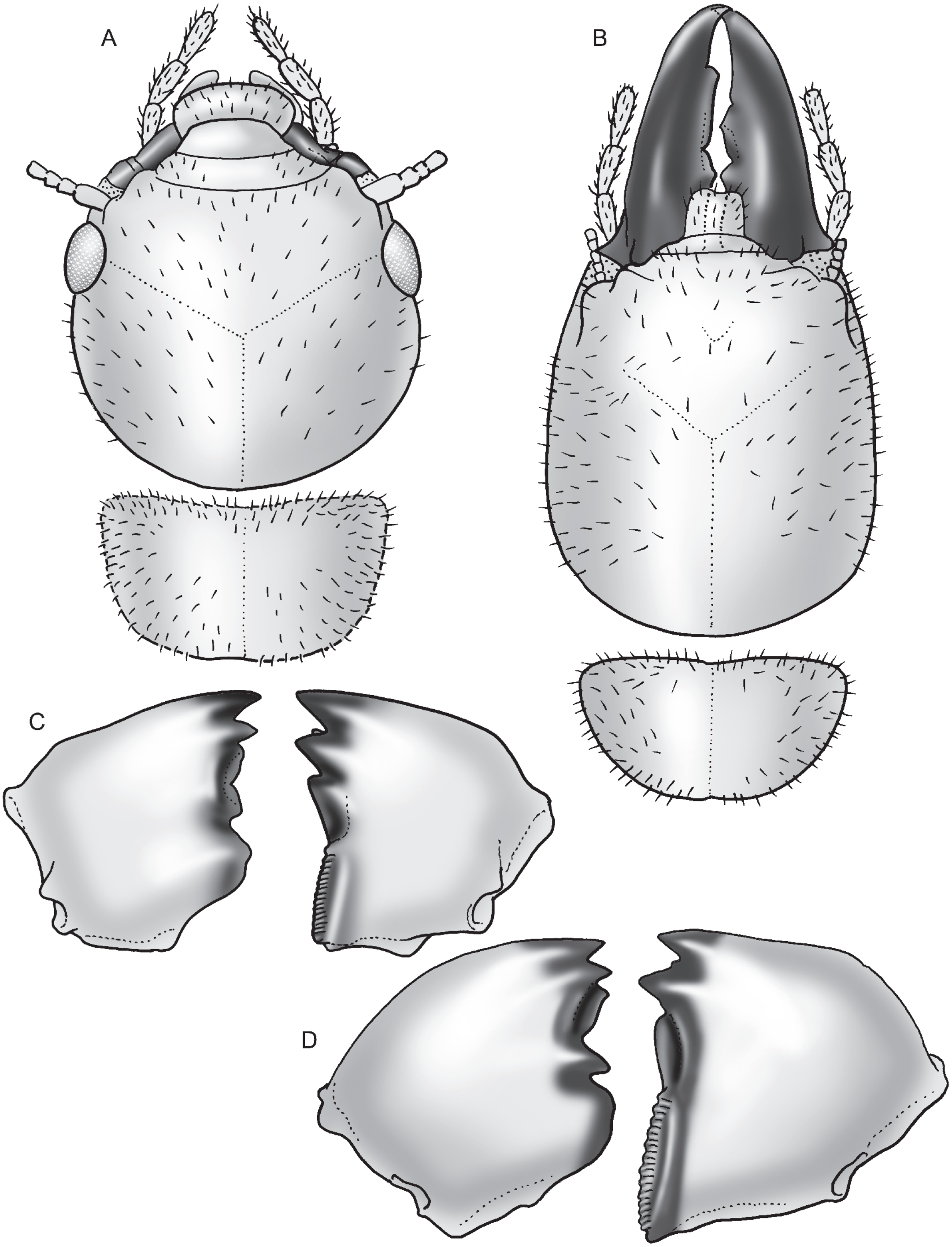


FIGURE 32. Representative Archotermopsidae. **A–C.** *Zootermopsis angusticollis* (Hagen). **A.** Head and pronotum of imago. **B.** Head and pronotum of soldier. **C.** Imago mandibles. **D.** Imago mandibles of *Hodotermopsis* sp. Not to the same scale.

strongly muscular, with chitinized armature, folds divided into columns (sclerotized, with scaly surface) and pulvilli (nonsclerotized), columns I and II short, rectangular, with prominent blade-shaped crenulated tooth in each, pulvilli I longer than columns, pulvilli II smaller than I, stomodeal valve long; midgut or mesenteron, long, cylindrical, forming an anticlockwise, circular ring, first dorsally, then ventrally under gizzard, ending in hind gut, ring diameter very wide, no mixed segment, anterior coecae 4–5, at gizzard-midgut junction; Malpighian tubules 10, inserted at midgut–hind gut junction, long, following a tortuous course around the gut; hind gut with first proctodeal segment (P1) short, cylindrical, enteric valve (P2) short, funnel shaped, well invaginated in paunch (P3), cushions in P1 in posterior third only, most developed in anterior part of P2 (cf. Mastotermitidae and Hodotermitidae), cuticular armature of cushions generally well developed, more elaborate in P2 than in P1, P1 and P2 with spines and scales; paunch (P3) dilated and elongated, containing symbiotic flagellates; P3–P4 loop strongly twisted, opening of P2 into P3 more posterior than in Kalotermitidae, thus openings of P2 and P4 at opposite ends of elongated P3 (adjoining in Kalotermitidae); P4 a long tube, with a muscular rectal valve with folds near junction with P5, armature of valve with several hundred pectinated scales; P5 dilated (abridged from Noirot, 1995b).

Additional Characters and Biology: No true worker caste, functions performed by pseudergates; symbiont protozoa present; strictly wood-dwelling; small colonies in rotting wood.

Genera Included: *Archotermopsis, Hodotermopsis,* †*Parotermes*, *Zootermopsis.*

Family †Cratomastotermitidae

Figure 62B

Imago: Head robust, longer than wide; eyes moderate sized; ocelli absent; fontanelle absent; Y-suture not visible; postclypeus large; pronotum large, wider than head. Legs: tarsi with five articles, tibial spurs 1:2:2 visible (probably more); arolium present. Cerci and abdominal styli not evident (latter presumably absent, but terminal structures observable only in a single specimen). Wings long and broad, with well-developed reticulations, like cross veins, forewing scale apparently large, probably shorter than hind-wing scale, with front margin arched, at least four major Rs branches, last branch with series of five lightly sclerotized, parallel, inferior branches that connect to M. Apex of Rs field encompassing wing apex in fore- and hind wings; hind wing with distinctive merging of Rs veins with inferior Rs vein near apex.

Soldier: Unknown.

Worker: Unknown.

Genus Included: †*Cratomastotermes*, from the Crato Formation, Early Cretaceous of Brazil.

Family Hodotermitidae

Figures 19; 24E–H; 25A, B; 39A–D; 33–35

Imago: Fontanelle absent; Y-suture present; eyes small; ocelli absent; antennae long and filamentous, with 23–32 articles; postclypeus flat in profile, short relative to width;

pronotum saddle shaped, narrower than head; imago-worker mandibles: left mandible with an apical tooth and three marginal teeth, second almost completely reduced and barely visible; right mandible with an apical tooth and two marginal teeth, subsidiary tooth absent at base of apical and first marginal tooth. Legs: tarsi with four articles; tibial spurs variable, 3:2–5:3–5; fore-, mid- and hind tibia with additional lateral spines (*Hodotermes, Microhodotermes*), 3:4:4; fore- and middle tibia without additional lateral spines (*Anacanthotermes*); arolium absent. Cerci with 1–5 articles; styli small, one jointed, generally present in both sexes. Sternal gland one, on fourth abdominal sternite. Forewing: scale small, not overlapping hind wing scale; Sc, R, and Rs sclerotized; Sc small, R and Rs arising from a common stem, Rs with several branches joining costal margin, apically several inferior branches extending to lower margin or tip of wing; M and Cu weak, M branched, several branches extending to lower margin; Cu with several branches; anal vein absent. Hind wing: Sc longer than in forewing; M arising at base of Rs; short anal vein present.

Soldier: Head large, thick dorsoventrally; mandibles stout; left with three marginal teeth, right with two marginal teeth; eyes rudimentary, with or without pigment; antennae with 22–33 articles; pronotum weakly saddle shaped, narrower than head; legs: tibial spurs variable, as in imago.

Worker: Gut: esophagus not separated from crop; crop very long, narrowed before gizzard, muscle sheath strong, surface with convolutions, vermiculate in appearance; gizzard cylindrical, strongly muscular, with chitinized armature, folds divided into columns (sclerotized, with scaly surface) and pulvilli (nonsclerotized), columns I and II short, with scaly surface and crenulated tooth in each, pulvilli I longer than columns, pulvilli II developed; stomodeal valve long; midgut or mesenteron long, cylindrical, forming an anticlockwise, circular ring, first dorsally, then ventrally under gizzard, ending in hind gut, ring diameter wide, no mixed segment, no coecae at gizzard-midgut junction; Malpighian tubules 8 (*Anacanthotermes*), 9–10 (*Hodotermes, Microhodotermes*), inserted at midgut–hind gut junction, long, following a tortuous course around the gut; hind gut with first proctodeal segment (P1) short, cylindrical, varying in length in different genera, enteric valve (P2) short and bulbous, well invaginated in paunch (P3), cushions extending from posterior half of P1, most developed in anterior part of P2 (cf. Mastotermitidae, Archotermopsidae, and Hodotermitidae), cuticular armature of cushions generally well developed, more elaborate in P2 than in P1, P2 with thick triangular spines, forming "shields" on posterior surface of groove between P1 and P2 (unique to Hodotermitidae); paunch (P3) dilated, hourglass shaped, containing symbiotic flagellates; P2–P4 loop strongly twisted with a huge dilation at end, opening of P2 into P3 as in Archotermopsidae; P4 a long tube, with a muscular rectal valve with folds near junction with P5, armature of valve with short spines; P5 dilated (abridged from Noirot, 1995b).

Additional Characters and Biology: True worker caste; symbiont protozoa present. Habitat: underground nests; savannah and semidesert harvesters, food consisting of grass, leaves, bark, and less woody twigs of shrubs, serious pests of grasslands.

Genera Included: *Anacanthotermes, Hodotermes, Microhodotermes.*

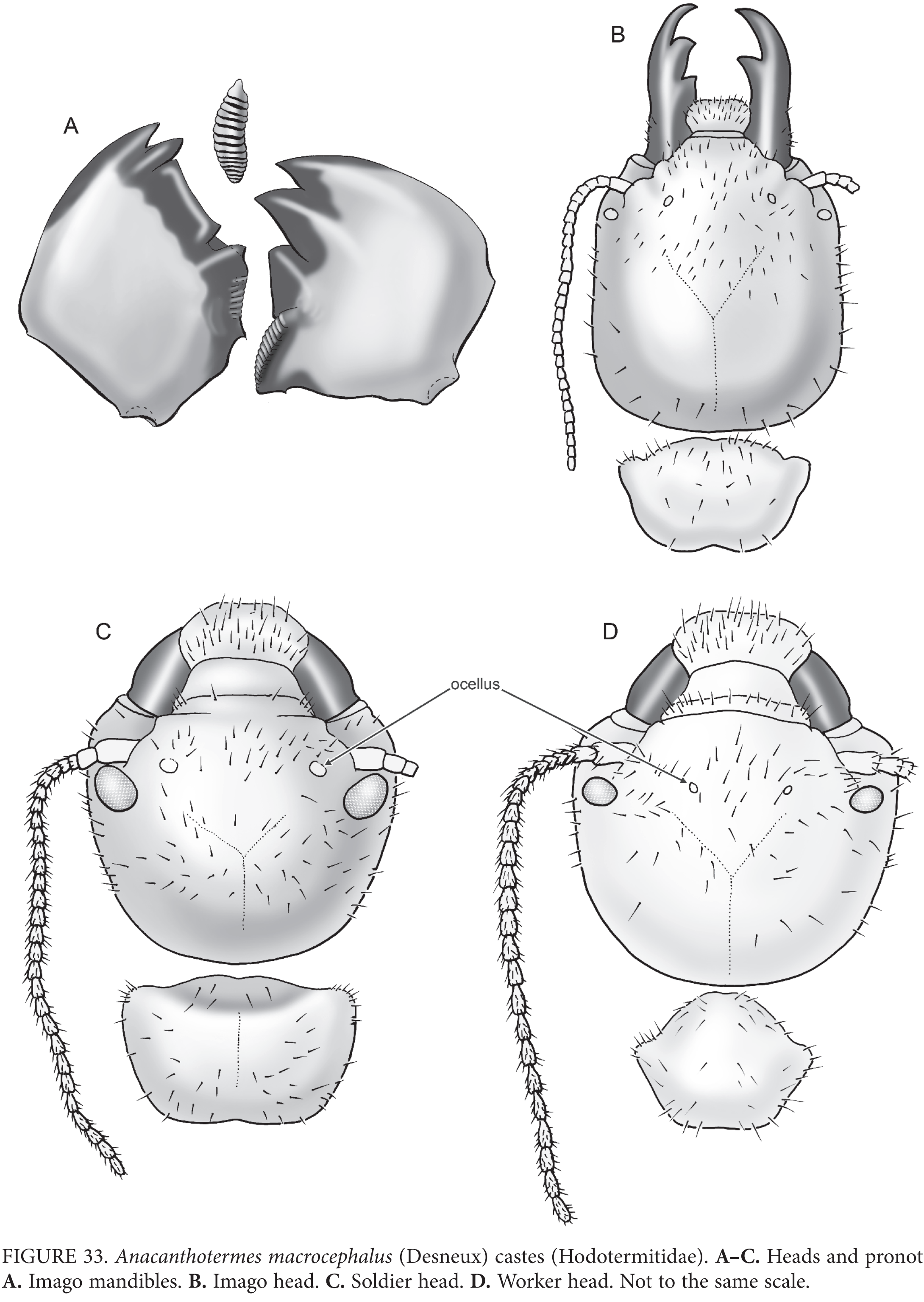


FIGURE 33. *Anacanthotermes macrocephalus* (Desneux) castes (Hodotermitidae). **A–C.** Heads and pronota. **A.** Imago mandibles. **B.** Imago head. **C.** Soldier head. **D.** Worker head. Not to the same scale.

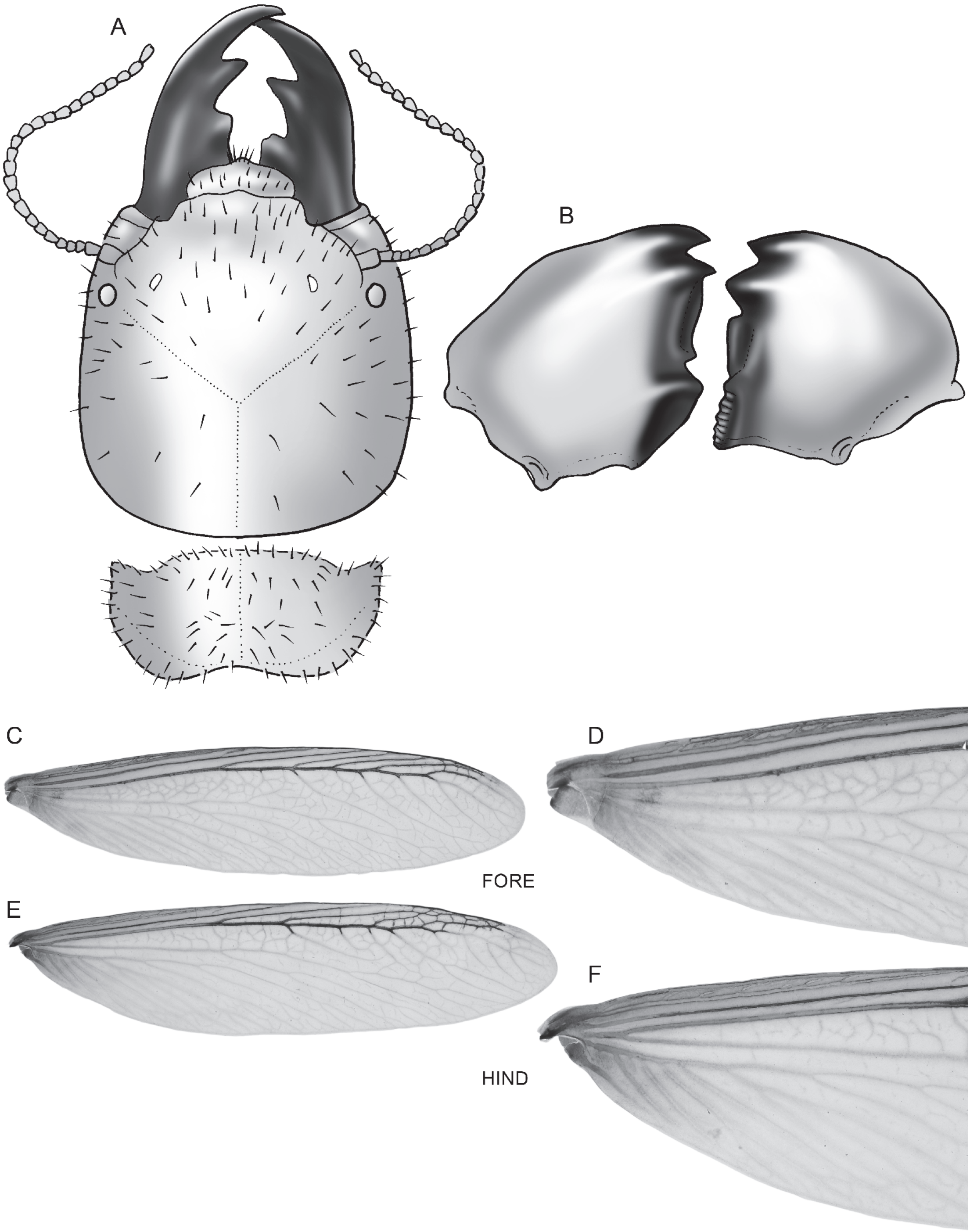


FIGURE 34. *Hodotermes mossambicus* (Hagen) (Hodotermitidae). **A.** Soldier head and pronotum. B. Imago mandibles. **C–F.** Wings. **C, D.** Forewings, entire and with detail of base. **E, F.** Hind wings, entire and with detail of base. Not to the same scale.

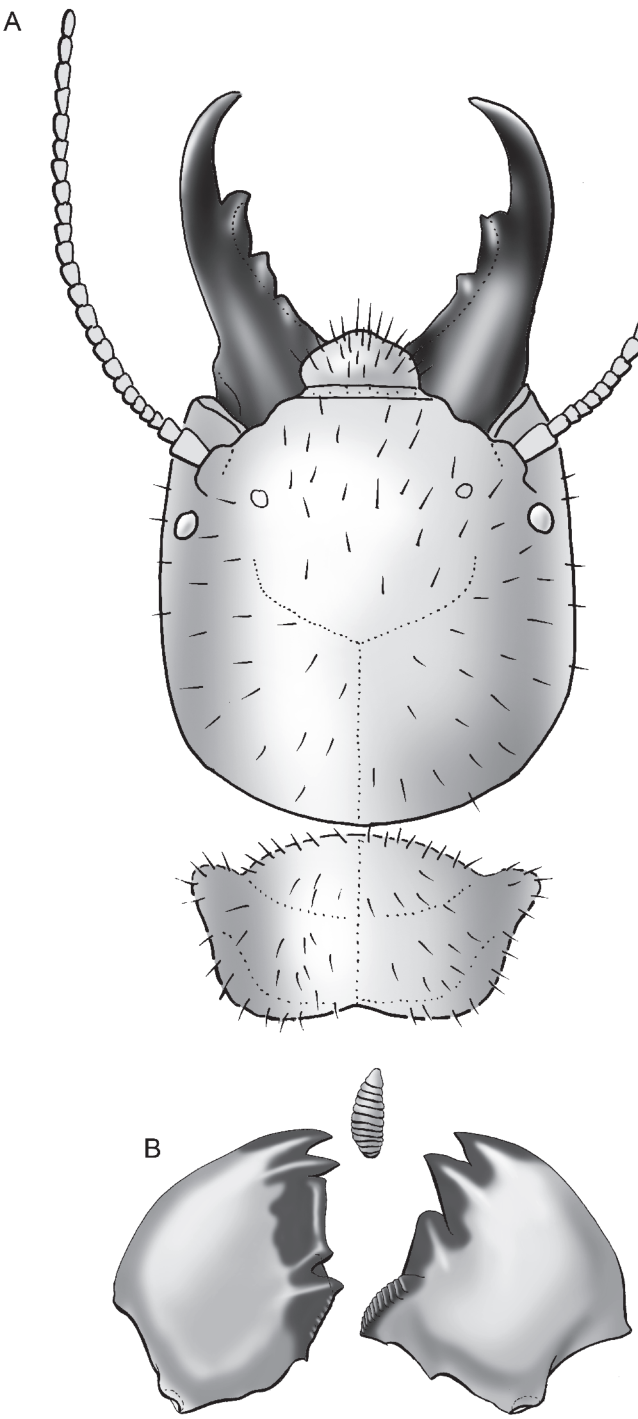


FIGURE 35. *Microhodotermes viator* (Latreille) (Hodotermitidae). **A.** Soldier head and pronotum. **B.** Imago mandibles, with molar plate. Not to the same scale.

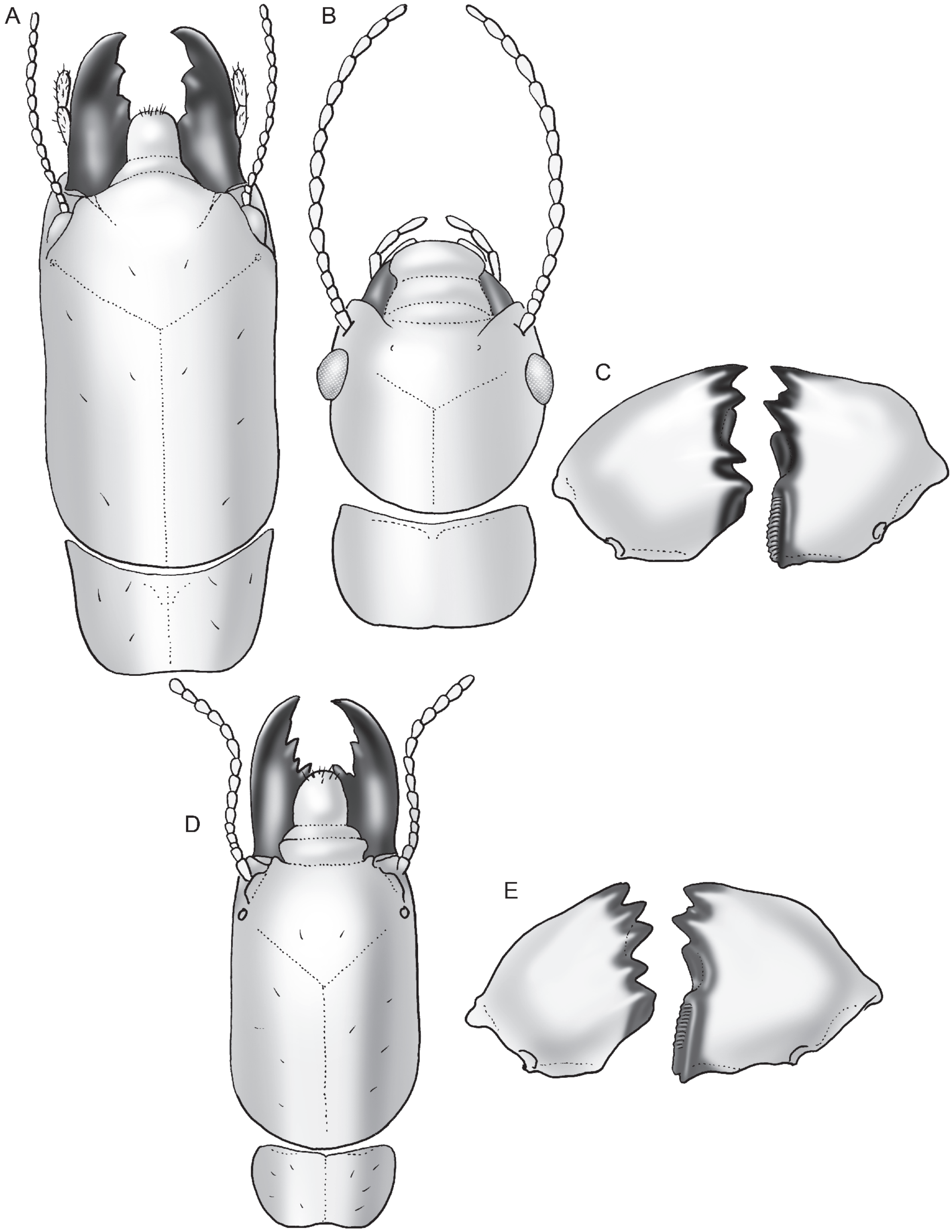


FIGURE 36. Exemplar Stolotermitidae. **A–C.** *Porotermes planiceps* (Sjöstedt). **A.** Soldier head and pronotum. **B.** Alate head and pronotum. **C.** Imago mandibles. **D, E.** *Stolotermes africanus* Emerson. **D.** Soldier head and pronotum. **E.** Imago mandibles.

Family Kalotermitidae

Figures 37–48

Imago: Fontanelle absent; Y-suture visible; eyes of varying sizes; ocelli present; antennae with 11–24 articles; postclypeus flat in profile, short relative to its width; pronotum flatly arched, as broad as or broader than head; imago-worker mandibles similar to Mastotermitidae. Left mandible with an apical and two distinct marginal teeth, first and third, as second fused with first, first and third separated by a notch; posterior margin of fused first + second shorter than or equal to anterior margin of third; right mandible with an apical and two marginal teeth. Legs: tarsi with four articles; tibial spurs 3:3:3, with additional spines (1–3) on middle tibia; arolium present or absent. Cerci with two articles. Sternal gland: one, on fifth abdominal sternite (as in Rhinotermitidae). Forewing: scale very large, overlapping hind-wing scale, costal margin strongly arched, except in *Glyptotermes* and *Eucryptotermes*; humeral suture well defined, arched, Sc, R1, and Rs heavily sclerotized, Sc short, R1 simple, Rs running parallel to costal margin, with a number of branches joining costal margin, except in *Glyptotermes* and *Calcaritermes,* in which Rs is unbranched; M either weak or strong, variable in position, joining wing tip of Rs either close to wing scale or far from it; Cu weak and unsclerotized, large number of branches joining lower (inner) margin; anal vein absent. Hind wing: subcosta absent; short anal vein present.

Soldier: Head robust, long, in some taxa subtruncate or phragmotic, Y-suture always present. Mandibles usually robust, dentition variable; left mandible with an apical tooth and three marginal teeth, all gradation of reduction to complete reduction of the three marginal teeth; right mandible with an apical tooth and two marginal teeth, in some species the two marginal teeth completely reduced. Antennae with 10–21 articles. Pronotum flat, almost as wide as head. Legs: tarsi with four articles; tibial spurs 3:3:3, with additional spines on middle tibia; arolium present or absent. Cerci with two articles.

Pseudergate: Gut: esophagus not separated from crop; crop elongated, not separated from gizzard, muscle sheath much reduced; gizzard strongly muscular, with chitinized armature, folds divided into columns (sclerotized, with scaly surface) and pulvilli (nonsclerotized), columns I and II wide, with large, prominent teeth, larger in II than in I, varying in shape with species, pulvilli I longer than columns, pulvilli II small but visible; stomodeal valve long; midgut or mesenteron somewhat short, cylindrical, forming an anticlockwise, circular ring, first dorsally, then ventrally under gizzard, ending in hind gut, ring diameter moderately wide (as in Stolotermitidae), no mixed segment, no coecae at gizzard-midgut junction (as in Rhinotermitidae); Malpighian tubules 8, inserted at midgut–hind gut junction long, following a tortuous course around the gut; hind gut with first proctodeal segment (P1) short, cylindrical, enteric valve (P2) well invaginated in paunch (P3), cushions extending entire length of P1 and P2, most developed in anterior part of P2 (cf. Mastotermitidae, Archotermopsidae, and Hodotermitidae), cuticular armature of cushions generally poorly developed, especially in P1, spines and scales varying with genera; paunch (P3) large, ovoid, containing symbiotic flagellates; P3–P4 loop untwisted (as in Rhinotermitidae and Serritermitidae), P2 opening into P3 anteriorly placed, relative to other families of lower termites (near the end of P3 where it joins P4);

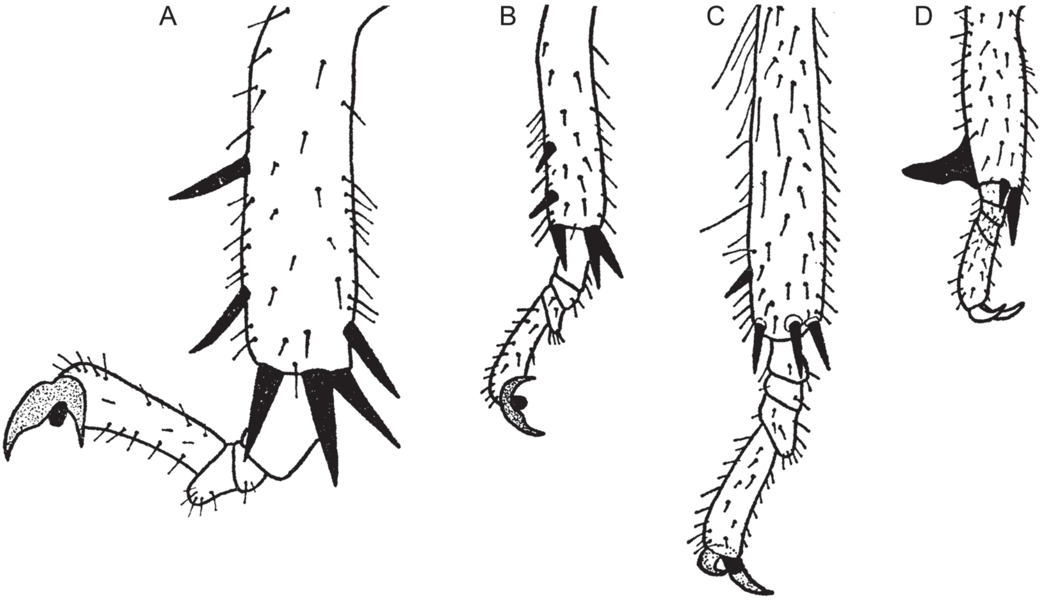


FIGURE 37. Legs of exemplar Kalotermitidae. **A.** *Proelectrotermes berendtii* (Pictet): right middle leg of imago. **B.** *Electrotermes affinis* (Hagen): right middle leg of imago. **C.** *Postelectrotermes praecox* (Hagen): middle leg of imago. **D.** *Calcaritermes imminens* (Snyder): left foreleg of soldier.

P4 a long tube, with a muscular rectal valve with folds near junction with P5, armature of the valve generally reduced (as in Rhinotermitidae); with few or no pectinated scales, P5 dilated (abridged from Noirot, 1995b).

Additional Characters and Biology: True worker caste absent, its functions performed by pseudergates; symbionts consisting of protozoa and bacteria, similar to Mastotermitidae. Habitat: nest in wood in small colonies, with irregular galleries filled with fecal pellets, no connection to soil, with the exception of *Paraneotermes,* which forages in soil; many serious pest species, in wooden structures and dead or standing trees.

Genera Included: *Allotermes, Bicornitermes, Bifiditermes, Calcaritermes, Ceratokalotermes, Comatermes, †Cratokalotermes, Cryptotermes, †Electrotermes, †Eotermes, Epicalotermes, Eucryptotermes, Glyptotermes, Incisitermes, †Kachinitermes, †Kachinitermopsis, Kalotermes, Marginitermes, Neotermes, †Oliogokalotermes, Paraneotermes, Postelectrotermes, Procryptotermes, †Proelectrotermes, †Prokalotermes, Proneotermes, Pterotermes, Rugitermes, Tauritermes.*

Family Mastotermitidae

Figures 11, 20, 21A–C, 23, 27D–F, 28A–B, 65A–C

Imago: Head large, with sides rounded; Y-suture not visible; fontanelle absent; eyes large; ocelli present, large; antennae moniliform, with 29–32 articles; postclypeus in profile flat, short relative to its width. Pronotum large, as wide as or wider than head. Imago-worker mandibles

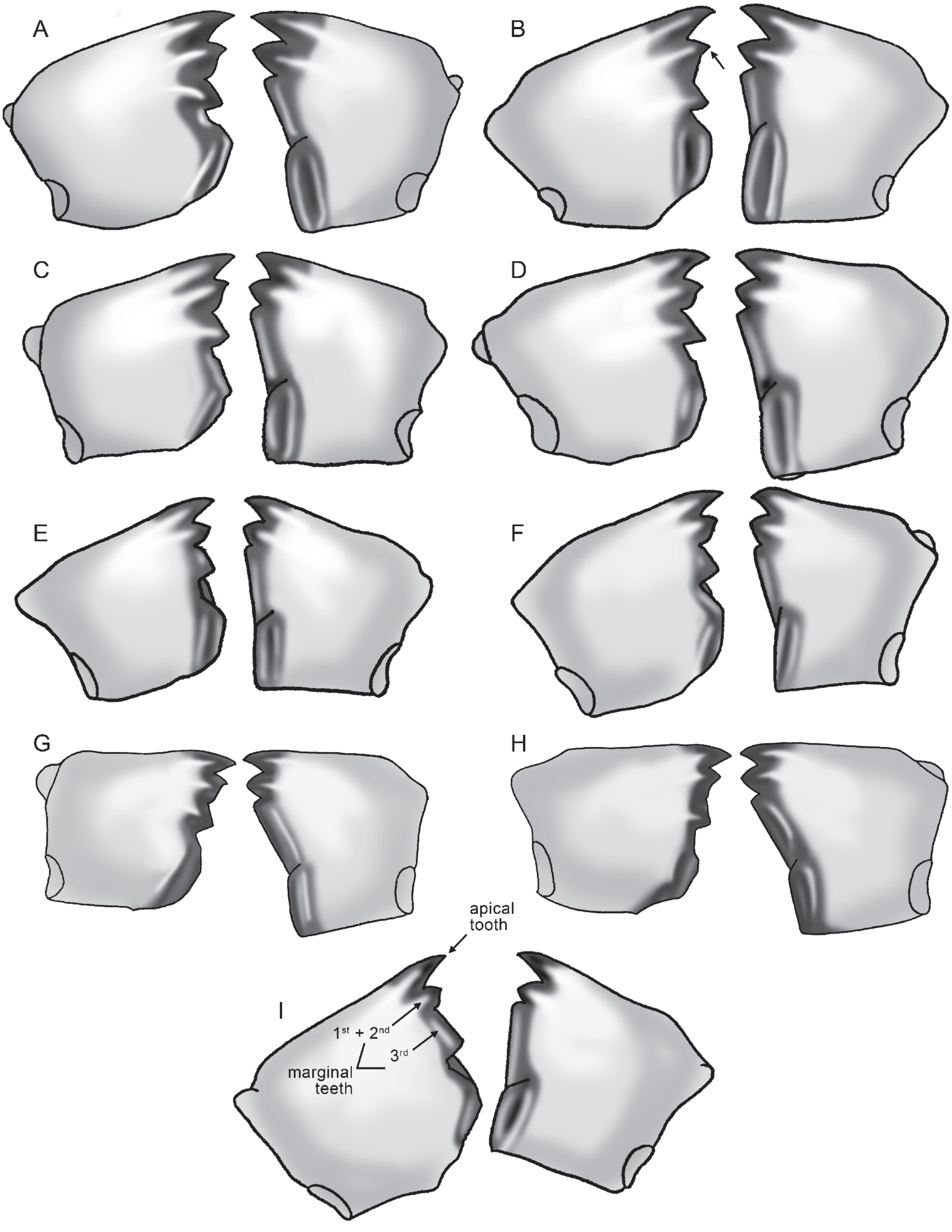


FIGURE 38. Imago mandibles of exemplar Kalotermitidae. **A.** *Kalotermes flavicollis* (Fabricius). **B.** *Paraneotermes simplicicornis* (Banks). **C.** *Ceratokalotermes spoliator* (Hill). **D.** *Incisitermes schwarzi* (Banks). **E.** *Bicornitermes bicornis* Krishna. **F.** *Bifiditermes madagascariensis* (Wasmann). **G.** *Glyptotermes tuberculatus* Froggatt. **H.** *Calcaritermes imminens* (Snyder). **I.** *Epicalotermes aethiopicus* Silvestri.

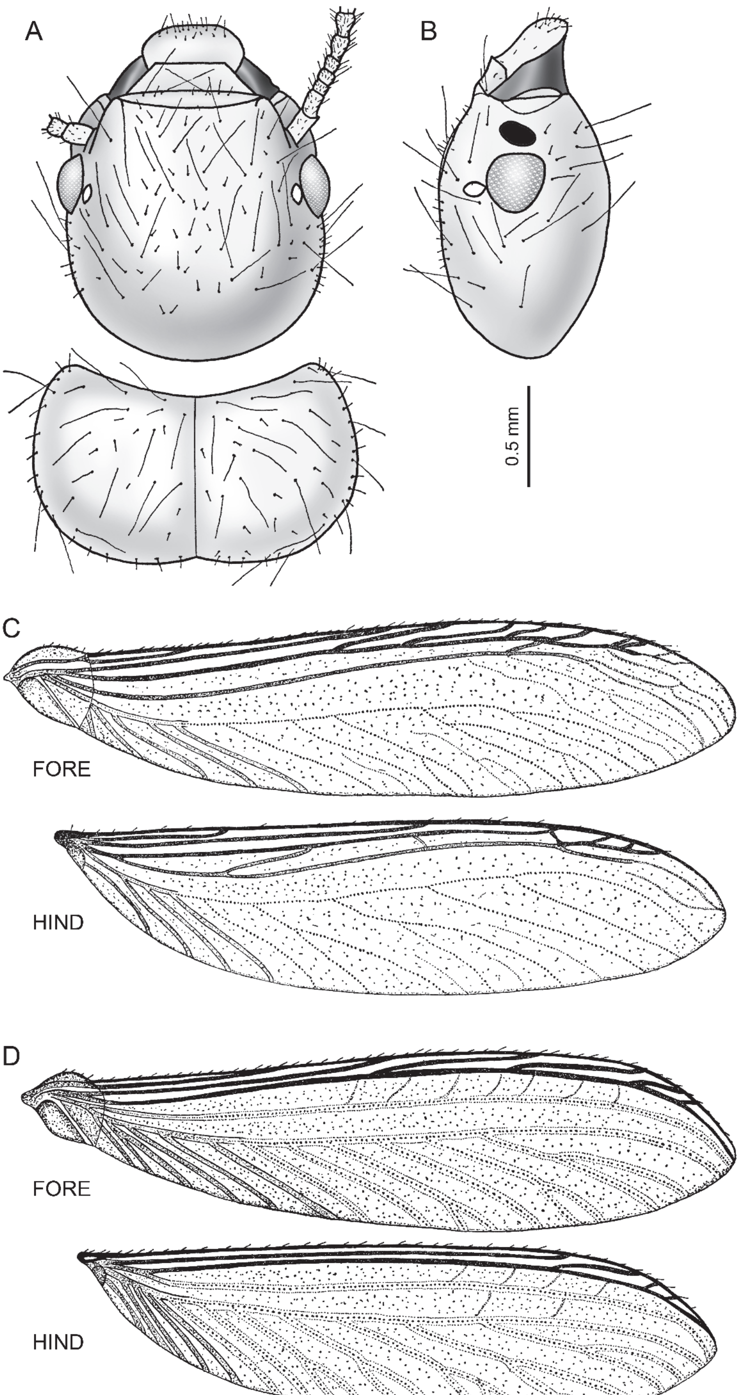


FIGURE 39. Imagoes of exemplar Kalotermitidae. *Comatermes perfectus* (Hagen): **A.** Head and pronotum, dorsal view; **B.** head, lateral view. **C.** *Paraneotermes simplicicornis* (Banks): forewing and hind wing. **D.** *Incisitermes schwarzi* (Banks): forewing and hind wing.

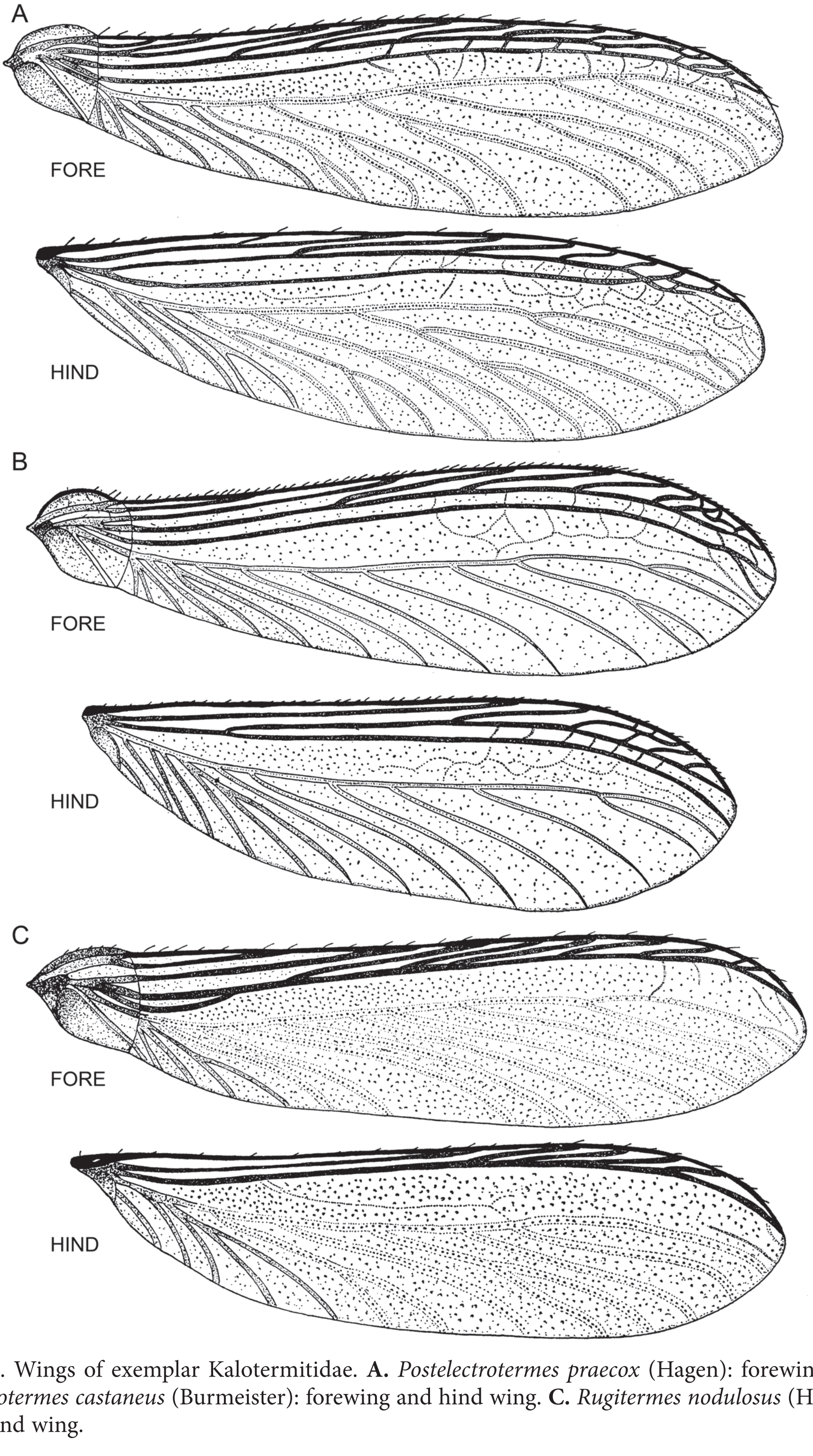


FIGURE 40. Wings of exemplar Kalotermitidae. **A.** *Postelectrotermes praecox* (Hagen): forewing and hind wing. **B.** *Neotermes castaneus* (Burmeister): forewing and hind wing. **C.** *Rugitermes nodulosus* (Hagen): forewing and hind wing.

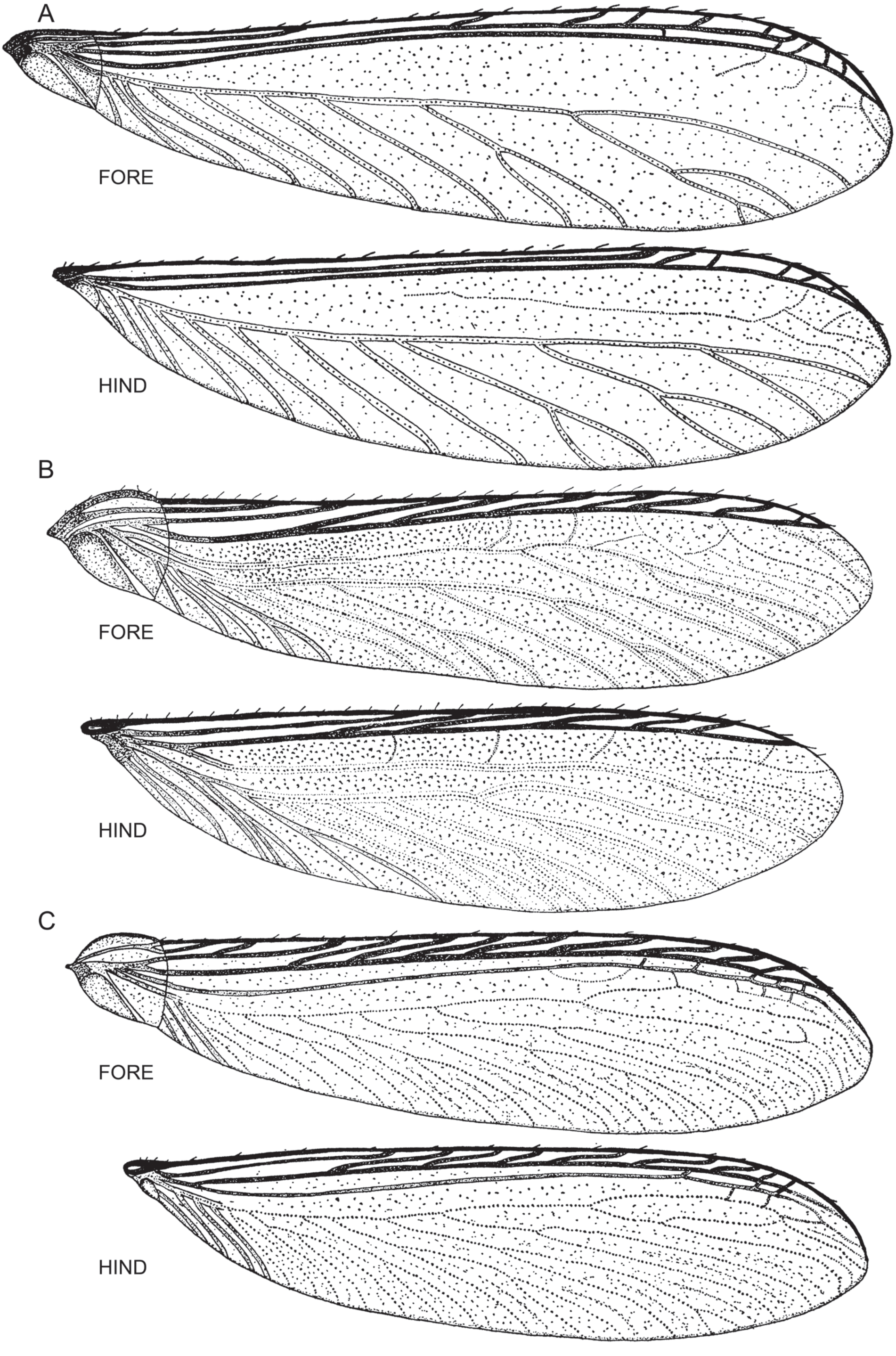


FIGURE 41. Wings of exemplar Kalotermitidae. **A.** *Eucryptotermes hagenii* (Müller): forewing and hind wing. **B.** *Kalotermes flavicollis* (Fabricius): forewing and hind wing. **C.** *Ceratokalotermes spoliator* (Hill): forewing and hind wing.

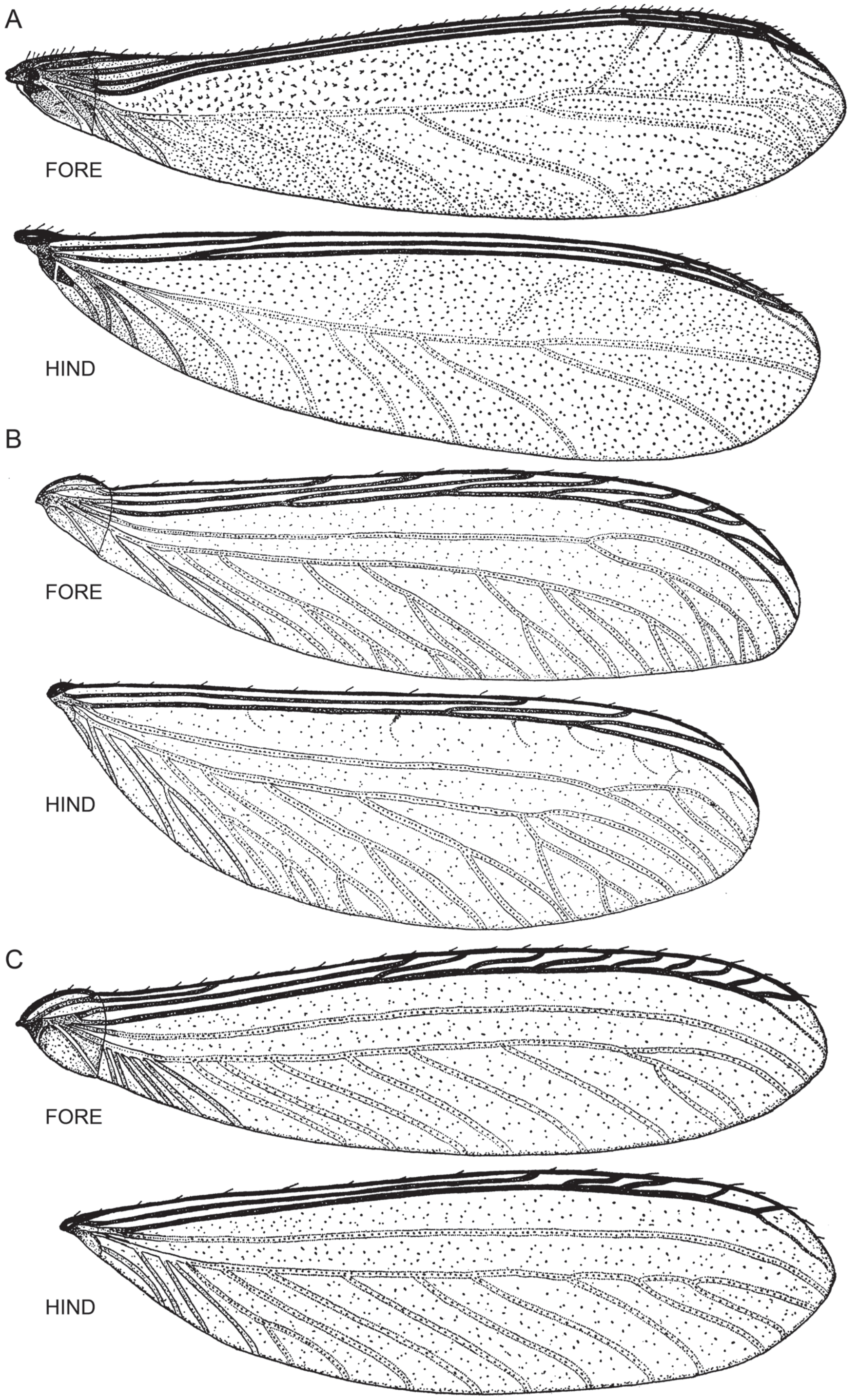


FIGURE 42. Wings of exemplar Kalotermitidae. **A.** *Glyptotermes canellae* (Müller): forewing and hind wing. **B.** *Pterotermes occidentis* (Walker): forewing and hind wing. **C.** *Marginitermes hubbardi* (Banks): forewing and hind wing.

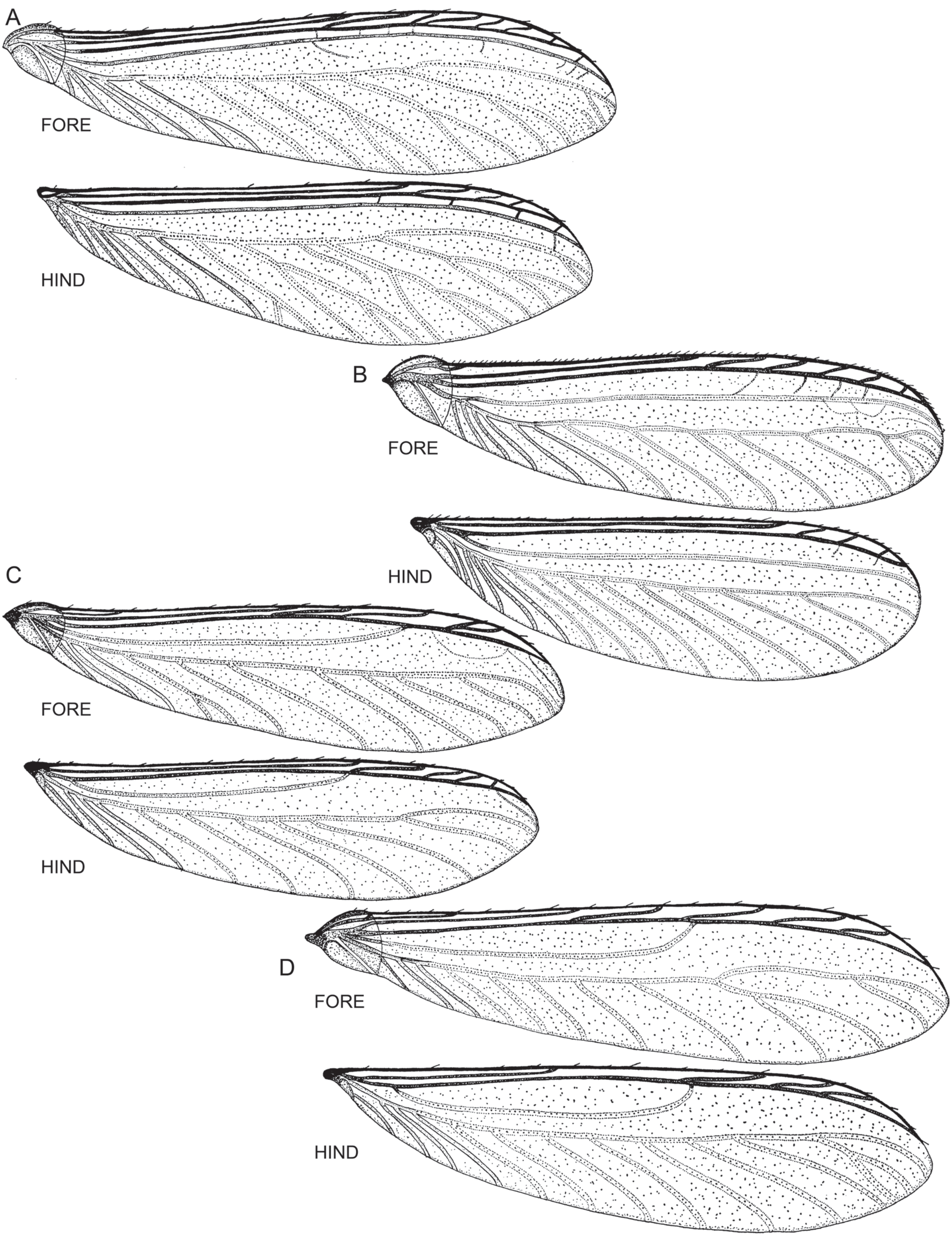


FIGURE 43. Wings of exemplar Kalotermitidae. **A.** *Proneotermes perezi* (Holmgren): forewing and hind wing. **B.** *Bifiditermes madagascariensis* (Wasmann): forewing and hind wing; **C.** *Cryptotermes cavifrons* Banks: forewing and hind wing; **D.** *Procryptotermes fryeri* (Holmgren): forewing and hind wing.

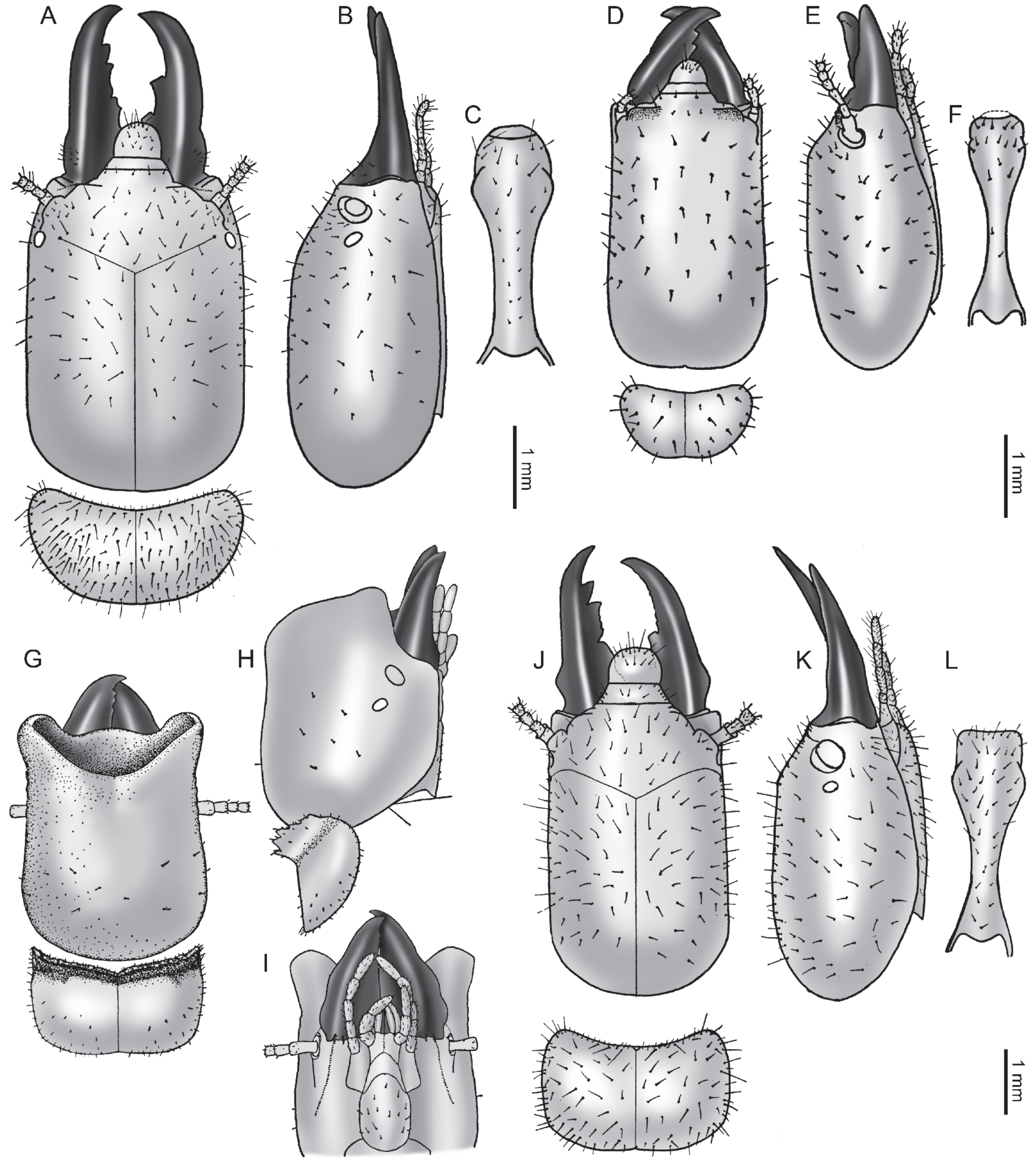


FIGURE 44. Soldiers of exemplar Kalotermitidae. *Neotermes castaneus* (Burmeister): **A.** Head and pronotum, dorsal view; **B.** head, lateral view; **C.** postmentum, ventral view. *Rugitermes nodulosus* (Hagen): **D.** Head and pronotum, dorsal view; **E.** head, lateral view; **F.** postmentum, ventral view. *Eucryptotermes hagenii* (Müller): **G.** Head and pronotum, dorsal view; **H.** head, lateral view; **I.** head, ventral view. *Kalotermes flavicollis* (Fabricius): **J.** Head and pronotum, dorsal view; **K.** head, lateral view; **L.** postmentum, ventral view.

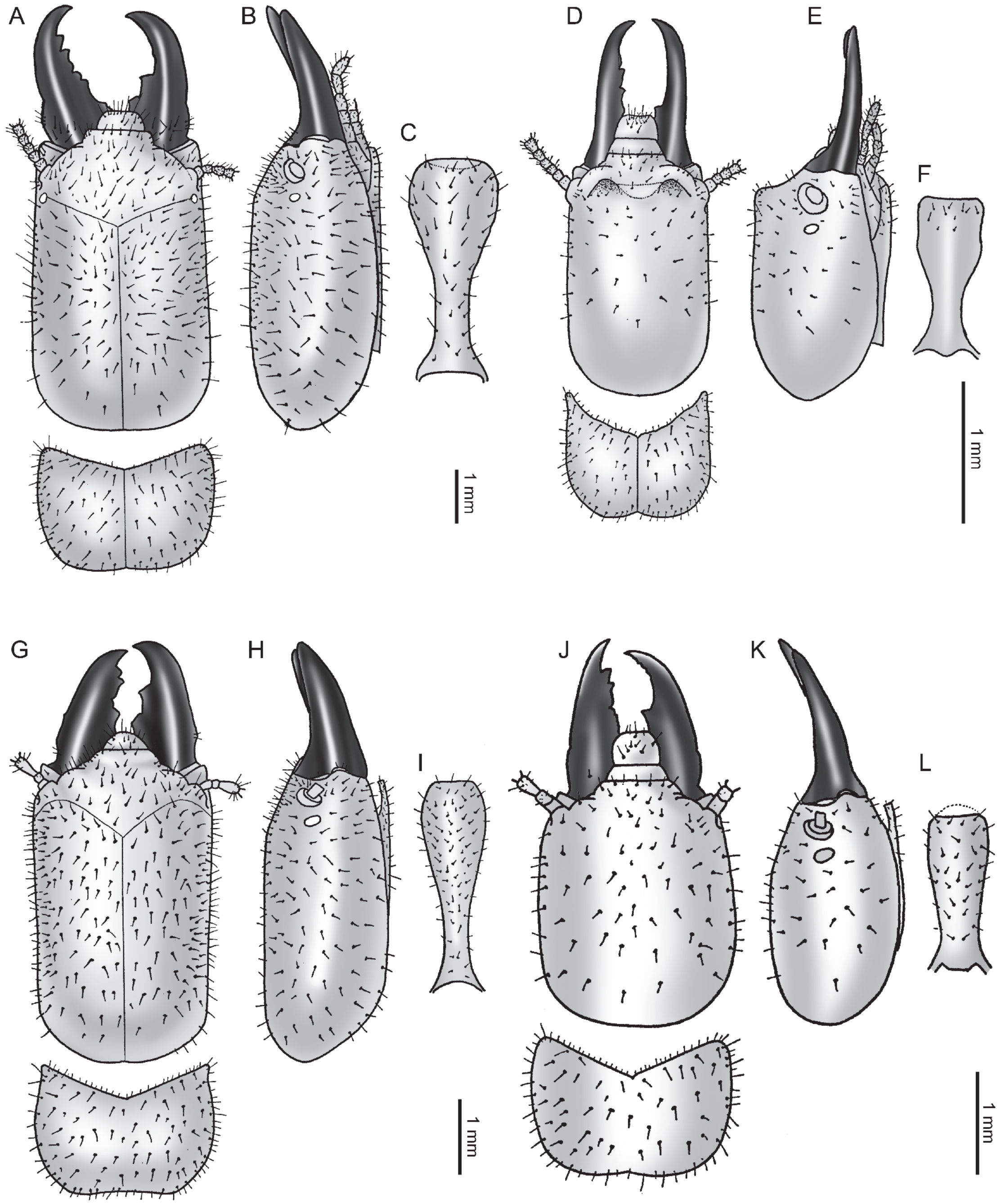


FIGURE 45. Soldiers of exemplar Kalotermitidae. *Paraneotermes simplicicornis* (Banks): **A.** Head and pronotum, dorsal view; **B.** head, lateral view; **C.** postmentum, ventral view. *Ceratokalotermes spoliator* (Hill): Soldier. **D.** Head and pronotum, dorsal view; **E.** head, lateral view; **F.** postmentum, ventral view. *Incisitermes schwarzi* (Banks): Large soldier. **G.** Head and pronotum, dorsal view; **H.** head, lateral view; **I.** postmentum, ventral view. *Incisitermes schwarzi* (Banks): Small soldier. **J.** Head and pronotum, dorsal view; **K.** head, lateral view; **L.** postmentum, ventral view.

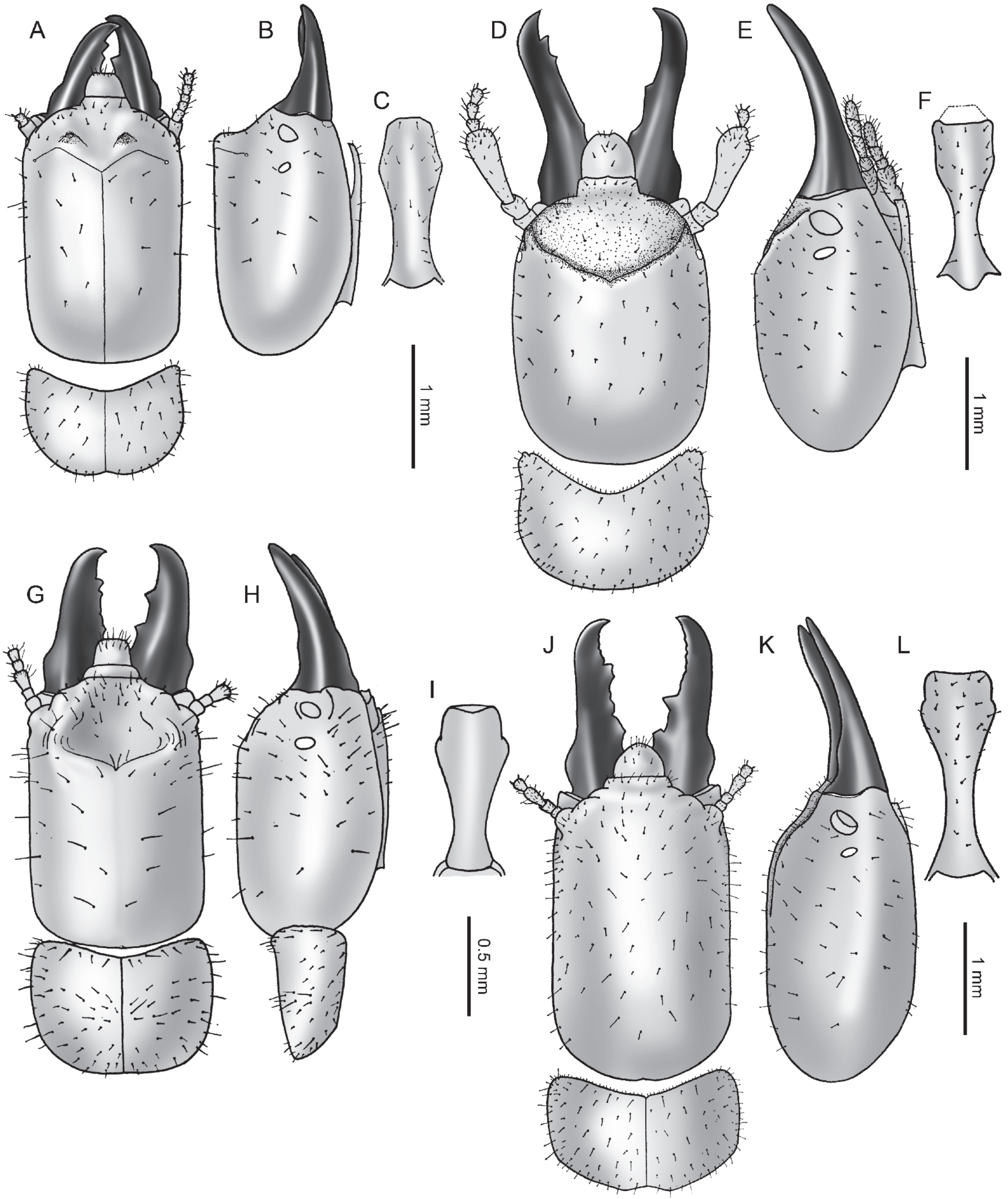


FIGURE 46. Soldiers of exemplar Kalotermitidae. *Glyptotermes tuberculatus* Froggatt: **A.** Head and pronotum, dorsal view; **B.** head, lateral view; **C.** postmentum, ventral view. *Marginitermes hubbardi* (Banks): **D.** Head and pronotum, dorsal view; **E.** head, lateral view; **F.** postmentum, ventral view. *Proneotermes perezi* (Holmgren): **G.** Head and pronotum, dorsal view; **H.** head, lateral view; **I.** postmentum, ventral view. *Bifiditermes madagascariensis* (Wasmann): **J.** Head and pronotum, dorsal view; **K.** head, lateral view; **L.** postmentum, ventral view.

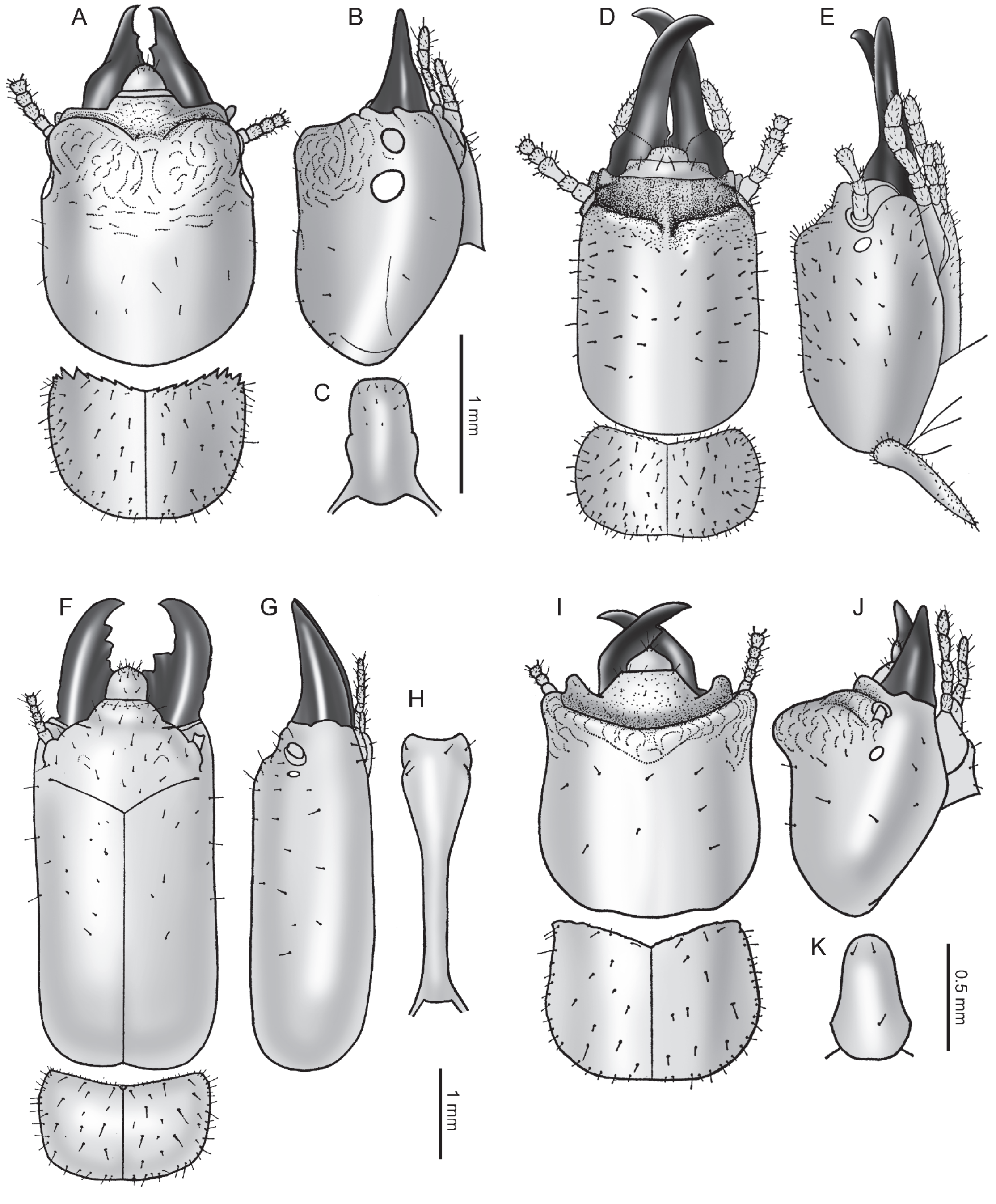


FIGURE 47. Soldiers of exemplar Kalotermitidae. *Bicornitermes bicornis* Krishna: **A.** Head and pronotum, dorsal view; **B.** head, lateral view; **C.** postmentum, ventral view. *Procryptotermes fryeri* (Holmgren): **D.** Head and pronotum, dorsal view; **E.** head and pronotum, lateral view. *Comatermes perfectus* (Hagen): **F.** Head and pronotum, dorsal view; **G.** head, lateral view; **H.** postmentum, ventral view. *Cryptotermes cavifrons* Banks: **I.** Head and pronotum, dorsal view; **J.** head, lateral view; **K.** postmentum, ventral view.

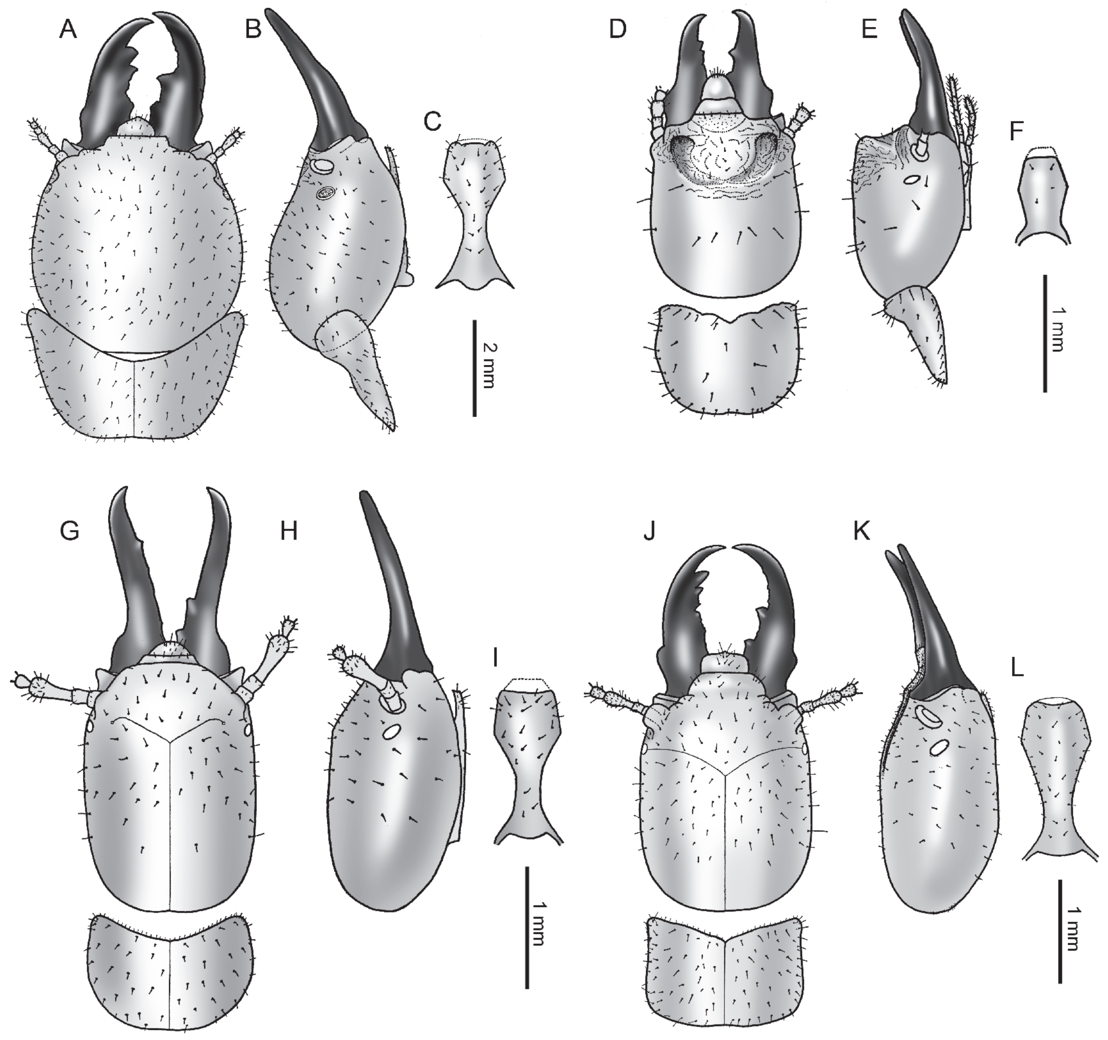


FIGURE 48. Soldiers of exemplar Kalotermitidae. *Pterotermes occidentis* (Walker): **A.** Head and pronotum, dorsal view; **B.** head and pronotum, lateral view; **C.** postmentum, ventral view. *Tauritermes taurocephalus* (Silvestri): **D.** Head and pronotum, dorsal view; **E.** head and pronotum, lateral view; **F.** postmentum, ventral view. *Allotermes paradoxus* Wasmann: **G.** Head and pronotum, dorsal view; **H.** head, lateral view; **I.** postmentum, ventral view. *Epicalotermes aethiopicus* Silvestri: **J.** Head and pronotum, dorsal view; **K.** head, lateral view; **L.** postmentum, ventral view.

similar to Kalotermitidae. Left mandible with an apical and two distinct marginal teeth, first and third, as second fused with first, first and third separated by a notch; posterior margin of fused first + second slightly longer than anterior margin of third. Right mandible with an apical and two marginal teeth. Legs: tarsi with five articles; tibial spurs 3:4:4; mid- and hind tibia with additional long spines; forecoxa with a projecting ridge; arolium present. Cerci with five articles. Sternal glands: three, on third, fourth, and fifth abdominal sternites. Wings: humeral plate absent in both wings. Forewing: reticulate; scale very large, overlapping hind-wing scale, costal margin of wing scale weakly arched; humeral suture well defined, strongly curved, not complete, terminating at inner end of anal region; Sc, R1, R2, R3, Rs, and M strongly sclerotized; Rs running parallel to costal margin, with several branches joining costal margin; M closer to Rs than to Cu, with branches radiating to apical margin; Cu weak, not sclerotized, with several branches joining lower margin; base of posterior anal vein represented only as dark pigmented area (also referred to as *basal stripe*). Hind wing: wing scale (basal) suture absent; anal lobe (anojugal) well developed, a feature unique among termites, but characteristic of roaches and mantids; single anal fold separated from anterior anal vein (multiple fanlike folds in blattids); posterior anal vein well developed.

Soldier: Head short and stout, broadly oval; eyes absent; mandibles stout, with two or three marginal teeth; antennae with 20–26 articles; pronotum large, saddle shaped, as wide as head. Legs: tarsi with five articles; tibial spurs 3:4:4; front margin of forecoxa with two pointed protuberances; foretibia with two mediolateral rows of short setae; forefemur with two mediolateral rows of short setae and additional long setae along the margin; arolium absent. Cerci with five articles.

Worker: Gut: esophagus not separated from crop; crop elongated, not separated from gizzard, muscle sheet well developed; gizzard strongly muscular, with chitinized armature, folds divided into columns (sclerotized, with scaly surface) and pulvilli (nonsclerotized), columns I and II elongated, with teeth on columns not prominent, pulvilli I small, pulvilli II reduced; stomodeal valve long; midgut or mesenteron long, cylindrical, forming an anticlockwise, circular ring, first dorsally, then ventrally under gizzard, ending in hindgut, ring diameter very wide, no mixed segment, with three small anterior bumps (= rudimentary coecae); Malpighian tubules 12–15 (possibly 16), inserted either singly or in pairs at midgut–hind gut junction, following a tortuous course around gut; hind gut with first proctodeal segment (P1) short, cylindrical, enteric valve (P2) well invaginated in paunch (P3), cushions (epithelial thickening) slightly prominent in posterior quarter of P1, more so in P2; cuticular armature of cushions with small scales; paunch (P3) large, dilated, divided into two unequal parts, separated by a sphincter, anterior smaller and more muscular than posterior, symbiotic protozoa only in posterior part; P3–P4 loop strongly twisted, P2 opening near sphincter; junction between paunch and colon (P4) with a huge armed sphincter, unique to this family; P4 a long tube, with a muscular rectal valve with folds near junction with rectum (P5), armature of valve with scales; P5 dilated (abridged from Noirot, 1995b).

Additional Characters and Biology: True worker caste present; eggs laid in pods (similar to ootheca in blattids); sperm multiflagellate; symbionts consisting of protozoa, spirochetes, bacteria. Habitat: found in logs, stumps of trees, or underground in large colonies; does not build mounds.

Genera Included: †*Blattotermes*, †*Garmitermes*, †*Idanotermes*, †*Khanitermes*, *Mastotermes*, †*Miotermes*†, †*Spargotermes*, †*Valditermes*.

Family Stolotermitidae

Figures 25C–D, 26, 28E–F, 36

Subfamily Porotermitinae

Imago: Fontanelle absent; Y-suture partially visible; eyes small; ocelli absent; antennae with 15–19 articles; postclypeus very short relative to width; pronotum faintly arched, narrower than head. Imago-worker mandibles: left with an apical tooth and three marginal teeth; right with an apical tooth and two marginal teeth, subsidiary tooth present at base of apical and first marginal tooth. Legs: tarsi with five articles; tibial spurs variable, 3:3:3 (*P. planiceps*), 3:3–4:2–4 (*P. adamsoni*); femur swollen; arolium absent. Cerci with 5 articles; styli short, present in males only. Forewing: wing membrane reticulated; scale either overlapping or just reaching hind-wing scale; all veins arising independently at wing suture; Sc not visible; R and Rs strongly developed and sclerotized; R simple or branched, with one or two subbranches extending to costal margin; Rs with variable number (5–8) of simple or forked offshoots extending to costal margin, one unsclerotized inferior branch extending to lower margin or tip of wing; M and Cu weak, branching variable; M closer to Cu than to Rs, with 4–6 branches and subbranches extending to lower margin; Cu with 5–10 branches and subbranches extending to lower margin; anal vein absent. Hind wing: R and Rs sclerotized, Rs and M arising from a common stem outside wing scale; Rs with 4–5 simple or forked branches extending to costal margin; M and Cu weak; M with 2–8 branches extending to lower margin; Cu with 4–10 branches and subbranches extending to lower margin; anal vein absent.

Soldier: Head long, somewhat flattened dorsoventrally; mandibles stout, with well-developed teeth; eyes rudimentary, with or without pigment; antennae with 13–19 articles; pronotum narrower than head. Legs: femur swollen; tibial spurs different from imago within same species, 3:2–4:2–3.

Pseudergate: Gut: esophagus not separated from crop; crop elongated, voluminous, slightly asymmetrical, muscle sheath reduced; gizzard strongly muscular, with chitinized armature, folds divided into columns (sclerotized, with scaly surface) and pulvilli (nonsclerotized), columns I and II short, rectangular, their cuticle poorly sclerotized, with prominent cylindrical, crenulated tooth in each, pulvilli I longer than columns (pulvilli II smaller than I), stomodeal valve long; midgut or mesenteron moderately long, cylindrical, forming an anticlockwise, circular ring, first dorsally, then ventrally under gizzard, ending in hind gut, ring diameter somewhat wide (similar to Kalotermitidae), no mixed segment, anterior coecae 3, at gizzard-midgut junction; Malpighian tubules 9, inserted at midgut–hind gut junction, long, following a tortuous course around the gut; hind gut with first proctodeal segment (P1) short, cylindrical, enteric valve (P2) short, cone shaped, well invaginated in paunch (P3), P1 shorter than P2, cushions in P1 poorly differentiated, nearly unarmed (i.e., with few spines and scales), most developed in anterior part of P2 (cf. Mastotermitidae and Hodotermitidae), cuticular armature of cushions more elaborate in P2, with pointed scales; paunch (P3) strongly dilated, shaped as in Kalotermitidae, containing symbiotic flagellates; P3–P4 loop less twisted than in Archotermopsidae, opening of P2 into P3 intermediate between those of Kalotermitidae and Archotermopsidae;

P4 a long tube, with a muscular rectal valve with folds near junction with P5, armature of valve with several hundred pectinated scales in each fold; P5 dilated (abridged from Noirot, 1995b).

Additional Characteristics and Biology: No true worker caste. Symbiotic protozoa present. Strictly wood dwelling; with soil connections (to ensure adequate moisture), nests in decaying logs and dead or living trees, some pest species.

Genera Included: †*Chilgatermes*, *Porotermes.*

Subfamily Stolotermitinae

Imago: Fontanelle absent; Y-suture present; eyes small; ocelli absent; antennae with 13–18 articles; postclypeus very short, relative to width; pronotum flat, narrower than head. Imago-worker mandibles: left with an apical tooth and three marginal teeth; right with an apical tooth and two marginal teeth, subsidiary tooth present at base of apical and first marginal tooth. Legs: tarsi with four articles; tibial spurs variable, 3:3:2 or 2:2:2; tibia without lateral spines; femur swollen; arolium absent. Cerci with 4–5 articles (fifth difficult to see *fide* Emerson). Wings dark, weakly reticulated, with dark micrasters. Forewing: scale overlapping hind-wing scale; all veins arising independently at wing suture; Sc, R, and Rs strongly sclerotized; Rs with 4–8 simple or forked subbranches extending to costal margin; M and Cu weak; M closer to Cu than to Rs; M with about 6 subbranches extending to lower margin; Cu with 3–5 branches extending to lower margin; anal vein absent. Hind wing: Sc absent; Rs and M arising from a common stem outside of wing scale; Rs with 4–6 branches and subbranches extending to costal margin; M and Cu weak; anal vein absent.

Soldier: Head long and markedly flattened dorsoventrally; mandibles with well-developed teeth; eyes rudimentary, pigmented; antennae with 14–19 articles; pronotum flat, narrower than head. Legs: femur swollen; tibial spurs as in imago; arolium absent.

Pseudergate: Gut: esophagus not separated from crop; crop elongated, voluminous, slightly asymmetrical, muscle sheath reduced; gizzard strongly muscular, with chitinized armature, folds divided into columns (sclerotized, with scaly surface) and pulvilli (nonsclerotized), columns I and II short, rectangular, their cuticle poorly sclerotized, with prominent conical, crenulated tooth in each, pulvilli I longer than columns (pulvilli II smaller than I), stomodeal valve long; midgut or mesenteron moderately long, cylindrical, forming an anticlockwise, circular ring, first dorsally, then ventrally under gizzard, ending in hind gut, ring diameter somewhat wide (similar to Kalotermitidae), no mixed segment, anterior coecae 2, at gizzard-midgut junction; Malpighian tubules 8, inserted at midgut–hind gut junction, long, following a tortuous course around the gut; hind gut with first proctodeal segment (P1) short, cylindrical, enteric valve (P2) short, cone shaped, well invaginated in paunch (P3), P1 shorter than P2, cushions in P1 poorly differentiated, nearly unarmed (i.e., with few spines and scales), most developed in anterior part of P2 (cf. Mastotermitidae and Hodotermitidae), cuticular armature of cushions more elaborate in P2, with narrow pointed scales; paunch (P3) strongly dilated, shaped as in Kalotermitidae, containing symbiotic flagellates; P3–P4 loop less twisted than in Archotermopsidae, opening of P2 into P3 intermediate between those of Kalotermitidae and Archotermopsidae; P4 a long tube, with a muscular rectal valve with folds near junction with

P5, armature of valve with several hundred pectinated scales in each fold; P5 dilated (abridged from Noirot, 1995b).

Additional Characters and Biology: No true worker caste; symbiotic protozoa present; strictly wood dwellers; nest in decaying logs.

Genus Included: *Stolotermes.*

Family †Termopsidae

Figure 65D, E

Imago: Eyes small, not prominent; ocelli absent; fontanelle absent; Y-suture present; antennae with at least 23 articles; pronotum slightly narrower than head. Legs: tarsi with five complete articles, tibial spurs 3:3–4:3, additional spines on mid- and hind tibia; arolium present. Cerci long, extending beyond tip of abdomen, with 5–6 articles. Styli present. Wings: distinctly reticulated, forewing scale with anterior margin only slightly arched (nearly straight), all veins originating inside of wing scale, Sc, R, R1, R2, and Rs heavily sclerotized, Rs with at least nine branches and subbranches encompassing a wide field in the apical third of the wing, M weak, running closer to Cu than to Rs, with 6–7 branches and subbranches, some reaching lower margin of wing, Cu weak with 8–9 branches and subbranches, anal vein absent.

Soldier: Unknown.

Worker: Unknown.

Genus Included: †*Termopsis.*

NEOISOPTERA

Family †Archeorhinotermitidae

Figures 64C, D

Imago: Head small, roundish, slightly longer than wide; fontanelle present; Y-suture absent; eyes medium sized; ocelli present, large; antennae with 13+ articles; postclypeus narrow, not prominently arched; pronotum narrower than head. Legs: tarsi with four articles, tibial spurs appear 3:2:2. Mandibles: left with a long, prominent, fingerlike apical tooth and three marginal teeth of approximately equal size, the apical tooth much longer than the three marginal teeth, fourth marginal tooth pointed and clearly visible from above (visible only in side vew in living species of Rhinotermitidae), outer margin with a prominent protuberance posterior to apical tooth; right with a small subsidiary tooth at base of upper margin of first marginal tooth, second marginal tooth prominent, equal in length to first marginal tooth, with its tip at the same level and its posterior margin with a medium sized cutting edge (longer in all other subfamilies of the Rhinotermitidae). Wings reticulate, without hairs or bristles; forewing scale covering hind wing scale (characteristic of the Rhinotermitidae); forewing with M vein simple, as strongly sclerotized as radial sector (Rs) and running midway between Rs and cubitus (Cu).

Soldier: Unknown.

Worker: Unknown.

Genus Included: †*Archeorhinotermes*, in mid-Cretaceous amber from Myanmar.

Family Rhinotermitidae

Figures 22A–C, 50–55

Imago: Fontanelle present, small to large; eyes variable in size, small to moderately large; ocelli present; pronotum flat, variable in width, narrower or wider than head. Imago-worker mandibles: left with an apical tooth and three marginal teeth; right with an apical tooth and two marginal teeth, subsidiary tooth present at base of apical and first marginal tooth. Legs: tarsi with four articles; tibial spurs 2:2:2 or 3:2:2; arolium absent. Cerci with two articles. Sternal gland: one, on fifth sternite. Wings: reticulate, membrane with or without hairs. Forewing: scale large, overlapping hind-wing scale (except in Psammotermitinae, Termitogetoninae); all veins arising independently from inside scale (except in Prorhinotermitinae, Psammotermitinae); costa fused with Sc, the fused vein running along entire interior margin of wing; Rs sclerotized, running close to costal margin; M vein present or absent, weak, running closer to Cu than to Rs, with branches extending to apex or lower margin; Cu weak, with several branches extending to lower margin; anal vein absent. Hind wing: costa-subcosta and Rs as in forewing; M arising from Rs, outside wing scale; cu as in forewing.

Soldier: Mono- or dimorphic. Head oval to rectangular; fontanelle present; antennae 12–19 articles; pronotum flat. Legs: tibial spurs 3:2:2 or 2:2:2; arolium absent. Cerci with two articles.

Worker: Gut: esophagus separated from crop (unlike other families of lower termites); crop shorter than in other lower termites, ovoid or subspherical, asymmetrical, with muscle sheath strongly reduced, as in Serritermitidae and Termitidae, cuticle with microsculpturing (furrows and striations); gizzard elongated, nearly cylindrical, strongly muscular, with chitinized armature, folds divided into columns (sclerotized, with scaly surface) and pulvilli (nonsclerotized), columns I and II elongated, their length equal to that of pulvilli I, pulvilli II reduced, teeth in columns I and II varying with genera (in *Prorhinotermes* teeth conspicuous but not prominent, longer in II than I, in *Reticulitermes* teeth conspicuous but not prominent, longer in I than II, in *Termitogeton* teeth without sclerotization, in *Rhinotermes, Coptotermes, Heterotermes,* and *Psammotermes* no teeth, but cuticle thickened and sclerotized front to back; stomodeal valve long, cuticle with longitudinal striations, as in Serritermitidae and Termitidae; midgut or mesenteron short, cylindrical, forming an anticlockwise, circular ring, first dorsally, then ventrally under gizzard, ending in hind gut, ring diameter narrow (as in Serritermitidae), no mixed segment, no anterior coecae at gizzard-midgut junction; Malpighian tubules 8, inserted at midgut–hind gut junction, long, following a tortuous course around the gut; hind gut with first proctodeal segment (P1) short, narrow at base, well invaginated in paunch (P3), P2 wider, cylindrical, enlarged posteriorly, cushions extending entire length of P1 and P2 (as in Kalotermitidae), cuticular armature of cushions generally well developed, cushion I on P2 more developed than that on P1, the inner pointed tip of cushion I on P2 (referred to as "eschutcheon" by Noirot) varying in shape and armature among the subfamilies, cushion I on P1 rectangular, cushion II distinct in P1, generally indistinct in P2 (Prorhinotermitinae,

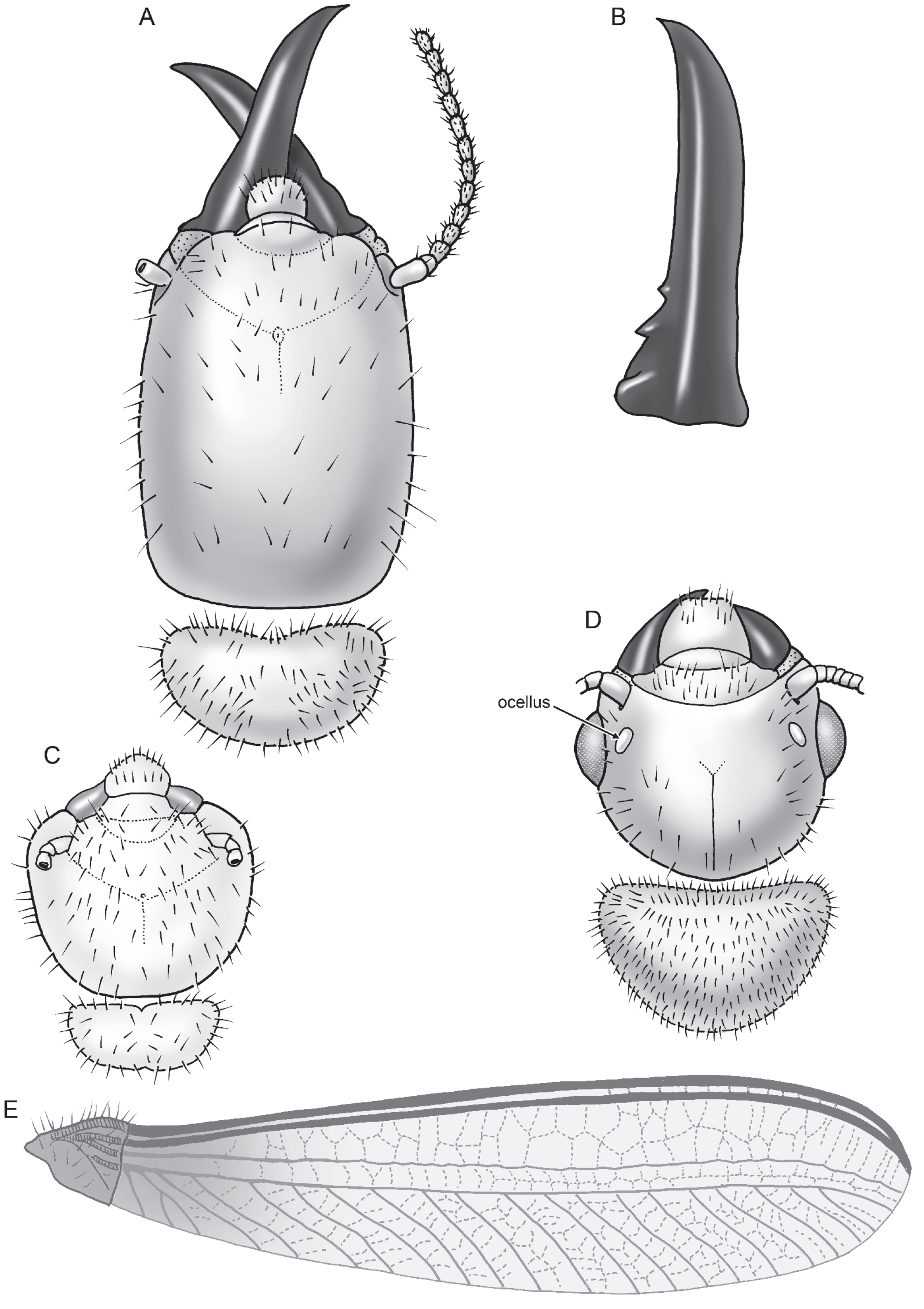


FIGURE 49. *Stylotermes* spp. (Stylotermitidae). **A–D.** *Stylotermes bengalensis* Mathur and Chhotani **E.** *Stylotermes fletcheri* Holmgren and Holmgren. **A.** Head and pronotum of soldier, dorsal view. **B.** Detail of soldier mandible. **C.** Head and pronotum of worker, dorsal view. **D.** Same, imago. **E.** Forewing. A, C, D to the same scale.

FIGURE 50. Imago heads of exemplar genera and species of Rhinotermitidae. **A.** *Psammotermes allocerus* Silverstri. **B.** *Coptotermes curvignathus* Holmgren. **C.** *Heterotermes platycephalus* Froggatt. **D.** *Dolichorhinotermes longilabius* (Emerson). **E.** *Schedorhinotermes* sp. **F.** *Termitogeton umbilicatus* (Hagen). Scanning electron micrographs; all scale lines = 0.5 mm.

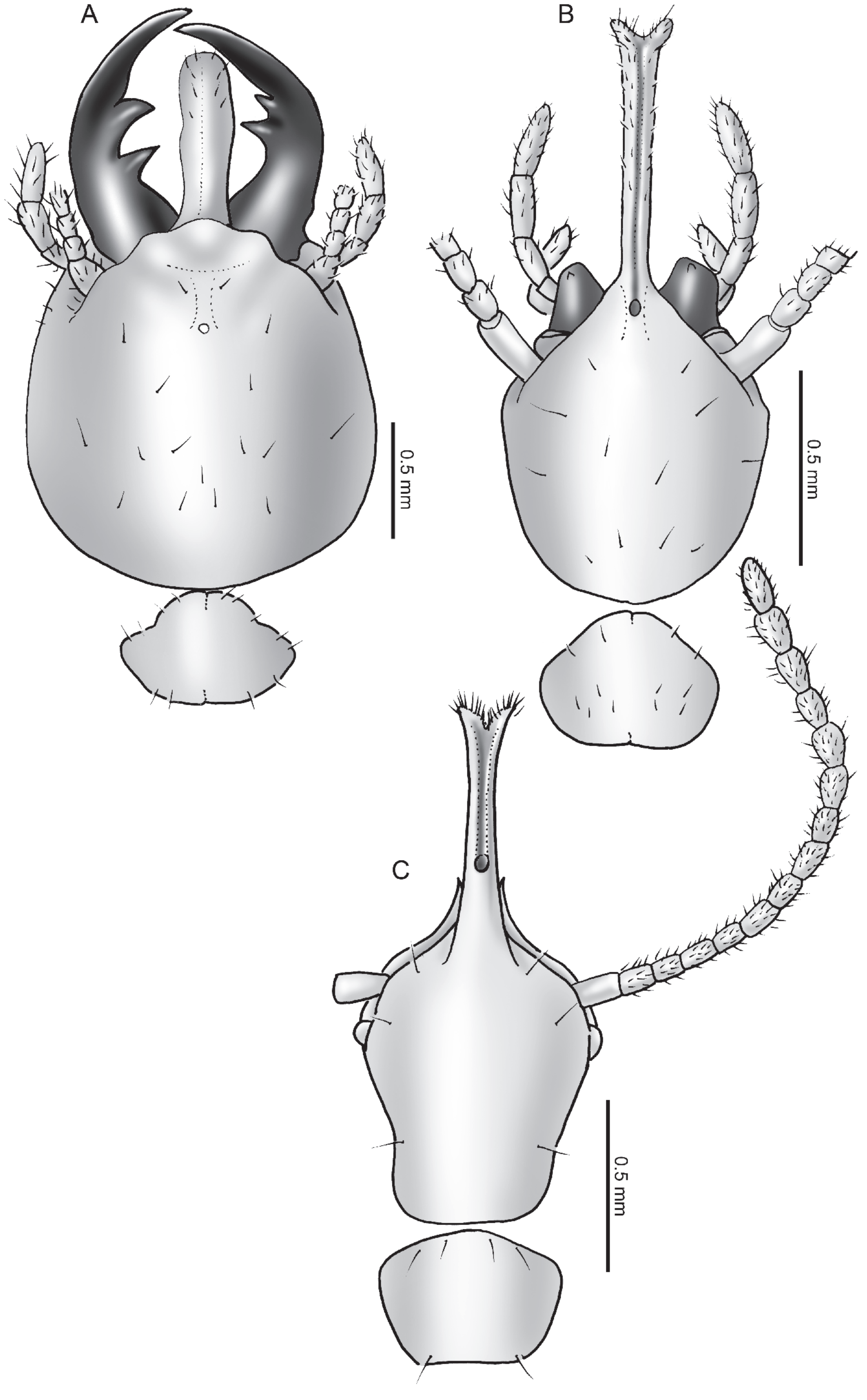


FIGURE 51. Soldiers of exemplar Rhinotermitidae. **A, B.** *Dolichorhinotermes laneiarius* Engel and Krishna. **A.** Major soldier. **B.** Minor soldier. **C.** *Acorhinotermes subfuscipes* (Emerson), minor soldier. Not to the same scale.

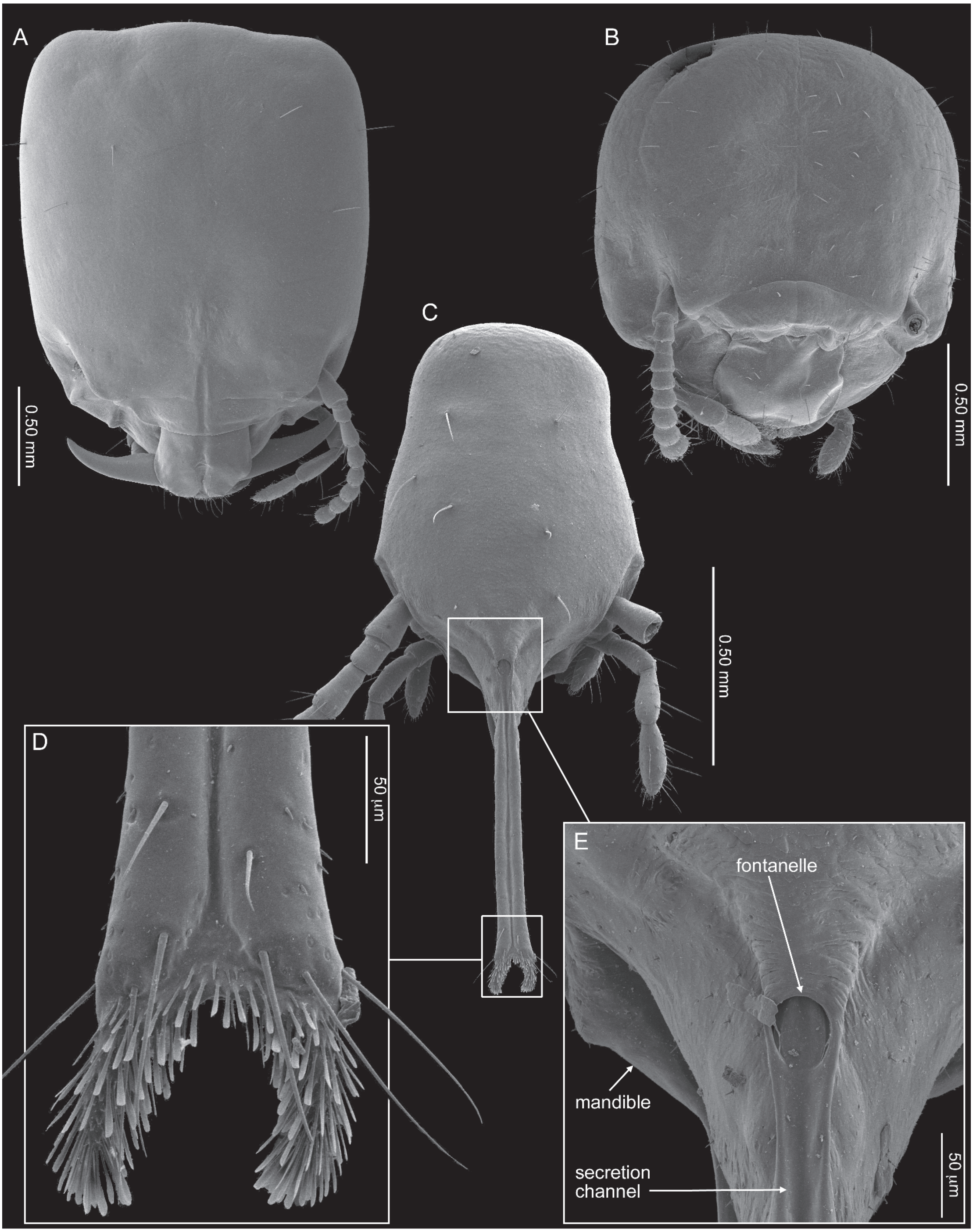


FIGURE 52. Heads of three of the four castes of *Rhinotermes marginalis* (Linnaeus) (Rhinotermitidae), frontal views (SEMs). **A.** Major soldier. **B.** Worker. **C–E.** Minor soldier. **C.** Entire head, with proboscis. **D.** Detail of tip of proboscis, showing brush that retains drop of defensive secretion. **E.** Detail of fontanelle.

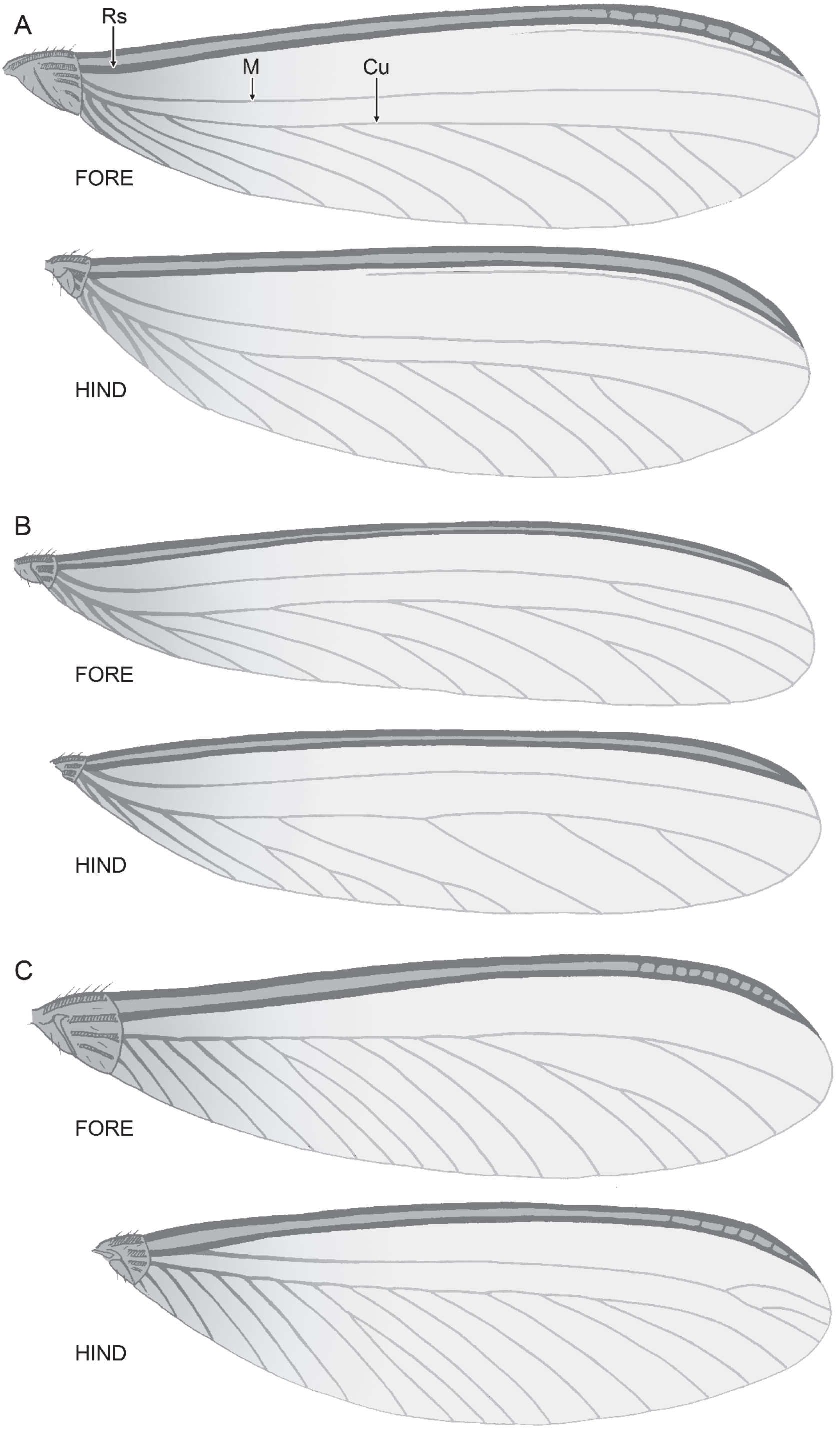


FIGURE 53. Fore- and hind wings of exemplar species and genera of Rhinotermitidae. **A.** *Coptotermes curvignathus* Holmgren. **B.** *Heterotermes platycephalus* Froggatt. **C.** *Prorhinotermes flavus* (Bugnion and Popoff).

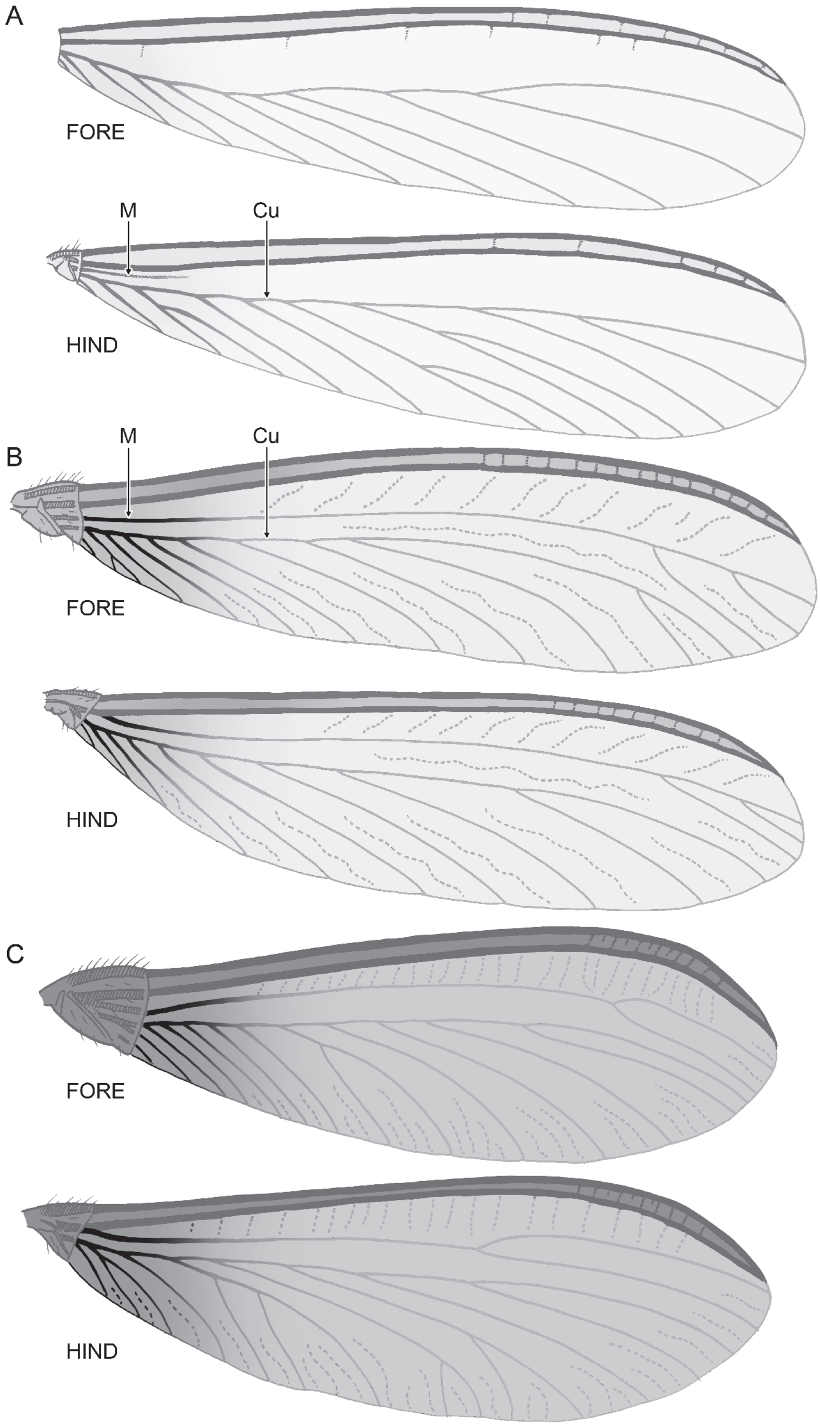


FIGURE 54. Fore- and hind wings of exemplar species and genera of Rhinotermitidae. **A.** *Psammotermes allocerus* Silvestri. **B.** *Reticulitermes flavipes* (Kollar). **C.** *Dolichorhinotermes longilabus* (Emerson).

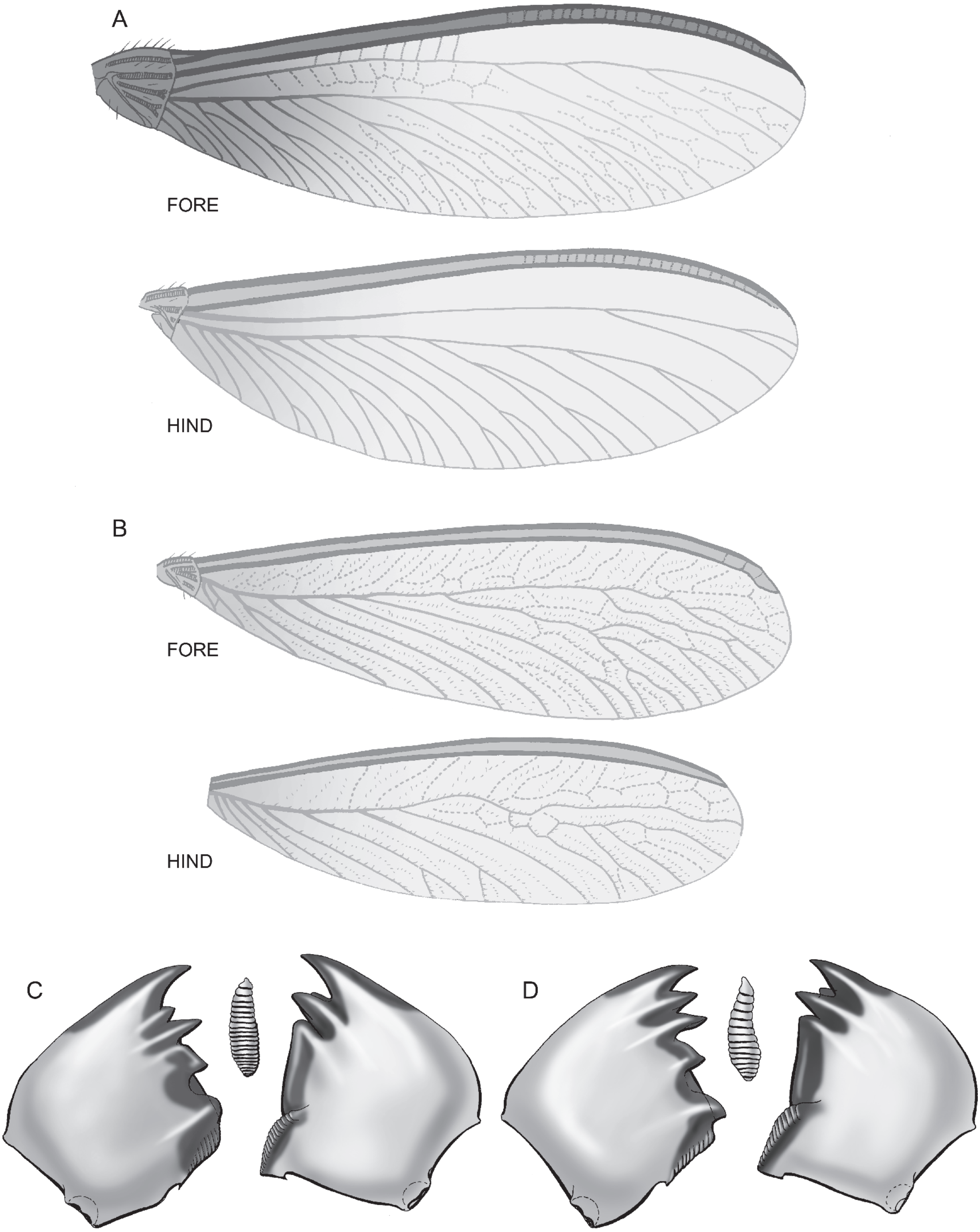


FIGURE 55. **A, B.** Fore- and hind wings of exemplar species and genera of Rhinotermitidae. **A.** *Schedorhinotermes* sp. (New Guinea). **B.** *Termitogeton umbilicatus* (Hagen). **C, D.** Worker mandibles of exemplar Rhinotermitidae. **C.** *Coptotermes acinaciformis* (Froggatt). **D.** *Reticulitermes flavipes* (Kollar).

Psammotermitinae, Termitogetoninae) or distinct (Heterotermitinae, Coptotermitinae, Rhinotermitinae); paunch (P3) dilated, containing symbiotic flagellates; P3–P4 loop untwisted (as in Kalotermitidae and Serritermitidae), P4 a long tube, with a very short muscular rectal valve with folds near junction with P5, armature of valve reduced, epithelium smooth or with a few unsclerotized scales; P5 dilated (abridged from Noirot, 1995b).

Additional Characters and Biology: True worker caste (except in Prorhinotermitinae); symbiont protozoa present.

Subfamily Coptotermitinae

Imago: Head almost semicircular; Y-suture generally not visible; fontanelle very small; eyes medium sized; ocelli present; antennae with 15–23 articles; postclypeus flat or slightly convex, short relative to width, with a median groove; pronotum flat. Imago-worker mandibles: left with one apical tooth and three marginal teeth, first marginal tooth smaller than apical, second marginal and third marginal tooth; right with an apical tooth and two marginal teeth, subsidiary tooth present at base of apical and first marginal tooth. Legs: tarsi with four articles; tibial spurs 3:2:2; arolium absent. Cerci with two articles; styli only in male. Sternal gland as in Rhinotermitidae. Wings densely hairy. Forewing as in Rhinotermitidae. Hind wing as in Rhinotermitidae.

Soldier: Head pear shaped; fontanelle prominent, large, roundish, opening in front at base of clypeus; frontal gland well developed. Mandibles saber shaped: left with several serrations at inner basal region and a projection below serrations; right without serrations. Antennae with 13–17 articles. Pronotum flat or faintly convex, with front margin slightly raised. Legs as in imago. Cerci as in Rhinotermitidae.

Additional Characters and Biology: Nest in logs, stumps, holes in trees, with soft carton deposits; some species forming definitive low mounds; many species are serious pests, introduced into several parts of the world.

Genus Included: *Coptotermes.*

Subfamily Heterotermitinae

Imago: Head: sides parallel below eyes; Y-suture distinct or indistinct; fontanelle very small, in middle of head; eyes small; ocelli very small, almost invisible; antennae with 12–19 articles; postclypeus weakly arched, shorter than half its width; pronotum flat, slightly narrower than head. Imago-worker mandibles: left with apical tooth and three marginal teeth, first marginal tooth equal to (*Reticulitermes*) or shorter than (*Heterotermes*) apical tooth, second marginal almost equal in length to apical tooth; right with apical tooth and two marginal teeth, subsidiary tooth present at base of apical and first marginal tooth. Legs: tibial spurs 3:2:2. Cerci as in Rhinotermitidae; styli in male only. Sternal gland as in Rhinotermitidae. Wings with few setae on membrane, venation as in Rhinotermitidae

Soldier: Head long and narrow, with parallel sides, frons strongly inclined; with or without dorsolateral protuberances; fontanelle small. Mandibles long, saber shaped, without teeth;

left with a large basal projection and four serrations above it; right with one or two minute serrations. Antennae with 12–19 articles. Labrum with tip pointed, needlelike, or blunt. Pronotum flat, narrower than head. Legs: tibial spurs as in imago. Cerci as in imago.

Additional Characters and Biology: Subterranean, with no discrete nests, in soil, colonies also in rotten logs or stumps of dead wood in contact with soil; some colonies found in mounds of other termites (*Heterotermes*); many pest species.

Genera Included: *Heterotermes, Reticulitermes.*

Subfamily Prorhinotermitinae

Imago: Head roundish to oval; fontanelle present, in middle of head; eyes small to medium sized; ocelli present; antennae with 17–22 articles; pronotum flat, narrower than head; postclypeus short relative to width, moderately arched; imago-worker mandibles: left with an apical tooth and three marginal teeth, second marginal same size as apical tooth, longer than first marginal tooth; right with apical tooth and two marginal teeth, subsidiary tooth present at base of apical and first marginal tooth. Legs: tibial spurs 3:2:2. Cerci as in Rhinotermitidae. Sternal gland as in Rhinotermitidae. Wings: membrane with few setae; forewing scale overlapping hind-wing scale, forewing Sc, R, and Rs as in Rhinotermitidae, M absent or present, when present arising from Cu, outside the wing scale (as in Psammotermitinae), in the middle or beyond the middle of the wing; in hind wing, M also arising from Cu (unlike all other rhinotermitids) or from the Rs, as in all other rhinotermitids.

Soldier: Dimorphic; head with sides rounded; fontanelle small, situated slightly beyond middle of head, groove present from fontanelle to clypeus; labrum without brush at tip; mandibles without teeth; antennae with 15–19 articles. Legs: tibial spurs 3:2:2.

Additional Characters and Biology: No true worker caste, unique to this subfamily of the Rhinotermitidae. Nest in decaying and dead trees, stumps, logs, or damp, decaying wood, with no connection to soil. Distribution mostly insular, rarely on mainland. Speculation that colonies can be transported in driftwood by ocean currents, thus accounting for wide distribution in islands of the South Pacific; some pest species.

Genera Included: *Prorhinotermes, †Zophotermes*.

Subfamily Psammotermitinae

Imago: Head nearly flat; Y-suture not visible; fontanelle prominent, located in middle; eyes small; ocelli present; antennae with 15–17 articles; postclypeus narrow, convex; pronotum flat, narrower than head. Imago-worker mandibles: left with apical tooth and three marginal teeth, first marginal tooth shorter than apical tooth and second marginal tooth, second marginal tooth subequal to apical tooth, third marginal tooth equal in length to second; right with apical tooth and two marginal teeth, subsidiary tooth present at base of apical and first marginal tooth. Legs: tibial spurs 3:2:2 (2:2:2 in *Glossotermes*). Cerci as in Rhinotermitidae; styli in male only. Sternal gland as in Rhinotermitidae. Wings: membrane transparent, anterior margin without setae; forewing scale not overlapping hind-wing scale, almost as long as hind wing scale. Forewing venation as in Rhinotermitidae, except the M arising from the Cu outside the wing scale (a character also present in Prorhinotermitinae). Hind wing as in Rhinotermitidae.

Soldier: Mono- or polymorphic; head flat, almost rectangular; fontanelle small to fairly prominent. Mandibles slightly hooked at tip, inner margin with 5–9 marginal teeth or large number of prominent, variable serrations. Antennae with 12–17 articles. Pronotum flat. Legs: tibial spurs as in imago. Cerci as in Rhinotermitidae.

Additional Characters and Biology: Subterranean nests in sandy soil in arid regions; some pest species.

Genus Included: *Psammotermes.*

Subfamily Rhinotermitinae

Imago: Head large, circular; fontanelle present, situated anteriorly, median groove running from fontanelle to clypeus; eyes large; ocelli present; antennae with 16–20 articles; Y-suture indistinct; pronotum flat, slightly narrower than head; postclypeus short, arched, with or without noselike projection. Imago-worker mandibles: left with an apical tooth and three marginal teeth, second marginal shorter than first; right with apical tooth and two marginal teeth, subsidiary tooth present at base of apical and first marginal tooth. Legs: tibial spurs 3:2:2. Cerci as in Rhinotermitidae, styli present in both sexes. Sternal gland as in Rhinotermitidae. Wings reticulate, with few setae. Fore- and hind wings as in Rhinotermitidae.

Soldier: Monomorphic (*Parrhinotermes, Acorhinotermes*) or dimorphic (*Schedorhinotermes, Rhinotermes, Dolichorhinotermes*). Head oval or roundish. Fontanelle small, situated anteriorly, deep, narrow groove running from fontanelle to base of clypeus (major soldier) or to tip of labrum (minor soldier). Labrum in minor soldier long, broad or narrow, in major soldier short; apex hyaline, with a "brush" at tip. Mandibles with teeth (in dimorphic species major soldier with teeth, minor soldier with teeth or reduced mandibles). Antennae with 13–19 articles. Pronotum flat.

Additional Characters and Biology: Nest in rotten logs, fence posts, or trunks of dead or living trees, or in deserted mounds of other species; not known to build specific mounds of their own. Pests of crops and timber.

Genera Included: *Acorhinotermes, Dolicorhinotermes, Macrorhinotermes, Parrhinotermes, Rhinotermes, Schedorhinotermes.*

Subfamily Termitogetoninae

Imago: Head triangular, dorsoventrally flattened. Y-suture partially visible; fontanelle present; eyes small; ocelli present; antennae with 15 articles; postclypeus short and flat; pronotum narrower than head, anterior margin projected medially. Imago-worker mandibles: left with an apical tooth and three marginal teeth, second marginal longer than apical or first marginal; right with apical tooth and two marginal teeth, subsidiary tooth present at base of apical and first marginal tooth. Legs: tibial spurs 2:2:2. Cerci as in Rhinotermitidae. Sternal gland as in Rhinotermitidae. Wings densely hairy, forewing scale not overlapping hind-wing scale, just reaching its anterior tip (unlike all other Rhinotermitidae, except Psammotermtinae), wing venation as in Rhinotermitidae, except M absent or indistinct in forewing.

Soldier: Head triangular, flattened dorsoventrally, posterior margins strongly sinuate, with medial projection; fontanelle small; mandibles without prominent teeth, small tooth and crenulations at basal region. Antennae with 13–15 articles. Pronotum flat, narrower than head, front margin with a medial projection. Legs: hind coxa swollen, tibial spurs 2:2:2, as in imago.

Additional Characters and Biology: Nest in damp, decaying tree trunks and under bark; the flattened body most likely an adaptation to living under bark

Genus Included: *Termitogeton.*

Family Serritermitidae

Figure 56

Imago: Fontanelle present, medium sized; eyes medium sized; Y-suture present; ocelli present; pronotum flat, narrower than head; antennae with 11–14 articles (13–14 in *Serritermes*; 11–13 in *Glossotermes*); postclypeus large, long, strongly arched, slightly shorter than half its width. Imago-worker mandibles: each with large apical tooth, marginal tooth widely separated from apical tooth; left with one (*Serritermes*) or two (*Glossotermes*) marginal teeth, molar plate with ridges and toothlike projection at apical end; right with one marginal tooth, molar plate with ridges and toothlike projection at apical end. Legs: tarsi with four articles; tibial spurs 2:2:2; arolium absent. Cerci with two articles, styli absent in both sexes. Sternal gland: one on fifth sternite. Wings reticulate, without setae. Forewing: scale large, extending almost to base of hind wing scale, but not overlapping; Sc and R present; Rs sclerotized, running parallel and close to costal margin; M indistinct, possibly coalesced with Cu; Cu arising independently from inside wing scale (separate at suture), with 18–19 branches; anal vein absent. Hind wing: Sc, R, Rs, and Cu similar to forewing; M arising from Rs near suture.

Soldier: Monomorphic. Head long, somewhat flat (*Glossotermes*) to thick (*Serritermes*), with curved sides. Fontanelle present, small, below vestigial eyes. Antennae with 12–15 articles (12–13 in *Serritermes,* 13–15 in *Glossotermes*). Labrum large, longer than wide, with sides rounded, tip hyaline. Mandibles long, narrow, slightly (*Glossotermes*) to distinctly hooked (*Serritermes*) at tip. Left: inner margin with serrations of equal size, reaching almost to base (*Serritermes*) or fine serrations on upper half and coarser serrations in lower (*Glossotermes*), and a toothlike projection and a notch at base. Right: inner margin with serrations on upper half (*Serritermes*) or without serrations (*Glossotermes*) and a toothlike projection at base (+ a notch at base in *Glossotermes*). Pronotum saddle shaped, indented in front, frontal lobe large. Legs: tibial spurs 2:2:2; arolium absent. Cerci with two articles.

Worker: Gut: esophagus not well separated from crop (much separated in Rhinotermitidae); crop conical, reduced in size and musculature, with muscle sheath strongly reduced, as in Rhinotermitidae and Termitidae, cuticle distinctly striated and with furrows; gizzard medium sized, with reduced chitinized armature, columns I and II unsclerotized, without teeth, but with a few conical spines, pulvilli 1 about twice as long as columns, pulvilli 2 very

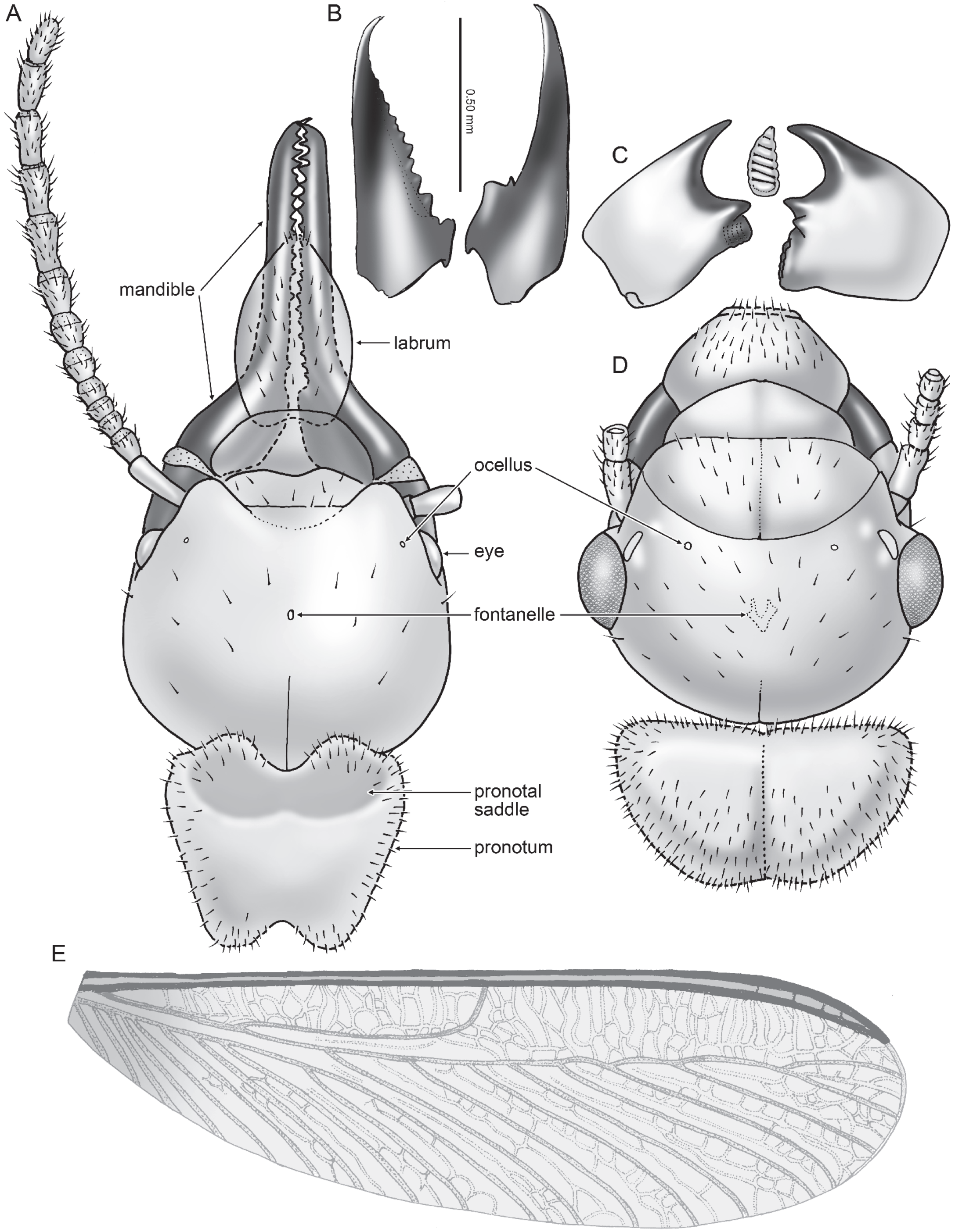


FIGURE 56. Exemplar Serritermitidae. **A, C–E.** *Serritermes serrifer* (Hagen and Bates). **A.** Head and pronotum of soldier *S. serrifer,* dorsal view. **B.** Soldier mandibles of *Glossotermes sulcatus* Cancello and DeSouza. **C.** Mandibles with molar plate of worker *S. serrifer.* **D.** Head and pronotum of imago. **E.** Forewing. Not to the same scale.

reduced; stomodeal valve short (unique among lower termites), cuticle with longitudinal striations, as in Rhinotermitidae and Termitidae; midgut or mesenteron short, cylindrical, forming an anticlockwise, circular ring, first dorsally, then ventrally under gizzard, ending in hind gut, ring diameter narrow (as in Rhinotermitidae), no mixed segment, no anterior coecae at gizzard-midgut junction; Malpighian tubules 8, inserted at midgut–hind gut junction, long, following a tortuous course around the gut; hind gut with first proctodeal segment (P1) short, cylindrical, P1 and P2 poorly differentiated (characteristic of the family), P2 invaginated in paunch (P3), P1 with 6 faint cushions, nearly unarmed; P2 cone shaped, shorter than P1, with 6 short, prominent cushions, cuticle on cushions with tiny scales and short curved spines; paunch (P3) strongly dilated, containing symbiotic flagellates; P3–P4 loop untwisted (as in Rhinotermitidae), P4 a long tube, with a very short muscular rectal valve with folds near junction with P5, rectal valve armature without scales; P5 dilated (abridged from Noirot, 1995b).

Additional Characters and Biology: True worker caste present; symbiont protozoa present. Nests in mounds, generally of *Cornitermes*; diet not known, might be vegetable detritus.

Genera Included: *Glossotermes, Serritermes.*

Family Stylotermitidae

Figure 49

Imago: Head nearly circular; fontanelle very small, sometimes not visible; eyes small to medium sized; ocelli present; antennae with 16–22 articles; postclypeus very short, faintly arched; pronotum flat. Imago-worker mandibles: left with one apical tooth and three marginal teeth, second marginal tooth very small, shorter than first marginal or apical tooth; right with an apical tooth and two marginal teeth, subsidiary tooth present at base of apical and first marginal tooth. Legs: tarsi with three articles; tibial spurs 3:2:2 (*Stylotermes*) or 2:2:2 (*Parastylotermes*). Cerci as in Rhinotermitidae. Sternal gland as in Rhinotermitidae. Wings reticulate, membrane without hairs. Forewing scale not overlapping hind-wing scale, almost touching tip of hind-wing scale: fore- and hind wing venation as in Rhinotermitidae.

Soldier: Head long, narrow; mandibles saber shaped, with one or two minute toothlike crenulations at base; fontanelle small; mandibles without prominent teeth, crenulations at inner basal region; antennae with 13–19 articles; pronotum flat.

Worker: Gut: see Rhinotermitidae.

Additional Characters and Biology: True worker caste present; symbiont protozoa present; small colonies, without discrete nest, in living and partially dead trees; some pest species.

Genera Included: †*Parastylotermes*, †*Prostylotermes*, *Stylotermes.*

Family Termitidae

Figures 29E–G, 30, 57–59

Imago: Fontanelle present; Y-suture present or absent; eyes small to large; ocelli present; antennae with 14–23 articles; postclypeus short to long, generally arched; pronotum saddle shaped. Imago-worker mandibles with apical tooth and two marginal teeth, except in some Termitinae (*Cavitermes, Crepititermes*) and Nasutitermitinae (*Mimeutermes*); left mandible with apical tooth shorter or longer than fused first plus second marginal tooth, third sometimes greatly reduced and represented as a rounded edge (*Amitermes, Drepanotermes*); right mandible with two marginal teeth, second marginal reduced or absent (*Jugositermes, Spinitermes, Tuberculitermes, Euchilotermes*). Legs: tarsi with four articles; tibial spurs 3:2:2 or 2:2:2, midtibia sometimes with additional spines. Cerci with two articles; styli present or absent. Sternal gland one, on fifth abdominal sternite. Forewing: scale short, not overlapping hindwing scale; membrane weakly or not reticulated; venation as in Rhinotermitidae.

Soldier: Caste present or absent; head shape variable; monomorphic, dimorphic, or trimorphic; fontanelle present; mandibles variable, short and stout, long and slender, or completely reduced as stubs (Nasutitermitinae), with or without teeth; biting or snapping type (symmetrical or asymmetrical). Antennae with 11–20 articles. Pronotum saddle shaped, narrower than head, anterior margin bilobed.

Worker: Crop musculature greatly reduced; gizzard without sclerotized tooth on columns I and II (unique to Termitidae); stomodeal valve with thin striations; midgut without caeca; Malpighian tubules 4 (2 in *Labidotermes*); no limiting groove between first proctodeal segment and enteric valve (P2); enteric valve armature within lumen of valve or everted into P3 (abridged from Noirot, 2001).

Additional Characters and Biology: True worker caste present; symbiotic protozoa absent, loss of proctodeal feeding; bacteria present.

Subfamily Apicotermitinae

Imago: Fontanelle present, small to large, oval, round, never slitlike, sometimes not visible; Y-suture generally not visible; antennae with 14–17 articles; labrum as broad as or broader than long, without transverse sclerotized band, tip partially hyaline; postclypus long, arched, longer than half its width. Imago-worker mandibles: left with apical tooth shorter (*Anoplotermes, Speculitermes* groups) or longer (*Apicotermes* group) than fused first plus second marginal tooth, posterior margin of first marginal tooth long and undulating, distinct notch or indentation between fused first plus second marginal tooth and third marginal tooth; right with first marginal tooth longer than second marginal tooth (all genera without soldiers), second marginal tooth reduced in some genera (*Apicotermes* group). Legs: forecoxa with longitudinal ridge on inner margin, with or without a protuberance and with fine, stiff setae and small scales; tibial spurs 3:2:2 or 2:2:2. Styli absent.

Soldier: Head with frontal gland weakly developed; fontanelle small, round, dotlike; antennae with 13–15 articles; legs as in imago; no soldier caste in all genera of the *Anoplotermes* group and some species of *Speculitermes.*

Worker: Gut: crop voluminous, asymmetrical; gizzard tubular, armature strongly reduced; generally no mixed segment, if present, on inner surface of mesentron or midgut; mesenteron-proctodeum junction transverse; Malpighian tubules 4 (2 in *Labidotermes*), swollen at base, attached separately to mesenteron some distance from mesenteron-proctodeum junction;

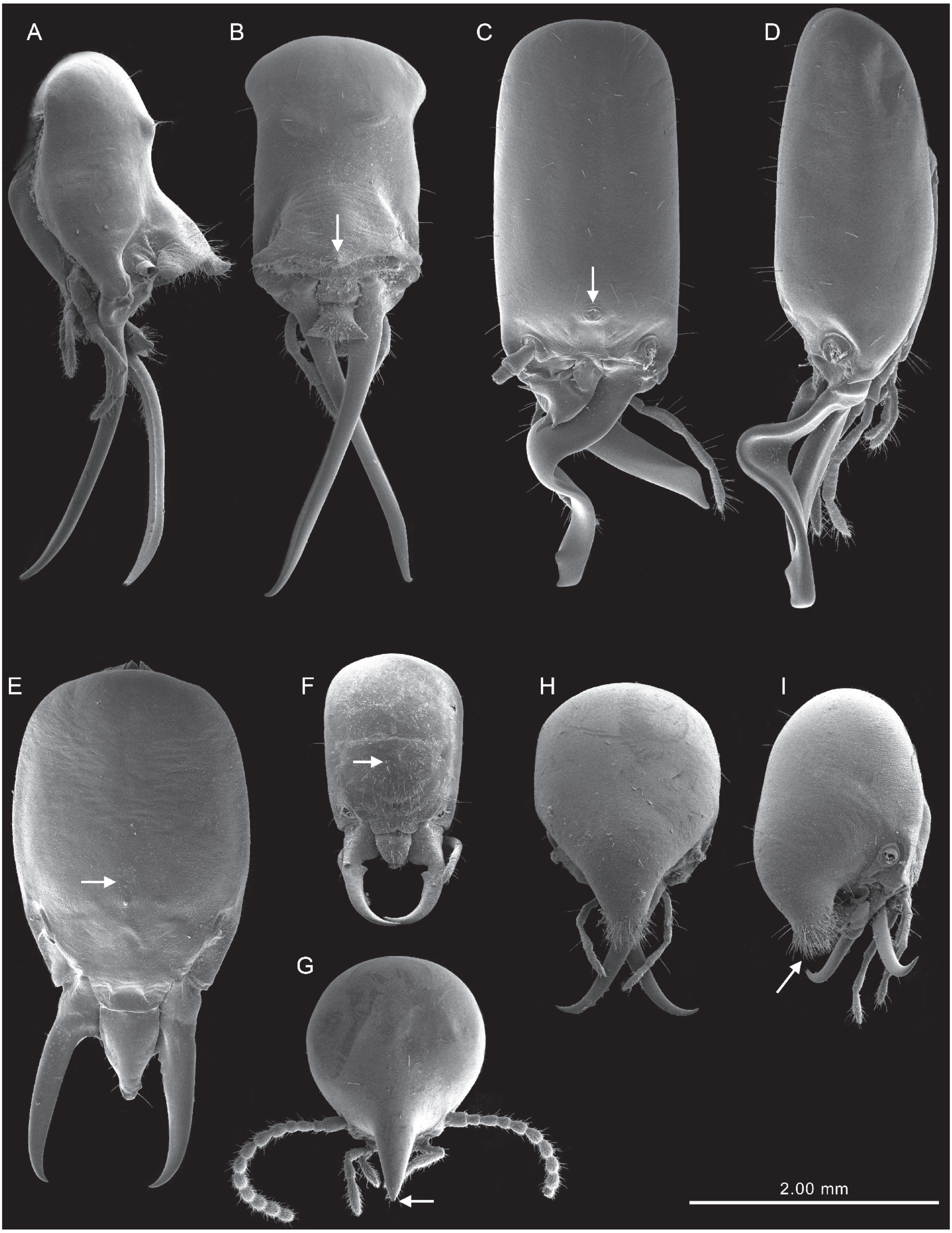


FIGURE 57. Heads of exemplar Termitidae soldiers (scanning electron micrographs). **A, B.** *Cavitermes tuberosus* (Emerson). **C, D.** *Dicuspiditermes santschii* (Silvestri). **E.** *Pseudacanthotermes militaris* (Hagen). **F.** *Amitermes minimus* Light. **G.** *Nasutitermes globiceps* (Holmgren). **H, I.** *Proboscitermes tubuliferus* (Sjöstedt).

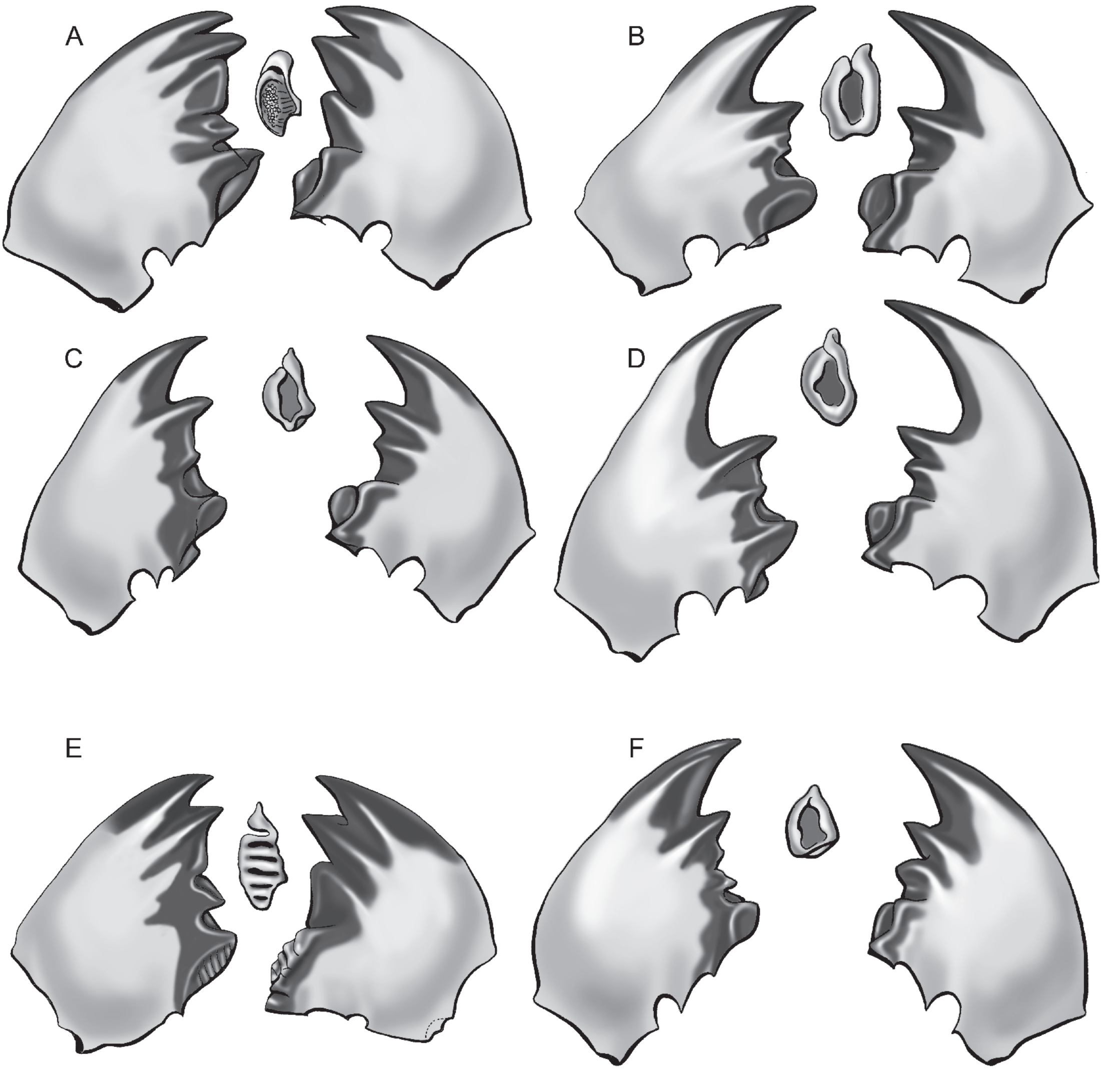


FIGURE 58. Mandibles with molar plates of exemplar species and genera of Termitidae (redrawn from Sands, 1998). **A, B.** Apicotermitinae. **A.** *Skatitermes psammophilus* Coaton. **B.** *Jugositermes* sp. **C, D.** Cubitermitinae. **C.** *Procubitermes arboricola* (Sjöstedt). **D.** *Megagnathotermes notandus* Silvestri. **E.** *Sphaerotermes sphaerothorax* (Sjöstedt) (Sphaerotermitinae). **F.** *Foraminitermes tubifrons* Holmgren (Foraminitermitinae).

Malpighian knot distinct; first proctodeal segment (P1) short or long; enteric valve strongly armed (in *Apicotermes* group and some genera of *Anoplotermes* group) or unarmed (in *Speculitermes* and some genera of *Anoplotermes* group); rectal valve without armature; for further variations in gut structure see Noirot, 2001.

Other Characters and Biology: Nests subterranean (with elaborate species-specific structure in *Apicotermes,* well described in the literature) or galleries in soil, rotten logs, under bark or stones or in mounds of other species; soil or humus feeders. In genera without soldiers, workers have developed a unique defense mechanisms, rupturing their abdomens by muscular

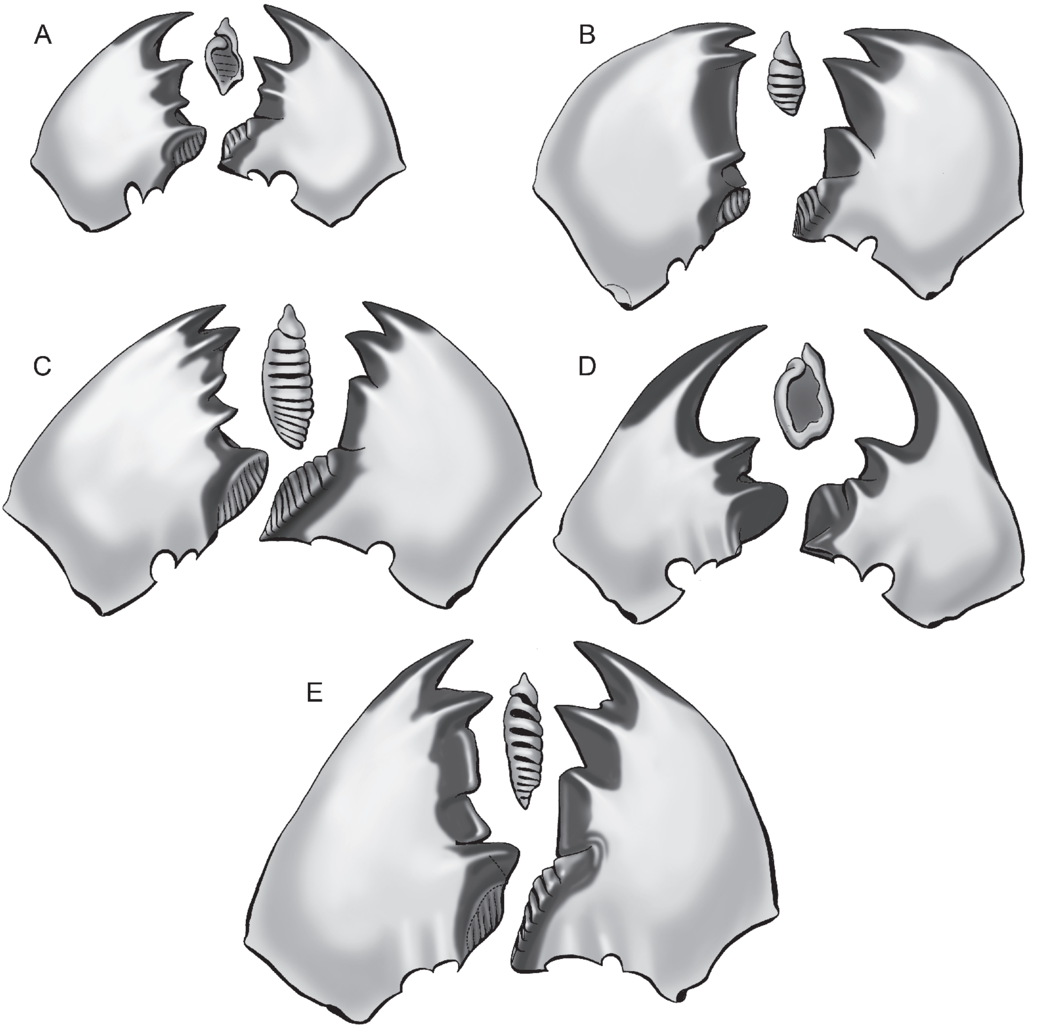


FIGURE 59. Mandibles with molar plates of exemplar species and genera of Termitidae (redrawn from Sands, 1998). **A.** *Termes hospes* (Sjöstedt) (Termitinae). **B–D.** Nasutitermitinae. **B.** *Trinervitermes trinervius* (Rambur). **C.** *Grallatotermes africanus* Harris. **D.** *Mimeutitermes edentatus* Sands. **E.** *Macrotermes bellicosus* (Smeathman) (Macrotermitinae).

contractions and spilling the abdominal contents over the attacker or depositing a drop of sticky fluid from the anus on the head of the predator, immobilizing it.

Genera Included: Three clades are recognized within this monophyletic subfamily (Sands, 1972; Noirot, 2001): *Apicotermes* Group (all Ethiopian genera without a soldier caste except one): *Acutidentitermes, Allognathotermes, Apicotermes, Coxotermes, Duplidentitermes, Euburnitermes, Heimitrmes, Hoplognathotermes, Jugositermes, Labidotrmes, Machadotermes, Phoxotermes, Rostrotermes, Skatitermes* (without soldier caste), *Trichotermes.*

Anoplotermes Group (Ethiopian and Neotropical, all genera soldierless except one): *Acholotermes, Acidnotermes, Adaiphrotermes, Aderitotermes, Adynotermes, Aganotermes, Alysco-*

termes, Amalotermes, Amicotermes, Anaorotermes, Anenteotermes, Anoplotermes, Apagotermes, Aparatermes, Asagarotermes, Astalotermes, Astratotermes, Ateuchotermes, Firmitermes (with soldier caste), *Grigiotermes, Longustitermes, Ruptitermes, Tetimatermes.*

Speculitermes Group (Oriental, soldier caste present, but few individuals): *Euhamitermes, Eurytermes, Indotermes, Speculitermes*

Subfamily Cubitermitinae

(elevated from tribe to subfamily)

Imago: Fontanelle present, small to large, usually round or oval, sometimes elongated; Y-suture generally indistinct; antennae with 15–17 articles; postclypeus mildly arched, long, length about half its width. Imago-worker mandibles: left with apical tooth longer than fused first plus second marginal tooth, posterior margin undulated, third marginal tooth small, reduced or absent in some genera (e.g., *Ophiotermes, Euchilotermes, Furculitermes*); right with apical tooth longer than first marginal tooth, posterior margin of second marginal tooth sinuate or straight, longer than anterior margin of second and posterior margin of first marginal tooth, second marginal tooth reduced or absent in some genera (e.g., *Ophiotermes, Euchilotermes, Furculitermes, Batillitermes*). Legs: tibial spurs 3:2:2, middle tibia with one or two extra subapical spines. Styli absent.

Soldier: Head generally subrectangular; frontal gland conspicuous; frons with or without projection (proboscis), when present front margin of projection in profile roundish or flattish; fontanelle conspicuous, sunken in a pit or groove, usually surrounded by brushlike setae; antennae with 14–15 articles. Labrum with anterior margin deeply or mildly concave, angular, sinuate, with pointed anterolateral corners. Mandibles biting type, robust or long, narrow, and slender, curved at tip, inner margins generally smooth or with fine serrations or tooth near base. Legs as in imago.

Worker: Gut: crop dilated; gizzard with regressed armature; mixed segment always present, cylindrical, with mesenteric tongue always on the outside (also in *Termes* group); Malpighian tubules 4, both pairs fused at a common base on Malpighian nodule at anterior part of mixed segment on midgut–hind gut junction; Malpighian knot present; enteric valve (P2) funnel shaped, six elongated cushions armed with numerous spines and six smaller cushions with few spines; paunch (P3) divided into two parts, P3a and P3b, P3a J-shaped, P3b S-shaped, a blind diverticulum or caecum present in P3b (characteristic of this subfamily), P3 usually without spines or setae; isthmus between P3 and P4 conspicuous, colon (P4) divided into two successive segments, P4a dilated; rectal valve well armed (abridged from Noirot, 2001).

Additional Characters and Biology: Nests subterranean or in mounds of other species, such as *Trinervitermes, Macrotermes, Odontotermes, Amitermes,* or epigeal mounds, such as the well-known mushroom-shaped dirt mounds of *Cubitermes,* with one or more caps used as rain-shedding devices. No economic significance.

Genera Included: Recent studies (Noirot, 2001; Inward et al., 2007) suggest that these African genera form a monophyletic group within the Termitinae; we are therefore placing these genera in a separate subfamily, Cubitermitinae: *Apilitermes, Basidentitermes, Batillitermes, Crenetermes, Cubitermes, Euchilotermes, Fastigitermes, Forficulitermes, Furculitermes, Lepidotermes, Megagnathotermes, Mucrotermes, Nititermes, Noditermes, Okavangotermes, Ophiotermes, Orthotermes, Ovambotermes, Pilotermes, Proboscitermes, Procubitermes, Profastigitermes, Thoracotermes, Trapellitermes, Unguitermes, Unicornitermes.*

Subfamily Foraminitermitinae

Imago: Head small, semicircular; Y-suture not visible; fontanelle punctiform, raised, situated at tip of projection (*Foraminitermes, Pseudomicrotermes*) or not raised (*Labritermes*); eyes moderately large; antennae 15–16 articles (12+ in *Labritermes*); postclypeus long, with or without medial line; pronotum distinctly saddle shaped (*Foraminitermes, Pseudomicrotermes*) or faintly so (*Labritermes*). Imago-worker mandibles: left with apical tooth longer (*Foraminitermes, Pseudomicrotermes*) or shorter (*Labritermes*) than fused first plus second marginal tooth, posterior margin of fused first plus second marginal tooth straight to undulating, sometimes with a faint notch between fused first plus second and third marginal tooth, third marginal tooth distinct (*Foraminitermes, Labritermes*) or reduced (*Pseudomicrotermes*), fourth marginal tooth (also referred to as molar tooth) hidden behind molar prominence; right with apical tooth longer or shorter than fused first plus second marginal tooth, as in left mandible, second marginal tooth well developed (less so in *Pseudomicrotermes*). Legs: tibial spurs 3:2:2, forecoxa with or without longitudinal ridge, without protuberance.

Soldier: Head with a small frontal projection (*Foraminitermes*) or without (*Pseudomicrotermes, Labritermes*). Fontanelle open at tip of projection (*Foraminitermes*) or situated just above frontal slope (*Pseudomicrotermes, Labritermes*), faint groove from fontanelle to base of labrum. Left mandible with upper inner margin faintly or distinctly serrated and a toothlike projection at base; lower part with four blunt crenulations (*Foraminitermes*), several coarser crenulations (*Pseudomicrotermes*), or coarser crenulations and an additional tooth (*Labritermes*); right mandible with a blunt tooth and a minute, thornlike point in basal region. Antennae with 12 (*Labritermes*) or 13–14 (*Foraminitermes, Pseudomicrotermes*) articles. Labrum with a hyaline tip, pointed or blunt. Legs: as in imago.

Worker: Gut: crop voluminous, not distinctly separated from gizzard; gizzard armature normal, but poorly sclerotized (*Labritermes*) or reduced (*Foraminitermes*); stomodeal valve very short; midgut or mesenteron long (shorter in *Foraminitermes, Pseudomicrotermes*); mesenteron-proctodeum (midgut–hind gut) junction simple, transverse, with mixed segment absent; Malpighian tubules 4, swollen at base, attached separately at mesenteron-proctodeum junction, extending forward for a short distance, then looping back toward hind gut; true Malpighian knot absent, Malpighian tubules adhering to proximal narrow portion of first proctodeal segment (P1) and dilated portion of third proctodeal segment (P3), forming a convoluted mass, referred to as "pseudo-Malpighian knot" (characteristic of this subfamily); P1 well developed, long, dilated posteriorly; enteric valve (P2) unarmed, without spines, invaginated directly into paunch (P3); P3 elongated, smaller than P1; isthmus between P3 and P4 indistinct; rectal valve unarmed (abridged from Noirot, 2001).

Additional Characters and Biology: Biology little known, generally collected in soil galleries sometimes associated with wood, one species (*Labritermes buttelreepeni*) builds a definitive nest.

Genera Included: *Foraminitermes, Labritermes, Pseudomicrotermes.*

Subfamily Macrotermitinae

Imago: Head medium-sized to large, oval to subcircular; fontanelle circular, minute, raised upward, inconspicuous in some genera; eyes bulging; ocelli large, oval; antennae with 15–20 articles; postclypeus arched, with median line, length in relation to width variable, less than half to more than half; labrum with transverse chitinized band, characteristic of the family; pronotum trapezoidal. Imago-worker mandibles: left with apical tooth shorter than fused first plus second marginal tooth, posterior margin of fused first + second long and sinuate, a faint notch between fused first + second and third marginal teeth, as in Apicotermitinae, right with (*Macrotermes*) or without (*Odontotermes*) a subsidiary tooth at base of apical and first marginal tooth. Tibial spirs 3:2:2. Wings long, costa thick, sclerotized, radius short, Rs sclerotized, running parallel to costa, M weak, arising separately from within the wing scale (*Macrotermes*) or from a stem common with Cu, outside the wing scale (*Odontotermes*); hind wing with M always branching from Rs, outside the wing scale.

Soldier: Monomorphic (*Porotermes, Allodontermes, Synacanthotermes, Odontotermes, Hypotermes, Microtermes, Ancistrotermes*), dimorphic (*Macrotermes, Pseudacanthotermes*), or trimorphic (*Acanthotermes*). Head in major soldier subrectangular to oval; fontanelle small, situated in middle of head (*Macrotermes*) or indistinct (*Odontotermes, Hypotermes, Microtermes, Ancistrotermes*). Mandibles thick, swordlike, without teeth, inner margins with crenulations (*Macrotermes, Hypotermes, Pseudacanthotermes, Acanthotermes*) or with teeth (*Odontotermes, Porotermes, Allodontotermes*). Antennae with 12–21 articles. Labrum with hyaline tip, pointed, obtuse, or lanceolate. Pronotum saddle shaped, with anterior and lateral margins with spines (*Acanthotermes, Pseudacanthotermes*) or with even margins without spines (*Macrotermes, Odontotermes, Ancistrotermes, Microtermes, Hypotermes*). Minor soldier smaller, half the size of major soldier, with much more slender mandibles and legs often proportionately longer. Legs: tibial spurs 3:2:2.

Worker: Gut: crop normally dilated; gizzard armed with sclerotized plates, columnar belt moderately sclerotized laterally with crenulated crests; midgut or mesenteron well developed, long and wide, largest gut compartment, volume larger than P2 + P3; no mixed segment (mesenteron attached posteriorly to the proctodeum in a simple transverse junction); mesenteric proctodeal junction with four posterior projections; Malpighian tubules 4, with ampulla at base, attached individually to gut wall at mesenteric proctodeal junction; no Malpighian knot; hind gut with first proctodeal segment (P1) short; enteric valve (P2), conical, ventral, enteric valve armature unsclerotized, not very elaborate (as in lower termites); paunch or third protodeal segment (P3), pyriform or U-shaped, cuticle terminally with microtrichiae; colon (P4) short, P3–P4 junction without isthmus, without bristles; rectal valve unarmed (abridged from Noirot, 2001).

Additional Characters and Biology: Builds subterranean nests to massive, spectacular, complex mounds; cultivates *Termitomyces* on fungus combs, unique to this family; several species of *Macrotermes, Odontotermes,* and *Microtermes* are serious pests to agricultural crops and trees (rubber and eucalyptus).

Genera Included: *Acanthotermes, Allodontotermes, Ancistrotermes, Eucasitermes, Hypotermes, Macrotermes, Megaprotermes, Microtermes, Odontotermes, Protermes, Pseudacanthotermes, Synacanthotermes.*

Subfamily Nasutitermitinae

Imago: Fontanelle present, commonly slitlike, oval, or bifurcate, sometimes not visible; Y-suture present or indistinct; antennae with 13–21 articles; labrum broader than long, without transverse sclerotized band, tip partially hyaline. Postclypeus weakly to strongly arched, short, less than half its width. Imago-worker mandibles: left with apical tooth size variable, shorter (*Nasutitermes* and other genera) or longer (*Subulitermes* and other genera) than fused plus second marginal tooth, third marginal tooth developed or reduced; right with two marginal teeth, second greatly reduced in some genera. Legs: tibial spurs 2:2:2. Styli absent.

Soldier: Monomorphic, dimorphic, or trimorphic. Head prolonged into a long nasus, frontal pore narrow, characteristic of the subfamily; frontal gland well developed; antennae with 11–21 articles; mandibles greatly reduced, nonfunctional, with or without points. Legs: Tibial spurs 2:2:2. Styli absent.

Worker: Gut: Dorsal torsion weak to conspicuous (*Nasutitermes* group) or always conspicuous (*Subulitermes* group); gizzard with moderately developed armature (*Nasutitermes* group) or with poorly developed armature (*Subulitermes* group); mixed segment with mesenteric tongue on external surface, of variable length and tubular (*Nasutitermes* group) or very short (in the Neotropical genera), slightly longer (in African genera), mesenteron-proctodeum junction circular or oblique (*Subulitermes* group); Malpighian tubules 4, generally strongly dilated at base, attached in two pairs to the mesenteron-proctodeum junction at beginning of mixed segment (*Nasutitermes* group) or tubules faintly swollen to not swollen at base, attached to mesenteron-proctodeum junction, the two pairs fused or not fused at base, in latter case tubules attached to a small Malpighian nodule; Malpighian knot always present, against mixed segment (*Nasutitermes* group) or against beginning of P1 or end of midgut or on mesenteron-proctodeal junction (*Subulitermes* group); P1 tubular, long to very long with posterior part bent before enteric valve, bending always dorsal and left of P5 (*Nasutitermes* group) or short (in Australian and African genera), longer (but not as long as in *Nasutitermes,* in Neotropical genera), straight, with a small bend at end (*Subulitermes* group); enteric valve (P2) cushions with two successive rings of spiny areas (*Nasutitermes* group) or without rings, well armed with short, robust, sclerotized spines or armature reduced (*Subulitermes* group); paunch (P3) when weakly bent undivided (pyriform or ovoid), when bent divided into two parts, with cuticular filaments (*Nasutitermes* group) or voluminous, divided into two parts by a constriction armed with sclerotized spines (*Subulitermes* group); P4 tubular, short (*Nasutitermes* group) or of variable length (*Subulitermes* group); rectal valve generally unarmed (*Nasutitermes* and *Subulitermes* groups) (abridged from Noirot, 2001).

Additional Characters and Biology: *Nasutitermes* Group: Generally xylophagous, feeding on wood, grass, leaf litter, decaying vegetable matter; nests are subterranean, arboreal, in hollow trees, nests of other species, or above ground constructed of carton or soil, some massive, attaining a height of 8–10 feet (*Nasutitermes triodiae*). Some genera are foragers, marching in columns and storing grass in their nests (e.g., *Trinervitermes, Hospitalitermes, Lacessititermes, Tenuirostritermes*). Some genera harbor inquiline species (*Constrictotermes*). Some are pest species, damaging agricultural crops, trees, and timber.

Subulitermes Group: Generally humivorous, feeding on humus and soil, nests are subterranean, in tree branches or decaying roots, or nests of other species.

Genera Included: *Nasutitermes* Group: *Ahmaditermes, Ampoulitermes, Antillitermes, Arcotermes, Baucaliotermes, Bulbitermes, Caetetermes, Caribitermes, Ceylonitermes, Coarctotermes, Coendutermes, Constrictotermes, Cortaritermes, Cucurbitermes, Diversitermes, Diwaitermes, Fulleritermes, Grallatotermes, Hirtitermes, Hospitalitermes, Kaudernitermes, Lacessititermes, Leptomyxotermes, Longipeditermes, Mycterotermes, Nasopilotermes, Nasutitermes, Ngauratermes, Niuginitermes, Obtusitermes, Occasitermes, Parvitermes, Peribulbitermes, Rhadinotermes, Roonwalitermes, Rotunditermes, Rounditermes, Sinonasutitermes, Tenuirostritermes, Triangularitermes, Trinervitermes, Tumulitermes, Velocitermes, Xiatermes.*

Subulitermes Group: *Aciculitermes, Afrosubulitermes, Agnathotermes, Angularitermes, Anhangatermes, Araujotermes, Atlantitermes, Australitermes, Ceylonitermellus, Convexitermes, Coatitermes, Cyranotermes, Eleanoritermes, Emersonitermes, Enetotermes, Ereymatermes, Eutermellus, Latisubulitermes, Leucopitermes, Macrosubulitermes, Malagasitermes, Malaysiotermes, Mimeutermes, Occultitrmes, Oriensubulitermes, Paraconvexitermes, Periaciculitermes, Postsubulitermes, Sabahitermes, Spatulitermes, Subulioiditermes, Subulitermes, Tarditermes, Verrucositermes.*

Subfamily Sphaerotermitinae

Imago: Head small, sides rounded; fontanelle present, punctiform; antennae with 15+ articles; labrum uniformly sclerotized, without a transverse chitinized band; postclypeus long, arched, with median line, length half its width. Imago-worker mandibles: left with apical tooth and two marginal teeth, apical tooth shorter than fused first plus second marginal tooth, posterior margin of fused first plus second somewhat sinuate, third marginal tooth fully developed as a distinct separate tooth; right with subsidiary at base of apical and first marginal teeth, 6–7 ridges on molar plate.

Soldier: Head with sides rounded; antennae with 13 articles; fontanelle in middle of head, inconspicuous. Mandibles: left without conspicuous teeth, inner margin with a few serrations and a blunt tooth at base; right with inner cutting edge smooth. Pronotum narrower than head, anterior and lateral margins even, without projecting spines.

Worker: Gut: crop normally dilated; gizzard armed with sclerotized plates with tooth, with small pulvilli attached posteriorly on columns, columns I and II with crenulated crests poorly developed, setae on pulvilli poorly developed, characteristic of this subfamily; midgut or mesenteron long (not as long as Macrotermitinae), no mixed segment (mesenteron attached posteriorly to the proctodeum in a simple transverse junction), without projections (cf. Macrotermitinae); Malpighian tubules 4, with ampulla at base, attached individually to gut wall at mesenteric proctodeal junction, no Malpighian knot; hind gut with first proctodeal segment (P1) short; enteric valve (P2) conical, ventral, enteric valve armature unsclerotized, not very elaborate; paunch, or third proctodeal segment (P3), pear shaped or U-shaped, microtrichiae present; colon (P4) short; P3, P4 junction with conspicuous, backward oriented bristles (unique among Isoptera); rectal valve unarmed (abridged from Noirot, 2001).

Additional Characters and Biology: Builds subterranean nests in rainforests, with convoluted galleries constructed of soil, feeding on rotting wood litter; no fungus combs, no association with symbiotic mycelium of *Termitomyces*; no economic significance (Sands, 1998).

Genus Included: Monotypic subfamily *Sphaerotermes.*

Subfamily Syntermitinae

Imago: Fontanelle generally large, depressed or convex (*Cornitermes, Procornitermes, Syntermes*), or small (e.g., *Armitermes*); Y-suture absent or partially visible; antennae with 13–21 articles; labrum broader than long, sometimes with a thin, white anterior lip (*Syntermes, Procornitermes*); postclypeus generally arched, long, longer than or equal to half its width, with a median line; pronotum with lateral margins with projections (*Syntermes*) or evenly rounded. Imago-worker mandibles: left with apical tooth shorter than posterior margin of fused first plus second marginal tooth, angle between apical and fused first plus second marginal tooth narrow, third marginal tooth small (as in *Syntermes, Cornitermes, Procornitermes, Rhynchotermes, Cahuallitermes*) or apical tooth longer than fused first plus second marginal tooth, angle between apical and fused first plus second wide (*Armitermes, Embiratermes, Paracornitermes, Labiotermes, Cyrilliotermes, Macuxitermes, Curvitermes*); right with apical tooth longer than or almost equal to first marginal tooth, second marginal tooth shorter than first marginal tooth (*Syntermes,* etc.), second marginal tooth very much reduced in some genera (e.g., *Curvitermes*). Legs: tibial spurs 3:2:2 or 2:2:2. Wings: unreticulated, membrane with fine setae; forewing: Sc, R and Rs sclerotized, R1 short, Rs running parallel to costal margin, M and Cu weak, M closer to Cu than to Rs, variably branched, Cu with several branches.

Soldier: Monomorphic or dimorphic; head with frontal tube (nasus) relative to length of mandibles short (*Syntermes, Procornitermes*) or very long and well developed (e.g., *Rhynchotermes*), tip of nasus flat, frontal pore wide and conspicuous (characteristic of this subfamily), frontal gland more or less developed, associated with muscle fibers (characteristic of this subfamily). Mandibles functional, well developed, adapted for biting, relative to nasus, long, straight, and stout (*Syntermes, Cornitermes, Procornitermes*) or short and strongly hooked (*Rhynchotrmes, Armitermes, Cyrilliotermes*), sickle shaped in some genera, with or without teeth. Antennae with 13–21 articles; labrum generally with hyaline tip; pronotum saddle shaped, narrower than head.

Worker: Gut: crop voluminous; gizzard armature normal, with well-developed narrow columns, longer than pulvilli; mixed segment long, mostly dilated, double, with dual lobes, overlapping first proctodeal segment (P1) (*Syntermes, Cornitermes, Labiotermes*) or reduced to one (inner or outer) lobe (*Procornitermes, Rhynchotermes, Cahuallitermes, Noirotitermes, Ibi-*

termes, Cyrilliotermes, Armitermes, Embiratermes, Curvitermes); Malpighian tubules 4, in two pairs fused at base, separately attached to mesenteron-proctodeum junction or the two pairs united at base (*Curvitermes, Cyrilliotermes, Armitermes*); P1 large and dilated (tubular in Nasutitermitinae); enteric valve ridges with spines (reduced armature in *Syntermes*); P3 smaller than P1, divided into two, with a dilated portion, followed by a bent, narrower tube; rectal valve with well-developed armature, with spines and scales (reduced in *Syntermes* and some species of *Procornitermes*).

Additional Characters and Biology: Some genera nest underground; others nest above ground, some constructing large mounds (as high as four meters in *Cornitermes*), some building arboreal carton nests, others colonizing abandoned nests of other termite species. In genera with elongated nasus and hooked mandibles, the mandibles are adapted to grasping the enemy while the defensive secretion is applied from the nasus. A few species are of minor economic importance, attacking young trees.

Genera Included: *Acangaobitermes, Armitermes, Cahuallitermes, Cornitermes, Curvitermes, Cyrilliotermes, Embiratermes, Ibitermes, Labiotermes, Macuxitermes, Noirotitermes, Paracurvitermes, Procornitermes, Rhynchotermes, Syntermes.*

Subfamily Termitinae

(represented by three groups)

Termes Group

Imago: Fontanelle present, minute to long, oval, round (*Angulitermes*), or slitlike (*Termes*); Y-suture generally not visible; antennae with 14–16 articles; postlypeus arched, long, length generally half its width. Imago-worker mandibles: left with apical tooth elongate, longer (e.g., *Termes, Tuberculitermes, Spinitermes, Capritermes, Quasitermes, Cristatitermes, Paracapritermes*), slightly shorter (e.g., *Hesperotermes*), or much shorter (e.g., *Neocapritermes, Planicapritermes*) than fused first plus second marginal tooth, third marginal tooth well developed (e.g., *Termes, Paracapritermes, Protocapritermes, Xylochomitermes, Apsenterotermes*) or absent (e.g., *Cavitermes, Crepititermes, Dihoplotermes, Cornicapritermes*); right with a long or short apical tooth, as in left mandible, second marginal tooth well developed (*Promirotermes, Angulitermes*), slightly reduced (e.g., *Paracapritermes, Termes, Hesperotermes, Neocapritermes*) or absent (e.g., *Cavitermes, Crepititermes, Dihoplotermes, Cornicapritermes*), posterior margin of second marginal tooth straight (vs. curved in *Pericapritermes* group). Legs: tibial spures 3:2:2 or 2:2:2, styli absent.

Soldier: Head subrectangular, frontal projection well developed, with a conical, pointed, or blunt tip (e.g., *Termes, Angulitermes, Dihoplotermes, Cornicapritermes*), much reduced (*Protocapritermes, Capritermes*), or absent (*Neocapritermes, Planicapritermes*). Fontanelle below projection surrounded by many setae; antennae with 14–15 articles; labrum with anterior margin straight, angular, or round, anterolateral corners pointed or rounded (labrum tongue shaped in *Planicapritermes*). Mandibles snapping type (except for *Spinitermes*): symmetrical or asymmetrical, symmetrical mandibles straight, long, rodlike, in profile curved, asymmetrical mandibles with left twisted or arched in middle, right bladelike, shorter than left. Legs: tibial spurs 3:2:2 or 2:2:2.

Worker: Gut: gizzard armature generally poorly sclerotized or moderately developed, as in *Amitermes* group; mixed segment present, mesenteric tongue on the outside, dilated or bilobed; Malpighian tubules 4, both pairs united at a common base (as in Cubitermitinae), ending in a conspicuous or reduced Malpighian nodule; Malpighian knot present; P1 variable in length, tubular or somewhat dilated; P2 cushions not well differentiated or barely visible, variably armed with spines; P3 mostly pyriform or J-shaped, divided into two parts (no diverticulum, as in Cubitermitinae), with poorly developed sclerotized spines (e.g., *Neocapritermes*) or no spines (e.g., Australian genera) (in *Pericapritermes* group this cuticular armature much more developed); rectal valve armed (abridged from Noirot, 2001).

Additional Characters and Biology: Nests subterranean, epigeal, under logs or stones, or in abandoned or occupied mounds of other termite species; some inquilinous species (e.g., *Inquilinitermes fur* in the nests of *Constrictotermes cyphergaster*); generally humus or soil feeders, some partially decayed wood feeders. A few species of minor economic importance.

Genera Included: Genera with symmetrical mandibles: *Angulitermes, Apsenterotermes, Cavitermes, Crepititermes, Cristatitermes, Dentispicotermes, Ekphysotermes, Ephelotermes, Genuotermes, Hapsidotermes, Hesperotermes, Inquilinitermes, Invasitermes, Lophotermes, Macrognathotermes,* ?†*Nanotermes, Orthognathotermes, Promirotermes, Saxatilitermes, Spinitermes, Termes, Tuberculitermes, Xylochomitermes.* Genera with asymmetrical mandibles: *Capritermes, Cornicapritermes, Dihoplotermes, Neocapritermes, Paracapritermes, Planicapritermes, Protocapritermes, Quasitermes.*

Pericapritermes Group

Imago: Fontanelle present, minute to large, punctate, ovoid, or oblong; Y-suture indistinct or partially visible; antennae with 14–15 articles; postclypeus strongly arched, length slightly less or almost equal to half its width. Imago-worker mandible: left with apical tooth shorter (e.g., *Homallotermes, Pericapritermes, Dicuspiditermes, Oriencapritermes*) or longer (e.g., *Kemneritermes, Procapritermes, Syncapritermes, Indocapritermes, Krishnacapritermes, Pseudocapritermes*) than fused first plus second marginal tooth, second marginal tooth prominent or reduced; right with apical tooth and two marginal teeth, shorter or longer than first marginal tooth, as in left mandible, second marginal tooth with anterior margin convex or straight, posterior margin concave. Legs: tibial spurs 3:2:2.

Soldier: Head rectangular; frontal gland small to moderate sized; frontal projection absent, except in *Mirocapritermes*; fontanelle small, located at slope of frons; antennae with 13–14 articles. Labrum with front margin moderately to deeply concave or straight, anterolateral corners pointed. Mandibles snapping type: left moderately to greatly twisted or arched in middle; right bladelike, shorter than left. Legs: tibial spurs 3:2:2, rarely 2:2:2; middle tibia sometimes with one or two additional spines (e.g., *Homallotermes, Dicuspiditermes, Pericapritermes*).

Worker: Gut: gizzard as in *Termes* group; mixed segment as in *Termes* group; Malpighian tubules 4, two pairs united at common base, opening at midgut–hind gut junction, Malpighian nodules always absent (present in *Termes* group); P1 short and tubular (always long in *Termes* group); P2 as in *Termes* group; P3 divisions poorly marked, armature well developed, with sclerotized spines (absent or hardly developed in *Termes* group); P4 very long; rectal valve armed (abridged from Noirot, 2001).

Additional Characters and Biology: Usually found in soil, under stone, bark, logs, or mounds of other termites, subterranean or aboveground nests against trees with rain-shedding caps and columns and ventilation pores (*Dicuspiditermes*). The asymmetrical mandibles are locked together and released with a loud click, flipping the soldier several inches in the air, speculated as defense or alarm behavior. Of no economic significance.

Genera Included: *Dicuspiditermes, Homallotermes, Indocapritermes, Kemneritermes, Krishnacapritermes, Labiocapritermes, Mirocapritermes, Oriencapritermes, Pericapritermes, Procapritermes, Pseudocapritermes, Sinocapritermes, Syncapritermes.*

Amitermes Group (= Amitermitinae)

Imago: Fontanelle present, small to large, round or oval, sometimes not clearly visible; Y-suture generally not visible; antennae with 12–18 articles; postclypeus generally arched, long, length usually half its width, divided by a line in middle. Imago-worker mandible: left with apical tooth and two marginal teeth (with the exception of *Protohamitermes,* which has three marginal teeth, a primitive character shared with Rhinotermitidae and other lower taxa), apical tooth generally shorter than fused first plus second marginal tooth (except in *Ahamitermes*), posterior margin of fused first plus second straight or roundish, third marginal tooth generally well developed (e.g., *Cephalotermes, Cylindrotermes, Prohamitermes, Globitermes, Microcerotermes*), somewhat reduced (*Synhamitermes, Eremotermes*), or greatly reduced and represented only by a round bulge (*Amitermes, Drapanotermes, Gnathamitermes*); right with apical tooth and two marginal teeth (subsidiary tooth at base of first marginal tooth in *Protohamitermes* and *Orientotermes,* a primitive feature found in the Rhinotermitidae and some lower termites), second marginal tooth with anterior margin very short, resembling a small, rounded hump, posterior margin long and straight (e.g., *Microcerotermes, Globitermes, Cephalotermes, Amitermes*) or well developed, with anterior margin angular and posterior margin curved (*Protohamitermes, Orientotermes*). Legs: tibial spurs generally 3:2:2, midtibia sometimes with one or two additional spines (2:2:2 in *Protohamitermes, Orientotermes*).

Soldier: Head pear shaped or long and narrow; frontal projection absent, except in some species of *Eremotermes*; fontanelle small, round, sometimes indistinct; antennae with 11–20 articles; labrum tongue shaped, rounded or slightly pointed at tip; postclypeus simple, not divided, except bilobed in *Amitermes*; mandibles short and robust or long and thin, usually each with one tooth or serrations on inner margin; tibial spurs as in imago.

Worker: Gut: gizzard armature moderately developed; mesenteron (midgut) short; mixed segment present, variable in shape; Malpighian tubules 4, each pair fused at base, attached to midgut–hind gut junction, in some genera each pair ending in a Malpighian nodule (in *Prohamitermes* tubules not paired, each ending in its own nodule); Malpighian knot always conspicuous, adhering to mesenteric tongue of mixed segment; P1 always long, usually tubular, sometimes dilated; P2 with six poorly sclerotized ridges, with straight spines; P3 large, usually pear shaped, sometimes with divisions, no armature present, isthmus between P3 and P4 distinct; P4 short; rectal valve mostly unarmed (some armature in *Globitermes* and *Protohamitermes*) (abridged from Noirot, 2001).

Additional Characters and Biology: Nests subterranean galleries, arboreal, in dead branches, logs, dung on ground, hard carton nests (*Microcerotermes*), or very tall mounds (e.g., the famous "compass mounds" of Australia, nearly 4 m high and 3 m long, built by *Amitermes meridionalis*); one species of *Incolitermes* is an inquiline in the nests of *Ahamitermes*; some species feed on grass and other vegetation. A few species are pests of agriculture and timber.

Genera Included: *Ahamitermes, Amitermes, Cephalotermes, Cylindrotermes, Drepanotermes, Eremotermes, Globitermes, Gnathamitermes, Hoplotermes, Incolitermes, Microcerotermes, Onkotermes, Orientotermes, Prohamitermes, Pseudhamitermes, Synhamitermes.*

PEST SPECIES OF ISOPTERA

Though in the public mind the very word *termite* conjures up images of devastation and destruction, surprisingly, not all termite species are pests. In fact, only a small number are responsible for the widespread ravages attributed to these insects. Of the nearly 3000 living species, only 371 (12.4%) have been reported in the literature as destructive, and only 104 (3.5%) are considered serious threats. Nevertheless, the damage inflicted by these relatively few species is monumental and far-reaching.

Termites attack and consume a variety of materials containing cellulose: paper, clothing, leather; agricultural crops such as sugar cane, grains, vegetables, fruit trees; other crops such as tea, coffee, rubber, coconut; forest trees; buildings and structural timbers; and even electric and telephone cables. Of this list (table 9) the most notable damage is done to structural wood in buildings and timber products. The financial loss resulting from this destruction is colossal, running into billions of dollars per year.

Termites are classified according to their habits into two main categories: wood dwelling and subterranean, and pest species may be of either type. The wood dwellers, all of which belong to the families Kalotermitidae, Stolotermitidae, and Archotermopsidae, typically enter the wood directly at the time of swarming and build their nests within it. Depending on the moisture content of the wood, these are subdivided into dry-wood (e.g., species of the genus *Cryptotermes*) and damp-wood termites (*Neotermes, Glyptotermes, Kalotermes, Incisitermes* of the family Kalotermitidae; *Stolotermes, Porotermes* of the family Stolotermitidae; *Zootermopsis* of the family Archotermopsidae). The subterranean termites are generally ground dwellers, some who construct underground definitive nests, some who inhabit diffuse nests in soil, others who build mounds, and a few who construct arboreal nests with connections to the soil. All subterranean termites gain access to their food supply by constructing tunnels or shelter tubes and all belong to the families Hodotermitidae, Mastotermitidae, Rhinotermitidae, Stylotermitidae, and Termitidae. These varied life styles make proper identification of species essential to effective control measures.

The most notorious pest species of termites are generally those that have been introduced into new geographical areas, usually as a result of human activity, and become invasive. Particularly menacing examples are *Cryptotermes brevis, Cryptotermes domesticus, Cryptotermes dudleyi, Coptotermes formosanus, Coptotermes gestroi, Reticulitermes flavipes,* and *Reticulitermes lucifugus.* Table 9 includes all of the species that have been cited as injurious in the literature. However, it must be noted that many such reports must be viewed provisionally, as the mere presence of a species in the proximity of damage is not sufficient to identify it as the source of the destruction; another species might be responsible, or the species in question might be consuming wood that is already dead, or the species might inflict damage too minimal for it to be defined as a pest.

TABLE 9. Pest Species of Isoptera (expanded from Harris 1961).
Pest status and identification of some species uncertain. * = Major pest species; field crops = cotton, vegetables.

	Tea/Coffee	Rubber	Cocoa	Coconut	Oil Palm	Groundnut	Sugar Cane	Fruit Trees	Grains	Pastures	Forest Trees	Field Crops	Buildings, Timber	Distribution
ARCHOTERMOPSIDAE														
Zootermopsis angusticollis													x	U.S.
Zootermopsis nevadensis													x	U.S.
HODOTERMITIDAE														
Anacanthotermes ahngerianus										x				Turkmenistan
Anacanthotermes macrocephalus								x		x	x			India, Pakistan
*Anacanthotermes ochraceus**								x					x	Algeria to Libya, Egypt, Sudan, Saudi Arabia
*Anacanthotermes septentrionalis**													x	Iran, Afghanistan, Turkmenistan
*Anacanthotermes vagans**													x	Iran, Iraq, Afghanistan, Pakistan
Hodotermes erithreensis										x				Ethiopia, Somalia
*Hodotermes mossambicus**									x	x		x	x	South Africa, East Africa
Microhodotermes viator										x			x	South Africa
KALOTERMITIDAE														
Bifiditermes beesoni								x			x		x	India
Bifiditermes improbus											x			Australia
Bifiditermes madagascarensis			x											Madagascar
Bifiditermes mutubae													x	Uganda
Ceratokalotermes spoliator											x		x	Australia
Comatermes perfectus	x													Colombia, Peru, Trinidad, Venezuela
*Crypotermes bengalensis**	x												x	Bangladesh, India
*Cryptotermes brevis**													x	U.S., Mexico, Guatemala, West Indies; Jamaica to Trinidad, Guyana Colombia, Brazil, Peru, Chile, Madeira, St. Helena, West Africa (Gambia to Nigeria), Uganda, South Africa, Madagascar, Australia, etc.
*Cryptotermes cavifrons**											x			Bahamas, Cuba, Bermuda, Puerto Rico, Haiti, Guatemala

Cryptotermes cubicoceps			x					x					x	Guyana, Brazil
*Cryptotermes cynocephalus**													x	Malaysia, Philippines
Cryptotermes declivus								x						China
*Cryptotermes domesticus**													x	Malaysia, Trinidad Vietnam, China, Japan, Sri Lanka, India, Pacific Is., etc.
*Cryptotermes dudleyi**													x	Australia, Malaysia, Philippines, India, Sri Lanka, East Africa, Seychelles, Colombia, Trinidad, Brazil, etc.
*Cryptotermes havilandi**	x							x					x	West Africa (Sierra Leone to Nigeria), Brazil, Trinidad, Guianas, Barbados, etc.
*Cryptotermes pallidus**													x	Mauritius
*Cryptotermes perforans**													x	Sri Lanka
*Cryptotermes primus**											x		x	Australia
*Cryptotermes roonwali**													x	India
Epicalotermes aethiopicus											x			Arabia
Eucryptotermes wheeleri													x	Brazil
Glyptotermes almorensis								x					x	India
Glyptotermes brevicornis											x			Australia
Glyptotermes ceylonicus	x	x												Sri Lanka
Glyptotermes coorgensis													x	India
*Glyptotermes dilatatus**	x	x						x			x			Sri Lanka
Glyptoterms kawaandae											x			Uganda
Glyptotermes pellucidus								x					x	Guyana, Venezuela
Glyptotermes pubescens											x			Puerto Rico
Glyptotermes tuberculatus											x		x	Australia, New Zealand
Incisitermes immigrans				x									x	Ecuador, Peru, Washington I.
*Incisitermes incisus**														Venezuela
*Incisitermes marginipennis**													x	Mexico, Guatemala
*Incisitermes minor**													x	U.S., Japan, China
Incisitermes repandus													x	Fiji
Incisitermes schwarzi													x	U.S.
*Incisitermes snyderi**											x		x	U.S., Puerto Rico
Kalotermes approximatus											x			Bermuda
Kalotermes brouni													x	New Zealand
Kalotermes flavicollis								x			x		x	Europe, North Africa, Turkey

TABLE 9. *Continued*

	Tea/Coffee	Rubber	Cocoa	Coconut	Oil Palm	Groundnut	Sugar Cane	Fruit Trees	Grains	Pastures	Forest Trees	Field Crops	Buildings, Timber	Distribution
*Kalotermes jepsoni**	x													Sri Lanka
Kalotermes sinaicus													x	Israel
*Marginitermes hubbardi**													x	U.S., Mexico
Neotermes aburiensis			x											West Africa
Neotermes andamanensis													x	India
Neotermes assmuthi								x					x	India
Neotermes bosei								x			x			India
Neotermes buxensis													x	India
Neotermes castaneus								x					x	West Indies, Brazil, Chile, Venezuela, Colombia
Neotermes chilensis								x					x	Chile
Neotermes fletcheri								x			x		x	India
Neotermes fulvescens								x						Brazil, Argentina
Neotermes gestri			x											Fernando Po, São Tomé, Principe
Neotermes gnathoferrum											x			Fiji
Neotermes greeni	x										x			Sri Lanka
*Neotermes insularis**											x			Australia
Neotermes jouteli											x			Dominican Republic
Neotermes laticollis				x									x	Seychelles
Neotermes malatensis								x						Philippines
Neotermes mangiferae								x					x	India
Neotermes megaoculatus								x					x	India
Neotermes microculatus													x	India
Neotermes papua			x											Papua New Guinea
Neotermes paraensis								x						Brazil
Neotermes rainbowi				x										Ellice Is.
Neotermes samoanus			x											Samoa
Neotermes sarasini			x											Samoa
*Neotermes tectonae**											x			Indonesia
Neotermes wagneri			x					x						Brazil
Paraneotermes simplicicornis								x			x			U.S.

Postelectrotermes bhimi	x													India
*Postelectrotermes militaris**	x										x			Sri Lanka
Postelectrotermes praecox													x	Madeira
Postelectrotermes pishinensis											x			Pakistan
Rugitermes occidentalis								x						Brazil, Argentina
Tauritermes vitulus								x					x	Brazil
MASTOTERMITIDAE														
*Mastotermes darwiniensis**							x	x			x			Australia, Papua New Guinea
RHINOTERMITIDAE														
Coptotermitinae														
*Coptotermes acinaciformis**							x	x			x		x	Australia, New Zealand
*Coptotermes amanii**											x	x	x	Somalia, Kenya, Tanzania, Malawi, Zambia, Zimbabwe
Coptotermes brunneus														
*Coptotermes ceylonicus**	x	x		x							x		x	Sri Lanka, India
*Coptotermes crassus**													x	Mexico, Honduras, Guatemala
*Coptotermes curvignathus**		x		x	x			x			x			Malaysia, Indonesia
Coptotermes elisae											x		x	Papua New Guinea
*Coptotermes formosanus**						x		x	x		x	x	x	Taiwan, China, Japan, Hawaii, Pacific Is., Sri Lanka, South Africa, U.S.
*Coptotermes frenchi**								x			x		x	Australia
*Coptotermes gaurii**													x	Sri Lanka
*Coptotermes gestroi**			x				x						x	Malaysia, Thailand, India, Madagascar, Mauritius, Jamaica, Brazil
*Coptotermes grandiceps**													x	Solomon Is.
*Coptotermes heimi**		x					x	x	x		x		x	India, Pakistan
*Coptotermes intermedius**													x	West Africa (Senegal to Nigeria)
*Coptotermes kishori**								x					x	India
*Coptotermes lacteus**													x	Australia
*Coptotermes michaelsoni**													x	Australia
*Coptotermes niger**				x				x			x		x	Panama, Guatemala, Belize, Brazil, Colombia, Panama
*Coptotermes obiratus**													x	Papua New Guinea
*Coptotermes pamuae**													x	Solomon Is.
Coptotermes sinabangensis				x										Indonesia

TABLE 9. *Continued*

	Tea/Coffee	Rubber	Cocoa	Coconut	Oil Palm	Groundnut	Sugar Cane	Fruit Trees	Grains	Pastures	Forest Trees	Field Crops	Buildings, Timber	Distribution
*Coptotermes sjostedti**			x									x	x	West Africa (Senegal to Cameroon), Congo, Angola, Uganda
Coptotermes testaceus		x	x				x	x				x	x	Bahamas, West Indies, Venezuela, Guianas, Trinidad, Surinam, Brazil, Chile, Peru, Bolivia, Brazil, Colombia, Ecuador, Venezuela
*Coptotermes travians**													x	Malaysia
*Coptotermes truncatus**				x									x	Seychelles, Madagascar
*Coptotermes vastator**							x						x	Philippines, Hawaii
Heterotermitinae														
Heterotermes aethiopicus													x	South Arabia, Sudan
Heterotermes assu													x	Brazil
*Heterotermes aureus**											x		x	U.S., Mexico
*Heterotermes balwanti**													x	India
Heterotermes cardini							x							Cuba, Dominican Republic
*Heterotermes ceylonicus**													x	Sri Lanka
*Heterotermes convexinotatus**								x	x				x	West Indies, Panama, Guatemala, Venezuela, Colombia
Heterotermes crinitus							x							Venezuela, Brazil, Guyana
Heterotermes ferox													x	Australia
*Heterotermes indicola**								x					x	India, Pakistan, Afghanistan, Sri Lanka
*Heterotermes longiceps**							x						x	Brazil, Argentina
*Heterotermes malabaricus**													x	India
Heterotermes paradoxus							x							Australia
*Heterotermes perfidus**											x		x	St. Helena
*Heterotermes philippinensis**							x						x	Philippines, Mauritius, Madagascar
Heterotermes sulcatus													x	Brazil
*Heterotermes tenuis**							x				x	x	x	West Indies, Guyana, Brazil, Paraguay, Argentina, Peru, Panama

Reticulitermes assamensis											x		x	India
*Reticulitermes chinensis**													x	China
*Reticulitermes flavipes**							x						x	U.S., Canada, Mexico, Germany, Austria, Chile
Reticulitermes fukienensis													x	China
*Reticulitermes hageni**													x	U.S.
*Reticulitermes hesperus**													x	U.S.
*Reticulitermes lucifugus**								x					x	Europe, Madeira, Algeria, Turkey, Uruguay, Israel
Reticulitermes saraswati													x	India
*Reticulitermes speratus**							x						x	Japan, Korea, China, Taiwan
*Reticulitermes tibialis**													x	U.S., Mexico
*Reticulitermes virginicus**													x	U.S.
Prorhinotermitinae														
Prorhinotermes flavus								x						India
Prorhinotermes inopinatus													x	Guam
*Prorhinotermes simplex**													x	U.S., Cuba, Puerto Rico, Jamaica
Prorhinotermes tibiaoensis													x	Philippines
Psammotermitinae														
Psammotermes allocerus													x	South Africa
*Psammotermes hybostoma**										x		x	x	North Africa (Algeria to Egypt), Senegal
Psammotermes rajasthanicus												x		Pakistan
Psammotermes voeltzkowi													x	Madagascar
Rhinotermitinae														
Dolichorhinotermes latilabrum													x	Bolivia, Brazil
Rhinotermes marginalis													x	Amazonia, Guianas
Schedorhinotermes intermedius							x						x	Australia
*Schedorhinotermes lamanianus**								x			x		x	Tanzania, South Africa
Schedorhinotermes logirostris					x									Malaysia
Schedorhinotermes malaccensis					x									Malaysia
Schedorhinotermes putorius			x										x	São Tomé
Schedorhinotermes sarawakensis													x	Malaysia
Schedorhinotermes solomonensis													x	Solomon Is.
Schedorhinotermes translucens													x	Malaysia

TABLE 9. *Continued*

	Tea/Coffee	Rubber	Cocoa	Coconut	Oil Palm	Groundnut	Sugar Cane	Fruit Trees	Grains	Pastures	Forest Trees	Field Crops	Buildings, Timber	Distribution
STOLOTERMITIDAE														
Stolotermitinae														
Stolotermes ruficeps													x	New Zealand
Porotermitinae														
*Porotermes adamsoni**											x			Australia
STYLOTERMITIDAE														
Stylotermes beesoni													x	India
Stylotermes bengalensis											x		x	India
Stylotermes chakratensis													x	India
Stylotermes dunensis													x	India
Stylotermes fletcheri								x					x	India
TERMITIDAE														
Apicotermitinae														
Anoplotermes pacificus							x				x	x		Argentina, Bolivia, Brazil, Paraguay, Peru
Anoplotermes schwarzi							x							Cuba
Macrotermitinae														
Allodontermes schultzi													x	South Africa
Allodontermes tenax				x								x		Tanzania
Ancistrotermes cavithorax								x			x		x	West Africa (Sierra Leone to Cameroon)
Ancistrotermes crucifer						x					x			Gambia, Nigeria
Ancistrotermes equatorius												x		Uganda
Ancistrotermes guineensis		x					x							Nigeria, Chad
Ancistrotermes latinotus						x	x					x		Congo, Tanzania, Central Africa, Zambia, Zimbabwe
Anistrotermes pakistanicus	x												x	Malaysia, Bangladesh
Hypotermes obscuriceps	x												x	Sri Lanka
Hypotermes xenotermitis											x			Myanmar
Macrotermes barneyi							x							China

Macrotermes bellicosis						x	x	x	x		x		x	West Africa, Sudan
Macrotermes carbonarius				x										Malawi
*Macrotermes convulsionarius**							x						x	India
Macrotermes falciger												x	x	South Africa, Zambia
Macrotermes gilvus							x						x	Malaysia, Philippines, Indonesia
Macrotermes khajuriai													x	India
Macrotermes natalensis	x					x					x		x	Central Africa, South Africa, Uganda, Sudan
Macrotermes subhyalinus			x	x		x	x	x	x		x	x	x	West, Central and East Africa, Sudan, Zimbabwe
*Megaporotermes giffardi**													x	Sierra Leone
Microtermes albopartitis												x		Tanzania
Microtermes aluco												x	x	Ghana, West Africa
Microtermes havilandi													x	South Africa
Microtermes incertoides													x	India
Microtermes jacobsoni	x													Indonesia
Microtermes kasaiensis												x		Zambia
Microtermes lepidus						x								Nigeria
Microtermes mycophagus							x					x	x	India, Pakistan
Microtermes naidensis												x		Yemen, Sudan
*Microtermes obesi**	x						x	x	x			x	x	India, Pakistan
*Microtermes redenianus**												x	x	Tanzania
Microtermes subhyalinus							x							Central Africa
Microtermes thoracalis						x						x		Sudan, Central Africa
Microtermes tragardhi							x						x	Sudan
Microtermes unicolor							x					x	x	India, Pakistan
Microtermes vadschaggae									x			x		Tanzania
Odontotermes assmuthi							x	x						India
Odontotermes anamallensis													x	India
*Odontotermes badius**						x	x					x	x	Angola, Kenya, Central Africa, Somalia, Uganda, Ethiopia, South Africa, Tanzania, Namibia
Odontotermes bellahunisensis				x									x	India
Odontotermes bhagwatii													x	India
Odontotermes brunneus													x	India
*Odontotermes ceylonicus**													x	Sri Lanka
Odontotermes classicus				x			x							Somalia

TABLE 9. *Continued*

	Tea/Coffee	Rubber	Cocoa	Coconut	Oil Palm	Groundnut	Sugar Cane	Fruit Trees	Grains	Pastures	Forest Trees	Field Crops	Buildings, Timber	Distribution
*Odontotermes distans**											x		x	India
*Odontotermes feae**											x		x	India, Bangladesh, Myanmar
*Odontotermes formosanus**	x						x	x	x				x	Taiwan, Vietnam, Cambodia, Thailand, Japan
Odontotermes gurdaspurensis									x		x		x	India
Odontotermes hainanensis							x	x			x	x		China
Odontotermes horai													x	India
*Odontotermes horni**	x			x				x					x	Sri Lanka
Odontotermes javanicus	x													Malaysia
Odontotermes kapuri													x	India
Odontotermes kibarensis													x	Uganda
*Odontotermes latericius**						x		x			x	x	x	East, Central and South Africa, Mozambique
Odontotermes latigula								x						India
Odontotermes lokanandi													x	India
Odontotermes longignathus	x													Malaysia
Odontotermes malabaricus													x	India
*Odontotermes microdentatus**											x		x	India
Odontotermes nilensis						x		x				x	x	Sudan, Senegal
*Odontotermes obesus**	x			x		x	x	x	x		x	x	x	India, Pakistan
*Odontotermes parvidens**	x							x			x	x		India, Myanmar, Pakistan
*Odontotermes pauperans**													x	West Africa (Senegal to Nigeria)
*Odontotermes redemanni**	x			x			x	x	x		x		x	Sri Lanka, India
Odontotermes smeathmani					x		x							Nigeria, Sudan
*Odontotermes taprobanes**							x							Sri Lanka
*Odontotermes transvaalensis**	x												x	South Africa, Zimbabwe
Odontotermes vulgaris						x								Senegal
*Odontotermes wallonensis**							x	x			x		x	India
Odontotermes zambesiensis												x		Tanzania
Pseudacanthotermes militaris	x		x				x				x	x		Nigeria, Malawi, Kenya, Tanzania
Pseudacanthotermes spiniger												x		Zambia

Nasutitermitinae														
Convexitermes convexifrons													x	Brazil, Peru
Cortaritermes fulviceps													x	Argentina, Brazil, Paraguay, Uruguay
Hospitalitermes birmanicus											x			Myanmar
Kauderintermes laticeps				x										Madagascar
Kaudernitermes nigritus				x										Madagascar
Nasutitermes acangussu													x	Brazil
Nasutitermes aquilinus											x		x	Argentina, Brazil, Paraguay
Nasutitermes anamalaiensis													x	India
Nasutitermes beckeri													x	India
Nasutiternes bivalens	x													Brazil
Nasutitermes brevioculatus							x							Brazil, Bolivia, Paraguay
Nasutitermes brunneus													x	India
Nasutitermes callimorphus													x	Brazil
Nasutitermes crassicornis													x	India
*Nasutitermes ceylonicus**				x									x	Sri Lanka
*Nasutitermes corniger**							x	x					x	Panama, Guatemala, Brazil, West Indies, Guyana
*Nasutitermes costalis**				x			x	x			x		x	West Indies, Guyana, Puerto Rico
Nasutitermes dunensis													x	India
Nasutitermes emersoni													x	India
*Nasutitermes ephratae**				x									x	Panama, Guatemala, West Indies
*Nasutitermes exitiosus**													x	Australia
Nasutitermes fletcheri													x	India
Nasutitermes gardneri													x	India
Nasutitermes globiceps							x						x	Paraguay, Bolivia
Nasutitermes guayanae													x	Brazil, Colombia, Guianas, Trinidad, Venezuela
Nasutitermes havilandi													x	Malaysia
Nasutitermes indicola													x	India
Nasutitermes jalpaigurensis													x	India
Nasutitermes longipennis													x	Australia
Nasutitermes luzonicus				x										Philippines
Nasutitermes matangensiformis													x	Vietnam
Nasutitermes mexicanus													x	Mexico
Nasutitermes novarumhebridarum				x										Solomon Is.
Nasutitermes nigriceps													x	Mexico, Guatemala, Jamaica

TABLE 9. *Continued*

	Tea/Coffee	Rubber	Cocoa	Coconut	Oil Palm	Groundnut	Sugar Cane	Fruit Trees	Grains	Pastures	Forest Trees	Field Crops	Buildings, Timber	Distribution
Nasutitermes octopilis								x						Brazil, Guyana
Nasutitermes parvonasutus							x							Taiwan
Nasutitermes peruanus								x						Bolivia, Brazil, Ecuador, Peru
Nasutitermes rippertii			x	x			x						x	Bahamas, Cuba
Nasutitermes surinamensis							x	x				x	x	Amazonia, Guianas
Nasutitermes thanensis													x	India
*Nasutitermes voeltzkowi**													x	Mauritius
Nasutitermes walkeri													x	Australia
Parvitermes antillarum							x							Dominican Republic
Parvitermes palliceps							x							Haiti
Trinervitermes biformis						x	x	x	x	x		x		India, Pakistan
Trinervitermes ebenerianus						x			x					Nigeria
Trinervitermes geminatus										x				Nigeria
Trinervitermes heimi							x							India
Trinervitermes rabidus								x	x			x		India
Trinervitermes trinervoides										x				South Africa
Velocitermes glabrinotus											x			Brazil
Syntermitinae														
Armitermes euamignathus											x			Bolivia, Brazil, Paraguay
Cornitermes bequaerti										x	x			Brazil
*Cornitermes cumulans**	x						x			x	x	x		Argentina, Brazil, Bolivia
Cornitermes ovatus							x							Brazil
*Cornitermes silvestrii**							x			x				Bolivia, Brazil
Procornitermes araujoi									x		x			Brazil
Procornitermes striatus	x						x	x	x		x			Argentina, Brazil, Paraguay, Uruguay
Procornitermes triacifer	x						x		x		x	x		Argentina, Bolivia, Brazil
Syntermes grandis							x							Bolivia, Brazil, Guianas
Syntermes insidians											x			Amazonia, Guianas
*Syntermes molestus**							x		x		x	x		Brazil
*Syntermes nanus**									x		x	x		Argentina, Brazil, Paraguay

Syntermes obtusus									x					Argentina, Bolivia, Brazil, Paraguay
Syntermes wheeleri									x					Brazil
Termitinae														
Amitermes amifer													x	Argentina, Brazil, Paraguay
Amitermes baluchistanicus								x						Pakistan
Amitermes belli													x	India, Pakistan
Amitermes evuncifer						x	x				x	x	x	Nigeria, Uganda
Amitermes excellans						x		x				x	x	Guyana, Brazil
Amitermes herbertensis							x						x	Australia
Amitermes latidens							x							Australia
Amitermes loennbergianus													x	Kenya
Amitermes neogermanus										x				Australia
Amitermes obeuntis													x	Australia
Amitermes obtusidens							x							Australia
Amitermes unidentatus													x	Mozambique
*Amitermes vilis**													x	Iran, Turkmenistan
Angulitermes dehraensis													x	Pakistan
Dicuspiditermes hutsoni	x													Sri Lanka
Drepanotermes rubriceps										x				Australia
Ephelotermes cheeli							x							Australia
Eremotermes nanus						x								Sudan
Eremotermes paradoxalis							x	x						India
Eremotermes sabaeus													x	South Arabia
Eurytermes ceylonicus	x													Sri Lanka
Globitermes globosus					x									Malaysia
*Globitermes sulphureus**					x						x		x	Malaysia, Thailand
Microcerotermes annandalei													x	India
Microcerotermes arboreus								x					x	Trinidad, Amazonia, Guianas
Microcerotermes baluchistanicus								x					x	Pakistan
Microcerotermes beesoni							x						x	India
Microcerotermes biroi				x										Solomon Is.
Microcerotermes bugnioni				x										Sri Lanka
Microcerotermes cameroni													x	India
Microcerotermes danieli				x									x	India
*Microcerotermes diversus**								x			x	x	x	Israel, Arabia, Iraq, Iran
Micerocerotermes edentaus			x											Ivory Coast

TABLE 9. *Continued*

	Tea/Coffee	Rubber	Cocoa	Coconut	Oil Palm	Groundnut	Sugar Cane	Fruit Trees	Grains	Pastures	Forest Trees	Field Crops	Buildings, Timber	Distribution
Microcerotermes exiguus							x						x	Venezuela, Brazil, Colombia, Trinidad, Nicaragua
Microcerotermes fletcheri								x					x	India
*Microcerotermes fuscotibialis**													x	Sierra Leone
Microcerotermes heimi													x	Pakistan
Microcerotermes labioangulatus													x	India
Microcerotermes losbanosensis				x			x						x	Philippines
Microcerotermes masaiaticus											x			Kenya
Microcerotermes minor											x		x	India
Microcerotermes nicobarensis				x										India
Microcerotermes palestinensis													x	Israel
Microcerotermes parviceps							x							Australia
Microcerotermes parvulus												x		Tanzania
Microcerotermes parvus			x											Congo, East Africa
*Miceroceroterme*s *raja*													x	India
Microcerotermes rambanensis													x	India
Microcerotermes solidus			x											Ghana
Microcerotermes strunckii							x	x					x	Brazil, Argentina
Microcerotermes subtilis				x									x	Seychelles
Microcerotermes theobromae			x											São Tomé
Microcerotermes tenuignathus													x	India, Pakistan
Microcerotermes turneri													x	Australia
*Neocapritermes opacus**											x			Argentina, Bolivia, Brazil, Ecuador, Paraguay, Peru
*Neocapritermes parvus**							x							Brazil Paraguay
Pericapritermes nitobei							x		x					China, Taiwan
Pseudocapritermes fletcheri	x													India
Sinocapritermes mushae									x					Taiwan
Termes fatalis							x	x						Amazonia, Guianas, Trinidad
Termes nigritus							x							Guyana
Termes riograndensis							x							Brazil

TERMITE EVOLUTION: DIVERSITY, DISTRIBUTIONS, PHYLOGENY, FOSSIL RECORD

At any one moment in evolutionary history, the diversity of organisms is a product of the speciation and extinctions that have preceded it. While ecological and genetic factors clearly affect the speciation and extinction of populations, and thus of species, understanding diversity also requires a historical context, for which phylogeny is the sine qua non. Understanding phylogenetic relationships are necessary for indentifying monophyletic taxa and for discerning evolutionary patterns. While it is typical for entomologists to examine phylogenetic relationships of living species only, we have made an effort to also include extinct termites here, since fossils are required for interpreting past diversity, the ages and divergence times of taxa, and extinctions.

The monophyly of the termites has probably never been seriously questioned, and indeed the Isoptera is defined by a large suite of specialized features or synapomorphies. These include the following: an imago-worker head that is prognathous (vs. opisthognathous as in roaches and hypognathous as in mantises); narrow, homonomous wings that dehisce along a basal suture; reduction of the crossveins into reticulations and loss of many longitudinal veins; reduction of the typical, large dictyopteran pronotum; highly reduced genitalia; and advanced sociality, or eusociality. Termites, in fact, are the only major group of social animals in which all species have morphologically distinct reproductives and soldiers (and usually workers), which are also comprised of both sexes, not just females.

The relationships of termites, however, to the two other major lineages of Dictyoptera, the Blattaria and Mantodea, have historically been controversial, with each of the four possible permutations having been proposed. These early studies, up to approximately the year 2000, have been amply reviewed (Kambhampati and Eggleton, 2000; Thorne et al., 2000; Eggleton, 2001; Grimaldi and Engel, 2005; Klass and Meier, 2006). In the past decade, evidence has accumulated that has established an undisputed sister-group relationship between termites and the relict wood roaches, *Cryptocercus*. This is the sole genus of the family Cryptocercidae, with seven known species: four in the southern Appalachians, one in the Cascade Mountains of northwestern North America, and two species in the Far East.

The concept of a *Cryptocercus*-termite relationship began with the classic work of Cleveland et al. (1934) on the similar symbiotic ciliate and flagellate protists shared between *Cryptocercus* and some basal termites (i.e., the protist genera *Leptospironympha* and *Trichonympha*). Besides harboring similar protist faunas, *Cryptocercus* also feeds on and nests within decaying wood in small colonies of parents and offspring. *Cryptocercus* are long-lived, monogamous, have extended parental care, and engage in transfer of protists among nestmates (reviewed in Grimaldi and Engel, 2005). Specialized structure of the proventriculus likewise supports this relationship (McKittrick, 1964; Klass, 1998), as do mandibular dentition (Ahmad, 1950) and other morphological features (Dietz et al., 2003; Grimaldi and Engel, 2005; Klass and Meier, 2006). It was the advent of molecular studies that fully corroborated the *Cryptocercus*-termite hypothesis (Lo et al., 2000; Inward et al., 2007a, 2007b; Legendre et al., 2008).

The view that termites are simply highly modified social roaches is no longer in dispute, but one question has arisen: if classification is to reflect phylogeny, shouldn't the Isoptera be demoted from an order to a subordinate taxon within Blattaria? The proposal has even been made that the name Isoptera be replaced with a family name (such as Termitidae, s.l.) and current families become subfamilies (Inward et al., 2007a). Lo et al. (2007), in response to this proposal, indicated that this would create unnecessary taxonomic chaos, and that Isoptera can be retained either as an unranked group or eventually be given some formal superfamilial grouping within Blattaria. This would preserve the internal classification of Isoptera and satisfy most needs for a phylogenetic classification. Thus, we are proposing an **Infraorder Isoptera** within the Order Blattaria, along with a few modifications of the taxonomic ranks within Blattaria (see classification summary and Engel et al. 2009).

Along with the recent activity in phylogenetics of termites has been the discovery and study of diverse fossil termites (figs. 60–65). The majority of termite fossils are preserved as compressions or impressions in sedimentary strata (e.g., fig. 60), and most of these are preserved as isolated wings. Wings are less susceptible to decay, which is why they are the most common type of insect remains in fossil deposits (Grimaldi and Engel, 2005). Wing venation in termites provides some phylogenetic information, such as the branching of Rs, M, and Cu veins, but there is a great deal of intraspecific variation, which unfortunately makes phylogenetic interpretation difficult based on venation alone. Moreover, many of the most systematically reliable characters for termites are of minute structures unlikely to be preserved in compressions, such as ocelli, sulci, tarsomeres and tibial spines, cerci, and mandibular dentition. Fortunately, insects preserved in amber (figs. 63–65), and ones preserved as 3-dimensional mineralized replicas (such as from the Miocene of Calico, California, and the very important Early Cretaceous Crato Formation of Brazil [Grimaldi et al., 2008: fig. 62]), generally preserve detailed 3-D structure. There are also fossilized remains of nests and galleries, generally referred to as ichnofossils. As a result, we have tended to place more emphasis in our interpretation of the termite fossil record on these well-preserved fossils. Tables 11 through 14 summarize the global diversity of living and extinct genera and species, and their distributions.

Several comprehensive phylogenetic studies on termites have been published within the past decade. These include the studies by Donovan et al. (2000), which used morphological and biological characters; and the molecular studies by Thompson et al. (2000: using 2 genes), Inward et al. (2007: 3 genes), and Legendre et al. (2008: 7 genes). Hypotheses on the relationships of families and some basal genera of termites are compared in figure 61. Relationships that agree in all or most of the hypotheses include the following: Mastotermitidae is the most basal living family; all other living termites comprise a monophyletic group; other groups that are definitively monophyletic are the Kalotermitidae, the two genera *Stolotermes* + *Porotermes* (now placed in the Stolotermitidae [Engel et al., 2009]), the harvester termites (*Anacanthotermes, Hodotermes,* and *Microhodotermes*: Hodotermitidae s.s.), those termites with a fontanelle (Neoisoptera), and the Termitidae. There also seems to be agreement in these major studies about the paraphyly of the Rhinotermitidae, though they differ as to relationships among rhinotermitids, as discussed below. Most recent is the morphological analysis of Engel et al. (2009), which included fossils with living taxa, and thus allows much more accurate interpretation of the termite fossil record.

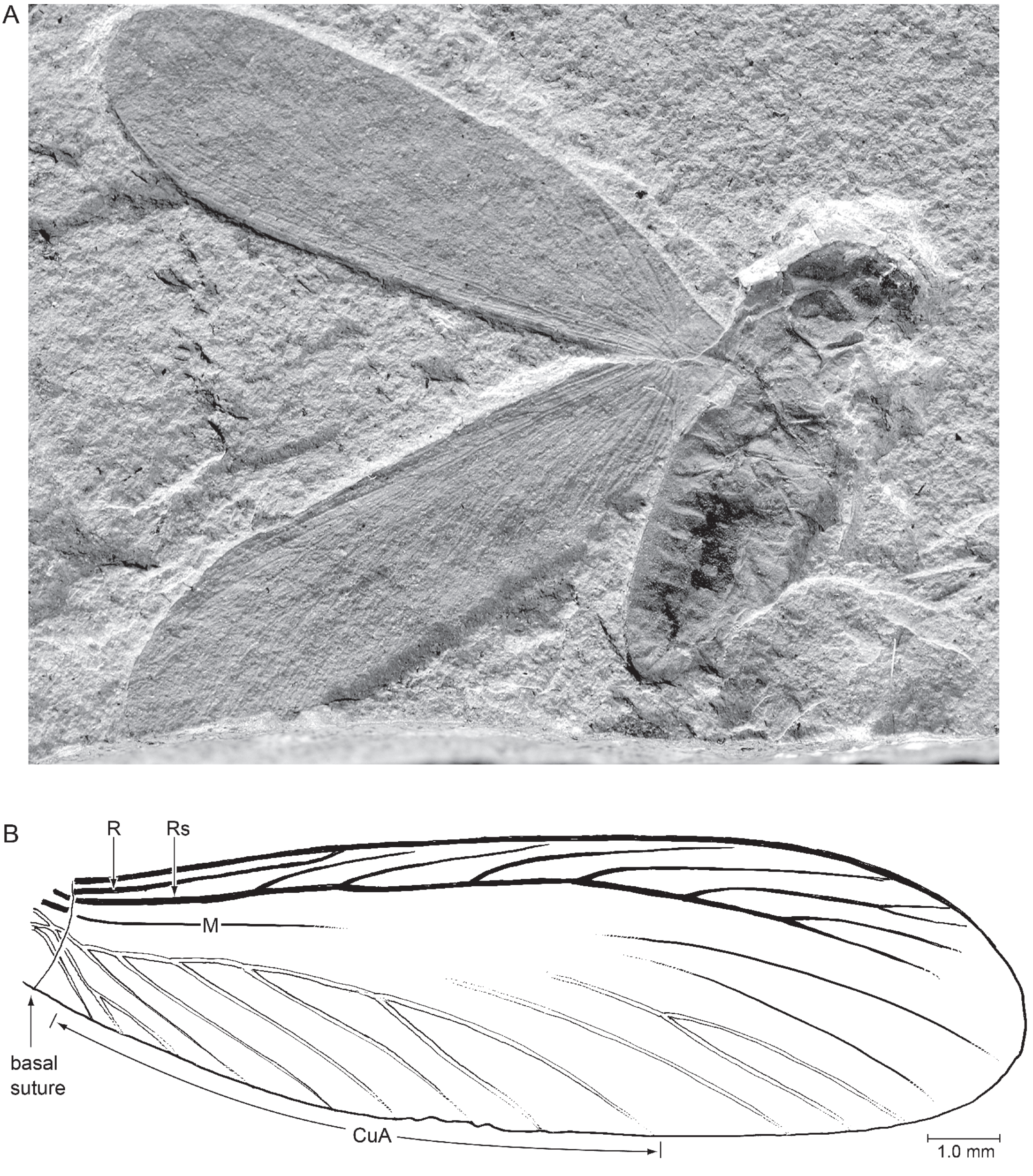


FIGURE 60. The oldest termite, *Baissatermes lapideus* Engel et al., from the Zaza Formation (Berriasian: ca. 135 myo) of Baissa, Transbaikal, Siberia. **A.** Photomicrograph of type and unique specimen. **B.** Venation of forewing, reconstructed from both wings.

Using a phylogenetic framework, the following is our attempt to synthesize various aspects of termite biology and their fossil record into an evolutionary narrative.

The earliest termites derive from the Early Cretaceous, 135–100 Mya, and in fact all species from the Cretaceous Period (145–65 Mya) are primitive (figs. 60, 62–64, 66). By "primitive" we mean they are either stem groups to all families of termites (i.e., *Cratomastermes*), to *Mastotermes* (several genera), to the Euisoptera, or to and among the basal living families including the Kalotermitidae. The most derived termite from the Cretaceous is the only one that possesses a fontanelle, *Archeorhinotermes rossi* (fig. 64C–D). Until recently (Engel et al., 2009), Isoptera was considered unique among major insect orders in having no extinct families, but this concept was merely an artifact of classifications that have not been based on phylogenetic study of the fossils. Almost all Cretaceous taxa, for example, were placed into a broad Hodotermitidae (Emerson, 1969; Nel and Paicheler, 1993; Thorne et al., 2000; Grimaldi and Engel, 2005). Engel et al. (2009) clarified the position of various Cretaceous genera that have either traditionally or provisionally been placed in the Hodotermitidae, such as *Meiatermes* (fig. 62D), *Carinatermes* (figs. 63A, B), and *Mariconitermes* (fig. 62A), and found that these are actually stem groups to the Euisoptera (see below). With the exception of *Archeorhinotermes* and *Proelectrotermes holmgreni* (both in 100 Myo Burmese amber; fig. 64E), all Cretaceous genera, where known, plesiomorphically have numerous antennomeres, a Y-shaped epicranial sulcus, five fully developed tarsomeres, numerous and well-developed superior branches of vein Rs, vein reticulations, a relatively large pronotum, and well-developed and serrated tibial spurs.

The most primitive Cretaceous termites—indeed, apparently the most basal of all known termites—is *Cratomastotermes wolfschwennegeri* Bechly from Brazil's Crato Formation (fig. 62B). As the name suggests, it was originally placed in the Mastotermitidae (Bechly, 2007), but this robust, heavy-bodied termite has features that are even more primitive than those of the mastotermitids, and so has been placed into a separate family, the **Cratomastotermitidae** (Engel et al., 2009). These are, namely, a very large, broad head (the presence/absence of ocelli is unknown), an exceptionally large pronotum, and wing venation in which the reticulations are actually developed as complete crossveins (in all living and extinct Mastotermitidae these crossvein reticulations do not join the longitudinal veins).

Mastotermes darwiniensis Froggatt is the sole living species of the family **Mastotermitidae**, and undisputedly the most basal living species of termite (figs. 11, 61, 66). It is found in the tropical, nonforested regions of northern Australia and has been introduced into southern New Guinea (fig. 67). Primitive features it retains are the following: large body size; ocelli; relatively large pronotum; hind wing with a large, fanlike anal lobe; numerous branches of veins Rs, M, and Cu; hind wing with barely developed basal suture; five tarsomeres; keeled fore coxae; multisegmented cerci; ovipositor (though internal) with valvulae; eggs laid in a vestigial ootheca; and specialized mycetocytes that harbor symbiotic *Blattabacterium* bacteria that are also found in roaches. It has been known for some time that *Mastotermes darwiniensis* is highly relict, since fossil *Mastotermes* are nearly global, from the Miocene through the Eocene of Europe (Emerson, 1965; Engel and Wappler, 2006), and in Miocene amber from Chiapas, Mexico (Krishna and Emerson, 1983), and the Dominican Republic (Krishna and Grimaldi, 1991), for a total of 13 extinct species of the genus. All three castes, in fact, are known for *Mastotermes electrodominicus* (Grimaldi and Engel, 2005). This species was also the subject of study for ancient DNA (DeSalle et al., 1992), though the authenticity of ancient DNA from amber fossils is doubtful (reviewed in Grimaldi and Engel, 2005). Fossil *M. electrodominicus* workers even yielded finely preserved remains of symbiotic protists from the hind-gut tissue (Wier et al., 2002). Despite the relict nature of *Mastotermes, M. darwiniensis* is a notorious pest with a very broad diet. Its distribution seems to be limited mostly by climate, which may have been the primary factor in the widespread extinction of *Mastotermes.*

There are seven other genera in the Mastotermitidae, all extinct and distributed throughout the world. The oldest apparent mastotermitid is *Valditermes brenane* Jarzembowski from Early Cretaceous Wealden clay of England. Its phylogenetic position has been disputed, but based on the long, straight anal edge of the incompletely preserved hind wing, it appears to have had a large anal lobe. Perhaps the most remarkable fossil mastotermitid is *Garmitermes succineus,* recently discovered in Baltic amber (Engel et al., 2007; fig. 65A–C). It is known only from a unique dealate specimen that is beautifully preserved, and it possesses features that are even more plesiomorphic than those in *Mastotermes*: a very large pronotum that wraps laterally, large lateral cervical sclerites, apical flagellomeres that are tapered, and plantular pads on the tarsi. Oddly, despite centuries of collecting and study of Baltic amber, this is the only known mastotermitid from that fossil deposit. In the study by Engel et al. (2009), Mastotermitidae were surprisingly defined as monophyletic, even though they have traditionally been defined on the basis of plesiomorphic morphological features. Monophyly of the family is weakly supported, though, based only on two homoplastic features, the presence of ocelli and the shape of the pronotum.

All the remaining Isoptera exclusive of the Mastotermitidae and Cratomastotermitidae are a monophyletic group that have been named the **Euisoptera** (Engel et al., 2009: fig. 66) based on the loss of various blattodean features of mastotermitids: absence of symbiotic *Blattabacterium* and ootheca (eggs instead are laid singly), complete loss of an ovipositor and an anal lobe/fan in the hind wing, as well as reduction in the size of the pronotum. There thus seems to be a sizeable phenotypic gap between the Mastotermitidae and the remaining termites. Relationships are ambiguous and contentious among those basal living genera of Euisoptera that traditionally have been classified in the Hodotermitidae and Termopsidae, as summarized in the classifications in table 10 and cladograms in figure 61.

One grouping of agreement among the major phylogenetic studies is the monophyly of the three genera of the "harvester" termites, *Anacanthotermes, Hodotermes,* and *Microhodotermes* (figs. 33–35), or what are classified as the **Hodotermitidae** s.s. (Engel et al., 2009: fig. 66). The molecular study by Inward et al. (2007) confirmed this close relationship, as did Legendre et al. (2008), though only the last two of these genera were included in that study. Morphologically and behaviorally the harvester termites share a suite of derived features: lacinia with one tooth subapical instead of both teeth apical, loss of soldier ocelli, the inferior branches of vein Rs parallel and diagonal to the trunk of Rs, and life in grasslands and steppes where they provision their nests with fragments of dried grasses and seeds. There are 21 species of harvesters (16 in *Anacanthotermes* alone), distributed throughout Africa and extending into the Middle

East, Eurasia, and to northwest India (fig. 67). Besides seeds and dried grasses, harvesters also feed on palm debris, herbivore dung, and occasionally on small amounts of wood. Some species of *Anacanthotermes* have been known to consume the straw embedded within the mud bricks of rural dwellings. The nests are a loose system of subterranean chambers and passages in the soil, marked on the surface by shallow mounds. Some of the chambers within the nest serve as "granaries." Although Engel et al. (2009) did not include the genus *Ulmeriella* in their analysis (which is known almost entirely from wings), *Ulmeriella* were possibly harvesters. This is the largest extinct genus of termites, with 11 described species, and is known from the Pliocene to the Oligocene of Asia, Europe, and North America (Emerson, 1968). The geo-

TABLE 10. Classifications of Some Basal Genera of Termites

Snyder, 1949a Emerson, 1955, 1968a, and 1968b Krishna, 1970	Grassé, 1949
Hodotermitidae	Hodotermitidae
Hodotermitinae	*Hodotermes*
Hodotermes	*Microhodotermes*
Microhodotermes	*Anacanthotermes*
Anacanthotermes	†*Ulmeriella*
†*Ulmeriella*	Termopsidae
Termopsinae	Termopsinae
†*Termopsis*	†*Termopsis*
Archotermopsis	*Archotermopis*
Hodotermopsis	*Hodotermopsis*
†*Parotermes*	*Zootermopsis*
Porotermitinae	†*Parotermes*
Porotermes	Porotermitinae
Stolotermitinae	*Porotermes*
Stolotermes	Stolotermitinae
†Cretatermitinae	*Stolotermes*
†*Cretatermes*	†Cretatermitinae
	[added in *Termitologia*]
Roonwal and Chhotani, 1989	Engel et al., 2009
Hodotermitidae	Hodotermitidae
Hodotermitinae	*Hodotermes*
Hodotermes	*Microhodotermes*
Microhodotermes	*Anacanthotermes*
Anacanthotermes	†Termopsidae
Porotermitinae	†*Termopsis*
Porotermes	Archotermopsidae
Stolotermitinae	*Archotermopsis*
Stolotermes	*Hodotermopsis*
†Cretatermitinae	*Zootermopsis*
†*Cretatermes*	†*Parotermes*
Termopsidae	Stolotermitidae
†*Termopsis* [presumed]	Porotermitinae
Archotermopsis	*Porotermes*
Hodotermopsis	Stolotermitinae
Zootermopsis	*Solotermes*

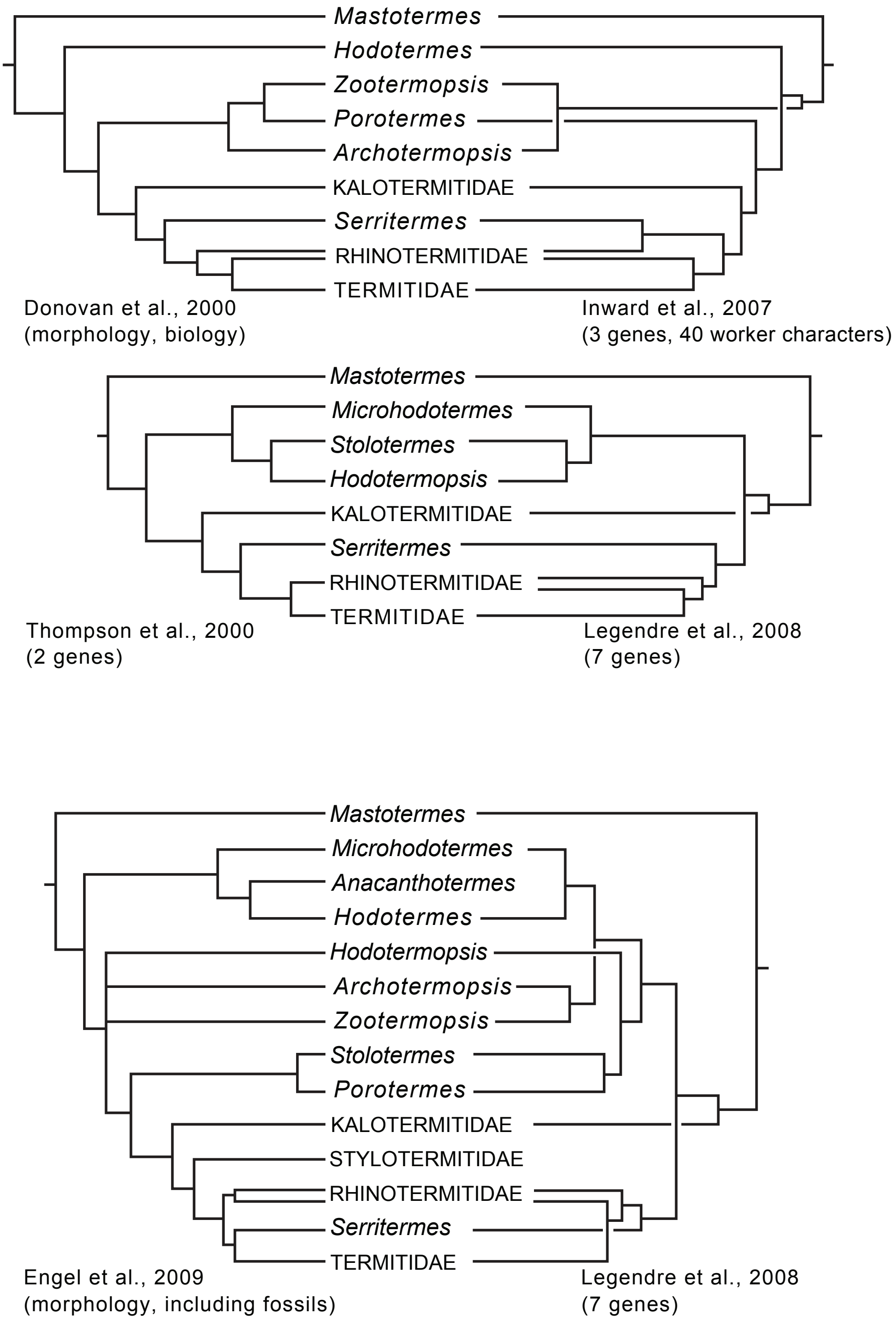


FIGURE 61. Five phylogenetic hypotheses for families and basal genera of Isoptera, based on morphology and/or nucleotide sequences. See text for discussion.

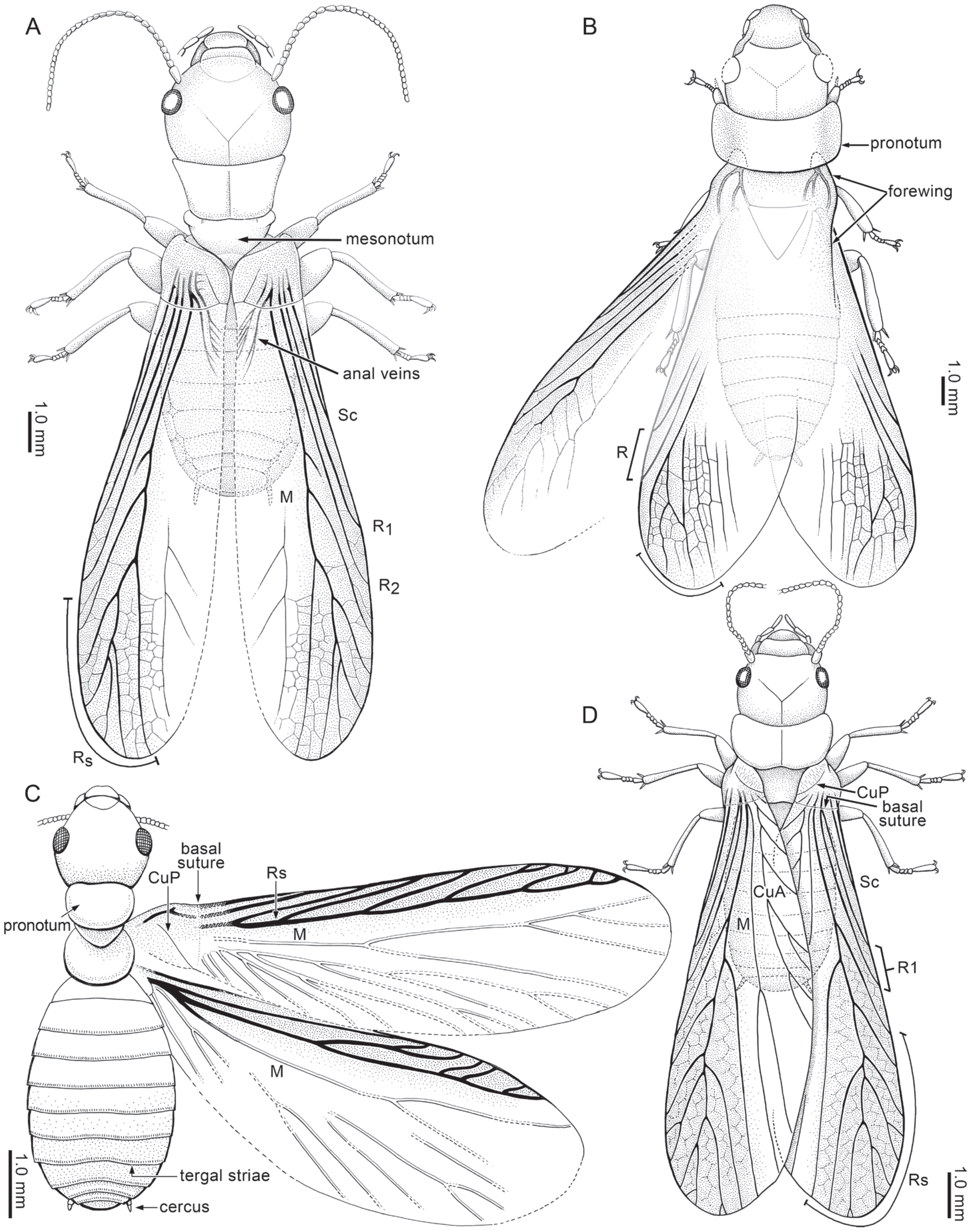


FIGURE 62. Reconstructions of four primitive fossil species and genera of termites from the Crato Formation, Early Cretaceous (Aptian, ca. 115 myo) of Brazil. **A.** *Mariconitermes talicei* Fontes and Vulcano. **B.** *Cratomastotermes wolfschwenningeri* Bechly. **C.** *Cratokalotermes santanensis* Bechly. **D.** *Meiatermes araripena* Krishna. Not to the same scale.

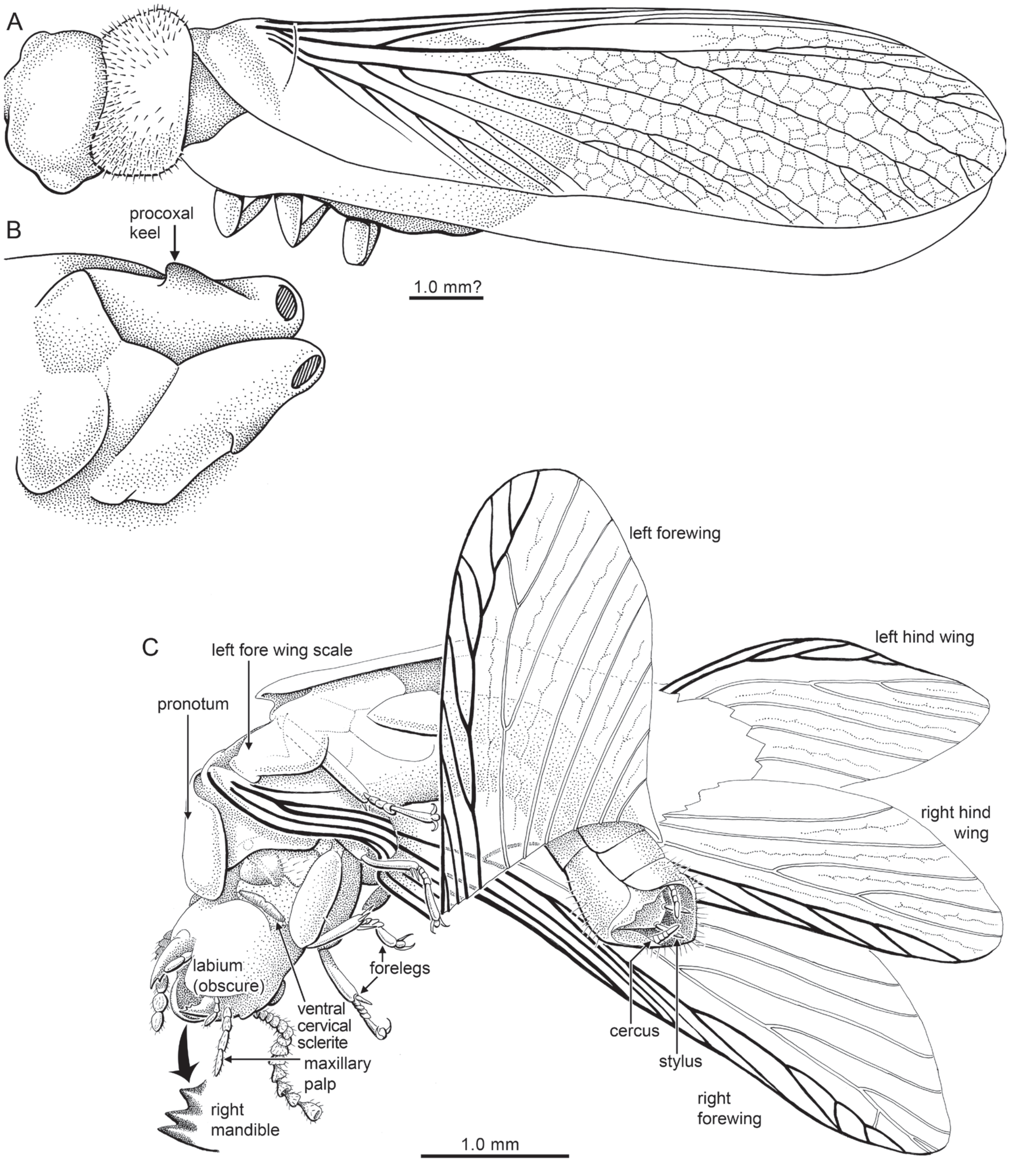


FIGURE 63. Primitive species and genera of fossil termites preserved in Cretaceous amber. **A, B.** *Carinatermes nascimbenei* Krishna and Grimaldi, in 90 myo amber from New Jersey. **A.** Dorsal habitus. **B.** Detail of bases of forelegs, showing plesiomorphic feature of coxal keels. **C.** *Melqartiterms myrrheus* Engel et al., from the Early Cretaceous of Lebanon, with dentition of right mandible. Illustrated as preserved; not to the same scale.

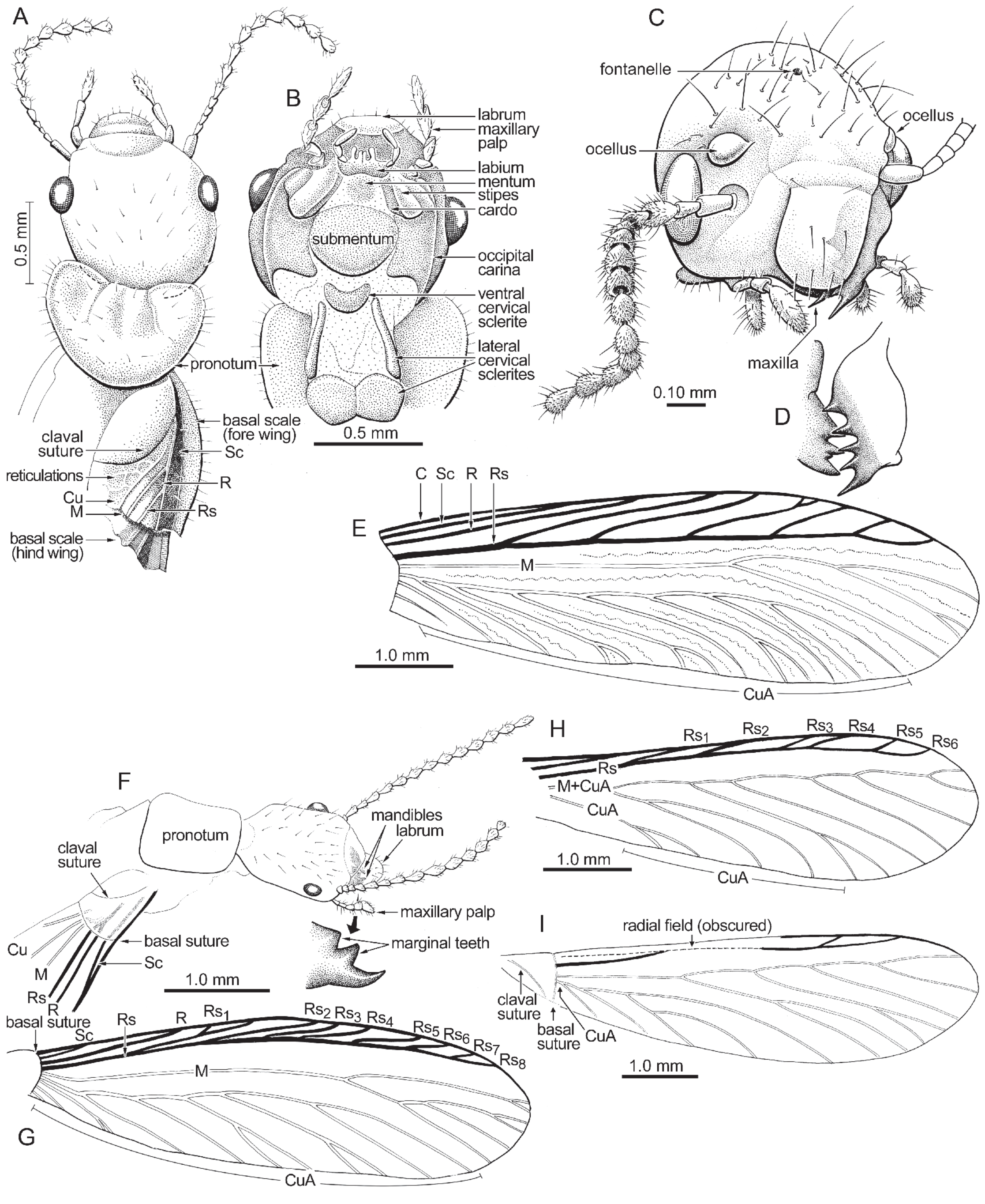


FIGURE 64. Diverse basal termites in mid-Cretaceous (98 myo) amber from northern Myanmar (Burma). **A, B.** *Mylacrotermes cordatus* Engel et al. **A.** dorsal view of head, pronotum, and wing bases. **B.** Ventral view of head and prothorax. **C, D.** *Archeorhinotermes rossi* Krishna and Grimaldi, the earliest and only Cretaceous neoisopteran. **C.** Frontal view of head. **D.** Detail of its unique mandibles. **E.** *Proelectrotermes holmgreni* Engel et al., forewing. **F, G.** *Tanytermes anawrahtai* Engel et al. **F.** Oblique dorsal view of head, pronotum, and wing base. **G.** Forewing. **H, I.** *Dharmatermes avernalis* Engel et al., forewings. All illustrated as preserved; not to the same scale.

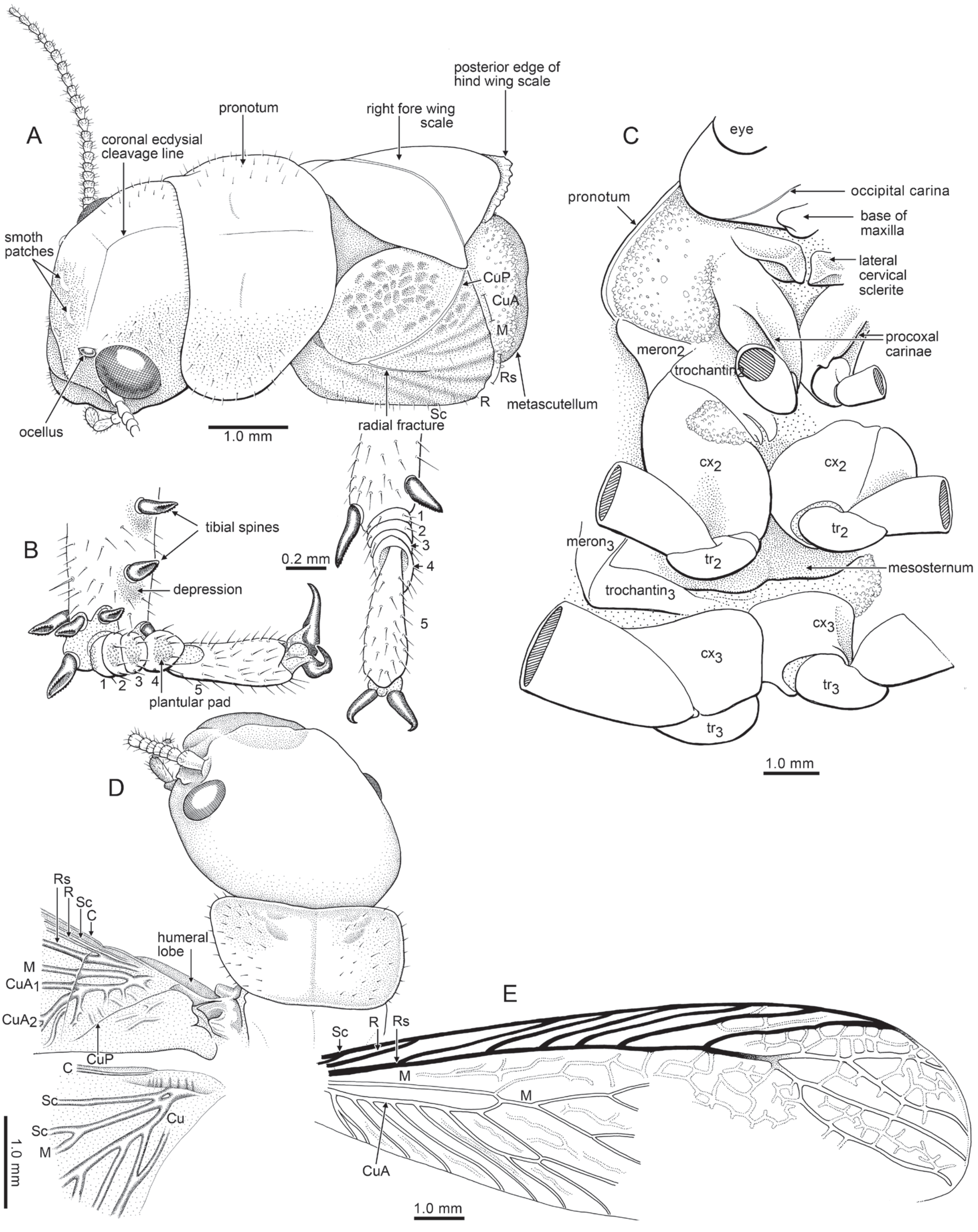


FIGURE 65. Exemplar termites in amber from the Eocene (ca. 42–45 myo) of the Baltic region. **A–C.** *Garmitermes succineus* Engel et al. (Mastotermitidae), dealate. **A.** Oblique dorsal view of head and thorax. **B.** Details of midleg (left) and foreleg (right). **C.** Ventral view of thorax. **D, E.** *Termopsis ukapirmasi* Engel et al. (Termopsidae s.s.). **D.** dorsal view of head, pronotum, and left wing bases. **E.** Wing. All illustrated as preserved; not to the same scale.

graphic and stratigraphic distribution of *Ulmeriella* suggests that the current range of the harvester termites is contracted and that the family, though phylogenetically basal, is rather young and no doubt originated and expanded with the grasslands in the Oligocene and Miocene. It is likely that the harvester termites are derived from one of the many stem-group Cretaceous termites.

Another very stable group comprises the two genera *Stolotermes* and *Porotermes,* each of which has traditionally been placed as a subfamily (Stolotermitinae and Porotermitinae, respectively) within the Hodotermitidae (Snyder, 1949a; Emerson, 1955, 1968a, 1968b; Krishna, 1970) or Termopsidae (Grassé, 1949), but which have recently been classified into a separate family, the **Stolotermitidae** (Engel et al., 2009: fig. 66). This group is biogeographically unique among all termites, the only species with a distribution that is a classic austral disjunction (Grimaldi and Engel, 2005; fig. 67). There are only 10 living species, most of which dwell and feed in rotting logs and tree trunks, although *Porotermes adamsoni* from eastern Australia attacks a variety of living trees and can be a serious timber pest. Two other species of *Porotermes* are *P. quadricollis,* from the wet temperate forests of Cautin Province, Chile, and *P. planiceps* Sjöstedt from South Africa (fig. 36A–C). *Stolotermes* occurs in southeast Australia (*S. australicus* Mjöberg, *S. victoriensis* Hill, *S. queenslandicus* Mjöberg), in New Zealand and Tasmania (*S. brunneicornis* [Hagen], *S. inopinus* Gay, and *S. ruficeps* Brauer), and in South Africa (*S. africanus* Emerson; fig. 36D–E). Austral disjunctions are classically interpreted as relicts of gondwanan drift, in which case these taxa would derive from the Cretaceous, although this interpretation is contradicted by various instances of austral insect fossils from the Northern Hemisphere (reviewed in Grimaldi and Engel, 2005). *Cretatermes carpenteri* Emerson (1967), from the Late Cretaceous of Labrador, has been interpreted on the basis of wing venation as similar to that of the Stolotermitidae, but Emerson classified it in a monotypic subfamily Cretatermitinae; otherwise there are no fossils of this group. *Cretatermes* was the first Cretaceous termite discovered and described.

Monophyly of the family **Archotermopsidae** (Engel et al., 2009) remains to be defined, although some of the molecular studies indicate a close relationship of two of the three genera placed in this family, *Archotermopsis* and *Zootermopsis* (Inward et al., 2007; Legendre et al., 2008). The relationships of the monotypic genus *Hodotermopsis* from southeast Asia (containing *H. japonicus* [= *H. sjostedti*]) are as yet unclear (Engel et al., 2009; Legendre et al., 2008). Morphologically, an apomorphic feature of this group is the reduced second tarsomere, which is not visible when viewed dorsally. *Archotermopsis* and *Zootermopsis* have a disjunct distribution, with two living species of the former genus, *A. wroughtoni* (in the Himalayan foothills of northern Afghanistan, Pakistan, and India) (fig. 31), *A. kuznetsovi* Beljaeva (from Vietnam), and three species of *Zootermopsis* found in western North America (fig. 32A–C). Close relationship of the fossil species *Archotermopsis tornquisti,* in Eocene Baltic amber, to the living species of the genus is supported by their unique lenticular eyes. The fossil genera *Parotermes* and *Gyatermes,* while known largely from wings, are likely archotermopsids. With the exception of *Zootermopsis laticeps* from Arizona and northern Mexico, which excavates nests in deciduous softwoods, the other three species of *Zootermopsis* and *Archotermopsis* construct simple, gallerylike nests within rotting conifer logs. A great deal of research has been done on

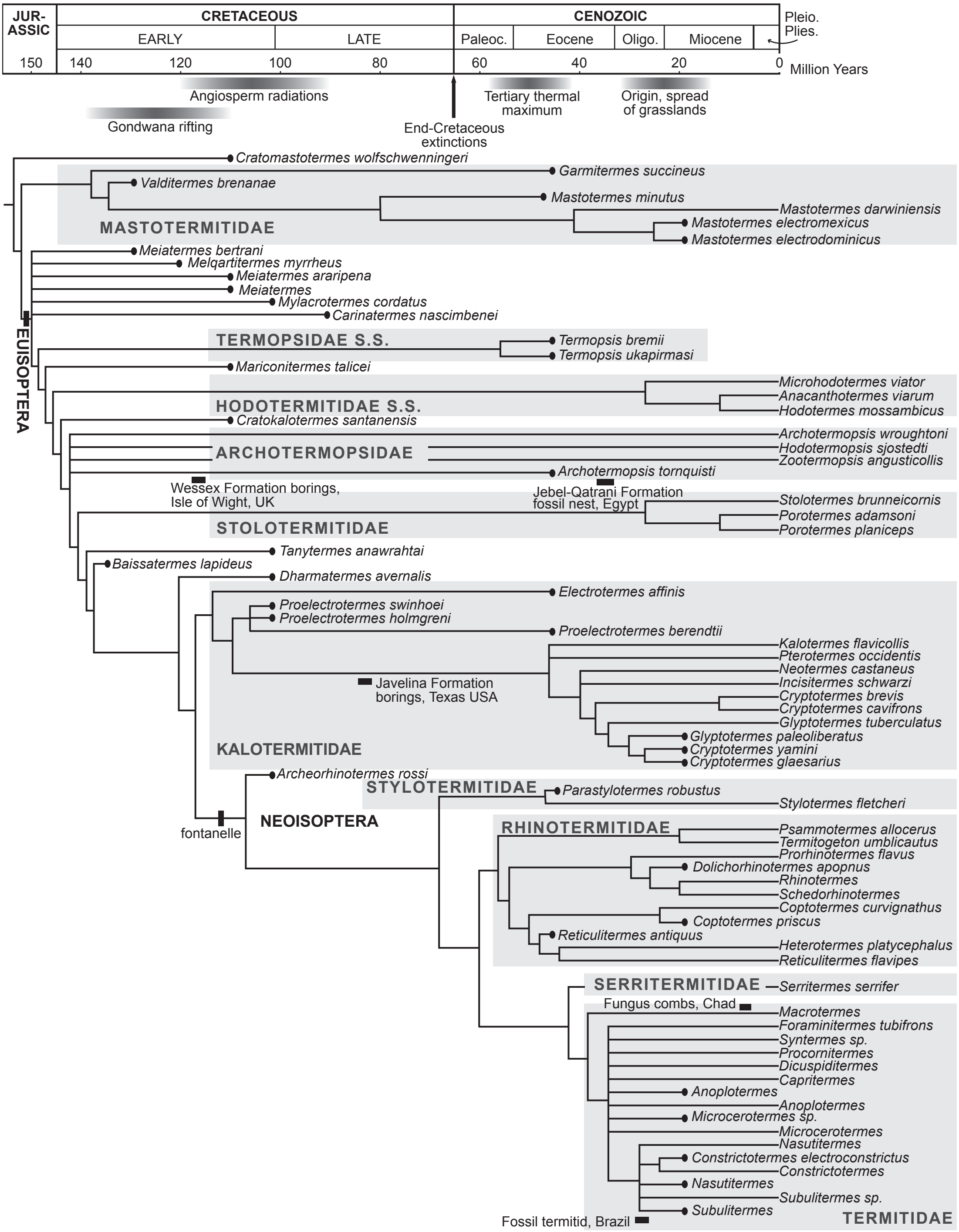


FIGURE 66. Phylogeny of the families and basal fossil genera of Isoptera (from Engel et al., 2009), shown with a geological time scale and significant geological and biological episodes. The classification in this treatise follows this arrangement of families.

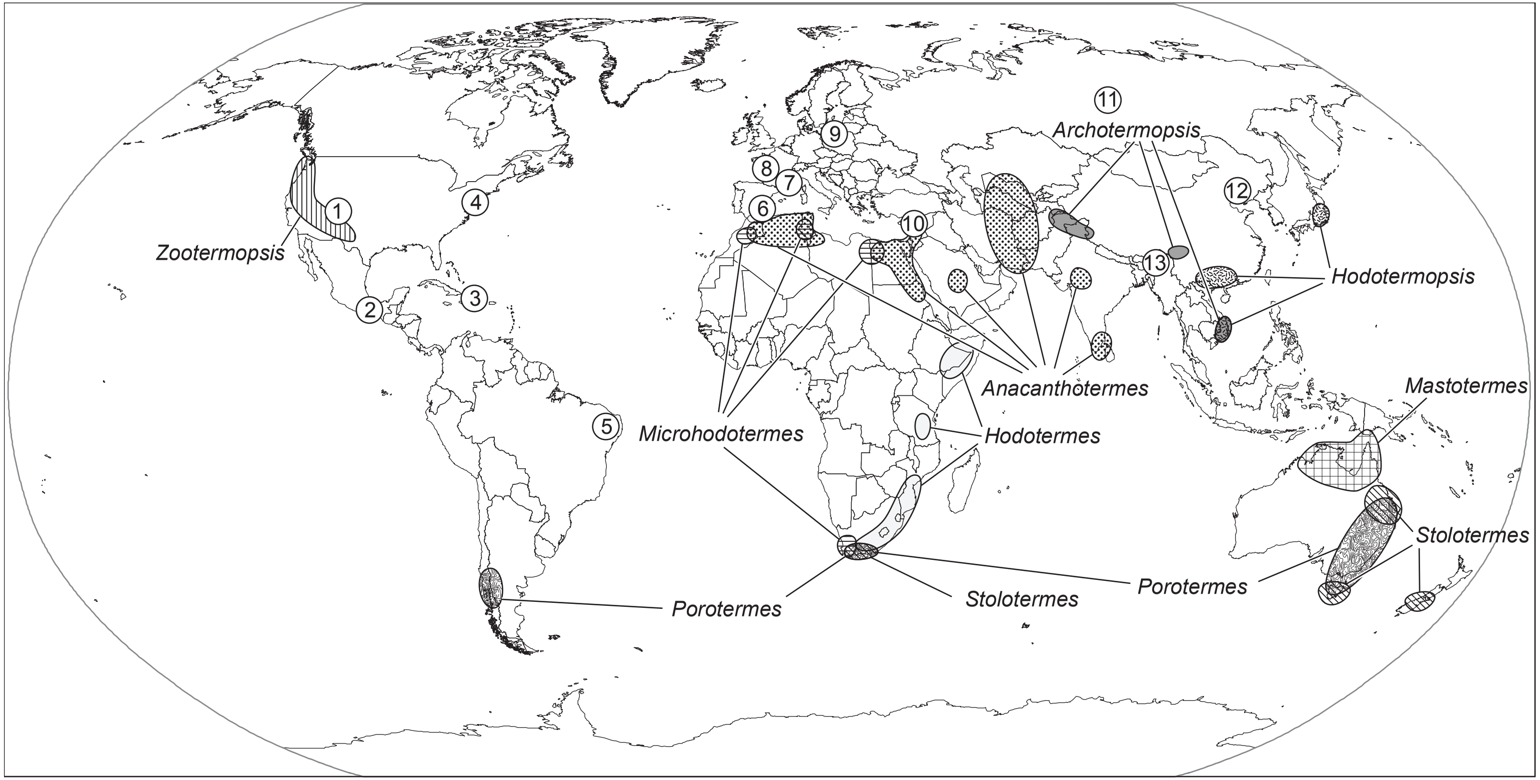


FIGURE 67. World distribution of living species in the basal families Mastotermitidae, Hodotermitidae s.s., Archotermopsidae, and Stolotermitidae, along with major fossil deposits for Isoptera (circled numbers). **1.** Florissant, Colorado (Late Eocene). **2.** Chiapas, Mexico (Miocene amber). **3.** Dominican Republic (Miocene amber). **4.** New Jersey amber (Late Cretaceous). **5.** Crato Formation, Brazil (Early Cretaceous). **6.** Montsec, Spain (Early Cretaceous). **7.** Aix-en-Provence, France (Oligocene). **8.** Eocene Oise amber, France. **9.** Eocene Baltic amber. **10.** Early Cretaceous amber from Lebanon. **11.** Baissa, Siberia (Early Cretaceous). **12.** Yixian Formation, China. **13.** Burmese amber (mid-Cretaceous). Fossils and disjunct Recent distributions indicate that basal termites were significantly more widespread.

Zootermopsis (e.g., Thorne, 1990, 1991; Thorne et al., 1993). Traditionally classified with these three living genera is the extinct genus from Baltic amber, *Termopsis* (Snyder, 1949a; Grassé, 1949; Emerson, 1955, 1968a, 1968b; Krishna, 1970; Roonwal and Chhotani 1989), but this genus appears phylogenetically basal to Archotermopsidae and even Hodotermitidae s.s., so **Termopsidae** s.s. has been proposed for *Termopsis* alone (Engel et al., 2009). There are two species of *Termopsis, T. bremii* and *T. ukapirmasi* (fig. 65C).

Monophyly of the "dry-wood" termites, family **Kalotermitidae**, is well established, based on morphological, behavioral, and genetic features (Krishna, 1961; Thompson et al., 2000; Inward et al., 2007; Legendre et al., 2008; Engel et al., 2009). Morphologically the kalotermitids are defined by the microstructure of the wing membrane (with either a pimplate or nodulose surface), a swollen humeral margin of the forewing scale, and three metatibial spurs. The common name derives from the habit of these termites excavating galleries in sound wood, either dead or living, sometimes even infesting dense tropical hardwoods like mahogany (e.g., some *Neotermes*). They are further distinctive in the loss of the worker caste. With 489 species (457 of them living) and 20 living genera, this is the second largest family of termites after the Termitidae. The monograph by Krishna (1961) on the genera remains the definitive reference for Kalotermitidae. Several interesting aspects of their biology relate to their wood-boring habits. One of these is that kalotermitids are dominant features of insular termite faunas, such as occur on islands in the Caribbean and the Pacific. Particularly for oceanic islands, colonization by kalotermitids is apparently facilitated by rafting in rather buoyant sound wood. Secondly, the soldiers of some genera are phragmotic, having plug-shaped heads used for blocking the openings to the galleries. In the most specialized phragmotic soldiers the frons is swollen, making the front of the head flat to concave, and the anterior half of the head with heavily sclerotized, wrinkled cuticle bearing short mandibles.

Traditionally, the Kalotermitidae were considered to be the sister group to the Mastotermitidae (Ahmad, 1950; Krishna, 1961), but, with the exception of Legendre et al. (2008), modern studies place the family as the sister group to Rhinotermitidae + Serritermitidae + Termitidae (Donovan et al., 2000; Thompson et al., 2000; Inward et al., 2007; Engel et al., 2009: fig. 61). Kalotermitidae are well represented as fossils in amber, the oldest of which are in 100 Myo Burmese amber, *Proelectrotermes swinhoei* and *P. holmgreni* (fig. 64E). Baltic amber contains three species of Kalotermitidae: *Electrotermes affinis, E. girardi,* and *Proelectrotermes berendtii.* The phylogenetic study of Engel et al. (2009) indicates that these extinct genera are stem groups to a crown group that consists of the living kalotermitids. Three species of Kalotermitidae are preserved in Miocene amber from the Dominican Republic, which belong to the speciose living genera *Cryptotermes, Glyptotermes,* and *Incisitermes.* The phylogenetic and stratigraphic positions of kalotermitid fossils thus indicate a Late Cretaceous divergence of living Kalotermitidae lineages from their extinct stem groups. There is even a well-preserved kalotermitid nest within in mineralized ("petrified") wood from the Late Cretaceous Javelina Formation of Texas (Rohr et al., 1986).

There are three monotypic genera that appear to be stem groups to the Kalotermitidae and Neoisoptera, which are *Dharmatermes avernalis* and *Tanytermes anawrahtai* in 100 Myo Burmese amber (fig. 64), and *Baissatermes lapideus,* a 135 Myo compression fossil from Siberia

(Engel et al., 2009; fig. 60). *Baissatermes* is the oldest fossil termite, whose phylogenetic position indicates that the basal divergences of Isoptera probably extended into the Late Jurassic. The **Neoisoptera** is a definitive monophyletic group distinguished by a unique synapomorphy, the presence of a fontanelle (Engel et al., 2009), which is a grouping that is also consistently defined on a genetic basis (Thompson et al., 2000; Inward et al., 2007; Legendre et al., 2008). *Archeorhinotermes rossi* Krishna and Grimaldi (fig. 64C, D), also in Burmese amber, was originally reported as the first Cretaceous Rhinotermitidae, placed in its own subfamily, the Archeorhinotermitinae (Krishna and Grimaldi, 2003); recent analysis indicates this species is a stem group to the Neoisoptera (Engel et al., 2009), and so should be placed in a separate family, the **Archeorhinotermitidae**. *Archeorhinotermes* has a distinctive left mandible, with four long, sharp marginal teeth (fig. 64D). Thus far, *Archeorhinotermes* is the only Cretaceous neoisopteran.

A genus that was not incorporated into the major studies (Donovan et al., 2000; Thompson et al., 2000; Inward et al., 2007; Legendre et al., 2008) is *Stylotermes,* formerly of the Rhinotermitidae (Stylotermitinae) (fig. 49). It is now placed in the **Stylotermitidae** along with the closely related fossil genus *Parastylotermes* (Engel et al., 2007b, 2009) by virtue of lacking some of the derived features of Rhinotermitidae s.s. (such as a clypeus keeled in profile, and strongly reticulate wings lacking setae on the membrane), as well as having the unique feature of three tarsomeres. There are 45 species of *Stylotermes,* all from southeast Asia where they have small colonies living in tunnels of sound or dying wood. *Parastylotermes* contains four species, three of which are compression or mineralized specimens from the Miocene of California and Washington, and the fourth is *P. robustus* (Rosen) in Eocene Baltic amber. Because of the incomplete nature of the Miocene specimens it is difficult to determine whether these are indeed stylotermitids. In the study by Engel et al. (2009), Stylotermitidae is the living sister group to the remaining Neoisoptera (fig. 66).

Relationships of the small living family **Serritermitidae** within Neoisoptera are somewhat ambiguous, with some hypotheses placing them as the living sister group to Rhinotermitidae + Termitidae (Donovan et al., 2000; Thompson et al., 2000), as closely related to some Rhinotermitidae (Inward et al., 2007), as a subfamily of Rhinotermitidae (Austin, 2004), or as the sister group to the Termitidae (Engel et al., 2009). Serritermitidae contains two genera and three species, *Serritermes* (monotypic: *serrifer* [Hagen and Bates]) and *Glossotermes* (*occulatus* Emerson and *sulcatus* Cancello and De Souza), all of which are from South America and generally nest in mounds of *Cornitermes* (Termitidae: Syntermitinae). *Glossotermes* was formerly classified in the Rhinotermitidae. Soldiers of both genera are particularly distinctive, possessing long, straight mandibles having numerous fine serrations on the inner edge (fig. 56).

The family **Rhinotermitidae**, a diverse assemblage of 335 living species in 12 genera and 6 subfamilies, is paraphyletic with respect to Termitidae. They nest in the ground or decaying logs and stumps, and infest moist, decaying wood in contact with the soil. There is significant disparity among the major studies as to which rhinotermitids are the sister group to Termitidae (fig. 68). According to Inward et al. (2007), there is a grade of at least four major rhinotermitid lineages, with Termitidae closely related to the most derived of these (fig. 68). The earlier study by Lo et al. (2004), which used portions of three mitochondrial genes, largely agrees with the results by Inward et al. (2007). Legendre et al. (2008) postulated that Termitidae is the

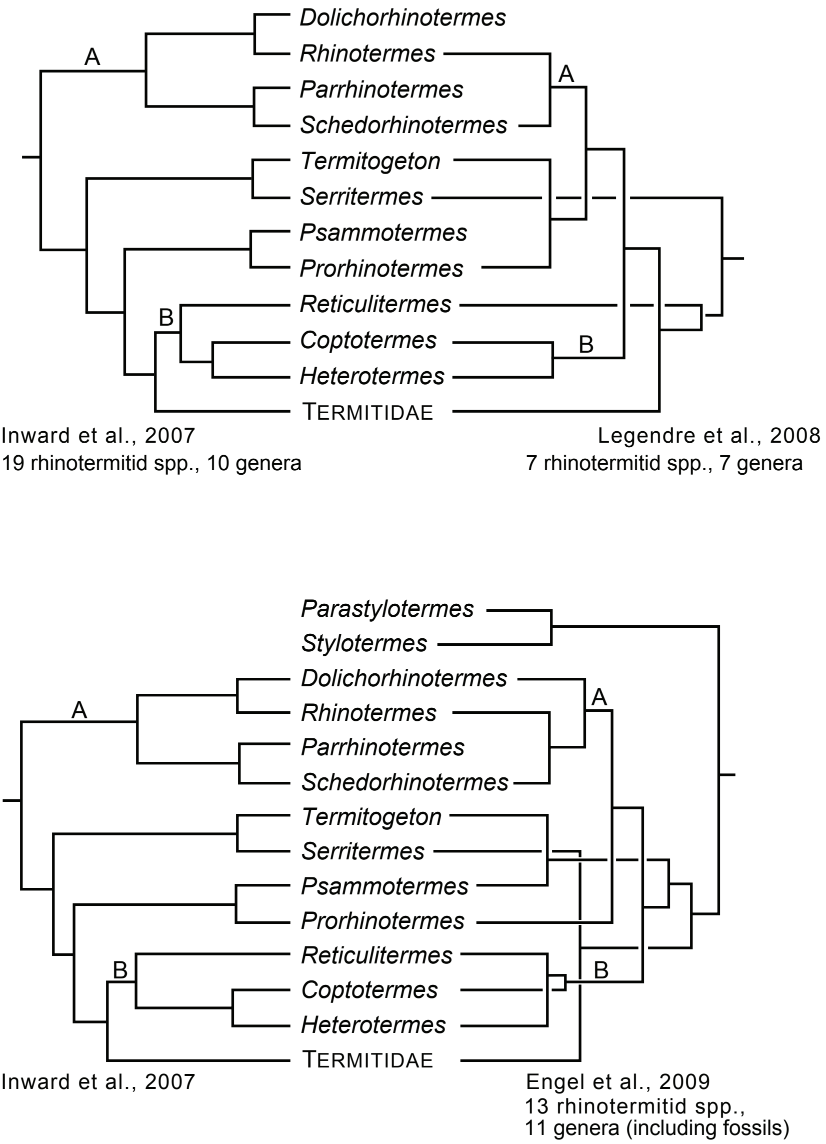


FIGURE 68. Comparisons of relationships among genera of Rhinotermitidae, based on hypotheses in three studies. Taxa in groups denoted by A and B are consistent among the studies (see text).

sister group to all Rhinotermitidae except *Reticulitermes,* and Engel et al. (2009) hypothesized a monophyletic Rhinotermitidae (sans *Stylotermes*) as sister group to Termitidae + Serritermitidae. Clearly, thorough study of rhinotermitid relationships is needed. Despite the ambiguities, a few groups of genera are consistently hypothesized, indicated as A and B in figure 68. Group A contains the genera *Dolichorhinotermes, Rhinotermes,* and *Schedorhinotermes,* and corresponds to the subfamily Rhinotermitinae; group B contains *Coptotermes, Heterotermes,* and *Reticulitermes,* and would correspond to the subfamilies Coptotermitinae and Heterotermitinae.

The group A genera, including the monotypic *Macrorhinotermes* from Borneo, are partly distinguished by having dimorphic soldiers. The minor soldiers of these species have a long labrum and bladelike mandibles lacking teeth; in those species with a very long labrum this structure is used for dispersing a defensive secretion. *Schedorhinotermes* contains 40 species throughout the IndoPacific; *Rhinotermes* and *Dolichorhinotermes* contain five and seven species, respectively, all of them Neotropical.

Group B contains the largest genera of the family and some of the most notorious termite pests. *Coptotermes* (71 species; circumtropical) has distinctive soldiers that bear a very large fontanelle, which exudes a "milky secretion, which sets to a rubbery mass on contact with air" when the soldiers are disturbed (Roonwal, 1970c: 336). The genus contains one of the world's most destructive termites, *C. formosanus* Shiraki (the "formosan termite"), a subtropical temperate species, which has been introduced nearly worldwide. Colonies of *C. formosanus* can reach over one million individuals. *Heterotermes* contains 31 species distributed in all tropical regions except central Africa, some of which are also significant pests. *Reticulitermes,* which contains 140 species, is very well known because it contains the most northerly termites. In the Palearctic, *Reticulitermes* extends to approximately 45°N latitude (through southern France, northern Italy, the Balkan states, east to the northern and eastern shores of the Black Sea). In the Nearctic, *Reticulitermes* extends to approximately 50°N in the west (because of the temperate rain forests along the coast of British Columbia), and in the east to about 43°N. The few species of *Reticulitermes* that range this far north clearly benefit by competitive release from other termites.

Two enigmatic genera of Rhinotermitidae are *Psammotermes* and *Termitogeton* (figs. 50A, F). *Psammotermes* contains six species from arid regions of Africa (Sahara, Namib), the Middle East, and western India. It is the only truly desert-dwelling genus of termites, with some species living in sand dunes while feeding on the windblown chaff of plant debris and ungulate dung. Like the harvesters, *Psammotermes* provision their subterranean nests with bits of dried grass, seeds, and similar material. At least some species are reported to have trimorphic soldiers (Roonwal, 1970c; Roonwal and Chhotani, 1989). *Termitogeton* contains only three species from southeast Asia, which are distinctive for the flat, cordate heads of the soldier and wing venation where vein M is virtually or entirely lost.

There are 18 fossil species of Rhinotermitidae, all belonging to living genera. Most of these are in Miocene amber from Mexico and the Dominican Republic (*Coptotermes, Dolichorhinotermes*) (Emerson, 1971; Schlemmermeyer and Cancello, 2000; Engel and Krishna, 2007c; Krishna and Grimaldi, 2009), and in Eocene Baltic amber (Engel et al., 2007b; Engel, 2008). *Coptotermes priscus* Emerson, in Dominican amber, is even known for all three castes. *Reticulitermes antiquus* (Germar) is the most common termite in Baltic amber; *Reticulitermes minimus* Snyder, also in Baltic amber, is one of the smallest known termites.

Termitidae is the largest family of termites with 2072 living species and 238 living genera, a diversity that has seriously impeded efforts at unraveling phylogeny. Traditional views of relationships have relied upon systems employing one or a few characters, such as the mandible structure of imago-workers and soldiers (Ahmad, 1950) as well as head (e.g., fontanelle) structure (Krishna, 1970). Studies by Noirot and coworkers on the structure of the digestive system (usually just called the "gut") have revealed significant variation, and thus have provided many morphological characters that correlate with habits and phylogenetic groupings (Noirot, 2001; Bitsch and Noirot, 2002; Sands, 1972; Donovan et al., 2000; Inward et al., 2007; figs. 69, 70). Although the study by Donovan et al. (2000) used 196 morphological and biological characters, many of these appear to have been overly "split" with multiple character states of questionable homology, which may explain the low support values for many of their clades. In general, other than the highly specialized heads of soldiers, the morphology of Termitidae is rather limited for deciphering relationships among such a diverse group, so molecular data promise to be particularly informative for this family. There have been several molecular studies analyzing Termitidae, but most of them have had very limited gene sampling (i.e., just COII: Miura et al., 1998; Austin et al., 2004; Ohkuma et al., 2004) or limited taxon sampling. The study by Legendre et al. (2008), for example, used sequences from seven genes, but only for 14 genera and species of Termitidae. The study by Inward et al. (2007) used only three genes, but for 240 species in over 100 genera of Termitidae—a taxon sampling that is unlikely to be duplicated. Thus, we are using this last study as the main reference for our discussion of termitid relationships.

Based on these and other studies, there are several unambiguous phylogenetic patterns and monophyletic groups in the Termitidae.

The **Macrotermitinae** is a monophyletic sister group to the rest of the Termitidae. This is a morphologically conservative group of 378 species in 12 genera that is behaviorally very specialized. These are the well-known fungus-growing termites that cultivate the mycelia of a Tricholomataceae (Basidiomycetes) fungus, *Termitomyces,* in the intricate galleries of their subterranean nests. Nest architecture is distinctive to most genera. This famous symbiosis has been studied for more than a century (Doflein, 1906; Petch, 1906; Bose, 1923; Heim, 1940; Grassé, 1994, 1945; Roonwal, 1962a; Batra and Batra, 1966; Sands, 1969; Rouland-Lefèvre, 2000). Workers forage outside the nest and apply feces to the nest walls on which the fungus grows. Mycelia and globular conidia of the fungus, on which the termites feed, metabolize the lignocellulose in the feces. Though many macrotermitines are dependent on this fungus, some apparently are not, and phylogenetically the various species of *Termitomyces* appear to be associated with particular genera of termites (Sands, 1969; Rouland-Lafèvre, 2002). Thus, the relationship appears completely analogous to the situation in the fungus-growing ants, the Attini. The ants also culture Tricholomataceae fungi on the walls of their nests, on which they feed, but for many of them the most intimate, coevolved symbiosis involves Lepiotaceae fungi (Chapela et al., 1994). In termites, such an intimate mutualism may have evolved from the habits of many Rhinotermitidae, which prefer to invade wood permeated by fungi, particularly by wet and soft rot fungi. While there is no known rhinotermitid-fungus symbiosis, the termites generally benefit nutritionally from wood conditioned by fungal mycelia, though this depends on the termite, the fungus species, and the type of wood. Some fungi, in fact, are toxic to termites. The large mounds of macrotermitines are familiar landmarks on the savannas of Africa, where most species occur. Some macrotermitines have spread to southern Asia as far as Sulawesi (but not to New Guinea or Australia). Oddly, despite the prevalence of macrotermitines in Africa, *Termitomyces* is considered to be absent from Madagascar, and may reflect the

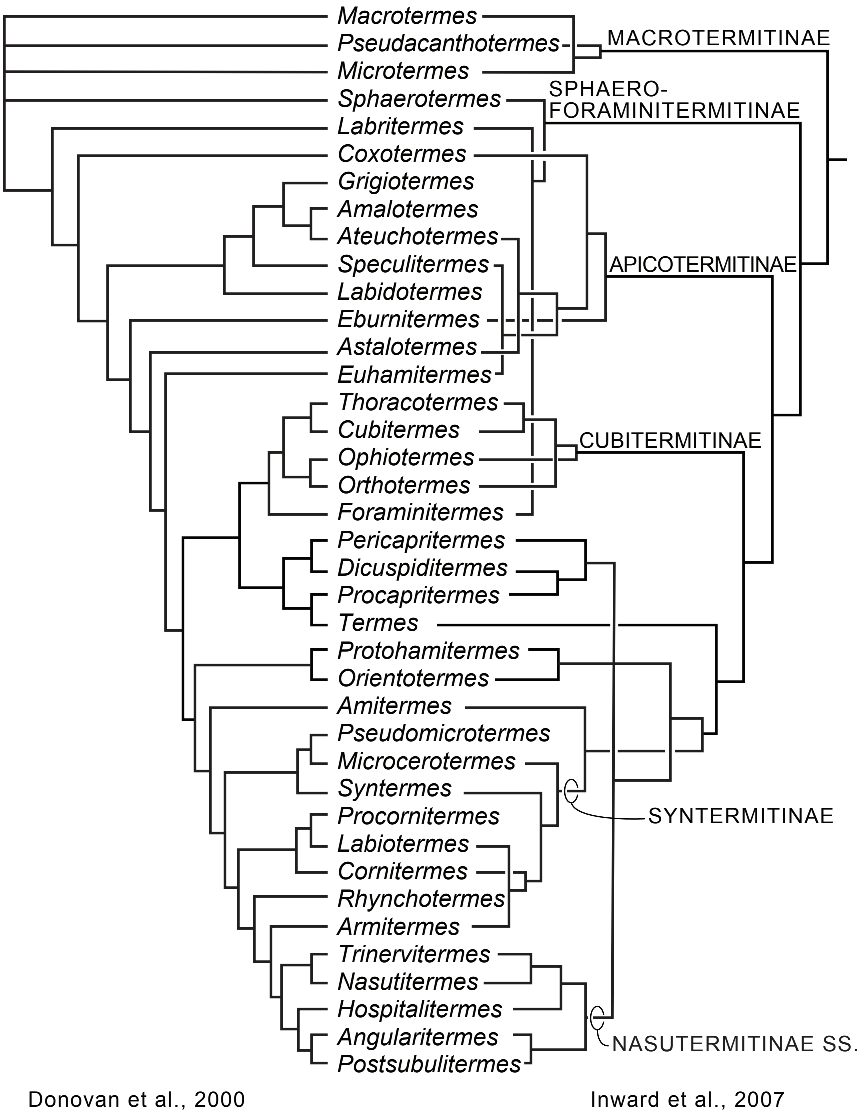


FIGURE 69. Comparisons of relationships among exemplar genera of Termitidae, based on two studies. Subfamilies are denoted. Relationships among the 235 genera of Termitidae present a significant challenge.

early separation of these landmasses. The only Malagasy macrotermitines are *Ancistrotermes kauderni, Microtermes sakalava* Cachan, and *M. divellens* Sjöstadt.

The only reports of macrotermitine fossils are of nests. One is a three-dimensional, silicified fungus comb from the Late Miocene (7 Myo) of Chad, putatively of *Odontotermes* (Duringer et al., 2006), though this genus is apparently poly- and paraphyletic (Inward et al., 2007). The other report concerns pillars of putatively Early Jurassic termites from South Africa, similar to those of modern *Macrotermes* or *Amitermes* (Bordy et al., 2004). A Jurassic termitid, let alone a macrotermitine, completely contradicts fossil and phylogenetic evidence, which otherwise indicates an entirely Tertiary origin of the Termitidae, as we discuss elsewhere in this

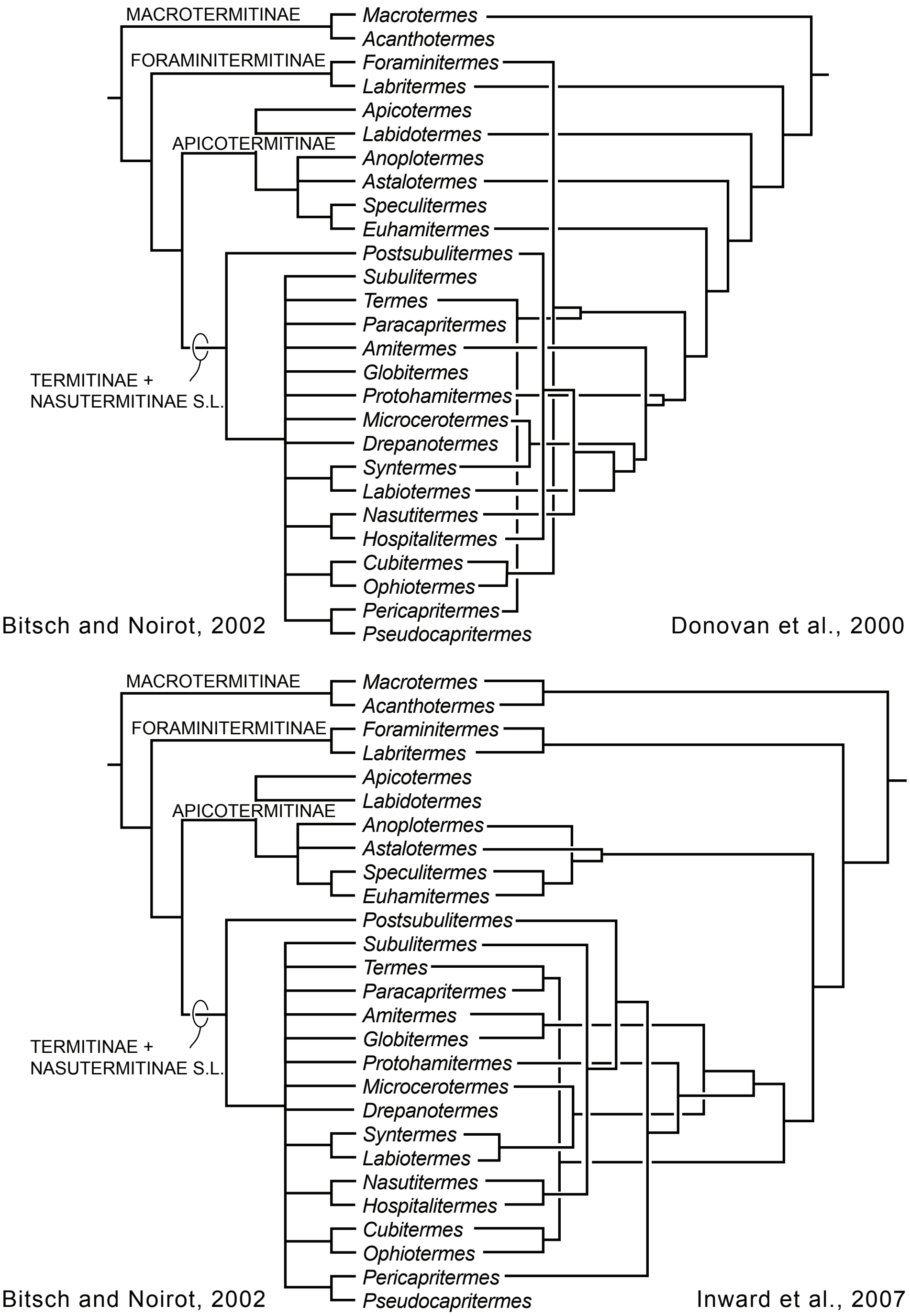


FIGURE 70. Comparisons of relationships among exemplar genera of Termitidae, based on three studies, by Bitsch and Noirot (2002) (based on gut morphology), by Donovan et al. (2000) (based on various morphological characters), and by Inward et al. (2007), based on nucleotide sequences. Macrotermitinae are consistently hypothesized to be the basal clade of Termitidae, with Apicotermitinae intermediate, and Nasutitermitinae highly derived.

chapter. Genise et al. (2005) provided detailed reasons as to why these pillars were even doubtfully of termites, but even if they were we must concur that "an assessment of the possibility of these [fossil nests] being modern structures made with ancient sediments should have been made" (Genise et al., 2005: 306).

The remainder of the Termitidae sans Macrotermitinae are probably monophyletic, based on the genetic evidence and a few morphological characters (such as loss of styli in soldiers and workers, and a bilobed worker pronotum). The basalmost taxon in the nonmacrotermitine Termitidae is a small group of three genera and eight species: the genera *Sphaerotermes* (African only) and *Foraminitermes* (African and Asian), and the Asian genus *Labritermes* (from the Malay Archipelago west of Bali). These are now placed into two subfamilies, the **Sphaerotermitinae** (monogeneric) and the **Foraminitermitinae** (which also includes *Labritermes* and *Pseudomicrotermes*) (Engel and Krishna, 2004a). All are denizens of tropical forests, where they feed on soils. Soil feeding is a highly specialized lifestyle in termites, which evolved exclusively and multiple times among Termitidae in the lowland tropical forests of southern Asia, central Africa, and the neotropics (see the review by Brauman et al., 2000). Soil feeders consume the actual, mineralized particles of soil beneath the humus, another stratum exploited by different groups of Termitidae. Soil feeders have generally converged on a syndrome of features: very light sclerotization of the body, proportionally few soldiers per colony, and small colonies of only a few hundred to a few dozen individuals living in amorphous, subterranean nests. They comprise some two-thirds of termitid genera and nearly half of all termite species, but they are also taxonomically the poorest known guild of termites because the colonies are so obscure.

The next basal group after the Foraminitermitinae is the **Apicotermitinae**. In the broad sense this subfamily genetically has grouped into it *Eburnitermes, Jugositermes, Allognathotermes,* and *Coxotermes* (Inward et al., 2007), which appear to be a grade to a definitively monophyletic group where the soldier caste has been lost (the Apicotermitinae s.l.). Apicotermitine workers of at least some genera defend the colony in a most peculiar way: as suicide bombers that douse their attackers with digesta from their exploded abdomen. The Apicotermitinae are largely forest-dwelling soil feeders in Africa, although the closely related genera *Euhamitermes* and *Speculitermes* are Asian, and the large genus *Anoplotermes* is Neotropical (of which there are dozens of undescribed species, and one view holds that this genus should be split into more than a dozen genera [Eggleton, 2000]). There are nine fossil species of *Anoplotermes* in Miocene Dominican amber (Krishna and Grimaldi, 2009).

After the Apicotermitinae, the next subfamily of Termitidae are the **Cubitermitinae**. These are soil feeders with highly specialized guts, some of which build earthen mounds and account for a large proportion of the animal biomass in African forest soils (Eggleton, 2000). Cubitermitinae appears to be the sister group to all of the remaining Termitidae. The subfamily is entirely African, and thus there is a clear biogeographic pattern indicating that the basal lineages of the Termitidae are African (with a few genera that spread to Asia). Almost certainly, *the origin and early diversification of the Termitidae was within sub-Saharan Africa,* then more derived lineages (such as various Termitinae and Nasutitermitinae) spread throughout southern Asia, Australia, and the New World.

The subfamily **Termitinae** presents a significant taxonomic and phylogenetic problem, since it appears to be both para- and polyphyletic (Inward et al., 2007), although monophyletic groups of termitine genera are readily defined. One such group is an Australian lineage comprised of genera that inhabit grasslands and subtropical forests such as *Cristatermes, Ephelotermes, Macrognathotermes, Paracapritermes,* and *Xylochomitermes*. Another such group is a Neotropical lineage comprised of *Cavitermes, Dihoplotermes,* and *Spinitermes,* though the last of these genera is probably para- and polyphyletic. A large group of at least 10 genera occurs in various regions, including the cosmopolitan genus *Amitermes* (comprised of 114 described species), a group related to the so-called mandibulate genera, the entirely Neotropical **Syntermitinae** (Engel and Krishna, 2004a).

Two competing hypotheses account for the origins of nasute soldiers: the *diphyletic* hypothesis (Emerson, 1949l; Ahmad, 1950; Sands, 1957a; Sen-Sarma, 1968; Krishna, 1970), where the nasute soldier and subsequent reduction of mandibles evolved independently in syntermitines and nasutitermitines; and the monophyletic hypothesis, where the syntermitines are interpreted as a basal grade to the nasutitermitines, which bear vestigial mandibles (Holmgren, 1912; Hare, 1937; Miller, 1986). The recent evidence from DNA sequences (Inward et al., 2007) supports a diphyletic origin and is further reflected by the structure of the frontal pore itself: it is broad, flat, and ringed with fine hairs in the syntermitines, but minute and simple in the nasutitermitines. Indeed, the frontal gland secretions of the two groups also differ. Nasutitermitines squirt secretion (which contains diterpenes [Prestwich, 1983; Prestwich and Collins, 1981b]) in a fine stream that reaches more than several times the body length. Syntermitines apply to attackers large droplets of secretion that contain no diterpenes. In several syntermitine genera such as *Rhynchotermes* and *Armitermes,* the soldier mandibles are large hooks shaped like ice tongs, which are used to grasp an attacker while smearing it with the secretion.

Closely related to the Nasutitermitinae s.s. are two distinctive, monophyletic groups. One is a small group of two genera, *Orientotermes* and *Protohamitermes* (which inhabit forests of peninsular Asia and Borneo). These and the Australian genus *Invasitermes* are the only other termitids besides apicotermitines that have lost the soldier caste, and where workers defend the colony as "suicide bombers" like apicotermitines. In contrast to this is another group, of more than six genera and 100 species from Asia, whose soldiers have elaborately specialized mandibles: *Discupiditermes, Homallotermes, Mirocapritermes, Pericapritermes, Procapritermes,* and *Sinocapritermes.* These soldiers have asymmetrical "snapping" mandibles, wherein the left mandible has a large kink near the middle, such that scissoring of the right mandible over the left creates a sudden snap (fig. 57). The soldier is propelled into the air if the snapping mandibles are touched to the ground, or it propels an attacker into the air if the mandibles are beneath an attacker. Interestingly, there appears to have been four origins of these bizarre mandibles in Termitidae according to Inward et al. (2007): once each in the African genus *Capritermes,* in the Neotropical genera *Neocapritermes* and *Planicapritermes,* and in the Oriental *Dicuspiditermes* and related genera.

The subfamily **Nasutitermitinae** s.s. is the largest monophyletic subfamily of termites, with 76 genera and approximately 600 species (Termitinae has more species, but it is not monophyletic). This group is defined by soldiers with vestigial mandibles and a nasus having a minute pore at the apex (figs. 22f, 57). There are some generic groups in this subfamily, most of which correspond to geographic regions. Group A, the *Subulitermes group,* is Neotropical; group B (*Fulleritermes* group) is African; groups C, D, and E are Asian; and group F is a group of mostly grass-feeding genera that are endemic to Australia. Amongst the Asian generic groups, group C (the *Hospitalitermes* group) is particularly interesting, since these are dark-bodied termites that forage exposed and in processions during the day (and thus resemble ants), feeding on lichens and sooty molds. The last group (G) includes the large genus *Nasutitermes,* which is a circumtropical genus of over 250 species, many of which construct large arboreal carton nests. Among *Nasutitermes* are smaller endemic genera (e.g., *Coarctitermes, Malagasitermes, Trinervitermes, Tumulitermes*). While the suggestion has been made that *Nasutitermes* needs to be split to accomodate the endemic genera, it is probably more appropriate phylogenetically and taxonomically to synonymize at least some of these small genera into *Nasutitermes.* The oldest nasutitermitines are 17 species in Miocene Dominican amber, which include the soldiers of several genera and species (Krishna and Grimaldi, 2009).

Summary

Termites diverged from a common ancestor with cryptocercid wood roaches some time in the latter half of the Jurassic about 150–160 Mya, though as of June, 2012 the oldest termite is the 135 Myo *Baissatermes* from the Early Cretaceous of Siberia. The ancestral termite was certainly wood feeding, harbored diverse symbiotic protists in its hindgut, and was social (though not necessarily having morphologically defined castes, as all termites have today). Diverse termites from later in the Cretaceous are all stem-group taxa, indicating that the divergences of the modern basal families—Masotermitidae, Termopsidae s.s., Hodotermitidae s.s., Archotermopsidae, Stolotermitidae, and Kalotermitidae—took place in the Early Cretaceous, with diversification within each of these families being probably mostly Tertiary. Extensive extinction of the living basal families rendered most of them with modern ranges that are disjunct and/or highly endemic, particularly *Mastotermes* (which was formerly global), as well as Archotermopsidae and Stolotermitidae. All Cretaceous and Early Tertiary termites doubtless retained ancestral features of harboring symbiotic protists and of feeding on wood, as do the basal families today along with the Rhinotermitidae (except for the havesters, Hodotermitidae s.s., which feed on grasses). With the development of the fontanelle, colonies evolved a highly effective new mechanism for defense. This, plus the development of fungus and bacterial symbioses in the Termitidae, along with profound changes in the digestive system and diverse diets (including grass, soil, and humus feeding), must have allowed the exploitation of new habitats, and eventually the construction of massive nests harboring hundreds of thousands to millions of siblings. Termites were relatively rare components of insect faunas until the diversification of family Termitidae (which contains two-thirds of all termite species) in approximately the Late Oligocene. All basal lineages of the Termitidae are African, indicating that this continent harbored the origin and early diversification of the family, sometime in the Tertiary, perhaps 45–55 Mya. The Termitidae subsequently spread throughout the world's tropics into one of the most recent radiations of an ecologically keystone animal group.

TABLE 11. Number of Recognized Genera and Species in Each Family (and in Subfamilies of Termitidae)

	Living Genera	Fossil Genera (only)	Total Genera	Living Species	Fossil Species	Total Species
†Archeorhinotermitidae		1	1		1	1
Archotermopsidae	3	1	4	6	4	10
†Cratomastotermitidae		1	1		1	1
Hodotermitidae	3		3	21		21
Kalotermitidae	21	8	29	456	33	489
Mastotermitidae	1	7	8	1	25	26
Rhinotermitidae	12	1	13	315	19	334
Serritermitidae	2		2	3		3
Stolotermitidae	2	1	3	10	3	13
Stylotermitidae	1	2	3	45	6	51
Termitidae						
Apicotermitinae	42		42	202	8	210
Cubitermitinae	26		26	156		156
Foraminitermitinae	3		3	10		10
Macrotermitinae	12		12	373	2	375
Nasutitermitinae	77		77	596	18	614
Sphaerotermitinae	1		1	1		1
Syntermitinae	15		15	99		99
Termitinae	61	1	62	637	7	647
TOTALS (Termitidae)	238		238	2072	35	2107
†Termopsidae		1	1		5	5
Unplaced		28	28		41	41
GRAND TOTALS	282	51	331	2933	173	3106

TABLE 12. Number of Living Species in Each Genus by Geographical Region
(numbers in parentheses = species common to other regions)*

	Number of Species	Australian	Papuan	Oriental	Palaearctic	Ethiopian	Nearctic	Neotropical	Unknown
ARCHOTERMOPSIDAE									
Archotermopsis	2			2 (1)	(1)				
Hodotermopsis	1			(1)	(1)				
Zootermopsis	3						3		
TOTAL (Archotermopsidae)	6			3	2		3		
HODOTERMITIDAE									
Anacanthotermes	16			2 (1)	15 (2)	(1)			
Hodotermes	2					2			
Microhodotermes	3				2	1			
TOTAL (Hodotermitidae)	21			2	17	4			
KALOTERMITIDAE									
Allotermes	3					3			
Bicornitermes	4					4			
Bifiditermes	12	1		3	1	7			
Calcaritermes	12			1			1	10	
Ceratokalotermes	1	1							
Comatermes	1							1	
Cryptotermes	69	17 (4)	9 (4)	18 (4)	(2)	10 (4)	(4)	30 (5)	
Epicalotermes	6				1	5			
Eucryptotermes	2							2	
Glyptotermes	127	6	8	74 (4)	5 (4)	12		26	
Incisitermes	29	2 (1)	5 (3)	6 (1)	(2)		6 (4)	16 (4)	1
Kalotermes	20	10		1	4	3	(1)	2 (1)	
Marginitermes	2						2 (1)	(1)	
Neotermes	117	1	14 (1)	57 (1)		20	(3)	26 (3)	
Paraneotermes	1						1		
Postelectrotermes	17			7	3	7			
Procryptotermes	14	1	3	3		3		4	
Proneotermes	2							2	
Pterotermes	1						1		
Rugitermes	13		1					12	
Tauritermes	3							3	
TOTAL (Kalotermitidae)	456	39	40	170	18	74	19	135	1
MASTOTERMITIDAE									
Mastotermes	1	1							
TOTAL (Mastotermitidae)	1	1							
RHINOTERMITIDAE									
Coptotermitinae									
Coptotermes	67	7	10 (4)	44 (7)	(5)	8 (3)	(3)	6 (4)	
Heterotermitinae									
Heterotermes	30	9 (2)	(2)	8 (1)	4 (2)	2 (1)	2 (1)	8 (1)	
Reticulitermes	138			112 (16)	37 (17)		6 (2)	(2)	
Prorhinotermitinae									
Prorhinotermes	11	(1)	3 (1)	4		1	(1)	3 (1)	
Psammotermitinae									
Psammotermes	6			(1)	4 (3)	4 (2)			

TABLE 12. *Continued*

	Number of Species	Australian	Papuan	Oriental	Palaearctic	Ethiopian	Nearctic	Neotropical	Unknown
Rhinotermitinae									
Acorhinotermes	1							1	
Dolicorhinotermes	7							7	
Macrorhinotermes	1			1					
Parrhinotermes	13	1	2	10 (1)	(1)				
Rhinotermes	5							5	
Schedorhinotermes	34	6 (1)	7 (4)	22 (3)		2			
Termitogetoninae									
Termitogeton	2		(1)	2 (1)					
TOTAL (Rhinotermitidae)	315	24	25	204	51	17	12	32	
SERRITERMITIDAE									
Serritermes	1							1	
Glossotermes	2							2	
TOTAL (Serritermitidae)	3							3	
STOLOTERMITIDAE									
Porotermitinae									
Porotermes	3	1				1		1	
Stolotermitinae									
Stolotermes	7	6				1			
TOTAL (Stolotermitidae)	10	7				2		1	
STYLOTERMITIDAE									
Stylotermes	45			45					
TOTAL (Stylotermitidae)	45			45					
TERMITIDAE									
Apicotermitinae									
Acholotermes	5					5			
Acidnotermes	1					1			
Acutidentitermes	1					1			
Adaiphrotermes	3					3			
Aderitotermes	2					2			
Adynotermes	1					1			
Aganotermes	1					1			
Allognathotermes	3					3			
Alyscotermes	2					2			
Amalotermes	1					1			
Amicotermes	12					12			
Anaorotermes	1					1			
Anenteotermes	10					10			
Anoplotermes	28						1	27	
Apagotermes	1					1			
Aparatermes	2							2	
Apicotermes	13					13			
Asagarotermes	1					1			
Astalotermes	17					17			
Astratotermes	6					6			
Ateuchotermes	8					8			
Coxotermes	1					1			

TABLE 12. *Continued*

	Number of Species	Australian	Papuan	Oriental	Palaearctic	Ethiopian	Nearctic	Neotropical	Unknown
Duplidentitermes	3					3			
Eburnitermes	1					1			
Euhamitermes	24			24					
Eurytermes	6			6					
Firmitermes	1					1			
Grigiotermes	2							2	
Heimitermes	2					2			
Hoplognathotermes	3					3			
Indotermes	10			10					
Jugositermes	1					1			
Labidotermes	1					1			
Longustitermes	1							1	
Machadotermes	3					3			
Phoxotermes	1					1			
Rostrotermes	1					1			
Ruptitermes	4							4	
Skatitermes	2					2			
Speculitermes	12			12					
Tetimatermes	1							1	
Trichotermes	3					3			
TOTAL (Apicotermitinae)	202			52		112	1	37	
Cubitermitinae									
Apilitermes	1					1			
Basidentitermes	8					8			
Batillitermes	2					2			
Crenetermes	5					5			
Cubitermes	67					67			
Euchilotermes	4					4			
Fastigitermes	1					1			
Forficulitermes	1					1			
Furculitermes	8					8			
Lepidotermres	9					9			
Megagnathotermes	2					2			
Mucrotermes	2					2			
Nitiditermes	1					1			
Noditermes	7					7			
Okavangotermes	2					2			
Ophiotermes	7					7			
Orthotermes	2					2			
Ovambotermes	1					1			
Pilotermes	1					1			
Proboscitermes	2					2			
Procubitermes	9					9			
Profastigitermes	1					1			
Thoracotermes	4					4			
Trapellitermes	1					1			
Unguitermes	7					7			
Unicornitermes	1					1			
TOTAL (Cubitermitinae)	156					156			

TABLE 12. *Continued*

	Number of Species	Australian	Papuan	Oriental	Palaearctic	Ethiopian	Nearctic	Neotropical	Unknown
Foraminitermitinae									
Foraminitermes	6					6			
Labritermes	3			3					
Pseudomicrotermes	1					1			
TOTAL (Foraminitermitinae)	10			3		7			
Macrotermitinae									
Acanthotermes	1					1			
Allodontermes	3					3			
Ancistrotermes	16			7		9			
Eucasitermes	1			1					
Hypotermes	13			13					
Macrotermes	59			41 (1)	3 (2)	17 (1)			
Megaprotermes	1					1			
Microtermes	66			12 (2)	(5)	53 (3)			1
Odontotermes	199		(1)	110 (8)	2 (7)	87			
Protermes	5					5			
Pseudacanthotermes	6					6			
Synacanthotermes	3					3			
TOTAL (Macrotermitinae)	373		1	184	10	185			1
Nasutitermitinae									
Aciculitermes	2			2					
Afrosubulitermes	1					1			
Agnathotermes	2							2	
Ahmaditermes	22			21	1				
Ampoulitermes	1			1					
Angularitermes	6							6	
Anhangatermes	1							1	
Antillitermes	1							1	
Araujotermes	4							4	
Arcotermes	1			1					
Atlantitermes	8							8	
Australitermes	3	3							
Baucaliotermes	1					1			
Bulbitermes	33			33					
Caetetermes	1							1	
Caribitermes	1							1	
Ceylonitermellus	2			2					
Ceylonitermes	2			2					
Coarctotermes	4					4			
Coatitermes	4							4	
Coendutermes	1							1	
Constrictotermes	7							7	
Convexitermes	2							2	
Cortaritermes	3							3	
Curcubitermes	3			3					
Cyranotermes	4							4	
Diversitermes	5							5	
Diwaitermes	3	(1)	3 (1)						
Eleanoritermes	1			1					
Emersonitermes	1			1					

TABLE 12. *Continued*

	Number of Species	Australian	Papuan	Oriental	Palaearctic	Ethiopian	Nearctic	Neotropical	Unknown
Enetotermes	1					1			
Ereymatermes	3							3	
Eutermellus	5					5			
Fulleritermes	4					4			
Grallatotermes	7		2	4		1			
Hirtitermes	3			3					
Hospitalitermes	35		3	32					
Kaudernitermes	4					4			
Lacessititermes	19			19					
Leptomyxotermes	1					1			
Leucopitermes	4			4					
Longipeditermes	2			2					
Macrosubulitermes	1	1							
Malagasitermes	1					1			
Malaysiotermes	2			2					
Mimeutermes	6					6			
Mycterotermes	1				(1)	(1)			
Nasopilotermes	1			1					
Nasutitermes	250	20 (5)	21 (5)	114 (5)	14 (5)	20	(2)	71 (2)	
Ngauratermes	1							1	
Niuginitermes	2		2						
Obtusitermes	3							3	
Occasitermes	2	2							
Occultitermes	2	2							
Oriensubulitermes	2			2					
Paraconvexitermes	3							3	
Parvitermes	9							9	
Periaciculitermes	1			1					
Peribulbitermes	3			3					
Postsubulitermes	1					1			
Rhadinotermes	1					1			
Roonwalitermes	1			1					
Rotunditermes	2			2					
Rounditermes	1							1	
Sabahitermes	2			2					
Sinonasutitermes	11			11					
Spatulitermes	1					1			
Subulioiditermes	3			3					
Subulitermes	6							6	
Tarditermes	1					1			
Tenuirostritermes	5						2 (1)	4 (1)	
Triangularitermes	1							1	
Trinervitermes	21			7	(2)	14 (2)			
Tumulitermes	17	17 (1)	(1)						
Velocitermes	10							10	
Verrucositermes	2					2			
Xiatermes	2			2					
TOTAL (Nasutitermitinae)	596	46	32	282	18	70	4	162	
Sphaerotermitinae									
Sphaerotermes	1					1			
TOTAL (Sphaerotermitinae)	1					1			

TABLE 12. *Continued*

	Number of Species	Australian	Papuan	Oriental	Palaearctic	Ethiopian	Nearctic	Neotropical	Unknown
Syntermitinae									
Acangaobitermes	1							1	
Armitermes	10							10	
Cahuallitermes	2							2	
Cornitermes	14							14	
Curvitermes	2							2	
Cyrilliotermes	4							4	
Embiratermes	14							14	
Ibitermes	3							3	
Labiotermes	10							10	
Macuxitermes	1							1	
Noirotitermes	1							1	
Paracurvitermes	1							1	
Procornitermes	5							5	
Rhynchotermes	7							7	
Syntermes	23							23	
TOTAL (Syntermitinae)	99							99	
Termitinae									
Ahamitermes	3	3							
Amitermes	111	58 (2)	3 (2)	4 (1)	12 (5)	23 (4)	9 (1)	11 (1)	
Angulitermes	29			21	4 (2)	6 (2)			
Apsenterotermes	5	5							
Capritermes	1					1			
Cavitermes	5							5	
Cephalitermes	1					1			
Cornicapritermes	1							1	
Crepititermes	1							1	
Cristatitermes	6	6							
Cylindrotermes	8							8	
Dentispicotermes	5							5	
Dicuspiditermes	20			20 (1)	(1)				
Dihoplotermes	1							1	
Divinotermes	3							3	
Drepanotermes	24	24							
Ekphysotermes	5	5							
Ephelotermes	6	6 (1)	(1)						
Eremotermes	10			6	2	2			
Genuotermes	1							1	
Globitermes	7			7					
Gnathamitermes	4						(2)	4 (2)	
Hapsidotermes	5	5							
Hesperotermes	1	1							
Homallotermes	4			4					
Hoplotermes	1							1	
Incolitermes	1	1							
Indocapritermes	1			1					
Inquilinitermes	3							3	
Invasitermes	2	2							
Kemneritermes	1			1					
Krishnacapritermes	2			2					
Labiocapritermes	1			1					

TABLE 12. *Continued*

	Number of Species	Australian	Papuan	Oriental	Palaearctic	Ethiopian	Nearctic	Neotropical	Unknown
Lophotermes	9	9							
Macrognathotermes	4	4 (1)	(1)						
Microcerotermes	148	14 (4)	13 (4)	49 (4)	20 (8)	57 (4)		7	
Mirocapritermes	8			8					
Neocapritermes	17							17	
Onkotermes	2							2	
Oriencapritermes	1			1					
Orientotermes	1			1					
Orthognathotermes	15							15	
Paracapritermes	4	4							
Pericapritermes	40		4	21 (1)	2 (1)	14			
Planicapritermes	2							2	
Procapritermes	13			13					
Prohamitermes	2			2					
Promirotermes	10					10			
Protocapritermes	2	1	1						
Protohamitermes	1			1					
Pseudhamitermes	2			2					
Pseudocapritermes	18			18					
Quasitermes	1					1			
Saxatilitermes	1	1							
Sinocapritermes	16			16					
Spinitermes	5							5	
Syncapritermes	1			1					
Synhamitermes	5			5					
Termes	24			8		8		8	
Tuberculitermes	3					3			
Xylochomitermes	6	6							
TOTAL (Termitinae)	640	155	23	214	41	126	11	100	
GRAND TOTAL (living species)	2937	273	120	**1160	157	753	51	569	2

*Note that a single species may overlap more than one region; therefore, numbers for genera with overlapping species will not equal the figure in the Number of Species column.

**This figure is skewed by the unusually large number of species described from China, many of which may prove to be invalid.

Biogeographical Regions:

Australian: Australia, Tasmania, New Zealand.

Ethiopian: Africa south of Tropic of Cancer, South Arabia (Yemen, United Arab Emirates), Fernando Po, São Tomé, Zanzibar, Pemba and Mafia, Madagascar, Comoros, Seychelles, Europa, Mauritius, Réunion.

Nearctic: North America (include Mexico north of Tropic of Cancer, exclude southern tip of Florida).

Neotropical: South America, North America (southern tip of Florida, around Miami; Mexico south of Tropic of Cancer), Central America, Galapagos and Cocos Islands.

Oriental: Indian subcontinent [India, Pakistan (exclude Baluchistan), Sri Lanka], southern China, Myanmar, Thailand, Laos, Vietnam, Cambodia, Indonesia (include Sulawesi but exclude Irian Jaya), Philippines, Taiwan.

Papuan: New Guinea, Moluccas, Amboina, Pacific islands of Melanesia, Micronesia, Polynesia, Hawaii.

Palaearctic: Europe, Eurasia, Japan, Korea, northern China, Africa north of Tropic of Cancer (Algeria, Egypt, Libya, Tunisia, Morocco), Iran, Iraq, Afghanistan, Pakistan (Baluchistan); Near East: Jordan, Saudi Arabia, Kuwait, Israel, Syria, Qatar, Oman.

TABLE 13. Number of Fossil Species in Each Genus by Continent and Age
(A = amber inclusion; C = compression fossil; Co = copal). Nomina dubia not added to totals.

	Australia	Asia	Europe	Africa	North America	South America	Cretaceous	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Type	Total Species
†ARCHEORHINOTERMITIDAE														
†*Archeorhinotermes*		1					1						A	1
TOTAL (†Archeorhinotermitidae)		1					1							1
ARCHOTERMOPSIDAE														
Archotermopsis			1					1					A	1
Hodotermopsis		1								1			C	1
†*Parotermes*					1				1				C	1
Zootermopsis					1				1				C	1
TOTAL (Archotermopsidae)		1	1		2			1	2	1				4
†CRATOMASTOTERMITIDAE														
†*Cratomastotermes*						1	1						C	1
TOTAL (Cratomastotermitidae)						1	1							1
KALOTERMITIDAE														
Calcaritermes						1				1			A	1
†*Cratokalotermes*						1	1						C	1
Cryptotermes					1	2				3			A, C	3
†*Electrotermes*			3					3					A	3
†*Eotermes*			1						1				C	1
Glyptotermes		1		1		2				3		1	A, C, Co	4
Incisitermes						2				2			A	2
†*Kachinitermes*		1					1						A	1
†*Kachinitermopsis*		1					1						A	1
Kalotermes		3	4					2	1	4			C	7
Neotermes			1						1				C	1
†*Oligokalotermes*			1						1				C	1
†*Proelectrotermes*		2	2		1		2	1	1	1			A, C	5
†*Prokalotermes*					2				2				C	2
TOTAL (†Kalotermitidae)		8	12	1	4	8	5	6	7	14		1		33
MASTOTERMITIDAE														
†*Blattotermes*	1		1		1			2	1				C	3
†*Garmitermes*			1					1					A	1
†*Idanotermes*			1					1					A	1
†*Khanitermes*		1					1						C	1
Mastotermes			11		1	1	1	3	4	5			A, C	13
†*Miotermes*			4							4			C	4
†*Spargotermes*						1		1					C	1
†*Valditermes*			1				1						C	1
TOTAL (Mastotermitidae)	1	1	19		2	2	3	8	5	9				25
RHINOTERMITIDAE													A	1
Coptotermitinae														
Coptotermes						4				4			A	4
Heterotermitinae														
Heterotermes			1			1		1		1			A	2
Reticulitermes			6		3			2	3	3	1		A, C	9

TABLE 13. *Continued*

	Australia	Asia	Europe	Africa	North America	South America	Cretaceous	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Type	Total Species
Prorhinotermitinae														
†*Zophotermes*		1						1					A	1
Rhinotermitinae														
Dolichorhinotermes						2				2			A	2
Rhinotermes			1							1			C	1
TOTAL (Rhinotermitidae)		1	8		3	7		4	3	11	1			19
STOLOTERMITIDAE														
Porotermitinae														
†*Chilgatermes*				1					1				C	1
Stolotermitinae														
Stolotermes	1	1								2			C	2
TOTAL (Stolotermitidae)	1	1		1					1	2			C	3
STYLOTERMITIDAE														
†*Parastylotermes*		1	1		3			2		3			A, C	5
†*Prostylotermes*		1						1					A	1
TOTAL (Stylotermitidae)		2	1		3			3		3				6
TERMITIDAE														
Apicotermitinae														
Anoplotermes						8				8			A	8
Macrotermitinae														
Macrotermes			2							2			C	2
Nasutitermitinae														
Atlantitermes						3				3			A	3
Caribitermes						1				1			A	1
Constrictotermes						1				1			A	1
Nasutitermes						9				9			A	9
Parvitermes						1				1			A	1
Subulitermes						2				2			A	2
Velocitermes						1				1			A	1
Termitinae														
Amitermes						1				1			A	1
Gnathamitermes					1					1			C	1
Microcerotermes						2				2			A	2
†*Nanotermes*		1						1					1	1
Termes			1			1			1	1			A, C	2
TOTAL (Termitidae)		1	3		1	30		1	1	33				35
†TERMOPSIDAE														
†*Termopsis*			5					2	1	2			A, C	5
TOTAL (Termopsidae)			5					2	1	2				5
UNPLACED														
†*Aiuruocatermes*						1			1				C	1
†*Aragonitermes*			1				1						A	1
†*Asiatermes*		1					1						C	1
†*Baissatermes*			1				1						C	1

TABLE 13. *Continued*

	Australia	Asia	Europe	Africa	North America	South America	Cretaceous	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Type	Total Species
†*Cantabritermes*			1				1						A	1
†*Cretarhinotermes*						1	1						C	1
†*Dharmatermes*		1					1						A	1
†*Francotermes*			1							1			C	1
†*Gyatermes*			1							1			C	1
†*Huaxiatermes*		1					1						C	1
†*Jitermes*		1					1						C	1
†*Lebanotermes*		1					1						A	1
†*Mariconitermes*						1	1						C	1
†*Meiatermes*			1			2	3						C	3
†*Melqartitermes*		1					1						A	1
†*Mesotermopsis*		2					2						C	2
†*Morazatermes*			1				1						A	1
†*Mylacrotermes*		1					1						A	1
†*Paleotermopsis*			1						1				C	1
†*Santonitermes*			1				1						A	1
†*Syagriotermes*			1				1						A	1
†*Tanytermes*		1					1						A	1
†*Ulmeriella*		2	7		2				4	4	3		C	11
†*Yanjingtermes*		1					1						C	1
†*Yongdingia*		1					1						C	1
†Carinatermitinae														
†*Carinatermes*					1		1						A	1
†Cretatermitinae														
†*Cretatermes*					1		1						C	1
†Lutetiatermitinae														
†*Lutetiatermes*			1				1						A	1
Nomina dubia														
†Caatingatermitinae														
†*Araripetermes*						1	1						C	1
†*Caatingatermes*						1	1						C	1
†*Nordestinatermes*						1	1						C	1
†Eutermitinae														
†*Eutermes*			1										A	1
TOTAL (unplaced)		14	18		4	5	26		6	6	3			41
TOTAL SPECIES (fossil species)	2	30	67	2	19	56	33	25	26	81	4	1		173

TABLE 14. Ichnofossil Species in Each Genus by Continent and Age

	Africa	North America	South America	Triassic	Cretaceous	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Total Species
Hodotermitidae											
†*Coatonichnus*	1							x	x		1
Kalotermitidae											
†*Cycalichnus*			1		x						1
†Krausichnidae											
†*Fleaglellius*	1					x	x				1
†*Krausichnus*	2					x	x				2
†*Tacuruichnus*			1						x		1
†*Termitichnus*	3					x	x	x		x	3
†*Vondrichnus*	2					x	x	x	x		2
Termitidae											
Macrotermitinae											
†*Microfavichnus*	1							x	x		1
Syntermitinae											
†*Syntermesichnus*			1					x			1
TOTAL											13

SUMMARY CLASSIFICATION OF ISOPTERA
(Modified from Engel, Grimaldi, and Krishna 2009)

Genera Arranged in Alphabetical Order within Families

Order BLATTARIA Burmeister
  Infraorder ISOPTERA Brullé
    Family †Cratomastotermitidae Engel, Grimaldi, and Krishna
        †*Cratomastotermes* Bechly

    Family Mastotermitidae Desneux
        †*Blattotermes* Riek
        †*Garmitermes* Engel, Grimaldi, and Krishna
        †*Idanotermes* Engel
        †*Khanitermes* Engel, Grimaldi, and Krishna
        Mastotermes Froggatt
        †*Miotermes* Rosen
        †*Spargotermes* Emerson
        †*Valditermes* Jarzembowski

  Parvorder EUISOPTERA Engel, Grimaldi, and Krishna
    Family incertae sedis
      = †Cretatermitinae Emerson
        †*Asiatermes* Ren
        †*Cretatermes* Emerson
        †*Huaxiatermes* Ren
        †*Mesotermopsis* Engel and Ren
      = †Lutetiatermitinae Schlüter
        †*Lutetiatermes* Schlüter
      = †Carinatermitinae Krishna and Grimaldi
        †*Carinatermes* Krishna and Grimaldi

    Genera incertae sedis
        †*Aiuruocatermes* Martins-Neto and Pesenti
        †*Aragonitermes* Engel and Delclòs
        †*Ardatermes* Kaddumi
        †*Baissatermes* Engel, Grimaldi, and Krishna
        †*Cantabritermes* Engel and Delclòs
        †*Cretarhinotermes* Bechly
        †*Dharmatermes* Engel, Grimaldi, and Krishna
        †*Francotermes* Weidner and Riou
        †*Gyatermes* Engel and Gross
        †*Jitermes* Ren
        †*Lebanotermes* Engel, Azar, and Nel

- †*Mariconitermes* Fontes and Vulcano
- †*Meiatermes* Lacasa-Ruiz and Martínez-Delclòs
- †*Melqartitermes* Engel, Grimaldi, and Krishna
- †*Morazatermes* Engel and Delclòs
- †*Mylacrotermes* Engel, Grimaldi, and Krishna
- †*Paleotermopsis* Nel and Paicheler
- †*Santonitermes* Engel, Nel, and Perrichot
- †*Syagriotermes* Engel, Nel, and Perrichot
- †*Tanytermes* Engel, Grimaldi, and Krishna
- †*Ulmeriella* Meunier
- †*Yanjingtermes* Ren
- †*Yongdingia* Ren

Family †Termopsidae Holmgren, s.s.
- †*Termopsis* Heer

Family Archotermopsidae Engel, Grimaldi, and Krishna
- *Archotermopsis* Desneux
- *Hodotermopsis* Holmgren
- †*Parotermes* Scudder
- *Zootermopsis* Emerson

Family Hodotermitidae Desneux
- *Anacanthotermes* Jacobson
- *Hodotermes* Hagen
- *Microhodotermes* Sjöstedt

Family Stolotermitidae Holmgren
- Stolotermitinae Holmgren
  - *Stolotermes* Hagen
- Porotermitinae Emerson
  - †*Chilgatermes* Engel, Pan, and Jacobs
  - *Porotermes* Hagen

Family Kalotermitidae Froggatt
- *Allotermes* Wasmann
- *Bicornitermes* Krishna
- *Bifiditermes* Krishna
- *Calcaritermes* Snyder
- *Ceratokalotermes* Krishna
- *Comatermes* Krishna
- †*Cratokalotermes* Bechly
- *Cryptotermes* Banks
- †*Electrotermes* Rosen
- †*Eotermes* Statz
- *Epicalotermes* Silvestri

- *Eucryptotermes* Holmgren
- *Glyptotermes* Froggatt
- *Incisitermes* Krishna
- †*Kachinitermes* Engel, Grimaldi, and Krishna
- †*Kachinitermopsis* Engel and Delclòs
- *Kalotermes* Hagen
- *Marginitermes* Krishna
- *Neotermes* Holmgren
- †*Oligokalotermes* Nel
- *Paraneotermes* Light
- *Postelectrotermes* Krishna
- *Procryptotermes* Holmgren
- †*Proelectrotermes* Rosen
- †*Prokalotermes* Emerson
- *Proneotermes* Holmgren
- *Pterotermes* Holmgren
- *Rugitermes* Holmgren
- *Tauritermes* Krishna

Nanorder NEOISOPTERA Engel, Grimaldi, and Krishna

Family †Archeorhinotermitidae Krishna and Grimaldi
- †*Archeorhinotermes* Krishna and Grimaldi

Family Stylotermitidae Holmgren and Holmgren
- †*Parastylotermes* Snyder and Emerson
- †*Prostylotermes* Engel and Grimaldi
- *Stylotermes* Holmgren and Holmgren

Family Rhinotermitidae Froggatt
- Coptotermitinae Holmgren
  - *Coptotermes* Wasmann
- Heterotermitinae Froggatt
  - *Heterotermes* Froggatt
  - *Reticulitermes* Holmgren
- Prorhinotermitinae Quennedey and Deligne
  - *Prorhinotermes* Silvestri
  - †*Zophotermes* Engel
- Psammotermitinae Holmgren
  - *Psammotermes* Desneux
- Rhinotermitinae Froggatt
  - *Acorhinotermes* Emerson
  - *Dolichorhinotermes* Snyder and Emerson
  - *Macrorhinotermes* Holmgren
  - *Parrhinotermes* Holmgren

    - *Rhinotermes* Hagen
    - *Schedorhinotermes* Silvestri
  - Termitogetoninae Holmgren
    - *Termitogeton* Desneux

- Family Serritermitidae Holmgren
    - *Glossotermes* Emerson
    - *Serritermes* Wasmann

- Family Termitidae Latreille
  - Sphaerotermitinae Engel and Krishna
    - *Sphaerotermes* Holmgren
  - Macrotermitinae Kemner
    - *Acanthotermes* Sjöstedt
    - *Allodontermes* Silvestri
    - *Ancistrotermes* Silvestri
    - *Eucasitermes* Silvestri
    - *Hypotermes* Holmgren
    - *Macrotermes* Holmgren
    - *Megaprotermes* Ruelle
    - *Microtermes* Wasmann
    - *Odontotermes* Holmgren
    - *Protermes* Holmgren
    - *Pseudacanthotermes* Sjöstedt
    - *Synacanthotermes* Holmgren
  - Foraminitermitinae Holmgren
    - *Foraminitermes* Holmgren
    - *Labritermes* Holmgren
  - Apicotermitinae Grassé and Noirot
    - *Acholotermes* Sands
    - *Acidnotermes* Sands
    - *Acutidentitermes* Emerson
    - *Adaiphrotermes* Sands
    - *Aderitotermes* Sands
    - *Adynotermes* Sands
    - *Aganotermes* Sands
    - *Allognathotermes* Silvestri
    - *Alyscotermes* Sands
    - *Amalotermes* Sands
    - *Amicotermes* Sands
    - *Anaorotermes* Sands
    - *Anenteotermes* Sands
    - *Anoplotermes* Müller

        Apagotermes Sands
        Aparatermes Fontes
        Apicotermes Holmgren
        Asagarotermes Sands
        Astalotermes Sands
        Astratotermes Sands
        Ateuchotermes Sands
        Coxotermes Grassé and Noirot
        Duplidentitermes Emerson
        Eburnitermes Noirot
        Euhamitermes Holmgren
        Eurytermes Wasmann
        Firmitermes Sjöstedt
        Grigiotermes Matthews
        Heimitermes Grassé
        Hoplognathotermes Silvestri
        Indotermes Roonwal and Sen-Sarma
        Jugositermes Emerson
        Labidotermes Deligne and Pasteels
        Longustitermes Bourguignon and Roisin
        Machadotermes Weidner
        Phoxotermes Collins
        Rostrotermes Grassé
        Ruptitermes Matthews
        Skatitermes Coaton
        Speculitermes Wasmann
        Tetimatermes Fontes
        Trichotermes Sjöstedt
    Syntermitinae Engel and Krishna
        Armitermes Wasmann
        Cahuallitermes Constantino
        Cornitermes Wasmann
        Curvitermes Holmgren
        Cyrilliotermes Fontes
        Embiratermes Fontes
        Ibitermes Fontes
        Labiotermes Holmgren
        Macuxitermes Cancello and Bandeira
        Noirotitermes Cancello and Myles
        Paracurvitermes Constantino and Carvalho
        Procornitermes Emerson
        Rhynchotermes Holmgren

- *Syntermes* Holmgren
- Nasutitermitinae Hare
  - *Aciculitermes* Emerson
  - *Afrosubulitermes* Emerson
  - *Agnathotermes* Snyder
  - *Ahmaditermes* Akhtar
  - *Ampoulitermes* Mathur and Thapa
  - *Angularitermes* Emerson
  - *Anhangatermes* Constantino
  - *Antillitermes* Roisin, Scheffrahn, and Křeček
  - *Araujotermes* Fontes
  - *Arcotermes* Fan
  - *Atlantitermes* Fontes
  - *Australitermes* Emerson
  - *Baucaliotermes* Sands
  - *Bulbitermes* Emerson
  - *Caetetermes* Fontes
  - *Caribitermes* Roisin, Scheffrahn, and Křeček
  - *Ceylonitermellus* Emerson
  - *Ceylonitermes* Holmgren
  - *Coarctotermes* Holmgren
  - *Coatitermes* Fontes
  - *Coendutermes* Fontes
  - *Constrictotermes* Holmgren
  - *Convexitermes* Holmgren
  - *Cotaritermes* Matthews
  - *Curcubitermes* Li and Ping
  - *Cyranotermes* Araujo
  - *Diversitermes* Holmgren
  - *Diwaitermes* Roisin and Pasteels
  - *Eleanoritermes* Ahmad
  - *Emersonitermes* Mathur and Sen-Sarma
  - *Enetotermes* Sands
  - *Ereymatermes* Constantino
  - *Eutermellus* Silvestri
  - *Fulleritermes* Coaton
  - *Grallatotermes* Holmgren
  - *Hirtitermes* Holmgren
  - *Hospitalitermes* Holmgren
  - *Kaudernitermes* Sands and Lamb
  - *Lacessititermes* Holmgren
  - *Leptomyxotermes* Sands

  - *Leucopitermes* Emerson
  - *Longipeditermes* Holmgren
  - *Macrosubulitermes* Emerson
  - *Malagasitermes* Emerson
  - *Malaysiotermes* Ahmad
  - *Mimeutermes* Silvestri
  - *Mycterotermes* Sands
  - *Nasopilotermes* Gao, Lam, and Owen
  - *Nasutitermes* Dudley
  - *Ngauratermes* Constantino and Acioli
  - *Niuginitermes* Roisin and Pasteels
  - *Obtusitermes* Snyder
  - *Occasitermes* Holmgren
  - *Occultitermes* Emerson
  - *Oriensubulitermes* Emerson
  - *Paraconvexitermes* Cancello and Noirot
  - *Parvitermes* Emerson
  - *Periaciculitermes* Li
  - *Peribulbitermes* Li
  - *Postsubulitermes* Emerson
  - *Rhadinotermes* Sands
  - *Roonwalitermes* Bose
  - *Rotunditermes* Holmgren
  - *Rounditermes* Ensaf, Ponchel, and Nel
  - *Sabahitermes* Thapa
  - *Sinonasutitermes* Li and Ping
  - *Spatulitermes* Coaton
  - *Subulioiditermes* Ahmad
  - *Subulitermes* Holmgren
  - *Tarditermes* Emerson
  - *Tenuirostritermes* Holmgren
  - *Triangularitermes* Matthews
  - *Trinervitermes* Holmgren
  - *Tumulitermes* Holmgren
  - *Velocitermes* Holmgren
  - *Verrucositermes* Emerson
  - *Xiatermes* Gao and He
- Cubitermitinae Weidner
  - *Apilitermes* Holmgren
  - *Basidentitermes* Holmgren
  - *Batillitermes* Uys
  - *Crenetermes* Silvestri

  - *Cubitermes* Wasmann
  - *Euchilotermes* Silvestri
  - *Fastigitermes* Sjöstedt
  - *Forficulitermes* Emerson
  - *Furculitermes* Emerson
  - *Lepidotermes* Sjöstedt
  - *Megagnathotermes* Silvestri
  - *Mucrotermes* Emerson
  - *Nitiditermes* Emerson
  - *Noditermes* Sjöstedt
  - *Okavangotermes* Coaton
  - *Ophiotermes* Sjöstedt
  - *Orthotermes* Silvestri
  - *Ovambotermes* Coaton
  - *Pilotermes* Emerson
  - *Proboscitermes* Sjöstedt
  - *Procubitermes* Silvestri
  - *Profastigitermes* Emerson
  - *Thoracotermes* Wasmann
  - *Trapellitermes* Sands
  - *Unguitermes* Sjöstedt
  - *Unicornitermes* Coaton
- Termitinae Latreille
  - *Ahamitermes* Mjöberg
  - *Amitermes* Silvestri
  - *Angulitermes* Sjöstedt
  - *Apsenterotermes* Miller
  - *Capritermes* Wasmann
  - *Cavitermes* Emerson
  - *Cephalotermes* Silvestri
  - *Cornicapritermes* Emerson
  - *Crepititermes* Emerson
  - *Cristatitermes* Miller
  - *Cylindrotermes* Holmgren
  - *Dentispicotermes* Emerson
  - *Dicuspditermes* Krishna
  - *Dihoplotermes* Araujo
  - *Divinotermes* Carrijo and Cancello
  - *Drepanotermes* Silvestri
  - *Ekphysotermes* Miller
  - *Ephelotermes* Miller

Eremotermes Silvestri
Genuotermes Emerson
Globitermes Holmgren
Gnathamitermes Light
Hapsidotermes Miller
Hesperotermes Gay
Homallotermes John
Hoplotermes Light
Incolitermes Gay
Indocapritermes Chhotani
Inquilinitermes Matthews
Invasitermes Miller
Kemneritermes Ahmad and Akhtar
Krishnacapritermes Chhotani
Labiocapritermes Krishna
Lophotermes Miller
Macrognathotermes Silvestri
Microcerotermes Silvestri
Mirocapritermes Holmgren
†*Nanotermes* Engel and Grimaldi
Neocapritermes Holmgren
Onkotermes Constantino, Liotta, and Giacosa
Oriencapritermes Ahmad and Akhtar
Orientotermes Ahmad
Orthognathotermes Holmgren
Paracapritermes Hill
Pericapritermes Silvestri
Planicapritermes Emerson
Procapritermes Holmgren
Prohamitermes Holmgren
Promirotermes Silvestri
Protocapritermes Holmgren
Protohamitermes Holmgren
Pseudocapritermes Kemner
Pseudohamitermes Holmgren
Quasitermes Emerson
Saxatilitermes Miller
Sinocapritermes Ping and Xu
Spinitermes Wasmann
Syncapritermes Ahmad and Akhtar
Synhamitermes Holmgren

        - *Termes* Linnaeus
        - *Tuberculitermes* Holmgren
        - *Xylochomitermes* Miller

- Nomina dubia
    - †Caatingatermitinae Martins-Neto, Ribeiro-Júnior, and Prezoto
        - †*Araripetermes* Martins-Neto, Ribeiro-Júnior, and Prezoto
        - †*Caatingatermes* Martins-Neto, Ribeiro-Júnior, and Prezoto
        - †*Nordestinatermes* Martins-Neto, Ribeiro-Júnior, and Prezoto
    - †Eutermitinae Holmgren
        - †*Eutermes* Heer

THE TAXONOMIC COMPENDIUM

In this Compendium letters after dates in citations are for identification only and do not indicate sequence of publication; thus, citations with identical dates may not appear in alphabetical order. In the few instances in which names and dates of different authors coincide, initials are given to distinguish the "outlier" from the more commonly cited investigator. Geographical coordinates (in square brackets) and Latin terms such as *nom. nov.* are cited exactly as they appear in the original publications and as a result are not consistent in style. All other square brackets indicate the present authors' remarks. Contemporary names for localities are used throughout (Sulawesi, Myanmar, Sri Lanka), except where the equivalent is not clear (Congo, Borneo) or the reference is broad (America, Africa). Historical names used by earlier authors are in parentheses. First references for valid taxa names are in bold fonts, with synonyms listed subsequently in nonbold fonts. † indicates a fossil taxon. The closing date for entries is June 2011.

Nomenclatural Changes Made in This Work

Kalotermitidae:

Eucryptotermes hagenii (Müller, 1873). **Reinstated name**.
Incisitermes snyderi (Light, 1933). **Lectotype selected**.
Calotermes maroccoensis Sjöstedt, 1904; synonymized with *Kalotermes flavicollis* (Fabricius, 1793). **New synonymy**.
Neotermes major Snyder, 1922; synonymized with *Neotermes connexus* Snyder, 1922. **New synonymy**.
Neotermes concavifrons Cachan, 1949; synonymized with *Neotermes europae* (Wasmann, 1910). **New synonymy**.
Glyptotermes alaotranus Cachan, 1951; synonymized with *Postelectrotermes longiceps* (Cachan, 1949). **New synonymy**.
Proneotermes delphinensis Cachan, 1951; synonymized with *Postelectrotermes longus* (Holmgren, 1910). **New synonymy**.

Rhinotermitidae:

Coptotermes mauricianus (Rambur, 1842); **Species revivisco** and **new combination**.
Termes arda Fabricius, 1781. **Lectotype selected**.
Reticulitermes huangi Krishna, this work, **nomen novum** for *Tsaitermes hunanensis* Li and Ping, 1983, now *Reticulitermes hunanensis,* a name preoccupied by *Reticulitermes* (*Planifrontotermes*) *hunanensis* Tsai and Peng, 1980.
Rhinotermes (*Schedorhinotermes*) *celebensis* (Holmgren, 1911). **Lectotype selected**.
Schedorhinotermes robustior Silvestri, 1909. **Status novus**.
Schedorhinotermes tenuis (Oshima, 1923). **New combination**.

Macrotermitinae

Parahypotermes Zhu et al., 1990; synonymized with *Hypotermes* Holmgren, 1913. **New synonymy**.

Hypotermes manyunensis (Zhu and Huang, 1990). **New combination**.

Hypotermes ruiliensis (Zhu and Wang, 1990). **New combination**.

Hypotermes yingjiangensis (Huang and Zhu, 1990). **New combination**.

Macrotermes zhui Krishna, this work, **nomen novum** for *Macrotermes latinotus* Zhu and Luo, 1985, which is preoccupied by *Macrotermes gilvus latinotus* Kemner, 1934.

Eutermes fenerivensis Sjöstedt, 1914; synonymized with *Microtermes kauderni* Holmgren, 1909. **New synonymy**.

Microtermes magnoculus Krishna, this work; **nomen novum** for *Microtermes somaliensis* Sjöstedt, 1927, as the name is preoccupied by *M. somaliensis* (Sjöstedt, 1912).

Odontotermes sundaicus form *esuriens* Kemner, 1934; synonymized with *Odontotermes billitoni* Holmgren, 1913. **New synonymy**.

Apicotermitinae:

Mirotermes (*Cubitermes*) *natalensis* form *obscurus* Holmgren, 1913; synonymized with *Alyscotermes kilimandjaricus* (Sjöstedt, 1907). **New synonymy**.

Anoplotermes burmeisteri (Czerwinski, 1901). **New combination**.

Euhamitermes shillongensis (Roonwal and Chhotani, 1960). **New combination**.

Hoplognathotermes angolensis Weidner, 1974. **Status novus**.

Syntermitinae:

Armitermes holmgreni Snyder, 1926 synonymized with *Armitermes heyeri* Wasmann, 1915. **New synonymy**.

Nasutitermitinae:

Bulbitermes fulvus (Tsai and Chen, 1963). **New combination**.

Bulbitermes pusillus (Holmgren, 1914). **New combination**.

Eutermes mitis Sjöstedt, 1902; synonymized with *Kaudernitermes laticeps* (Wasmann, 1897). **New synonymy**

Kaudernitermes nigritus (Wasmann, 1897). **New combination**.

Kaudernitermes salebrithorax (Sjöstedt, 1904). **New combination**.

Milesnasitermes Dudley, 1890, *Eutermes costalis* Holmgren. **Selected as type species**.

Milesnasitermes Dudley, 1890; synonymized with *Nasutitermes* Dudley, 1890. **New synonymy**.

Nasutitermes crinitus Krishna and Grimaldi, this work; **nomen novum** for *Nasutitermes pilosus* Krishna and Grimaldi, as the name is preoccupied by *Nasutitermes pilosus* Snyder, 1926.

Nasutitermes hexianensis Krishna, this work; **nomen novum** for *Havilanditermes communis* Li and Xiao, 1989, which is a junior homonym of *Nasutitermes communis* Tsai and Chen, 1963.

Nasutitermes longirostris sabahicola Engel and Krishna, this work; **nomen novum** for *Nasutitermes longirostris minor* Thapa, which is a junior secondary homonym of *Nasutitermes minor* (Holmgren, 1906).

Nasutitermes matangensiformis christmasensis Krishna, this work; **nomen novum** for *Eutermes* (*Eutermes*) *matangensiformis obscurus* Holmgren, 1913, as the name is preoccupied by *Eutermes* (*Eutermes*) *insularis obscurus* Holmgren, 1910.

Nasutitermes obscurus (Holmgren, 1906). **New combination**.

Nasutitermes mauritianus (Wasmann, 1910a): [**Status novus** as correct name for taxon].

Tenuirostritermes strenuus (Hagen, 1860). **New combination**.

Eutermes (*Eutermes*) *sandakensis* Oshima, 1914c [*Eutermes* (*Eutermes*) *sandakanensis* by Oshima, 1914a (**unjustified emendation**)].

Cubitermitinae:

Cubitermes bilobatus form *curta* Sjöstedt, 1926; synonymized with *Cubitermes bilobatus* (Haviland, 1898). **New synonymy**.

Cubitermes fungifaber var. *elongata* Sjöstedt, 1924; synonymized with *Cubitermes fungifaber* (Sjöstedt, 1896). **New synonymy**.

Cubitermes sankurensis form *elongata* Sjöstedt, 1926; synonymized with *Cubitermes sankurensis* Wasmann, 1911. **New synonymy**.

Ophiotermes receptus (Sjöstedt, 1913). **New combination**.

Procubitermes curvatus Silvestri, 1914. **Status novus**.

Procubitermes sinuosus Silvestri, 1914. **Status novus**.

Termitinae:

Amitermes gestroanus (Sjöstedt, 1912). **New combination**.

Microcerotermes pauliani Krishna, this work; **nomen novum** for *Gibbotermes longiceps* Cachan, 1951 (now *Microcerotermes longiceps*), a junior secondary homonym of *Microcerotermes longiceps* Cachan, 1949.

Microcerotermes transiens Rosen, 1912. **Status revivisco**.

Pericapritermes metatus Silvestri, 1914. **Raised to species rank**.

Pericapritermes emersoni Krishna, 1968; synonymized with *Pericapritermes nigerianus* Silvestri, 1914. **New synonymy**.

Procapritermes dakshinae (Chhotani and Ferry, 1995). **New combination**.

Procapritermes keralai (Chhotani and Ferry, 1995). **New combination**.

Procapritermes zhangfengensis (Yang, Zhu and Huang, 1995). **New combination**.

Pseudhamitermes longignathus (Ahmad, 1965). **New combination**.

Termes capensis (Silvestri, 1914). **New combination**.

Museums and Repositories

The following abbreviations have been used for the institutions in which the type specimens are held:

ACCU	Instituto de Ecología y Sistemática, Academia de Ciencias de Cuba, Capdevila, KM 3, Boyeros, Ciudad de La Habana, Cuba
AM	Australian Museum, Sydney, NSW, Australia
AMNH	American Museum of Natural History, New York
ANIC	Australian National Insect Collection, CSIRO, Canberra, ACT, Australia
BCOT	Beihai Control Office of Termites, Guangxi, China
BMNH	Natural History Museum (formerly British Museum (Natural History)), London, UK
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii
BSIPL	Birbal Sahni Institute of Paleobotany, Lucknow, India
CAS	California Academy of Sciences, San Francisco, California
CGM	Cairo Geological Museum, Cairo, Egypt
CHM	Charlestown Museum, Charleston, South Carolina
CICC	Chengdu Institute of Termite Control, Chengdu, China
CITC	Chongqing Institute of Termite Control, Chongqing, China
CMFE	Civico Museo “Federico Eusebio,” Alba, Italy
CMNH	Chicago Museum of Natural History, Chicago, Illinois
CNAR	Centre National d’Appui a la Recherche, N’Jdamena, Chad
COM	Colombo Museum, Colombo, Sri Lanka
CPT	The Fundación Conjunto Paleontológico de Teruel-Dinópolis, Teruel, Spain
CUMZ	Cambridge University Museum of Zoology, Cambridge, UK
DEIB	Deutsches Entomologisches Institut, Eberswalde, Germany
DGAP	Divisão de Geologia e Mineralogia, Avenida Pasteur, 404, Praia Vermelha, Rio de Janeiro, Brazil
DRSJ	Desert Regional Station (Zoological Survey of India), Jodhpur, Rajasthan, India
DZUB	Departamento de Zoologia, Universidade de Brasilia, Brasilia, Brazil
DZUC	Departaments de Zoologia da Universidade de Coimbra, Coimbra, Portugal
DZUP	Departamento de Zoologia, Univerisdade Federal do Paraná, Curitiba, Brazil
DZVU	Universidad de Uruguay, Montevideo, Uruguay
EMAG	Ernst-Moritz Arndt Collection, Museum der Stadt Greifswald, Greifswald, Germany
ENAR	Departamento de Entomologia, Universidade Federal Rural do Rio de Janeiro, Brazil
ERMNH	Eternal River Museum of Natural History, Amman, Jordan (personal collection of H.F. Kaddumi)
FACENAC	Facultad de Ciencias Exactas y Naturales Agrimensura, Universidad Nacional del Nordeste, Argentina
FDFI	Forest Deparment, Colo-i-Suva, Fiji Islands
FESG	Forest Experiment Station, Gulfport, Mississippi
FIB	Fujian Institute of Biology, Fuzhou, Fujian Province, China
FMNH	Field Museum of Natural History, Chicago, Illinois
FRCS	Forest Research Centre, Sandakan, Sabah, Malaysia
FRI	Forest Research Institute, Dehradun, Uttarakhand, India
FRIK	Forest Research Institute, Kepong, Malaysia

FRIP	Forest Research Institute, Peshawar, Pakistan
FSCA	Florida State Collection of Arthropods, Gainsville, Florida
FTLD	University of Florida, Fort Lauderdale Research and Education Center, Davie, Florida
GBW	Geologischen Bundesanstalt, Wien, Austria
GIEC	Guangdong (Kwangtung) Institute of Entomology, Guangzhou, China
GIF	Guizhou Institute of Forestry, Guiyang, Guizhou Province, China
GIUG	Geologisch-Paläotologisches Institut, Universität Göttingen, Germany
GMR	Geological Museum, Rostock, Germany
GMZ	Geological Museum, Zurich, Switzerland
GPIUH	Geologisch-Palälontologischen Institut der Universitäd Halle, Germany
GUNR	Department of Geosciences of the University of Rennes, Rennes, France
GUQ	Department of Geology, University of Queensland, Queensland, Australia
HMIM	Hayk Mirzayans Insect Museum, Insect Taxonomy Research Department, Plant Pests and Diseases Research Institute, Tehran, Iran
HNHM	Hungarian Natural History Museum, Budapest, Hungary
HTCC	Huanan Tropical Crops College Tan-Hsien (Dan-Xian) Hainan Island, China
IAH	Instituto Alexander von Humbolt, Arthropod collection, Villa de Leyva, Boyac, Colombia
IARI	Entomology Division of the Indian Agriculture Research Institute, New Delhi, India
IEA	Instituto di Entomologia Agraria, Portici, Italy
IEIL	Institut d'Estudios Illerdenses, Lleida, Spain
IFAN	Instituto Fondamental d'Afrique Noir, Dakar, Senegal
IFH	Institute of Forestry, Changsha, Hunan Province, China
IIAA	Instituto de Investigação Agronómica de Angola, Nova Lisboa, Angola
INHM	Iraq Natural History Museum, Baghdad, Iraq
INPA	Instituto Nacional de Pesquisas de Amazonia, Manaus, Brazil
IPM	Iwate Prefectural Museum, Morioka-shi, Iwate, Japan
IPNC	Institut des Parcs. Nationaux du Conge Belge, Tervuren, Belgium = Musée Royal de l'Afrique Centrale
ISH	Institut für Seefischerei, Hamburg, Germany
ISM	L'Institute Scientifique de Madagascar, Tervuren, Belgium = Musée Royal de l'Afrique Centrale
IZTAS	Institute of Zoology, Turkmenian Academy of Sciences, Ashkhabad, Turkmenistan
KIZK	Kunming Institute of Zoology, Academia Sinica, Kunming, China
KMNH	Kitakyushu Museum of Natural History and Human History, Kitakyushu, Fukuoka, Japan
KU	University of Kansas, Museum of Natural History, Lawrence, Kansas
KUEL	Entomology Laboratory of Kyushu University, Kyushu, Japan
LACM	Los Angeles County Museum, Los Angeles, California
LRFC	L.R. Fontes Collection, São Paulo, Brazil (personal collection)
LZFD	Laboratoire Zoologique, Faculté des Sciences, Dijon, France
MACN	Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" e Instituto Nacional de Investigaciones de las Ciencias Naturales, Buenos Aires, Argentina
MAVC	Collection of M.A. Vulcano, São Paulo, Brazil
MCFC	Museu de la Ciència, la Fundació La Caixa, Barcelona, Spain
MCG	Museo Civico di Storia Naturale "Giacomo Doria," Genoa, Italy

MCNA	Museo de Ciencias Naturales de Álava (Álava Province), Vitoria-Gasteiz, Álava, Spain
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
MD	Museu do Dundo, Dundo, Angola
MEUV	Museu de Entomologia da Universidade Federal de Viçosa Minas Geraias, Brazil
MHNAP	Muséum d'Histoire Naturelle d'Aix-en-Provence, France
MHNB	Muséum d'Histoire Naturelle (Naturhistorisches Museum), Basel, Switzerland
MJG	Landesmuseum Joanneum, Graz (Abteilung für Zoologie), Austria
MLP	Museo de La Plata, La Plata, Buenos Aires, Argentina
MLU	Martin Luther Universität, Halle-Wittenberg, Germany
MNHA	Museo Nacional de Historia Natural del Paraguay (Asunción)
MNHP	Muséum National d'Histoire Naturelle, Paris, France
MNM	Mainzer Naturhistorische Museum, Germany
MPEG	Museu Paraense "Emiliano Goeldi," Belém
MPUC	Museum of Paleontology, University of California, Berkeley
MW	Museum Wasmann, Valkenburg, the Netherlands
MZB	Museum Zoologicum Bogoriense, Bogor, Indonesia
MZBB	Museum Zoologicum Bogoriense, Bogor, Java, Indonesia
MZBC	Museum Zoologicum Bogoriense, Cibinong, Indonesia
MZD	Museum zu Déva, Transylvania, Romania
MZUF	Museo Zoologico, Università, Firenze, Italy
MZUSP	Museu de Zoologia, Universidade de São Paulo, Brazil
NAP	Institute of Zoology, Academia Sinica (formerly National Academy of Peiping), Beijing, China
NCIP	National Collection of Insects, Pretoria, South Africa
NHMB	Naturhistorisches Museum, Basel, Switzerland
NHMG	Naturhistoriska Museet, Göteborg, Sweden
NHMM	Natuurhistorisch Museum Museum of Maastricht, Maastricht, the Netherlands
NHMW	Naturhistorisches Museum, Wien, Austria
NHRM	Naturhistoriska Riksmuseet, Stockholm, Sweden
NITN	Nanjing Institute of Termite Control, Nanjing, China
NMBZ	National Museum, Bulawayo, Zimbabwe
NMK	National Museum, Nairobi, Kenya
NMM	Naturhistorisches Museum Mainz, Landessammlung für Naturkunde Rheinland-Pfalz, Mainz, Germany
NMNS	National Museum of Natural Science, Taichung, Taiwan
NMV	Museum of Victoria, Melbourne, Victoria, Australia
NSMT	National Science Museum (Natural History), Tokyo, Japan
NTU	National Taiwan Univeristy, Entomology Department, Taipei, Taiwan
NWUC	Northwest University, Xi'an, Shaanxi Province, China
NZAC	New Zealand Arthropod Coll. Landcare Research (formerly N.Z. Arthropod Coll. DSIR), Mt. Albert, Auckland, New Zealand
ONHM	Oman Natural History Museum, Muscat, Oman
OSUC	Oregon State University, , Corvallis, Oregon
OUM	Hope Department Entomology, Oxford University, Oxford, UK
PEFO	Petrified Forest National Park Museum, Holbrook, Arizona
PIFU	Paläontologisches Institut, Freien Univerität, Berlin, Germany

PIM	Paleontological Institute Moscow, Moscow, Russia
PNCR	Institut des Parcs Nationaux du Congo et du Rwanda, Tervuren, Belgium = Musée Royal de l'Afrique Centrale
PU	Princeton University, Princeton, New Jersey
QITC	Quzhou Institute of Termite Control, Quzhou, Zhejiang Province, China
RGMC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium
RIB	Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium
RIOU	Riou, B., collection, Laboratoire de Prehistorie, Institut des Sciences de la Terre, Dijon, France (pers. coll.)
RMNH	Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden, the Netherlands
ROMTE	Royal Ontario Museum, Department of Entomology, Toronto, Ontario, Canada
SAM	South African Museum, Cape Town, South Africa
SAMA	South Australian Museum, Adelaide, SA, Australia
SBP	Sociedade Brasileira de Paleoartropodologia, Brazil
SCSC	Department Biology, St. Cloud State College, St. Cloud, Minnesota
SEMK	Snow Entomological Museum, University of Kansas, Lawrence
SFRI	Sichuan Forestry Research Institute, Chengdu, Sichuan Province, China
SHNM	Shangdong Natural History Museum, Jinan, Shandong Province, China
SIES	Shanghai Institute of Entomology, Academia Sinica, Shanghai, China
SKU	Syiah Kuala University, Darussalam, Banda Aceh, Indonesia
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
STI	Swiss Tropical Institute, Basel, Switzerland,
SUM	Stellenbosch University, Cape Town, South Africa
TFRI	Taiwan Forestry Research Institute, Taipei, Taiwan
TTMB	Természettudom nyi Múzeum, Budapest, Hungary
UCB	University of California, Berkeley, California
UCRs	University of California, Riverside, California
UCV	Universidad Central de Venezuela, Maracay, Venezuela
UDLZ	Universite de Dakar, Laboratorie de Zoologie, Dakar, Senegal
UEFS	Universidade Estadual de Feira de Santana, Brazil
UFPB	Universidade Federal da Paraíba, Paraíba, Brazil
UGB	Universidade Guarulhos, Paleontological collection, Geosciences, Guarulhos, Brazil
UGCA	University of Georgia, Museum of Natural History Collection of Arthropods, Athens, Georgia
UKZI	Department of Zoology, University of Kerala, Trivandrum, India
ULK	Université Lovanium, Kinshasa, Zaire
UMMZ	University of Michigan, Michigan, Ann Arbor, Michigan
UMZC	University Museum, Department of Zoology, Cambridge, UK
UONZ	Depatment of Geology, University of Otago, Dunedin, New Zealand
UOP	University of Panama, Panama, Panama
UPLE	Laboratoire d'Evolution des Etres Organises (University of Paris), Paris, France
UPLM	Univeristy of Philippines Los Banos Museum of Natural History, Los Banos, Laguna Province, Philippines
USNM	US National Museum, Smithsonian Institution, Washington, DC
UZM	Universitetets Zoologiske Museum, Copenhagen, Denmark

WITC	Wuhan Institute of Termite Control, Wuhan, Hubei Province, China
YITC	Yichang Institute of Termite Control, Yichang, Hubei Province, China
YPM	Yale University, Peabody Museum, New Haven, Connecticut
ZAHC	Zhejiang Agricultural University, Plant Protection Department, Hangzhow, China
ZIHS	Zoötomiska Institute, Hogskolas, Stockholm, Sweden
ZIL	Academy of Sciences, Zoological Institute, St Petersburg, Russia
ZIUL	Zoologischen Institut der Universität, Leipzig, Germany
ZMA	Zoölogisch Museum, Universiteit van Amsterdam, Amsterdam, the Netherlands
ZMB	Museum für Naturkunde an der Universität Humbolt zu Berlin, Berlin, Germany
ZMH	Zoologisches Museum für Hamburg, Hamburg, Germany
ZMLP	Department of Zoology, University of Punjab, Lahore, Pakistan
ZMLU	Zoologiska Instituet, Universitets Lund, Lund, Sweden
ZMM	Moscow State University, Moscow, Russia
ZMUC	Zoological Museum, University of Copenhagen, Copenhagen, Denmark
ZSI	Zoological Survey of India, Calcutta, West Bengal, India
ZSID	Northern Regional Station, Zoological Survey of India, Dehra Dun, Uttarkhand, India
ZSIN	Zoological Survey of India, Northern Regional Station, Dehradun, Uttarkhand, India
ZSM	Zoologische Staatssammlung des Bayerischen Staates, München, Germany
ZTI	Eidgenössischen Polytechnikums (Technical Institute), Zurich
ZUPL	Department of Zoology, University of Punjab, Lahore, Pakistan

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