

## Phylogeny and classification of tribe Aedini (Diptera: Culicidae)

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The phylogeny and classification of tribe Aedini are delineated based on a cladistic analysis of 336 characters from eggs, fourth-instar larvae, pupae, adult females and males, and immature stage habitat coded for 270 exemplar species, including an outgroup of four species from different non-aedine genera. Analyses of the data set with all multistate characters treated as unordered under implied weights, implemented by TNT version 1.1, with values of the concavity constant  $K$  ranging from 7 to 12 each produced a single most parsimonious cladogram (MPC). The MPCs obtained with  $K$  values of 7–9 were identical, and that for  $K = 10$  differed only in small changes in the relationships within one subclade. Because values of  $K < 7$  and  $> 10$  produced large changes in the relationships among the taxa, the stability of relationships exemplified by the MPC obtained from the  $K = 9$  analysis is used to interpret the phylogeny and classification of Aedini. Clade support was assessed using parsimony jackknife and symmetric resampling. Overall, the results reinforce the patterns of relationships obtained previously despite differences in the taxa and characters included in the analyses. With two exceptions, all of the groups represented by two or more species were once again recovered as monophyletic taxa. Thus, the monophyly of the following genera and subgenera is corroborated: *Aedes*, *Albuginosus*, *Armigeres* (and its two subgenera), *Ayurakitia*, *Bothaella*, *Bruceharrisonius*, *Christophersiomyia*, *Collessius* (and its two subgenera), *Dahlia*, *Danielsia*, *Dobrotworskyius*, *Downsiomyia*, *Edwardsaedes*, *Finlaya*, *Georgecraigius* (and its two subgenera), *Eretmapodites*, *Geoskusea*, *Gilesius*, *Haemagogus* (and its two subgenera), *Heizmannia* (and subgenus *Heizmannia*), *Hopkinsius* (and its two subgenera), *Howardina*, *Hulecoeteomyia*, *Jarnellius*, *Kenknighthia*, *Lorrainea*, *Macleaya*, *Mucidus* (and its two subgenera), *Neomelaniconion*, *Ochlerotatus* (subgenera *Chrysoconops*, *Culicelsa*, *Gilesia*, *Pholeomyia*, *Protoculex*, *Rusticoidus* and *Pseudoskusea*), *Opifex*, *Paraedes*, *Patmarkisia*, *Phagomyia*, *Pseudarmigeres*, *Rhinoskusea*, *Psorophora* (and its three subgenera), *Rampamyia*, *Scutumyia*, *Stegomyia*, *Tanakaius*, *Udaya*, *Vansomerenis*, *Verrallina* (and subgenera *Harbachius* and *Neomacleaya*), *Zavortinkius* and *Zeugomyia*. In addition, the monophyly of *Tewarius*, newly added to the data set, is confirmed. *Heizmannia* (*Mattinglyia*) and *Verrallina* (*Verrallina*) were found to be paraphyletic with respect to *Heizmannia* (*Heizmannia*) and *Verrallina* (*Neomacleaya*), respectively. The analyses were repeated with the 14 characters derived from length measurements treated as ordered. Although somewhat different patterns of relationships among the genera and subgenera were found, all were recovered as monophyletic taxa with the sole exception of *Dendroskusea* **stat. nov.** Fifteen additional genera, three of which are new, and 12 additional subgenera, 11 of which are new, are proposed for monophyletic clades, and a few lineages represented by a single species, based on tree topology, the principle of equivalent rank, branch support and the number and nature of the characters that support the branches. *Acartomyia* **stat. nov.**, *Aedimorphus* **stat. nov.**, *Canraedes* **stat. nov.**, *Cornetius* **stat. nov.**, *Geoskusea* **stat. nov.**, *Levua* **stat. nov.**, *Lewnielsenius* **stat. nov.**, *Rhinoskusea* **stat. nov.** and *Sallumia* **stat. nov.**, which were previously recognized as subgenera of various genera, are elevated to generic status. *Catageiomyia* **stat. nov.** and *Polyleptiomyia* **stat. nov.** are resurrected from synonymy with *Aedimorphus*, and *Catatassomyia* **stat. nov.** and *Dendroskusea* **stat. nov.** are resurrected from synonymy with *Diceromyia*. *Bifidistylus* **gen. nov.** (type species: *Aedes lamborni* Edwards) and *Elpeytonius* **gen. nov.** (type species: *Ochlerotatus apicoannulatus* Edwards) are described as new for species previously included in *Aedes* (*Aedimorphus*), and *Petermattinglyius* **gen. nov.** (type species: *Aedes iyengari* Edwards) and *Pe. (Aglaonotus)* **subgen. nov.** (type species: *Aedes whartoni* Mattingly) are described as new for species previously included in *Aedes* (*Diceromyia*). Four additional subgenera are recognized for species of *Ochlerotatus*, including *Oc. (Culicada)* **stat. nov.**

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(type species: *Culex canadensis* Theobald), **Oc. (*Juppius*) subgen. nov.** (type species: *Grabhamia caballa* Theobald), **Oc. (*Lepidokeneon*) subgen. nov.** (type species: *Aedes spilotus* Marks) and **Oc. (*Woodius*) subgen. nov.** (type species: *Aedes intrudens* Dyar), and seven are proposed for species of *Stegomyia*: **St. (*Actinothrix*) subgen. nov.** (type species: *Stegomyia edwardsi* Barraud), **St. (*Bohartius*) subgen. nov.** (type species: *Aedes pandani* Stone), **St. (*Heteraspidion*) subgen. nov.** (type species: *Stegomyia annandalei* Theobald), **St. (*Huangmyia*) subgen. nov.** (type species: *Stegomyia mediopunctata* Theobald), **St. (*Mukwaya*) subgen. nov.** (type species: *Stegomyia simpsoni* Theobald), **St. (*Xyele*) subgen. nov.** (type species: *Stegomyia desmotes* Giles) and **St. (*Zoromorphus*) subgen. nov.** (type species: *Aedes futunae* Belkin). Due to the unavailability of specimens for study, many species of *Stegomyia* are without subgeneric placement. As is usual with generic-level groups of Aedini, the newly recognized genera and subgenera are polythetic taxa that are diagnosed by unique combinations of characters. The analysis corroborates the previous observation that 'Oc. (*Protomacleaya*)' is a polyphyletic assemblage of species.

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## INTRODUCTION

Theobald (1901a, b, 1903, 1907, 1910) provided the first major treatment of family Culicidae, but he did not recognize tribal categories. Many of the taxa currently placed in tribe Aedini were included in his subfamily Culicinae.

Edwards (1932) included dixid and chaoborid midges as subfamilies of Culicidae and regarded the 'true mosquitoes' as members of a third subfamily, Culicinae, which at that time included 1,400 species divided among three tribes, Anophelini, Megarhinini and Culicini. He divided the tribe Culicini (1,184 species), based primarily on adult characters, into five groups, the *Aedes*, *Culex*, *Sabethes*, *Theobaldia* and *Uranotaenia* Groups. His *Aedes* Group comprised seven of the eight genera that later authors (see below) included in tribe Aedini, namely *Aedes* (with many subgenera), *Armigeres*, *Eretmapodites*, *Haemagogus*, *Heizmannia*, *Opifex* and *Psorophora*. Edwards (1932) recognized *Zeugomyia*, the eighth genus included in the traditional classification of Aedini, as a component of his *Uranotaenia* Group rather than the *Aedes* Group. Thus, Edwards (1932) was the first comprehensive treatment of the taxa currently included in tribe Aedini.

In his study of the Afrotropical mosquitoes, Edwards (1941) followed his 1932 generic arrangement and reiterated that 'The large and cosmopolitan genus *Aedes* includes a great diversity of species and is not easy to define as a whole'. He recognized nine subgenera and divided them between two groups based primarily on the structure of the genitalia and the maxillary palpus of the males. One group consisting of three subgenera was defined primarily by the presence of finger-like claspettes that arise from the basosternal area of the gonocoxite, and an undivided, scoop-like phallosome without teeth. The other group of six

subgenera was defined by the presence of setose basal lobes or plaques in place of claspettes, and a phallosome comprised of two lateral plates bearing various teeth. However, Edwards (1941) noted that 'some small and anomalous subgenera do not fit easily into either of these groups . . .'. He also used the development of the male maxillary palpus in a key to separate five of the subgenera included in the second group.

Stone (1957) removed dixid and chaoborid midges from Culicidae and restricted the family to the Culicinae of Edwards (1932). This brought about changes in subfamily and tribal designations that were adopted by Stone, Knight & Starcke (1959) in their world catalogue of mosquitoes. This classification recognized subfamilies Anophelinae, Culicinae and Toxorhynchitinae, and two tribes within Culicinae, Culicini and Sabethini. Belkin (1962) disagreed with this change and retained Edwards' subfamily structure, but re-organized the classification of Culicinae ('true mosquitoes') to include 12 tribes instead of three. He retained Anophelini and Toxorhynchitini and recognized 10 tribes in place of Edwards' Culicini. At least some authors (e.g. Belkin, Heinemann & Page, 1970) continued to treat dixids and chaoborids as subfamilies of Culicidae until Knight & Stone (1977) once again excluded them from the family. Wood & Borkent (1989) firmly established that Chaoboridae, Corethrellidae, Culicidae and Dixidae were separate families within superfamily Culicoidea (infraorder Culicomorpha) based on a cladistic analysis of suborder Nematocera.

Belkin (1962) defined tribe Aedini to include the seven genera of Edwards' (1932) *Aedes* Group and genus *Zeugomyia*, and proposed a division of genus *Aedes* based on characters of the male genitalia (i.e. proctiger with or without cercal setae and a simple or complex aedeagus) and the fourth-instar larvae (i.e. presence or absence of seta 12-I). However, his study was based primarily on taxa from the South Pacific

that included 12 subgenera of *Aedes* and two other genera of Aedini. Belkin noted that whereas his groupings appeared to be natural it was quite probable that the defining characters would not hold up outside the South Pacific area. He also pointed out that 'Many of the subgenera of *Aedes* appear to be heterogeneous complexes of superficially similar forms, and it is very probable that they will have to be subdivided into smaller natural groups'. He realized that 'Lumping all small taxa into groups of a convenient size but of indefinite affinities does nothing but obscure relationships'. Additionally, he recognized that genus *Aedes* must be studied on a worldwide basis, and all life stages examined, before it could be truly evaluated, understood and possibly reorganized.

Family Culicidae currently includes 3,521 species and Aedini, the largest tribe, includes 1,255 formally recognized species (<http://mosquito-taxonomic-inventory.info>, accessed 2 November 2009). After more than a century of study, mosquito taxonomy is still largely at the descriptive level (alpha taxonomy) and relatively little attention has been given to the development of a natural classification (beta taxonomy). Zavortink (1990) pointed out that 'At the beta level of taxonomy, . . . the species are studied in greater detail and reclassified into smaller and more numerous genera that indicate their genetic relationships more accurately'. Using a mathematical equation that expresses the graphical distribution of species per genus in those groups of organisms that have achieved the beta level of taxonomy, Zavortink calculated that the total number of genera in Culicidae (based on about 3,200 species in 1990) should be 225. In proportion to the family, a tribe the size of Aedini should theoretically include 87 genera. Zavortink (1994), while discussing the 'state of mosquito systematics', noted two goals of systematics that apply to the present study: '. . . to arrange . . . species in a classification that reflects their evolutionary relationships' and 'to provide unique names for the species and other taxa in the classification so that information about these taxa may be communicated'.

Authors who have studied multiple generic-level taxa of Aedini explicitly recognized that the larger genera (especially *Aedes* in the traditional broad sense) and subgenera were heterogeneous, i.e. polyphyletic. Belkin (1962) stated that 'the currently accepted classification of Edwards (1932, 1941) is far from being a satisfactory one' and 'the internal classification of Aedini is in need of thorough revision'. Belkin (1962), in his discussion of the systematics of *Aedes*, also stated that 'characters used by Edwards (1932: 129–178; 1941: 106–223) for the definition of the subgenera are often very superficial and unsatisfactory'.

The reclassification of tribe Aedini began with the removal of *Verrallina*, *Ayurakitia* and *Ochlerotatus* from

the composite *Aedes* (Reinert, 1999d, 2000a, 2000b, respectively). This was followed by a phylogenetic analysis of Aedini (Reinert, Harbach & Kitching, 2004) in which most genera and subgenera of the tribe were shown to be well-defined monophyletic taxa whereas some large groups, e.g. *Aedimorphus*, *Finlaya*, *Ochlerotatus* and *Stegomyia*, were found to be polyphyletic. Two subsequent studies (Reinert, Harbach & Kitching, 2006, 2008) examined the phylogeny of *Finlaya* and *Ochlerotatus*. Each of the three studies (Reinert *et al.*, 2004, 2006, 2008) successively showed remarkable congruence despite differences in the taxa and morphological characters analysed in each. As a result of those studies, 62 genera were formally proposed for the species included in tribe Aedini.

Reinert *et al.* (2004, 2006, 2008) pointed out that few molecular studies of Aedini have been published. Wesson, Porter & Collins (1992) examined the relationships of six aedine species (four 'Aedes', one *Haemagogus*, one *Psorophora*) based on rDNA ITS2 sequence data. Besansky & Fahey (1997) included three 'Aedes' and one *Haemagogus* among 13 mosquito species in a study of relationships based on sequence data for the nuclear protein-coding *white* gene. Kumar, Black & Rai (1998) investigated the relationships of 15 culicine species representing six 'genera', including nine species of 'Aedes' and one each of *Armigeres* and *Haemagogus*. More recently, Cook *et al.* (2005) investigated the relationships among 20 species of 'Aedes' representing six traditionally recognized subgenera, including *Aedes* (one species), *Aedimorphus* (1), *Diceromyia* (2), *Halaedes* (3), *Ochlerotatus* (10) and *Stegomyia* (3), based on sequence data for the cytochrome oxidase c subunits I and II (COI, COII) of mitochondrial DNA. Behbahani *et al.* (2005) used ITS2 sequences to construct a phylogenetic tree for five species of *Stegomyia*. The results of Wesson *et al.* (1992), Besansky & Fahey (1997) and Kumar *et al.* (1998) indicated a paraphyletic Aedini, but these studies provided little insight into the phylogeny and classification of the tribe because they included very few generic-level taxa and few species. For example, whereas *St. aegypti* and *St. albopicta* formed a strongly supported sister pair in the *white*-gene phylogeny of Besansky & Fahey (1997), they were not placed in a congeneric relationship in the ITS2 phylogeny of Wesson *et al.* (1992) or the RFLP phylogeny of Kumar *et al.* (1998). All three of these studies included '*Ochlerotatus* (*Protomacleaya*) *triseriatus*', which was strongly paired with *Psorophora* in the phylogeny of Wesson *et al.* (1992) and with *Haemagogus* in the phylogenies of Besansky & Fahey (1997) and Kumar *et al.* (1998). It is interesting to note that Wesson *et al.* (1992) suggested that *Aedes sensu auctorum* should be split into two genera, one including '*Oc. (Pro.) triseriatus* (as *Ae. (Pro.) triseria-*

tus) along with species of *Haemagogus* and *Psorophora*. The COI and COII phylogenies of Cook *et al.* (2005) agreed with respect to species-level groupings, but because sequences for neither gene were available for all the species analysed, it was 'difficult to draw firm conclusions regarding the interspecies relationships'. Support for supraspecific clades was either very low or meaningless in cases where higher-level taxa were represented by several samples of a single species. In general, clade support, assessed by bootstrap proportions, was slightly higher for the COII phylogeny. Whereas the monophyly of *Diceromyia taylori* + *Di. furcifer* (as *Ae. taylori* and *Ae. furcifer*) was weakly supported in the COI phylogeny, it was very strongly supported (bootstrap value = 99) in the COII phylogeny. Likewise, the monophyly of *St. luteocephala* + (*St. albopicta* + *St. aegypti*) (as species of *Aedes*) received low support in the COI phylogeny and modest support (bootstrap value = 53) in the maximum likelihood tree of COII sequences. Eight species of '*Ochlerotatus*' included in the analysis of COI data (COII data were not available) were placed in a sister-group relationship to *Oc. (Rusticoides) rusticus* (as *Ae. rusticus*), which was sister to *Ae. cinereus*, but all of the internal branches were only weakly supported. The three species of *Halaedes* (not included in the COI phylogeny) formed a strongly supported clade in the COII phylogeny (bootstrap value = 99) comprised of *ashworthi* + (*wardangensis* + *australis*) (as *Aedes* species). Overall, the results of Cook *et al.* (2005) are not inconsistent with those of Reinert *et al.* (2004). Rey *et al.* (2001) used a 763-bp segment of the mitochondrial COI gene to examine the phylogenetic relationships of 14 species (12 endemic in France) traditionally placed in genus *Aedes*. Overall, the relationships inferred from their analyses support the generic status of *Aedes*, *Ochlerotatus* and *Stegomyia* proposed by Reinert (2000b) and Reinert *et al.* (2004). More recently, Shepard, Andreadis & Vossbrinck (2006) showed that species of *Aedes* (four species) and *Ochlerotatus* (15 species from the northeastern United States) fall into two separate and distinct clades based on phylogenetic analyses of the 18S subunit of rDNA. Thus, the elevation of *Ochlerotatus* to generic level by Reinert (2000b) based on morphological data is corroborated by mitochondrial and ribosomal DNA sequence data. Cywinska, Hunter & Hebert (2006) and Kumar *et al.* (2007) reported on the genetic divergence of 37 Canadian and 63 Indian mosquito species, respectively, based on short fragments of the cytochrome c oxidase I (COI) region of mitochondrial DNA ('barcodes') used to provide species identification. The study of Cywinska *et al.* (2006) included 24 species of '*Aedes*' (genera *Aedes* and *Ochlerotatus* of Reinert *et al.*, 2004, 2006) and that of Kumar *et al.* (2007) included 27 aedine

species of genera '*Aedes*', *Armigeres*, *Collessius*, *Diceromyia*, *Fredwardsius*, *Heizmannia*, *Lorrainea*, *Phagomyia*, *Rhinokusea*, *Stegomyia* and *Verrallina* (all *sensu* Reinert *et al.*, 2004, 2006). Neighbour-joining (NJ) trees were used to cluster haplotypes, and the distinct clusters were interpreted as species. Neighbour-joining is a phenetic method, not a phylogenetic method, and the observed clusters are based on overall similarity, not synapomorphy; hence, the relationships among the species portrayed in the NJ trees of Cywinska *et al.* (2006) and Kumar *et al.* (2007) are not relevant to the conclusions drawn from the cladistic analyses of Reinert *et al.* (2004, 2006, 2008).

Our previous studies (Reinert *et al.*, 2004, 2006, 2008) examined the higher-level relationships within Aedini, *Finlaya* (and allied taxa) and *Ochlerotatus* (and allied taxa), respectively. The aim of the present study is a comprehensive assessment of the phylogeny and classification of tribe Aedini, to include previously studied taxa and a selection of available species that more thoroughly represent the diversity of *Aedimorphus*, *Diceromyia* and *Stegomyia*. An underlying hypothesis to be tested is the principle of equivalent rank and the integrity of generic-level taxa that we previously recognized based on this principle. To avoid confusion, species of uncertain generic and subgeneric placement, and generic-level names used in the previous sense that include these species, are enclosed within single quotation marks to distinguish them from formally recognized monophyletic taxa.

## MATERIALS AND METHODS

The present study includes the 270 species listed in Table 1 (see also for authorship and geographical distribution). The ingroup comprises 266 species of Aedini and the outgroup consists of the four non-aedine species used in our previous studies (Reinert *et al.*, 2004, 2006, 2008): *Culex quinquefasciatus*, *Culiseta inornata*, *Mansonia titillans* and *Orthopodomyia signifera*. The ingroup taxa include the type species of most genus-level names. Unfortunately, specimens of several important species that we wanted to include in the analysis were unavailable or had several missing life stages. The internal classification of some genera, e.g. *Eretmapodites* and Afrotropical *Stegomyia*, is hampered because numerous species have unknown immature stages.

The data (Appendix 1) comprise 336 characters from eggs (4), fourth-instar larvae (97), pupae (39), females (101), males (14), female genitalia (30), male genitalia (50) and habitat of immature stages (1). Individually reared, pin-mounted adults with associated slide-mounted fourth-instar larval and pupal exuviae were studied when available. A phase contrast or differential interference contrast microscope

**Table 1.** Species Examined

The following species were examined in detail during the comparative morphological analysis. An asterisk (\*) following a species-author combination denotes a type species of a generic-level taxon. Geographical distribution of species is indicated by region: 1, Nearctic; 2, Palaearctic; 3, Afrotropical; 4, Oriental; 5, Australasian (including western Pacific Islands); 6, Neotropical. An asterisk following a geographic region indicates a relatively recent introduction.

| Genus                                       | Subgenus                        | Species                                       | Distribution |
|---|---------------------------------|---|--------------|
| <b>Aedini ingroup taxa</b>                  |                                 |   |              |
| <i>Abraedes</i> Zavortink                   |                                 | <i>papago</i> (Zavortink)*                    | 1            |
| <i>Aedes</i> Meigen                         |                                 | <i>cinereus</i> Meigen*                       | 2            |
|   |                                 | <i>esoensis</i> Yamada                        | 2            |
| ' <i>Aedes</i> ' <i>sensu auctorum</i>      | ' <i>Aedimorphus</i> ' Theobald | <i>albocephalus</i> (Theobald)                | 3            |
|   |                                 | <i>alboscuteclatus</i> (Theobald)             | 2,4,5        |
|   |                                 | <i>apicoannulatus</i> (Edwards)               | 3            |
|   |                                 | <i>argenteopunctatus</i> (Theobald)           | 3            |
|   |                                 | <i>caecus</i> (Theobald)                      | 4            |
|   |                                 | <i>culicinus</i> Edwards                      | 4            |
|   |                                 | <i>cumminsii</i> (Theobald)                   | 3            |
|   |                                 | <i>dalzieli</i> (Theobald)                    | 3            |
|   |                                 | <i>dentatus</i> (Theobald)                    | 3            |
|   |                                 | <i>domesticus</i> (Theobald)*                 | 3            |
|   |                                 | <i>eritreae</i> Lewis                         | 3            |
|   |                                 | <i>gibbinsi</i> Edwards                       | 3            |
|   |                                 | <i>irritans</i> (Theobald)                    | 3            |
|   |                                 | <i>lamborni</i> Edwards                       | 3            |
|   |                                 | <i>mediolineatus</i> (Theobald)               | 4            |
|   |                                 | <i>ochraceus</i> (Theobald)                   | 3            |
|   |                                 | <i>orbitae</i> Edwards                        | 4            |
|   |                                 | <i>pallidostriatus</i> (Theobald)             | 4            |
|   |                                 | <i>pampangensis</i> (Ludlow)                  | 4            |
|   |                                 | <i>pipersalatus</i> (Giles)                   | 4            |
|   |                                 | <i>punctifemoris</i> (Ludlow)                 | 4            |
|   |                                 | <i>quasiunivittatus</i> (Theobald)            | 3            |
|   |                                 | <i>simulans</i> (Newstead & Carter)           | 3            |
|   |                                 | <i>taeniorhynchoides</i> (Christophers)       | 4            |
|   |                                 | <i>tarsalis</i> (Newstead)                    | 3            |
|   |                                 | <i>trimaculatus</i> (Theobald)                | 4            |
|   |                                 | <i>vexans vexans</i> (Meigen)                 | 1,2,3,4,5    |
|   | ' <i>Canraedes</i> ' Edwards    | <i>cancricomes</i> Edwards*                   | 4            |
|   |                                 | <i>masculinus</i> Mattingly                   | 4            |
|   |                                 | <i>penghuensis</i> Lien                       | 4            |
|   | ' <i>Cornetius</i> ' Huang      | <i>cozi</i> Cornet*                           | 3            |
| <i>Alanstonea</i> Mattingly                 |                                 | <i>brevitibia</i> (Edwards)                   | 4            |
| <i>Albuginosus</i> Reinert                  |                                 | <i>marshallii</i> (Theobald)*                 | 3            |
|   |                                 | <i>ngong</i> (van Someren)                    | 3            |
| <i>Armigeres</i> Theobald                   | <i>Armigeres</i>                | <i>breinli</i> (Taylor)                       | 5            |
|   |                                 | <i>subalvatus</i> (Coquillett)                | 2,4          |
|   | <i>Leicesteria</i> Theobald     | <i>flavus</i> (Leicester)                     | 4            |
|   |                                 | <i>longipalpis</i> (Leicester)*               | 4            |
| <i>Ayurakitia</i> Thurman                   |                                 | <i>griffithi</i> Thurman*                     | 4            |
|   |                                 | <i>peytoni</i> (Reinert)                      | 4            |
| <i>Aztecaedes</i> Zavortink                 |                                 | <i>ramirezi</i> (Vargas & Downs)*             | 1            |
| <i>Belkinius</i> Reinert                    |                                 | <i>aurotaeiatus</i> (Edwards)*                | 4            |
| <i>Borichinda</i> Harbach & Rattanarithikul |                                 | <i>cavernicola</i> Rattanarithikul & Harbach* | 4            |
| <i>Bothaella</i> Reinert                    |                                 | <i>eldridgei</i> (Reinert)                    | 4            |
|   |                                 | <i>helenae</i> (Reinert)*                     | 4            |

Table 1. Continued

| Genus   | Subgenus  | Species                               | Distribution |
|---|---|---------------------------------------|--------------|
| <i>Bruceharrisonius</i> Reinert                       |   | <i>alektorovi</i> (Stackelberg)       | 2            |
|   |   | <i>greenii</i> (Theobald)*            | 4            |
| <i>Christophersomyia</i> Barraud                      |   | <i>gombakensis</i> (Mattingly)        | 4            |
|   |   | <i>thomsoni</i> (Theobald)*           | 4            |
| <i>Collessius</i> Reinert,<br>Harbach & Kitching      | <i>Alloeomyia</i> Reinert,<br>Harbach & Kitching<br><i>Collessius</i> | <i>banksi</i> (Edwards)               | 4            |
|   |   | <i>pseudotaeniatus</i> (Giles)*       | 4            |
|   |   | <i>elsiae</i> (Barraud)               | 4            |
|   |   | <i>macfarlanei</i> (Edwards)*         | 4            |
| <i>Dahlia</i> Reinert,<br>Harbach & Kitching          |   | <i>echinus</i> (Edwards)              | 2            |
| <i>Danielsia</i> Theobald                             |   | <i>geniculata</i> (Olivier)*          | 2            |
|   |   | <i>albotaeniata</i> Leicester*        | 4            |
|   |   | <i>harperi</i> (Knight)               | 4            |
| <i>Diceromyia</i> Theobald                            |   | <i>franciscoi</i> (Mattingly)         | 4            |
|   |   | <i>furcifer</i> (Edwards)*            | 3            |
|   |   | <i>iyengari</i> (Edwards)             | 4            |
|   |   | <i>meronephada</i> (Dyar & Shannon)   | 4            |
|   |   | <i>micropterus</i> (Giles)            | 4            |
|   |   | <i>periskelata</i> (Giles)            | 4            |
|   |   | <i>reginae</i> (Edwards)              | 4            |
|   |   | <i>scanloni</i> (Reinert)             | 4            |
|   |   | <i>taylori</i> (Edwards)              | 3            |
|   |   | <i>whartoni</i> (Mattingly)           | 4            |
| <i>Dobrotworskyius</i> Reinert,<br>Harbach & Kitching |   | <i>alboannulatus</i> (Macquart)       | 5            |
| <i>Downsiomyia</i> Vargas                             |   | <i>tubbutiensis</i> (Dobrotworsky)*   | 5            |
|   |   | <i>leonis</i> (Colless)               | 4            |
|   |   | <i>nivea</i> (Ludlow)*                | 4            |
| <i>Edwardsaedes</i> Belkin                            |   | <i>bekkui</i> (Mogi)                  | 2            |
|   |   | <i>imprimens</i> (Walker)*            | 2,4,5        |
| <i>Eretmapodites</i> Theobald                         |   | <i>chrysogaster</i> Graham            | 3            |
|   |   | <i>quinquevittatus</i> Theobald*      | 3            |
| <i>Finlaya</i> Theobald                               |   | <i>kochi</i> (Dönitz)*                | 5            |
|   |   | <i>poicilia</i> Theobald              | 4,5          |
| <i>Fredwardsius</i> Reinert                           |   | <i>vittatus</i> (Bigot)*              | 2,3,4        |
| <i>Georgecraigius</i> Reinert,<br>Harbach & Kitching  | <i>Georgecraigius</i>   | <i>atropalpus</i> (Coquillett)*       | 1,2*         |
|   | <i>Horsfallius</i> Reinert,<br>Harbach & Kitching                     | <i>epactius</i> (Dyar & Knab)         | 1,6          |
|   |   | <i>fluviatilis</i> (Lutz)*            | 6            |
| <i>Gilesius</i> Reinert, Harbach<br>& Kitching        |   | <i>pulchriventer</i> (Giles)*         | 2,4          |
| <i>Gymnetopa</i> Coquillett                           |   | <i>mediovittata</i> (Coquillett)*     | 6            |
| <i>Haemagogus</i> Williston                           | <i>Conopostegus</i> Dyar  | <i>leucoelaenus</i> (Dyar & Shannon)* | 6            |
|   |   | <i>leucotaeniatus</i> (Komp)          | 6            |
|   | <i>Haemagogus</i>   | <i>equinus</i> Theobald               | 6            |
|   |   | <i>splendens</i> Williston*           | 6            |
| <i>Halaedes</i> Belkin                                |   | <i>australis</i> (Erichson)*          | 5            |
| <i>Heizmannia</i> Ludlow                              | <i>Heizmannia</i>   | <i>complex</i> (Theobald)             | 4            |
|   |   | <i>scintillans</i> Ludlow*            | 4            |
|   | <i>Mattinglyia</i> Lien   | <i>achaetae</i> (Leicester)           | 4            |
|   |   | <i>catesi</i> (Lien)*                 | 4            |
| <i>Himalaius</i> Reinert,<br>Harbach & Kitching       |   | <i>gilli</i> (Barraud)*               | 4            |

**Table 1.** *Continued*

| Genus   | Subgenus   | Species                                | Distribution |
|---|--|--|--------------|
| <i>Hopkinsius</i> Reinert,<br>Harbach & Kitching    | <i>Hopkinsius</i>                                | <i>embuensis</i> (Edwards)             | 3            |
|   |  | <i>ingrami</i> (Edwards)*              | 3            |
| <i>Howardina</i> Theobald                           | <i>Yamada</i> Reinert,<br>Harbach & Kitching     | <i>albocinctus</i> (Barraud)           | 4            |
|   |  | <i>seoulensis</i> (Yamada)*            | 2            |
|   |  | <i>sexlineata</i> (Theobald)           | 6            |
| <i>Huaedes</i> Huang                                |  | <i>wauensis</i> (Huang)*               | 5            |
| <i>Hulecoeteomyia</i> Theobald                      |  | <i>chrysolineata</i> (Theobald)*       | 4            |
|   |  | <i>sherki</i> (Knight)                 | 4            |
| <i>Indusius</i> Edwards                             |  | <i>pulverulentus</i> (Edwards)*        | 4            |
| <i>Isoaedes</i> Reinert                             |  | <i>cavaticus</i> (Reinert)*            | 4            |
| <i>Jarnellius</i> Reinert,<br>Harbach & Kitching    | <i>Jarnellius</i>                                | <i>sierrensis</i> (Ludlow)             | 1            |
|   |  | <i>varipalpus</i> (Coquillett)*        | 1            |
| <i>Lewnielsenius</i> Reinert,<br>Harbach & Kitching |  | <i>muelleri</i> (Dyar)*                | 1            |
|   |  | <i>chungi</i> (Lien)*                  | 4            |
| <i>Jihlienius</i> Reinert,<br>Harbach & Kitching    |  |  |              |
| <i>Kenknighthia</i> Reinert                         |  | <i>dissimilis</i> (Leicester)*         | 4            |
|   |  | <i>harbachi</i> (Reinert)              | 4            |
| <i>Kompia</i> Aitkin                                |  | <i>purpureipes</i> (Aitken)*           | 1            |
| <i>Leptosomatomyia</i> Theobald                     |  | <i>aurimargo</i> (Edwards)*            | 5            |
| <i>Lorrainea</i> Belkin                             |  | <i>amesii</i> (Ludlow)                 | 4            |
|   |  | <i>dasyorrhus</i> (King & Hoogstraal)* | 5            |
| <i>Luius</i> Reinert, Harbach<br>& Kitching         |  | <i>fengi</i> (Edwards)*                | 4            |
| <i>Macleaya</i> Theobald                            | <i>Chaetocruuiomyia</i><br>Theobald              | <i>wattensis</i> (Taylor)              | 5            |
|   | <i>Macleaya</i>                                  | <i>tremula</i> Theobald*               | 5            |
| <i>Molpemyia</i> Theobald                           |  | <i>pecuniosa</i> (Edwards)             | 5            |
| <i>Mucidus</i> Theobald                             | <i>Mucidus</i>                                   | <i>alternans</i> (Westwood)*           | 5            |
|   |  | <i>laniger</i> (Wiedemann)             | 4            |
| <i>Pardomyia</i> Theobald                           |  | <i>aurantius</i> (Theobald)*           | 4,5          |
|   |  | <i>quadripunctis</i> (Ludlow)          | 4            |
|   |  | <i>lineatopenne</i> (Ludlow)           | 4,5          |
| <i>Neomelaniconion</i><br>Newstead                  |  | <i>palpale</i> Newstead*               | 3            |
| <i>Ochlerotatus</i> Lynch<br>Arribáizaga            | <i>Acartomyia</i> Reinert,<br>Harbach & Kitching | <i>zammitii</i> (Theobald)*            | 2            |
|   | <i>Buvirilia</i> Reinert,<br>Harbach & Kitching  | <i>edgari</i> (Stone & Rosen)*         | 5            |
| <i>Chrysoconops</i> Goeldi                          |  | <i>fulvus fulvus</i> (Wiedemann)*      | 6            |
|   |  | <i>fulvus pallens</i> (Ross)           | 1,6          |
| <i>Culicelsa</i> Felt                               |  | <i>mitchellae</i> (Dyar)               | 1            |
|   |  | <i>taeniorhynchus</i> (Wiedemann)*     | 1,6          |
| <i>Empihals</i> Reinert,<br>Harbach & Kitching      |  | <i>vigilax</i> (Skuse)*                | 3*,4,5       |
| <i>Geoskusea</i> Edwards                            |  | <i>baisasi</i> (Knight & Hull)         | 4            |
|   |  | <i>longiforceps</i> (Edwards)          | 5            |
| <i>Gilesia</i> Theobald                             |  | <i>aculeatus</i> (Theobald)*           | 5            |
|   |  | <i>mcdonaldi</i> (Belkin)              | 5            |
| <i>Levua</i> Stone & Bohart                         |  | <i>geoskusea</i> (Amos)*               | 5            |
| <i>Ochlerotatus</i>                                 |  | <i>infirmatus</i> (Dyar & Knab)        | 1            |
|   |  | <i>scapularis</i> (Rondani)*           | 1,6          |

Table 1. *Continued*

| Genus                                | Subgenus                                 | Species                                     | Distribution |
|--------------------------------------|--|---|--------------|
|                                      | <i>Protoculex</i> Felt                   | <i>pertinax</i> (Grabham)                   | 6            |
|                                      |  | <i>serratus</i> (Theobald)*                 | 6            |
|                                      | <i>Pholeomyia</i> Reinert,               | <i>calcariae</i> (Marks)*                   | 5            |
|                                      | Harbach & Kitching                       | <i>flavifrons</i> (Skuse)                   | 5            |
|                                      | <i>Pseudoskusea</i> Theobald             | <i>bancroftianus</i> (Edwards)              | 5            |
|                                      |  | <i>postspiraculosus</i> (Dobrotworsky)      | 5            |
|                                      | <i>Rhinoscusea</i> Edwards               | <i>longirostris</i> (Leicester)*            | 4,5          |
|                                      |  | <i>wardi</i> (Reinert)                      | 4            |
|                                      | <i>Rusticoides</i> Shevchenko            | <i>refiki</i> (Medschid)*                   | 2            |
|                                      | & Prudkina                               | <i>rusticus</i> (Rossi)                     | 2            |
|                                      | <i>Sallumia</i> Reinert,                 | <i>hortator</i> (Dyar & Knab)*              | 6            |
|                                      | Harbach & Kitching                       |   |              |
|                                      | Unassigned to subgenus                   | <i>albifasciatus</i> (Macquart)             | 6            |
|                                      |  | <i>andersoni</i> (Edwards)                  | 5            |
|                                      |  | <i>aurifer</i> (Coquillett)                 | 1            |
|                                      |  | <i>caballus</i> (Theobald)                  | 2,3          |
|                                      |  | <i>calumnior</i> (Belkin, Heinemann & Page) | 6            |
|                                      |  | <i>campestris</i> (Dyar & Knab)             | 1            |
|                                      |  | <i>canadensis canadensis</i> (Theobald)     | 1            |
|                                      |  | <i>cantans</i> (Meigen)                     | 2            |
|                                      |  | <i>cantator</i> (Coquillett)                | 1            |
|                                      |  | <i>caspius</i> (Pallas)                     | 2            |
|                                      |  | <i>communis</i> (de Geer)                   | 1,2          |
|                                      |  | <i>diantaeus</i> (Howard, Dyar & Knab)      | 1,2          |
|                                      |  | <i>dorsalis</i> (Meigen)                    | 1,2,4        |
|                                      |  | <i>excrucians</i> (Walker)                  | 1,2          |
|                                      |  | <i>fitchii</i> (Felt & Young)               | 1,2          |
|                                      |  | <i>flavescens</i> (Müller)                  | 1,2          |
|                                      |  | <i>grossbecki</i> (Dyar & Knab)             | 1            |
|                                      |  | <i>hexodontus</i> (Dyar)                    | 1,2          |
|                                      |  | <i>impiger</i> (Walker)                     | 1,2          |
|                                      |  | <i>intrudens</i> (Dyar)                     | 1,2          |
|                                      |  | <i>nivalis</i> (Edwards)                    | 5            |
|                                      |  | <i>pionips</i> (Dyar)                       | 1,2          |
|                                      |  | <i>pullatus</i> (Coquillett)                | 1,2          |
|                                      |  | <i>punctor</i> (Kirby)                      | 1,2          |
|                                      |  | <i>ratcliffei</i> (Marks)                   | 5            |
|                                      |  | <i>riparius</i> (Dyar & Knab)               | 1,2          |
|                                      |  | <i>spencerii spencerii</i> (Theobald)       | 1            |
|                                      |  | <i>pilotus</i> (Marks)                      | 5            |
|                                      |  | <i>squamiger</i> (Coquillett)               | 1            |
|                                      |  | <i>sticticus</i> (Meigen)                   | 1,2          |
|                                      |  | <i>stimulans</i> (Walker)                   | 1            |
|                                      |  | <i>theobaldi</i> (Taylor)                   | 5            |
|                                      |  | <i>thibaulti</i> (Dyar & Knab)              | 1,2          |
| ' <i>Ochlerotatus</i> ' <i>sensu</i> | ' <i>Finlaya</i> ' <i>sensu auctorum</i> | <i>biocellatus</i> (Taylor)                 | 5            |
| <i>auctorum</i>                      |  | <i>candidoscutellum</i> (Marks)             | 5            |
|                                      |  | <i>crossi</i> (Lien)                        | 4            |
|                                      |  | <i>keefei</i> (King & Hoogstraal)           | 5            |
|                                      |  | <i>oreophilus</i> Edwards                   | 2,4          |



Table 1. *Continued*

| Genus  | Subgenus  | Species                                 | Distribution         |
|--|---|---|----------------------|
|  | ' <i>Protomacleaya</i> '<br><i>sensu auctorum</i> | <i>brelandi</i> (Zavortink)             | 1                    |
|  |   | <i>burgeri</i> (Zavortink)              | 1                    |
|  |   | <i>galindoi</i> (Schick)                | 6                    |
|  |   | <i>homoeopus</i> (Dyar)                 | 6                    |
|  |   | <i>knabi</i> (Coquillett)               | 6                    |
|  |   | <i>kompi</i> (Vargas & Downs)           | 6                    |
|  |   | <i>terrens</i> (Walker)                 | 6                    |
|  |   | <i>triseriatus</i> (Say)*               | 1                    |
|  |   | <i>zoosophus</i> (Dyar & Knab)          | 1                    |
| <i>Opifex</i> Hutton                             | <i>Nothoskusea</i><br>Dumbleton                   | <i>chathamicus</i> (Dumbleton)*         | 5                    |
|  | <i>Opifex</i>                                     | <i>fuscus</i> Hutton*                   | 5                    |
| <i>Paraedes</i> Edwards                          |   | <i>barraudi</i> Edwards*                | 4                    |
|  |   | <i>ostentatio</i> (Leicester)           | 4                    |
| <i>Patmarksia</i> Reinert,<br>Harbach & Kitching |   | <i>argyronotum</i> (Belkin)             | 5                    |
|  |   | <i>papuensis</i> (Taylor)*              | 5                    |
| <i>Phagomyia</i> Theobald                        |   | <i>gubernatoris</i> (Giles)*            | 4                    |
|  |   | <i>lophoventralis</i> (Theobald)        | 4                    |
| <i>Pseudarmigeres</i> Stone<br>& Knight          |   | <i>argenteoventralis dumni</i> (Evans)* | 3                    |
|  |   | <i>michaelikati</i> (van Someren)       | 3                    |
| <i>Psorophora</i> Robineau-<br>Desvoidy          | <i>Grabhamia</i><br>Theobald                      | <i>columbiae</i> (Dyar & Knab)          | 1,6                  |
|  |   | <i>jamaicensis</i> Theobald*            | 6                    |
|  | <i>Janthinosoma</i><br>Lynch Arribálzaga          | <i>cyanescens</i> (Coquillett)          | 1,6                  |
|  |   | <i>ferox</i> (von Humboldt)             | 1,6                  |
|  | <i>Psorophora</i>                                 | <i>ciliata</i> (Fabricius)*             | 1,6                  |
|  |   | <i>howardii</i> Coquillett              | 1,6                  |
| <i>Rampamyia</i> Reinert,<br>Harbach & Kitching  |   | <i>albilabris</i> (Edwards)             | 5                    |
|  |   | <i>notoscripta</i> (Skuse)*             | 5                    |
| <i>Scutomyia</i> Theobald                        |   | <i>albolineata</i> Theobald*            | 4,5                  |
|  |   | <i>arboricola</i> (Knight & Rozeboom)   | 4                    |
| <i>Skusea</i> Theobald                           |   | <i>pembaensis</i> (Theobald)*           | 3                    |
| <i>Stegomyia</i> Theobald                        |   | <i>aegypti</i> (Linnaeus)*              | 1*,2*,3,4*,<br>5*,6* |
|  |   | <i>africana</i> Theobald                | 3                    |
|  |   | <i>albopicta</i> (Skuse)                | 1*,2,3*,4,5,<br>6*   |
|  |   | <i>annandalei</i> Theobald              | 4                    |
|  |   | <i>apicoargentea</i> Theobald           | 3                    |
|  |   | <i>bromeliae</i> (Edwards)              | 3                    |
|  |   | <i>chemulpoensis</i> (Yamada)           | 2                    |
|  |   | <i>craggi</i> Barraud                   | 4                    |
|  |   | <i>deboeri</i> (Edwards)                | 3                    |
|  |   | <i>dendrophila</i> (Edwards)            | 3                    |
|  |   | <i>desmotes</i> Giles                   | 4                    |
|  |   | <i>edwardsi</i> Barraud                 | 4                    |
|  |   | <i>futunae</i> (Belkin)                 | 5                    |
|  |   | <i>gardnerii gardnerii</i> Ludlow       | 4                    |
|  |   | <i>luteocephala</i> Newstead            | 3                    |
|  |   | <i>mediopunctata</i> Theobald           | 4                    |
|  |   | <i>metallica</i> (Edwards)              | 3                    |
|  |   | <i>pandani</i> (Stone)                  | 5                    |
|  |   | <i>perplexa</i> Leicester               | 4                    |
|  |   | <i>poweri</i> Theobald                  | 3                    |
|  |   | <i>riversi</i> (Bohart & Ingram)        | 4                    |
|  |   | <i>saipanensis</i> (Stone)              | 5                    |
|  |   | <i>scutellaris</i> (Walker)             | 5                    |

Table 1. Continued

| Genus  | Subgenus                    | Species                                    | Distribution         |
|--|-----------------------------|--|----------------------|
|  |                             | <i>simpsoni</i> Theobald                   | 3                    |
|  |                             | <i>unilineata</i> (Theobald)               | 3                    |
|  |                             | <i>wadai</i> (Tanaka, Mizusawa & Saugstad) | 2                    |
|  |                             | <i>w-albus</i> Theobald                    | 4                    |
|  |                             | <i>woodi</i> (Edwards)                     | 3                    |
| <i>Tanakaius</i> Reinert,<br>Harbach & Kitching    |                             | <i>savoryi</i> (Bohart)                    | 2                    |
|  |                             | <i>togoi</i> (Theobald)*                   | 1*,2,4               |
| <i>Tewarius</i> Reinert                            |                             | <i>agastyai</i> (Tewari & Hiriyan)*        | 4                    |
|  |                             | <i>reubenae</i> (Tewari & Hiriyan)         | 4                    |
| <i>Udaya</i> Thurman                               |                             | <i>argyrurus</i> (Edwards)*                | 4                    |
|  |                             | <i>lucaris</i> Macdonald & Mattingly       | 4                    |
| <i>Vansomerenis</i> Reinert,<br>Harbach & Kitching |                             | <i>luteostriata</i> (Robinson)             | 3                    |
|  |                             | <i>pulchrithorax</i> (Edwards)*            | 3                    |
| <i>Verrallina</i> Theobald                         | <i>Harbachius</i> Reinert   | <i>nobukonis</i> (Yamada)                  | 2                    |
|  |                             | <i>yusafi</i> (Barraud)*                   | 4                    |
|  | <i>Neomacleaya</i> Theobald | <i>indica</i> (Theobald)*                  | 4                    |
|  |                             | <i>pseudomediofasciata</i> (Theobald)      | 4                    |
|  | <i>Verrallina</i>           | <i>butleri</i> (Theobald)*                 | 4,5                  |
|  |                             | <i>carmenti</i> (Edwards)                  | 5                    |
| <i>Zavortinkius</i> Reinert                        |                             | <i>fulgens</i> (Edwards)                   | 3                    |
|  |                             | <i>longipalpis</i> (Grünberg)*             | 3                    |
| <i>Zeugnomyia</i> Leicester                        |                             | <i>gracilis</i> Leicester*                 | 4                    |
|  |                             | <i>lawtoni</i> Baisas                      | 4                    |
| <b>Non-aedine outgroup taxa</b>                    |                             |  |                      |
| <i>Culex</i> Linnaeus                              | <i>Culex</i>                | <i>quinquefasciatus</i> Say                | 1*,2*,3,4*,<br>5*,6* |
| <i>Culiseta</i> Felt                               | <i>Culiseta</i>             | <i>inornata</i> (Williston)                | 1                    |
| <i>Mansonia</i> Blanchard                          | <i>Mansonia</i>             | <i>titillans</i> (Walker)*                 | 1,6                  |
| <i>Orthopodomyia</i> Theobald                      |                             | <i>signifera</i> (Coquillett)              | 1,6                  |

with 400× magnification is needed to observe the very slender distal parts of many setae of larvae and pupae for the measurement of total length. Pinned adults were examined with a binocular stereomicroscope utilizing cold white light delivered by a fiber-optic illumination system. An adjustable examination stage with biaxial rotation capability (see fig. 125.3 in Russell *et al.*, 1963) allowed observation and illumination of specimens at any angle.

In general, we examined three to six specimens (range 1–20) of each life stage and structure for each species. However, we had to code some characters from literature sources for those taxa where specimens of certain life stage were unavailable (i.e. characteristics of most eggs and some fourth-instar larvae and pupae). Examples of species not available in the larval stage are ‘*Ae. (Adm.) apicoannulatus*, *Hs. (Mat.) catesi*, *Oc. andersoni*, *Oc. (Phl.) flavifrons*, *Oc. (Chs.) fulvus fulvus* and *Oc. nivalis*, and the pupal stage are ‘*Ae. (Adm.) apicoannulatus*, ‘*Ae. (Adm.) argenteopunctatus*, *Db. alboannulatus* and *Oc. (Chs.) fulvus fulvus*. Missing data are denoted by a ‘?’ in the data set (Appendix 1). States of continuous characters

were determined either by clear gaps in the observed counts or measurements (e.g. character 36), or by reference to observed intraspecific variation (e.g. character 50). Characters that could not be scored due to absence of homologous structures (‘dependent characters’) are indicated by a dash ‘–’, e.g. conditions of setae 6-S and 9-S on the larval siphon of *Mansonia*, which lacks these setae. All multistate characters were initially treated as unordered. However, it may be argued that continuous measurement characters, such as lengths or ratios derived from lengths, should be treated as ordered sequences (Thiele, 1993). Hence we also undertook analyses with the 14 such length ratio characters (13, 14, 17, 20, 62, 67, 72, 84, 107, 138, 161, 273, 280 and 318; see below) treated as ordered. Polymorphic characters are explicitly coded as exhibiting only those states observed. A few characters used in our previous studies (Reinert *et al.*, 2004, 2006, 2008) were re-evaluated and modified, and a number of new characters were added to complete the present data set.

Specimens from the following collections were examined during the study: National Museum of Natural

History, Smithsonian Institution, Washington, District of Columbia, USA; The Natural History Museum, London, UK; Bohart Museum, University of California, Davis, California, USA; Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario, Canada; Department of Zoology and Entomology, University of Queensland, Brisbane, Australia; Australian National Insect Collection, CSIRO Division of Entomology, Canberra, Australia; Laboratoire/Cellule Entomologie, EID Méditerranée, Montpellier, France; Connecticut Agricultural Experiment Station, New Haven, Connecticut, USA; Florida State Collection of Arthropods, Division of Plant Industry, Gainesville, Florida, USA; Florida Medical Entomology Laboratory, University of Florida, Vero Beach, Florida, USA; National Institute of Malariology, Parasitology and Entomology, Hanoi, Vietnam; Center for Research in Medical Entomology, Madurai, Tamil Nadu, India; Vector Control Research Center, Indira Nagar, Pondicherry, India; Laboratoire de Taxonomie des Vecteurs, Centre IRD de Montpellier, France; and the collection of the first author.

Abbreviations used in the text for generic-level taxa follow Reinert (2001a) and Reinert *et al.* (2006, 2008). New generic-level taxa proposed herein are described in the section following the 'Concluding Comments'. Abbreviations for all genera of Aedini recognized as a result of the present study are listed in the 'Abbreviations of Aedine Genera' section following the 'New Generic-Level Taxa'. All currently valid species of Aedini, with their generic and subgeneric placement, are listed in Appendix 2. Due to the unavailability of specimens for study and inadequate published descriptions, some species could not be assigned to generic-level taxa with certainty and remain in the category of *incertae sedis*.

## CHARACTER DESCRIPTIONS

Adult characters were derived from females unless otherwise noted. Males of many species often have fewer setae and scales than females, and would skew the coding of some character states. Setal branching characters are coded to reflect observed intraspecific variation; hence, some such characters are coded in the form of '(0) single; (1) branched' whereas others are coded in the form of '(0) single or two-branched; (1)  $\geq 3$  branches' (or similar form) to reflect the actual development of the particular seta in each species.

Anatomical nomenclature and chaetotaxy follow Harbach & Knight (1980, 1982) except for terms proposed by Reinert (1990, 1999c, 2000c, 2002a, 2008a). Many structures of characters used in the present study are illustrated in these publications. However, references to character states illustrated

in other publications are provided in the explanations of the characters listed below.

## EGGS

Reinert (2005) noted that the egg stage has been described and/or illustrated for only approximately 16% of the species of Aedini, and provided a list of those species with their literature citations. The egg characters are coded as missing, in part or in total, for approximately half of the taxa included in this study. Eggs of various species are illustrated in numerous articles, e.g. Howard, Dyar & Knab (1913), Horsfall & Craig (1956), Craig & Horsfall (1960), Ross & Horsfall (1965), Forattini (1965, 1996), Myers (1967), Kalpage & Brust (1968), Mattingly (1970, 1971, 1974), Horsfall, Voorhees & Cupp (1970), Horsfall & Voorhees (1972), Reinert (1972a, c), Matsuo, Yoshida & Kunou (1972), Moriya, Yabe & Harada (1972, 1973), Matsuo, Lien & Yoshida (1974a), Matsuo, Yoshida & Lien (1974b), Hinton (1981), Linley (1989), Linley & Chadee (1990, 1991), Chadee & Bennett (1990), Linley, Geary & Russell (1991a, b, c, 1992), Linley & Craig (1993, 1994), Service, Duzak & Linley (1997) and Alencar *et al.* (2003, 2005, 2008).

1. *Oviposition, eggs laid*: (0) singly; (1) in a raft; (2) in a mass. Egg deposition is unknown for numerous aedine species and are coded (?). Many of the species for which the egg-laying habits are known deposit their eggs singly. Macdonald (1960) reviewed the unusual egg-laying habits of species of *Ar.* (*Leicestertia*) and indicated that perhaps most females attach and hold their egg-masses between both hindlegs, the eggs lying at an angle formed by each tibia and first tarsomere. The egg-mass is later deposited on the water surface in a plant cavity. Other species of the subgenus deposit their eggs in ribbons (state 2) directly on the water surface. In general, *Ar.* (*Leicestertia*) eggs hatch about two days after being laid, which is somewhat similar to the egg rafts of most species of *Culex*. The eggs of subgenus *Armigeres* and other aedine genera, e.g. *Aedes*, *Ochlerotatus*, *Psorophora* and *Stegomyia*, are laid singly, can withstand a period of dryness and will not hatch until they have been immersed in water.

2. *Anterior end, shape*: (0) tapered; (1) flattened to slightly rounded; (2) elongate and narrow. Aedine taxa have eggs with state (0) (see Linley, 1990: figs 1 and 4, '*Ae.* (*Adm.*) *vexans* and *Oc.* (*Och.*) *infirmatus*). See Howard *et al.* (1913: fig. 669, *Or. signifera*) for example of state (1) and Linley, Linley & Lounibos (1986: fig. 1, *Ma. titillans*) for state (2).

3. *Width at midlength*: (0) somewhat expanded; (1) greatly expanded, more or less diamond-shaped in

lateral outline. Most known aedine eggs exhibit state (0) (see examples in Ross & Horsfall, 1965: fig. 188, *St. aegypti*; fig. 189, '*Oc. (Pro.) triseriatus*'; fig. 204, *Oc. dorsalis*). Examples of eggs with the midlength greatly expanded often appear more or less diamond-shaped in lateral outline (see Marshall, 1938: fig. 57h; Service *et al.*, 1997: figs 13 and 14a, *Oc. (Rus.) rusticus*; Horsfall *et al.*, 1970: figs 32A and 33A, *Ps. (Pso.) ciliata* and *Ps. (Pso.) howardii*; Linley *et al.*, 1991: fig. 12, *Mu. (Muc.) alternans*).

4. *Outer chorion, cell pattern*: (0) absent or weakly developed; (1) well developed; (2) with spiny appearance, cells with elongate anteriorly inclined tubercle. See the literature cited in the introduction to EGGS and for characters 2 and 3.

#### LARVAE (FOURTH-INSTARS)

5. *Labiogula, length*: (0) < width; (1)  $\geq$  width. Labiogular width is measured from the outer margins of the posterior tentorial pits. Length of the labiogula is measured from the caudolateral angle of the dorsomentum to the posterior margin of the collar. See Belkin (1962: figs 243, 303 and 314, *Fl. franclemonti* (Belkin), *Lo. dasyorrhus* and *St. aegypti*) for examples of state (0) and his figures 234, 277 and 298 (*Pm. argyronotum*, *Mu. (Muc.) alternans* and '*Ae. (Adm.) alboscuteallatus*') for state (1).

6. *Antenna, ratio of length to median length of dorsal apotome (DAP)*: (0)  $\leq$  0.40; (1)  $\geq$  0.42. This character is determined by dividing the antennal shaft length by the DAP median length (larval exuviae preferred to whole larvae). Antennae vary from short (see Tanaka, Mizusawa & Saugstad, 1979: figs 99 and 101, *Ta. togoi* and *Ta. savoryi*) to long (see Tanaka *et al.*, 1979: figs 102 and 104, *Hk. (Yam.) seoulensis* and *Br. alektorovi* (= *kobayashii* Nakata); Hopkins, 1952: fig. 62, *Va. pulchrithorax*).

7. *Antenna, spicules*: (0) absent; (1) present. Some aedine species have antennae without spicules, e.g. *Abraedes* (see Zavortink, 1972: fig. 34, *Ab. papago*), *Aztecaedes*, *Finlaya*, *Gymnometopa*, *Halaedes*, *Kompia* and *Stegomyia*. Other species have few, normally small and scattered spicules, e.g. *Downsiomyia*, *Haemagogus*, *Howardina*, *Kenknightia* (see Reinert, 1990: fig. 24, *Ke. dissimilis*) and *Zavortinkius* whereas many species have numerous, normally well-developed spicules covering all or most of the antenna, e.g. *Aedes* (see Tanaka *et al.*, 1979: fig. 134, *Ae. yamadai* Sasa, Kano & Takahasi), *Mucidus*, *Psorophora*, *Tanakaius* and *Oc. (Rusticooidus)*.

8. *Seta 1-A, ratio of length to antennal width at point of attachment*: (0)  $\leq$  3.0; (1)  $\geq$  3.1. Seta 1-A is nor-

mally moderately long to long ( $\geq$  3.1 times width of antenna) in most Aedini, e.g. '*Oc. (Protomacleaya)*' (see figures in Zavortink, 1972) and *Zavortinkius*, but this seta is short ( $\leq$  3.0 times width of antenna) in some taxa, e.g. *Armigeres* (see Steffan, 1968: figs 2, 4, 6, 8, 10 and 12, *Ar. (Armigeres)* species), *Opifex* and most *Stegomyia* (see Belkin, 1962: figs 208 and 314, *Op. (Opi.) fuscus* and *St. aegypti*).

9. *Seta 1-A, development*: (0) single or 2-branched; (1)  $\geq$  3 branches. Many species of Aedini have seta 1-A single (see Belkin, 1962: figs 231 and 357, *Ra. albilabris* and *Ar. (Arm.) breinli*) whereas others are multiple-branched (see Belkin, 1962: figs 267 and 282, *Oc. (Buv.) edgari* and *Ed. imprimens*). However, this seta is single or two-branched in some species, and it is also two-branched in some specimens of a few species in which seta 1-A is multiple-branched, which are scored (0,1).

10. *Setae 2,3-A, insertion on antenna*: (0) apical or nearly apical; (1) noticeably subapical. Setae 2- and 3-A are inserted apically on nearly apically on the antennae of most Aedini. However, they are noticeably subapical in *Oc. (Rhinokusea)* (see Reinert, 1976c: figs 12–14) and the outgroup species *Ma. titillans* (see Belkin *et al.*, 1970: fig. 50, *Ma. titillans*).

11. *Seta 1-C, development*: (0) spiniform; (1) single, thinner, distal part attenuate; (2) forked or branched, proximal part stout. Spiniforms are single setae, thickened throughout with a bluntly pointed or rounded apex (see Zavortink, 1972: fig. 56, *Hg. (Con.) leucotaeniatus*). Single setae are relatively slender, normally long and the distal part is attenuated. Species of *Ps. (Psorophora)* have seta 1-C spiniform, but very short (scored 0). Setae exhibiting state (1) are single, normally moderately to very thick proximally but attenuate distally (see Belkin, 1962: fig. 218, *Oc. (Geo.) longiforceps*; Hopkins, 1952: fig. 62, *Va. pulchrithorax*). Species of *Aedes*, *Verrallina* and *Za. longipalpis* have seta 1-C long, somewhat stouter than usual and the apices are blunt or bluntly pointed; these are scored here as (1). Those species exhibiting state (2) have seta 1-C thickened proximally and have two or more branches distally. Seta 1-C is branched in species of *Finlaya* and *Hw. walkeri* (see Berlin, 1969: fig. 18). This seta has up to six branches in some species of *Finlaya* (see Marks, 1947), and Bohart (1957) noted that it is 2–6 branched in *St. pandani*.

12. *Seta 4-C, insertion relative to seta 6-C*: (0) anterior; (1) at same level; (2) posterior. Seta 4-C is inserted mesal to seta 6-C and in state (1) it is at the same level as seta 6-C in a perpendicular line to the

longitudinal axis (midline) whereas in state (0) it is anterior to seta 6-C and in state (2) it is posterior to seta 6-C. The positions of setae 4–7-C are determined on head capsules, normally exuviae, that are horizontal with the thorax and abdomen. If the head is in a prognathous orientation and turned down anteriorly, these and other setae may appear to be positioned differently. This also applies to characters 16 and 19. See Belkin (1962) for illustrations of state (0) (figs 218 and 277, *Oc. (Geo.) longiforceps* and *Mu. (Muc.) alternans*) and state (2) (fig. 211, *Ha. australis*).

13. *Seta 4-C, ratio of length to median length of DAp:* (0)  $\leq 0.19$ ; (1) 0.21–0.38; (2) 0.40–0.81; (3)  $\geq 0.90$ . The lengths of setae 4–7-C are compared to the median length of the DAp, preferably in fourth-instar larval exuviae.

14. *Seta 5-C, ratio of length to median length of DAp:* (0)  $\leq 0.19$ ; (1) 0.21–0.38; (2) 0.41–0.81; (3)  $\geq 0.90$ . See the information under character 13.

15. *Seta 5-C, development:* (0) single; (1) branched. Larval seta 5-C is single in many aedine taxa, e.g. *Abraedes*, *Aztecaedes*, *Finlaya*, *Howardina*, *Kenknighthia* (most species) (see Reinert, 1990: figs 26 and 29, *Ke. harbachi* and *Ke. luzonensis* (Rozeboom)) and *Zavortinkius*. This seta is branched in other aedine taxa, e.g. *Aedes*, *Downsiomyia*, *Hulecoeteomyia* (see Knight, 1968: figs 3 and 7, *Hl. chrysolineata* and *Hl. sherki*), *Ochlerotatus* (subgenera *Geoskusea* and *Levua*) and *Tanakaius*.

16. *Seta 6-C, insertion relative to seta 7-C:* (0) anterior; (1) at same level or posterior. See illustrations in Tanaka *et al.* (1979: figs 99 and 123, *Ta. togoi* and *St. chemulpoensis*) for state (0) and their figures 128 and 131 (*Oc. (Geo.) baisasi* and *Ae. esoensis*) for state (1). Insertion of seta 6-C is normally anterior or posterior to the insertion of seta 7-C. In some taxa with setae 6-C inserted posterior to seta 7-C, it may be inserted at the same level as seta 7-C in a few specimens and is coded (1). See the information under character 12.

17. *Seta 6-C, ratio of length to median length of DAp:* (0)  $\leq 0.19$ ; (1) 0.21–0.38; (2) 0.41–0.81; (3)  $\geq 0.90$ . See the information under character 13.

18. *Seta 6-C, development:* (0) single; (1) branched. See Wood *et al.* (1979: pl. 47, *Oc. (Cul.) sollicitans* (Walker)) for an example of state (0) and their pl. 19 (*Ae. cinereus*) for state (1). *Leptosomatomyia aurimargo* has seta 6-C moderately long, stout, with long, slender aciculae in a patch on the proximal area and is coded (0).

19. *Seta 7-C, insertion relative to seta 5-C:* (0) anterior; (1) at approximately same level; (2) posterior. Tanaka *et al.* (1979) provided illustrations of state (0) (figs 104 and 126, *Br. alektorovi* and ‘*Ae. (Adm.) vexans nipponii* (Theobald)), state (1) (figs 116 and 122, *St. galloisi* (Yamada) and *St. wadai*) and state (2) (figs 96 and 99, *Hl. koreica* (Edwards) and *Ta. togoi*). See the information under character 12.

20. *Seta 7-C, ratio of length to median length of DAp:* (0)  $\leq 0.19$ ; (1) 0.21–0.38; (2) 0.41–0.81. See the information under character 13.

21. *Seta 7-C, development:* (0) single (rarely 2-branched); (1)  $\geq 3$  branches. See Reinert (1999c: figs 14 and 15, *Za. longipalpis* and *Za. geoffroyi* (Reinert)) for examples of state (0) and Zavortink (1972: figs 9 and 53, ‘*Oc. (Pro.) triseriatus* and *Ge. (Hor.) fluviatilis*) for examples of state (1).

22. *Seta 12-C, insertion relative to seta 13-C:* (0) mesal to or directly posterior; (1) lateral. Seta 13-C is longer and normally borne lateral to seta 12-C in Culicidae. For this reason, the longer seta in a mesal position relative to the other in some species of Aedini is interpreted as seta 13-C (see figure 277 of *Mu. (Muc.) alternans* in Belkin, 1962, labelled as 12-C). Some taxa have seta 12-C inserted in a line parallel to the longitudinal axis and posterior to seta 13-C (scored 0).

23. *Seta 13-C, development:* (0) single; (1) branched. Seta 13-C is normally single in many of the species of Aedini, e.g. *Ha. australis* and *Ra. albilabris* (see Belkin, 1962: figs 211 and 231). However, it is branched in a number of other taxa, e.g. *Aedes*, *Kenknighthia*, *Mucidus*, *Oc. (Geoskusea)* (see Belkin, 1962: figs 216 and 218), *Ochlerotatus* (subgenera *Levua* and *Rhinuskusea*), *Psorophora* and *Zavortinkius*. See the information under character 22.

24. *Seta 14-C, development:* (0) single; (1) branched. Seta 14-C is often single (see Tanaka *et al.*, 1979: figs 92 and 101, *Oc. intrudens* and *Ta. savoryi*) and may be slender or stiff and stout. The seta is branched (see Tanaka *et al.*, 1979: figs 102 and 119, *Hk. (Yam.) seoulensis* and *St. flavopicta* (Yamada)) and may be slender or stellate in some species.

25. *Seta 19-C:* (0) absent; (1) present. The occurrence of setae 18-C and 19-C ventrally on the cervical membrane of larvae belonging to 29 genera, 72 subgenera and 331 species of Culicidae was reported by Hochman & Reinert (1974). These authors also illustrated setae 18- and 19-C and discussed the

taxonomic importance and possible phylogenetic significance of seta 19-C.

26. *Ventromedian cervical sclerite*: (0) absent; (1) present. A small solid or fragmented sclerite is present on the ventromedian area of the cervix in many aedine larvae. It appears to be absent in some taxa, e.g. *Co. (Col.) macfarlanei*, *Ko. purpureipes*, *Mc. (Mac.) tremula*, *Mc. (Cha.) wattensis*, *Oc. (Lev.) geoskusea*, *Oc. (Rhinoskusea)*, *Psorophora*, *Zavortinkius* and the four non-aedine outgroup species. Reinert (1976a) provided a review and illustrations of this sclerite in Culicidae.

27. *Setae 1–3-P, insertion*: (0) not on common support plate; (1) two or three of these setae on common support plate. All or occasionally only two of setae 1–3-P are attached to a common setal support plate in several taxa, e.g. *Abraedes*, *Alanstonea*, *Ar. (Armigeres)*, *Ayurakitia*, *Bothaella*, *Gymnometopa*, *Haemagogus*, *Howardina*, *Huaedes*, *Kenknighthia*, *Oc. (Pseudoskusea)*, *Oc. (Rhinoskusea)*, *Scutomyia* and *Zeugomyia*. They are also attached to a common plate in the outgroup species *Cs. inornata* and *Cx. quinquefasciatus*. See Wood, Dang & Ellis (1979: pl. 15, *Oc. campestris*) for an example of state (0) and their plates 14 and 21, *Oc. aurifer* and *Oc. decticus* (Howard, Dyar & Knab), for examples of state (1).

28. *Seta 1-P, length relative to length of seta 2-P*: (0) equal or shorter; (1) longer. Seta 1-P is normally longer than seta 2-P in Aedini (see Belkin, 1962: figs 227 and 277, *Ra. notoscripta* and *Mu. (Muc.) alternans*), but it is shorter than or equal in length to 2-P in some taxa, e.g. *Finlaya* (see Belkin, 1962: figs 237 and 239, *Fl. bougainvillensis* (Marks) and *Fl. burnetti* (Belkin)), *Hw. walkeri*, *Ja. (Lew.) muelleri*, *St. tulagiensis* (Edwards) and *St. robinsoni* (Belkin) (see Belkin, 1962: figs 318 and 320, for the last two species).

29. *Seta 2-P, development*: (0) single; (1) branched. Belkin (1962) provided illustrations of state (0) (fig. 237, *Fl. bougainvillensis*) and state (1) (fig. 298, '*Ae. (Adm.) alboscuteclatus*').

30. *Seta 3-P, length relative to length of seta 2-P*: (0) shorter; (1) equal or longer. Seta 3-P is normally shorter than seta 2-P (see Belkin, 1962: figs 314 and 322, *St. aegypti* and *St. albopicta*), but it is longer in *Christophersiomyia* (see Abercrombie, 1977: figs 8 and 19, *Cr. chionodes* (Belkin) and *Cr. thomsoni*) and the outgroup species *Cs. inornata*.

31. *Seta 4-P, length relative to length of seta 3-P*: (0) equal or shorter; (1) longer. See Belkin (1962) for

examples of taxa with seta 4-P shorter than seta 3-P (figs 218 and 234, *Oc. (Geo.) longiforceps* and *Pm. argyronotum*) and taxa with seta 4-P longer than seta 3-P (figs 274 and 316, *Oc. (Lev.) geoskusea* and *Sc. albolineata*).

32. *Seta 4-P, development*: (0) single; (1) branched. Seta 4-P is single in a number of taxa, e.g. *Oc. excrucians* and *Ta. savoryi* (see Tanaka *et al.*, 1979: figs 82 and 99), whereas in other taxa it is branched (see Tanaka *et al.*, 1979: figs 79 and 102, *Oc. (Emp.) vigilax* and *Hk. (Yam.) seoulensis*).

33. *Seta 5-P, length relative to length of seta 6-P*: (0) equal or shorter; (1) longer. See Belkin (1962) for illustrations of state (0) (fig. 243, *Fl. franclemonti*) and state (1) (fig. 231, *Ra. albilabris*).

34. *Seta 5-P, development*: (0) single; (1) branched. Seta 5-P is single in several taxa, e.g. *Aedes* (see Tanaka *et al.*, 1979: fig. 134, *Ae. yamadai*), *Hg. (Conopostegus)*, *Isoaedes*, *Mucidus* and *Ochlerotatus* (subgenera *Geoskusea*, *Levua* and *Rhinoskusea*). In other taxa, this seta is branched, e.g. *Abraedes* (see Zavortink, 1972: fig. 34, *Ab. papago*), *Aztecaedes*, *Gymnometopa* and *Kompia*.

35. *Seta 7-P, development*: (0) single; (1) branched. Belkin (1962) illustrated state (0) (figs 211 and 277, *Ha. australis* and *Mu. (Muc.) alternans*), and state (1) (figs 267 and 271, *Oc. (Buv.) edgari* and *Oc. (Gil.) mcdonaldii*).

36. *Seta 8-P, ratio of length to length of seta 4-P*: (0)  $\leq 1.2$ ; (1)  $\geq 1.8$ . Seta 8-P is less than or equal to 1.2 times the length of seta 4-P in most taxa examined (see Tanaka *et al.*, 1979: fig. 99, *Ta. togoi*). It is more than or equal to 1.8 times the length of seta 4-P in *Aedes*, *Dn. alboteniata*, *Gc. (Hor.) fluviatilis*, *Oc. (Rusticoidus)*, *Ps. (Jan.) ferox*, *Ps. (Gra.) jamaicensis* (see Belkin *et al.*, 1970: figs 60 and 67) and the outgroup species *Cs. inornata*.

37. *Seta 8-P, development*: (0) single (occasionally 2-branched); (1) multiple-branched (occasionally 3-branched). A few taxa have seta 8-P single or occasionally 2-branched (see Belkin, 1962: figs 211 and 277, *Ha. australis* and *Mu. (Muc.) alternans*). Most taxa have seta 8-P multiple-branched, but it is occasionally only 3-branched (see Belkin, 1962: figs 239 and 316, *Fl. burnetti* and *Sc. albolineata*).

38. *Seta 13-P*: (0) absent; (1) present. Seta 13-P is present in a few species of Aedini, e.g. *Bothaella* (see Reinert, 1973c: figs 13 and 14, *Bo. helenae* and *Bo. eldridgei*), *Howardina* (Ioliota Group of Walkeri

Section, see Berlin, 1969), *St. hoguei* (Belkin), *St. robinsoni*, *St. tulagiensis* and *St. upolensis* (Marks) (see Belkin, 1962: figs 318, 320, 334 and 352). Harbach & Kitching (1998) noted the sporadic presence of seta 13-P in *Aedes* (*sensu auctorum* prior to Reinert *et al.*, 2004) and *Psorophora*.

39. *Seta 1-M, ratio of length to length of seta 2-M*: (0)  $\leq 2.5$ ; (1)  $\geq 3.5$ . See Tanaka *et al.* (1979: figs 99 and 111, *Ta. togoi* and '*Oc. (Fin.) oreophilus*) for examples of state (0) and their figure 104, *Br. alektorovi*, for state (1).

40. *Seta 1-M, development*: (0) single (rarely 2-branched); (1)  $\geq 3$  branches. Examples of state (0) in species of *Mu. (Mucidus)* are illustrated in Tyson (1970). Examples of state (1) in species of '*Oc. (Protomacleaya)*' are illustrated in Zavortink (1972).

41. *Seta 4-M, development*: (0) single; (1) branched. Many generic-level taxa of Aedini have seta 4-M branched (see Schick, 1970: figs 16 and 22, '*Oc. (Pro.) terrens* and '*Oc. (Pro.) berlini* (Schick)). Zavortink (1972) illustrated examples of state (0) (figs 32, 34, 37 and 40, *Ko. purpureipes*, *Ab. papago*, *Az. ramirezi* and *Gy. mediovitata*).

42. *Seta 7-M, length relative to length of seta 5-M*: (0) shorter; (1) equal or longer. Seta 7-M is normally shorter than seta 5-M (see Tanaka *et al.*, 1979: fig. 98, *Co. (Col.) hatorii* (Yamata)) in most Aedini; however, it is longer than seta 5-M in other taxa, e.g. *Eretmapodites*, *Ha. australis*, *Hi. gilli*, *Kompia*, *Macleaya*, *Oc. (Geoskusea)*, *Ps. (Jan.) ferox*, *Skusea*, *Tanakaius* (see Tanaka *et al.*, 1979: fig. 99, *Ta. togoi*) and the outgroup species *Cx. quinquefasciatus*.

43. *Seta 1-T, development*: (0) slender to slightly thickened; (1) very stout. Most species of Aedini have seta 1-T slender to slightly thickened (see Belkin, 1962: fig. 211, *Ha. australis*). Seta 1-T is distinctly stout in a few species, e.g. *Co. (Col.) hatorii* (see Tanaka *et al.*, 1979: fig. 98) and *Co. (Col.) elsiae* (see Barraud, 1934: fig. 39c).

44. *Seta 1-T, insertion*: (0) on integument; (1) on tubercle or plate. Tanaka *et al.* (1979) illustrated examples of state (0) (fig. 99, *Ta. togoi*) and state (1) (fig. 98, *Co. (Col.) hatorii*).

45. *Seta 2-T, development*: (0) single; (1) branched. See illustrations in Zavortink (1972: fig. 44, *Ja. (Lew.) muelleri*) for an example of a single seta 2-T and Belkin (1962: fig. 211, *Ha. australis*) for an example of a branched 2-T.

46. *Seta 4-T, development*: (0) single; (1)  $\geq 2$  branches, not stellate; (2)  $\geq 3$  branches, stellate. Stellate setae have three to numerous, moderately stout to stout, stiff branches that are truncate or bluntly pointed (not attenuate) and radiate in different directions from or near the base (starburst-shaped) (see Belkin, 1962: fig. 237, *Fl. bougainvillensis*). Branches of stellate setae often are of different lengths. In some species, e.g. *Az. ramirezi* and '*Oc. (Pro.) zoosophus*', this and some other setae approach the stellate condition except the branches are somewhat narrower and tend to be in one plane (fan-shaped). These are scored (1).

47. *Seta 6-T, development*: (0) single; (1) branched. Many taxa of Aedini have seta 6-T single (see Arnell & Nielsen, 1972: figs 9 and 13, *Ja. (Jar.) varipalpus* and *Ja. (Jar.) sierrensis*), whereas some taxa have seta 6-T branched (see Reinert, 1999c: fig. 14, *Za. longipalpis*).

48. *Seta 3-I, development*: (0) single; (1) branched. See Tanaka *et al.* (1979) for examples of state (0) (figs 114 and 116, *St. riversi* and *St. galloisi*) and state (1) (figs 131 and 134, *Ae. esoensis* and *Ae. yamadai*). Some specimens of a few species show an overlap of the two states and are scored (0,1).

49. *Seta 7-I, ratio of length to length of seta 6-I*: (0)  $< 0.45$ ; (1)  $\geq 0.55$ . Seta 7-I is relatively short in some species (see Belkin, 1962: fig. 208, *Op. (Opi.) fuscus*) but it is moderately long to long in other species, e.g. *Oc. (Geo.) longiforceps* and *Oc. (Lev.) geoskusea* (= *suvae* Stone & Bohart) (see Belkin, 1962: figs 218 and 274). Seta 7-I is longer than 6-I (state 1) in *Sc. platylepida* (Knight & Hull) (see Reinert & Ramalingam, 1983: fig. 2).

50. *Seta 7-I, development*: (0) single to 3-branched; (1)  $\geq 4$  branches. Seta 7-I is single or occasionally has two or three branches in most Aedini (see Belkin, 1962: fig. 227, *Ra. notoscripta*). However, it is thinner and has more than three branches in other taxa, e.g. *Mucidus* (see Belkin, 1962: fig. 277, *Mu. (Muc.) alternans*) and *Sk. pambaensis*. This seta has overlapping states in '*Oc. (Fin.) keefei*', *Op. (Opi.) fuscus* and *Ps. (Pso.) howardii*, and is scored (0,1).

51. *Seta 12-I*: (0) absent; (1) present. Seta 12-I is absent in a number of taxa, e.g. *Abraedes*, *Aedes*, *Armigeres*, *Ayurakitia*, *Aztecaedes*, *Bothaella*, *Christophersomyia*, *Eretmapodites*, *Gymnometopa*, *Heizmannia*, *Howardina*, *Isoaedes*, *Kompia*, *Scutomyia*, *Stegomyia*, *Udaya*, *Verrallina* and *Zeugnomyia*. Reinert (2000b) discussed the occurrence of seta 12-I in generic-level taxa previously included in *Aedes* and

*Ochlerotatus*. Seta 12-I is present in many other taxa (see Tanaka *et al.*, 1979: fig. 86, *Oc. communis*), e.g. *Bruceharrisonius*, *Collessius*, *Downsiomyia*, *Finlaya*, *Hulecoeteomyia*, *Kenknightsia*, *Molpemyia*, *Mucidus*, *Opifex*, *Ochlerotatus* (most species), *Patmarksia*, *Phagomyia*, *Psorophora*, *Rampamyia* and *Zavortinkius* (see Reinert, 1999c: fig. 14, *Za. longipalpis*). In the case of Section I of *Ochlerotatus*, Reinert (2000b) noted six exceptions, i.e. *Ja. laguna* (Arnell & Nielsen), *Ja. monticola* (Belkin & McDonald), *Ja. muelleri*, *Ja. varipalpus*, *Mc. (Cha.) tulliae* (Taylor) and *Oc. impiger daisetsuzanus* (Tanaka, Mizusawa & Saugstad). Arnell (1973) and Harbach & Kitching (1998) noted that seta 12-I was normally present in *Haemagogus*, but absent in a few species.

52. *Seta 1-II, development*: (0) single; (1)  $\geq 2$  branches, not stellate; (2)  $\geq 3$  branches, stellate. Belkin (1962) illustrated the three states of seta 1-II, i.e. state (0) (fig. 234, *Pm. argyronotum*), state (1) (fig. 231, *Ra. albilabris*) and state (2) (fig. 237, *Fl. bougainvillensis*).

53. *Seta 2-II, development*: (0) single; (1) branched. The developmental states of seta 2-II are illustrated in Belkin (1962): state (0) (fig. 218, *Oc. (Geo.) longiforceps*) and state (1) (fig. 237, *Fl. bougainvillensis*).

54. *Seta 3-II, development*: (0) single; (1) branched. Zavortink (1972) provided illustrations of state (0) (figs 32 and 34, *Ko. purpureipes* and *Ab. papago*) and state (1) (figs 18 and 28, '*Oc. (Pro.) kompi*' and '*Oc. (Pro.) knabi*').

55. *Seta 5-II, development*: (0) single; (1)  $\geq 2$  branches, not stellate; (2)  $\geq 3$  branches, stellate. Seta 5-II is branched in most Aedini, either stellate (see Belkin, 1962: fig. 237, *Fl. bougainvillensis*) or not stellate (state 1) (see Belkin, 1962: figs 227–229, *Ra. notoscripta*). This seta is single in a few taxa (see Reinert, 1979: fig. 5, *Ia. cavaticus*).

56. *Seta 6-II, length relative to length of seta 6-III*: (0) shorter; (1) equal or longer. See Tanaka *et al.* (1979: figs 102 and 104, *Hk. (Yam.) seoulensis* and *Br. alectorovi*) for state (0) and their figures 98 and 99, *Co. (Col.) hatorii* and *Ta. togoi*, for state (1).

57. *Seta 6-II, development*: (0) single; (1) branched. Seta 6-II is normally branched (see Belkin, 1962: figs 211 and 251, *Ha. australis* and *Fl. hollingsheadi*) in Aedini, but it is single in some taxa, e.g. *Alanstonea* (see Ramalingam & Ramakrishnan, 1971: fig. 2, *As. brevitibia*), *Ar. (Arm.) breinli*, *Eretmapodites*, *Molpemyia*, *Mucidus*, *Oc. (Levua)* and *Ve. (Harbachius)*.

58. *Seta 7-II, development compared to seta 7-I*: (0) similar; (1) different. Seta 7-II is often slightly shorter than seta 7-I. See Belkin (1962: fig. 208, *Op. (Opi.) fuscus*) for an example of state (0) and his figure 218 (*Oc. (Geo.) longiforceps*) for state (1). Seta 7-II is short, slender and 2-branched in *Gc. (Hor.) fluviatilis* and differs from seta 7-I, which is long, stout, aciculate and single (see fig. 53 in Zavortink, 1972), and is scored (1).

59. *Seta 8-II, development*: (0) single; (1) branched. See Zavortink (1972) for examples of state (0) (figs 32, 34 and 40, *Ko. purpureipes*, *Ab. papago* and *Gy. mediiovittata*), and his figures 4, 7 and 9 ('*Oc. (Pro.) hendersoni*' (Cockerell), '*Oc. (Pro.) brelandi*' and '*Oc. (Pro.) triseriatus*') for examples of state (1).

60. *Seta 6-III, development*: (0) single; (1) branched. Seta 6-III is single in some taxa, e.g. *Aedes*, *Bruceharrisonius*, *Isoaedes*, *Mo. pecuniosa*, *Mu. (Mucidus)* (see Tyson, 1970: fig. 17, *Mu. laniger*), *Ochlerotatus* (several species), '*Oc. (Fin.) candidoscutellum*', '*Oc. (Fin.) rubrithorax*' (Macquart), *Oc. (Geo.) longiforceps*, and the outgroup species *Ma. titillans* and *Or. signifera*. This seta is branched (see Tanaka *et al.*, 1979: figs 79 and 80, *Oc. (Emp.) vigilax* and *Oc. dorsalis*) in many taxa examined.

61. *Seta 3-V, ratio of length to length of setae 5-V*: (0)  $\leq 1.55$ ; (1)  $\geq 1.80$ . Seta 3-V is at least two times longer (often much longer) than seta 5-V in species of Section I of '*Ochlerotatus*' (as defined and illustrated by Reinert, 2000b) whereas it is shorter to 1.5 times the length of seta 5-V in species of Section II.

62. *Seta 1-VII, ratio of length to middorsal length of segment X*: (0)  $\leq 0.42$ ; (1) 0.48–0.85; (2)  $\geq 0.94$ . The middorsal length of segment X is measured along a straight line parallel to the longitudinal axis from the posterior margin of the saddle (minus marginal spicules) anteriorly to the first annulation in the membrane cephalad of the saddle. Fourth-instar larvae, not exuviae, should be used for measurements of segment X. Examples of the three character states are illustrated in Belkin (1962): for state (0) see fig. 271, *Oc. (Gli.) mcdonaldi*, for state (1) see fig. 265, *Oc. antipodeus* Edwards and for state (2) see fig. 332, *St. hebridea* (Edwards)).

63. *Seta 2-VII, insertion on tergum VII*: (0) on posterior 0.45 near seta 1-VII; (1) on anterior 0.40 far anterior to seta 1-VII. Seta 2-VII is inserted near seta 1-VII in most species examined (see Tanaka *et al.*, 1979: figs 95 and 102, *Hl. japonica* and *Hk. (Yam.) seoulensis*). See Berlin (1969: figs 18 and 44, *Hw.*



*walkeri* and *Hw. sexlineata*; Belkin, 1962: figs 237 and 251, *Fl. bougainvillensis*, *Fl. hollingsheadi*) for examples of state (1).

64. *Seta 2-VII, development*: (0) single; (1) branched. Seta 2-VII is single in many Aedini, e.g. *Bruceharri-sonius*, *Georgecraigius*, *Jarnellius*, *Kenknightia*, *Mucidus*, *Ochlerotatus* (subgenera *Geoskusea*, *Levua* and *Rhinoskusea*) (see Belkin, 1962: figs 218 and 274, *Oc. (Geo.) longiforceps* and *Oc. (Lev.) geoskusea*) and *Tanakaius*. This seta has two or more branches in other taxa, e.g. *Ayurakitia*, *Bothaella*, *Downsiomyia*, *Finlaya* (see Belkin, 1962: figs 237, 239 and 241, *Fl. bougainvillensis*, *Fl. burnetti* and *Fl. fijiensis* (Marks)), *Gymnometopa*, *Haemagogus*, *Howardina*, *Kompia*, *Scutomyia*, *St. futunae*, *St. robinsoni* and *St. tulagiensis*.

65. *Seta 3-VII, insertion relative to seta 1-VII*: (0) anterior; (1) at same level or posterior. Seta 3-VII is inserted anterior to seta 1-VII (see Belkin, 1962: figs 218 and 243, *Oc. (Geo.) longiforceps* and *Fl. franclemonti*) in most Aedini, e.g. *Downsiomyia*, *Edwardsaedes*, *Finlaya*, *Rampamyia* and *Stegomyia*. This seta is inserted at the same level or posterior to seta 1-VII in some taxa, e.g. *Ha. australis* (see Belkin, 1962: fig. 211), *Kenknightia*, *Opifex*, *Tanakaius* and *Oc. (Levua)*. See the information under character 12.

66. *Seta 3-VII, development*: (0) single; (1) branched. See Zavortink (1972: figs 32, 34, 37 and 40, *Ko. purpureipes*, *Ab. papago*, *Az. ramirezi* and *Gy. mediovittata*) for examples of state (0) and Reinert (1990: figs 24–32, *Kenknightia*) for examples of state (1).

67. *Seta 3-VII, ratio of length to middorsal length of segment X*: (0)  $\leq 0.42$ ; (1) 0.48–0.85; (2)  $\geq 0.94$ . See character 62 for the method used to measure the length of this seta. Tanaka *et al.* (1979) provided illustrations of state (0) (fig. 110, *Do. nishikawai* (Tanaka, Mizusawa & Saugstad)), state (1) (fig. 116, *St. galloisi*) and state (2) (fig. 96, *Hl. koreica* (Edwards)).

68. *Seta 10-VII, development*: (0) single; (1) branched. Seta 10-VII is single in many aedine taxa, e.g. *Abraedes*, *Downsiomyia*, *Georgecraigius*, *Gymnometopa*, *Haemagogus* (see figures in Arnell, 1973), *Kompia*, *Mu. (Mucidus)*, *Scutomyia*, *Stegomyia* and *Tanakaius*. This seta is branched in other taxa, e.g. *Aedes*, *Finlaya*, *Opifex* and *Halaedes* (see Belkin, 1962: figs 208 and 211, *Op. (Opi.) fuscus* and *Ha. australis*).

69. *Seta 12-VII, insertion relative to seta 13-VII*: (0) anterior; (1) at approximately same level; (2) poste-

rior. Most aedine taxa have seta 12-VII posterior to seta 13-VII (see Reinert, 1976c: figs 12 and 13, *Oc. (Rhi.) longirostris* and *Oc. (Rhi.) wardi*). This seta is inserted anterior to seta 13-VII (state 0) in a few taxa, e.g. *Hg. (Haemagogus)* (see figures in Arnell, 1973), *Howardina* (most species), *Kompia*, *Scutomyia* and *St. africana*, and at approximately the same level as seta 13-VII (state 1) in a few other taxa, e.g. *Abraedes*, *Gymnometopa* and *Hg. (Conopostegus)* (see figures in Zavortink, 1972). See the information under character 12.

70. *Seta 12-VII, development*: (0) single; (1) branched. Seta 12-VII is single in many Aedini, e.g. *Downsiomyia*, *Finlaya*, *Georgecraigius*, *Howardina* (see figures in Berlin, 1969), *Kompia* and nearly all *Stegomyia*. It is branched in other taxa, e.g. *Aedes*, *Oc. (Levua)*, *Opifex* and *Zavortinkius* (see Reinert, 1999c: fig. 14, *Za. longipalpis*).

71. *Setae 1,2-VIII, insertion*: (0) not on common setal support plate; (1) on common setal support plate. Setae 1,2-VIII are not attached to a common setal support plate (see Tanaka *et al.* 1979: figs 99 and 114, *Ta. togoi* and *St. riversi*) in most aedine taxa. They are inserted on a common setal support plate in some taxa, e.g. '*Ae. (Adm.) alboscuteclatus*', '*Ae. (Adm.) vexans vexans*', *Edwardsaedes*, *Mucidus* (see Belkin, 1962: figs 277 and 279, *Mu. (Muc.) alternans* and *Mu. (Pdo.) painei* (Knight)), *Ne. lineatopenne*, *Ne. palpale*, *Ochlerotatus* (some species) and *Ve. (Nma.) indica*. Setae 1,2-VIII in *St. desmotes* are usually both attached to the posterior margin of the comb plate, however this is not homologous to species with these two setae attached to a small setal support plate and is coded (0).

72. *Seta 1-VIII, ratio of length to length of seta 2-VIII*: (0)  $\leq 0.38$ ; (1) 0.50–0.95; (2)  $\geq 1.10$ . See Belkin (1962) for examples of state (0) (fig. 211, *Ha. australis*), state (1) (fig. 234, *Pm. argyronotum*) and state (2) (fig. 231, *Ra. albilabris*).

73. *Seta 1-VIII, development*: (0) single; (1) branched. Seta 1-VIII is normally branched in Aedini, e.g. *Oc. dorsalis* (see Tanaka *et al.*, 1979: fig. 98) and '*Oc. (Pro.) terreus*' (see Schick, 1970: fig. 16). It is single in a few taxa, e.g. *Co. (Col.) hatorii* (see Tanaka *et al.*, 1979: fig. 98) and *Oc. spilotus* (see Dobrotworsky, 1965: fig. 47).

74. *Seta 2-VIII, development*: (0) single; (1) branched. Seta 2-VIII is single and moderately long to long in many Aedini, e.g. *Hulecoeteomyia* (see Tanaka *et al.* 1979: fig. 95, *Hl. japonica japonica* (Theobald)), *Mu. (Mucidus)* and nearly all *Stegomyia*, but it is 2- or

3-branched in other taxa, e.g. *Aedes*, *Bruceharrisonius*, *Mu. (Pardomyia)*, *Opifex* (see Belkin, 1962: fig. 208, *Op. (Opi.) fuscus*), *Psorophora* and *Zavortinkius*. Also see the information under character 77.

75. *Seta 2-VIII, insertion*: (0) nearer to seta 1-VIII than to seta 3-VIII; (1) nearer to seta 3-VIII than to seta 1-VIII; (2) insertion approximately midway between setae 1- and 3-VIII. See Reinert (1974: fig. 54, *Ve. (Nma.) indica*) for an example of state (0), Berlin (1969: fig. 11, *Hw. fulvithorax*) for state (1) and Bohart (1957: figs 6a and 6c, *St. pandani* and *St. neopandani* (Bohart)) for state (2).

76. *Seta 3-VIII, development*: (0) simple; (1) aciculate. Tanaka *et al.* (1979) illustrated state (0) (fig. 125, '*Ae. (Adm.) alboscuteclatus*') and state (1) (fig. 99, *Ta. togoi*). A number of published illustrations of seta 3-VIII omit the aciculae or overemphasize its presence. This character here is based on observations of specimens with a phase contract microscope at 400x magnification. Many species of *Stegomyia* have the branches of seta 3-VIII with very few short, inconspicuous aciculae.

77. *Seta 4-VIII, development*: (0) single; (1) branched. Seta 4-VIII, like seta 2-VIII, is single in most Aedini. This seta is branched in many of the species that have seta 2-VIII also branched (see Belkin *et al.*, 1970: figs 56, 60 and 67, *Ps. (Pso.) ciliata*, *Ps. (Jan.) ferox* and *Ps. (Gra.) jamaicensis*). It is branched (state 1) in *Armigeres*, *Bruceharrisonius*, *Edwardsaedes*, *Eretmapodites*, *Halaedes*, *Oc. (Chs.) fulvus pallens*, *Oc. (Pcx.) atlanticus*, *Opifex*, *Psorophora* (most species) and the outgroup species *Ma. titillans*. Seta 4-VIII is both single and two-branched in a few species. Also see the information under character 74.

78. *Comb, scales*: (0) few to several in one or two irregular rows; (1) numerous in a patch. See examples in Belkin (1962: fig. 316, *Sc. albolineata*) for state (0) and his figure 243 (*Fl. franclemonti*) for state (1).

79. *Comb plate*: (0) absent; (1) present. A comb plate is normally present in *Psorophora* (see Belkin *et al.*, 1970: fig. 67, *Ps. (Gra.) jamaicensis*) and usually absent in most other Aedini. It is also present in some *Stegomyia* (e.g. *St. annandalei*, *St. craggi*, *St. desmotes*, *St. edwardsi*, *St. gurneyi* (Stone & Bohart), *St. maehleri* (Bohart), *St. malikuli* (Huang), *St. mediopunctata* and *St. perplexa*), *Sc. arboricola* (most specimens), *Do. dorseyi* (Knight), *Hg. (Hag.) capricornii* Lutz, *Hg. (Hag.) janthinomys* Dyar, *Mc. (Cha.) elchoensis* (Taylor) and *Mc. (Mac.) tremula*.

80. *Siphon, acus*: (0) absent; (1) present. An attached or detached acus located at the base of the siphon (in line with the pecten) is found in many aedine taxa, e.g. *Aedes*, *Bruceharrisonius*, *Downsiomyia*, *Edwardsaedes*, *Finlaya*, *Georgecraigius*, *Hulecoeteomyia*, *Jarnellius*, *Kompia* and *Ochlerotatus* (see Arnell, 1976: figs 31 and 37, *Oc. (Och.) infirmatus* and *Oc. (Och.) scapularis*). This structure is absent in other taxa, e.g. *Abraedes*, *Gymnometopa*, *Halaedes*, *Molpemyia* (see Reinert, 1993: fig. 8, *Mo. pecuniosa*), *Stegomyia* and *Zavortinkius*.

81. *Pecten*: (0) absent; (1) present. Pecten spines are absent from larvae of *Armigeres* and the outgroup species *Ma. titillans* and *Or. signifera*. Pecten spines are reduced in number and may be absent on one side (rarely both sides) of the siphon in species of *Eretmapodites* (see illustrations in Hopkins, 1952; Service, 1990). However, the larval stage is unknown for many species of this genus. Most aedine taxa have a pecten.

82. *Pecten spines, arrangement*: (0) evenly spaced; (1) distal one or more widely spaced. Pecten spines are evenly spaced in most aedine taxa (see Belkin, 1962: figs 227–229, *Ra. notoscripta*). Reinert (1979) noted that the distal one or more pecten spines are more widely spaced in some Aedini, e.g. *Aedes* (see Tanaka *et al.*, 1979: figs 131 and 132, *Ae. esoensis*), '*Ae. (Aedimorphus)*' (most species) (see illustrations in Hopkins, 1952), *Edwardsaedes*, *Isoaedes*, *Mucidus* (many species), *Neomelaniconion*, *Ochlerotatus* (numerous species), *Psorophora* (some species) and *Verrallina*. This condition also occurs in '*Ae. (Can.) masculinus*', *Huaedes*, *Paraedes*, the Dendrophilus Group of *Stegomyia* and some specimens of *St. aegypti*. Species without a pecten are coded (–). See the information under character 81.

83. *Seta 1-S, number*: (0) 1; (1)  $\geq 2$ . State (0) (see Tanaka *et al.*, 1979: fig. 101, *Ta. savoryi*) is the usual condition in Aedini. *Aedes* (see Tanaka *et al.*, 1979: fig. 131, *Ae. esoensis*) and *Oc. (Rusticooidus)* exhibit state (1). Accessory setae are typical of genus *Culex*, whereas seta 1-S at the base of the siphon is characteristic of many species of *Culiseta* Felt.

84. *Seta 1a-S, ratio of length to width of siphon*: (0)  $\leq 0.40$ ; (1) 0.43–1.12; (2) 1.15–1.99; (3)  $\geq 2.17$ . The length of seta 1a-S is compared to the width of the siphon of fourth-instar larvae at the point of insertion. See Belkin *et al.* (1970: fig. 60, *Ps. (Jan.) ferox*) for an example of state (0), (fig. 72: *Oc. (Pcx.) pertinax*) for state (1) and (fig. 56, *Ps. (Pso.) ciliata*) for state (2). See Hopkins (1952: fig. 88, '*Ae. (Adm.) argenteopunctatus*') for an example of state (3).

85. *Seta 1a-S, development*: (0) single; (1) branched. Seta 1a-S is branched in most Aedini (see Belkin *et al.*, 1970: fig. 69, *Oc. (Cul.) taeniorhynchus*) and single in a few taxa, e.g. *Ps. (Pso.) ciliata* (see Belkin *et al.*, 1970: fig. 56) and *Ps. (Pso.) howardii*.
86. *Seta 1a-S, insertion*: (0) within pecten; (1) distal to pecten; (2) basal to pecten. Belkin (1962) illustrated state (0) (fig. 218, *St. tulagiensis*), state (1) (fig. 298, '*Ae. (Adm.) alboscuteclatus*') and state (2) (fig. 185, *Cs. tonnoiri* (Edwards)). See the information under character 81 for taxa without a pecten, which are coded (-).
87. *Seta 6-S, length relative to distal width of siphon*: (0) equal or shorter; (1) noticeably longer. See Belkin (1962) (his fig. 314, *St. aegypti*) for state (0) and (his fig. 243, *Fl. franclemonti*) for state (1). Setae 6-S is absent from the highly modified siphon of *Ma. titillans* (see Belkin *et al.*, 1970: fig. 50), which is coded (-).
88. *Seta 8-S, length relative to distal width of siphon*: (0) shorter; (1) longer. Most taxa of Aedini have seta 8-S short (state 0). See illustrations in Belkin (1962: fig. 227, *Ra. notoscripta*) for state (0) and his figure 237 (*Fl. bougainvillensis*) for state (1).
89. *Seta 9-S, development*: (0) slender, nearly straight or slightly curved; (1) stout, hook-like. See Belkin (1962: figs 227 and 231, *Ra. notoscripta* and *Ra. albilabris*) for examples of state (0) and Marks (1949: figs 9 and 12, *Oc. normanensis* (Taylor) and *Oc. pseudonormanensis* (Marks)) for examples of state (1). Seta 9-S is absent from the highly modified siphon of *Ma. titillans*, which is coded (-).
90. *Sclerotization of segment X (saddle)*: (0) incomplete ventrally; (1) completely encircles segment. All species of Aedini have either a small or large dorsal saddle or sclerotization that completely encircles segment X. Many taxa have a saddle that is incomplete ventrally, e.g. *Aztecaedes* (see Zavortink, 1972: fig. 37, *Az. ramirezi*), *Bruceharrisonius*, *Georgecraigius*, *Gymnometopa*, *Haemagogus*, *Jarnellius*, *Mucidus*, *Ochlerotatus* (many species), *Paraedes* and *Zavortinkius*. A saddle that completely encircles segment X occurs in certain other taxa, e.g. *Huaedes*, *Ochlerotatus* (some species groups) (see illustrations in Arnell, 1976, Scapularis Group) and *Psorophora*. Reinert (2002a) provided illustrations of different developmental states of this character in Aedini.
91. *Saddle, acus*: (0) absent; (1) present. Some genera of Aedini do not have a saddle acus, e.g. *Aedes*, *Downsiomyia*, *Finlaya*, *Halaedes*, *Hulecoeteomyia*, *Stegomyia* and *Tanakaius* (see Tanaka *et al.*, 1979: figs 99 and 101, *Ta. togoi* and *Ta. savoryi*). An acus is present in other species, e.g. *Ochlerotatus* (many species) (see Wood *et al.*, 1979: pls 20 and 25, *Oc. communis* and *Oc. excrucians*). The acus is attached to the base of the saddle in most genera, but a small oval sclerite located in a similar position but normally detached from the base of the saddle occurs in some taxa, e.g. *Rampamyia*. *Orthopodomys signifera* has a narrow, basal, sclerotized band that is separated from the saddle. Because of its structure and location, it is not considered to be homologous with the acus in Aedini. An acus is present in the outgroup species *Cs. inornata*.
92. *Saddle, moderate to well-developed spicules on posterior margin*: (0) absent; (1) present. See Belkin (1962: fig. 314, *St. aegypti*) for an example of state (0) and his figure 237 (*Fl. bougainvillensis*) for an example of state (1).
93. *Seta 1-X, insertion*: (0) on saddle; (1) not on saddle. See Belkin (1962) for examples of state (0) (fig. 227, *Ra. notoscripta*) and state (1) (fig. 211, *Ha. australis*). Seta 1-X is inserted on the ventral or ventroposterior margin of the saddle in some taxa, e.g. *Ja. (Lew.) muelleri*, *Lorrainea*, *Mc. (Mac.) tremula*, *Oc. (Geo.) baisasi* and *Op. (Opi.) fuscus* (see Belkin, 1962: fig. 208), which are scored (0).
94. *Seta 2-X, ratio of length to length of seta 3-X*: (0)  $\geq 0.90$ ; (1)  $\leq 0.70$  (rarely 0.80). This seta is normally noticeably short in most Aedini, e.g. *Aedes* and *Ochlerotatus* (see Wood *et al.*, 1979: pls 19 and 30, *Ae. cinereus* and *Oc. hexodontus*). It is long in a few taxa, e.g. *Mucidus* (see Tyson, 1970: figs 17 and 20, *Mu. (Muc.) laniger* and *Mu. (Pdo.) aurantius aurantius*).
95. *Seta 2-X, development*: (0) single or 2-branched (rarely 3-branched); (1)  $\geq 5$  branches (rarely 4-branched). See the information under character 94.
96. *Seta 2-X, aciculate*: (0) absent; (1) present. Hopkins (1952) provided illustrations of state (0) (fig. 58, *Oc. caspius*) and state (1) (fig. 132, *Er. chrysogaster*).
97. *Seta 3-X, development*: (0) single; (1) branched. Seta 3-X is normally single in Aedini (see Zavortink, 1972: fig. 9, '*Oc. (Pro.) triseriatus*') but it is branched in some taxa, e.g. *Armigeres*, *Az. ramirezi* (see Zavortink, 1972: fig. 32), *Ed. imprimens*, *Er. quinquevittatus*, *Gy. mediovittata*, *Hw. sexlineata*, *Ko. purpureipes*, *St. futunae*, *Zeugnomyia* and the outgroup species *Cs. inornata* and *Ma. titillans* (see Belkin *et al.*, 1970: fig. 50).

98. *Ventral brush (seta 4-X), attachment*: (0) on integument; (1) on grid with transverse bars; (2) on grid with lateral and transverse bars; (3) on boss. Reinert (2002a) conducted a comparative analysis of the ventral brush and its attachment to segment X in Aedini and illustrated and discussed ancestral and derived forms.

99. *Preocratal/preboss setae (i.e. two or more setae anterior to grid or boss)*: (0) absent; (1) present. Setae of the ventral brush are normally paired but an occasional specimen may possess an odd number of setae. Some species, e.g. *Hg. (Hag.) splendens*, have a single unpaired preboss seta whereas other species have a single unpaired preocratal seta, these are scored (0). *Psorophora* have numerous preocratal setae that are inserted in the ventral margin of the saddle (see Belkin *et al.*, 1970: figs 56, 60 and 67, *Ps. (Pso.) ciliata*, *Ps. (Jan.) ferox* and *Ps. (Gra.) jamaicensis*).

100. *Seta 4a-X of ventral brush, ratio of length to length of seta 4c-X*: (0)  $\leq 0.25$ ; (1)  $\geq 0.70$ . The most caudal (posterior) seta of the ventral brush is designated seta 4a-X, the next cephalad (anterior) seta is 4b-X, and so on (see Belkin, 1962, Knight & Laffoon, 1971, Reinert, 2002a). Seta 4a-X is normally as long or longer than seta 4c-X, rarely moderately long, in Aedini. *Abraedes*, *Aztecaedes*, *Kompia* and *Ja. (Lew.) muelleri* have a short seta 4a-X relative to seta 4c-X (see Zavortink, 1972: figs 32, 34, 37 and 44).

101. *Seta 4d-X of ventral brush, development*: (0) single, plumose; (1) single or 2-branched (rarely 3-branched), not plumose; (2)  $\geq 5$  branches (rarely 4-branched), not plumose. See Huang (1968: fig. 2, *Hu. wauensis*) and Reinert (1993: fig. 8, *Mo. pecuniosa*) for examples of state (0). Belkin (1962) illustrated state (1) (fig. 350, *St. tongae* (Edwards)) and state (2) (fig. 269, *Oc. (Emp.) vigilax*). Also, see the information under character 100.

#### PUPAE

102. *Cephalothorax, clear unpigmented spots*: (0) absent; (1) present. Clear, unpigmented areas of the pupal cephalothorax (scutum and metanotum) are characteristic of *Finlaya* (see Belkin, 1962: figs 238, 244 and 252, *Fl. burnetti*, *Fl. freycinetiae* (Laird) and *Fl. knighti* (Stone & Bohart)). Some species of *Finlaya* also have clear, unpigmented areas on some abdominal terga. Berlin's (1969) illustrations of the pupal metanotum of *Hw. inaequalis* and *Hw. stenei* show an unpigmented lateral spot. Because no specimens of these two species were available for examination, it is uncertain if these spots are similar to those of *Finlaya*. *Alanstonea brevitibia* and *Be. aurotaeniatus*

have similar clear unpigmented spots. A small clear spot dorsal to the trumpet base was observed in the two available specimens of *Lu. fengi*, hence this character is scored (1) for this species.

103. *Trumpet, tracheoid area*: (0) absent; (1) present. The tracheoid area is absent in some taxa, e.g. *Alanstonea*, *Armigeres*, *Fredwardsius*, *Gymnometopa*, *Huaedes*, *Leptosomatomyia*, *Op. (Opifex)*, *Psorophora* (most species), *Skusea*, '*Ae. (Adm.) alboscuteclatus*' and the outgroup species *Cs. inornata* and *Or. signifera*. See the information under character 104.

104. *Trumpet, tracheoid area, development*: (0) weakly developed, at base; (1) well developed, distal to base. The tracheoid area is weakly developed at the base of the trumpet in most generic-level taxa of Aedini (see Belkin, 1962: figs 266, 281 and 321, *Oc. (Buv.) edgari*, *Ed. imprimens* and *St. albopicta*). It is subbasal and well developed in some aedine taxa, e.g. *Finlaya*, *Mucidus* (see Tyson, 1970: fig. 15, *Mu. (Pdo.) quadripunctis* and *Mu. (Pdo.) aurantius aurantius*), *Oc. (Rhinoskusea)* and the non-aedine outgroup species *Cx. quinquefasciatus* and *Ma. titillans* (see Belkin *et al.*, 1970: figs 33 and 51). Species without a tracheoid area are coded (-). See the information under character 103.

105. *Seta 1-CT, development relative to seta 3-CT*: (0) weakly developed, considerably shorter than seta 3-CT; (1) similar in thickness and length; (2) very strongly developed, considerably longer. See illustrations in Belkin (1962) for examples of state (0) (fig. 266, *Oc. (Buv.) edgari*), state (1) (fig. 233, *Pm. argyronotum*) and state (2) (fig. 242, *Fl. franclemonti*).

106. *Seta 5-CT, ratio of length to length of seta 4-CT*: (0)  $\leq 1.2$ ; (1)  $> 1.3$ . Seta 5-CT is shorter than or approximately as long as seta 4-CT in many taxa (see Reinert, 1972b: figs 8 and 9, *Ay. peytoni* and *Ay. griffithi*). This seta is noticeably longer than seta 4-CT in other taxa, e.g. *Kenknighthia* (see Reinert, 1990: figs 15 and 22, *Ke. dissimilis* and *Ke. pecori* (Reinert)) and *Hg. (Conopostegus)* (see Zavortink, 1972: figs 55 and 60, *Hg. (Con.) leucotaeniatus* and *Hg. (Con.) leucocelaenus*).

107. *Seta 7-CT, length relative to length of seta 6-CT*: (0) equal or shorter; (1) 1.2–5.0 times as long; (2)  $\geq 6.0$  times as long. Seta 7-CT is shorter than or as long as seta 6-CT in several taxa, e.g. *Ar. (Armigeres)*, *Bothaella*, *Eretmapodites*, many *Heizmannia*, some *Stegomyia* (see Belkin, 1962: fig. 313, *St. aegypti*) and *Zeugomyia*. For examples of state (1), see Belkin (1962: figs 207 and 210, *Op. (Opi.) fuscus* and *Ha. australis*), and for state (2) see Zavortink (1972: figs

60 and 62, *Hg. (Con.) leucocelaenus* and *Hg. (Con.) clarki* (Galindo, Carpenter & Trapido)).

108. *Seta 11-CT, development*: (0) single; (1) branched. See Belkin (1962) for examples of state (0) (fig. 226, *Ra. notoscripta*) and state (1) (fig. 266, *Oc. (Buv.) edgari*). Some species, e.g. *Bo. eldridgei*, *Bo. helenae*, *Hw. walkeri*, *Ia. cavaticus*, *Mo. pecuniosa*, *Oc. communis* and *Ps. (Gra.) columbiae*, show an overlap between the two alternatives in which seta 11-CT is single in some specimens and 2-branched in others (scored 0,1).

109. *Seta 13-CT*: (0) absent; (1) present. Seta 13-CT is present in a few species of Aedini, e.g. *Ab. papago*, *Be. aurotaeniatus* (see Reinert, 1980: fig. 1; Reinert, 1982: fig. 4), *St. futunae* (Belkin) and *St. rotumae* (Belkin) (see Belkin, 1962: figs 327 and 347). Examination of three paratypes of *Ab. papago* revealed a well-developed, two-branched seta on both sides of one exuvia, an alveolus on both sides of another, and neither seta nor alveolus on the third. Reinert (1980, 2000b) provided a review of seta 13-CT in Culicidae and Aedini.

110. *Seta 3-I, length relative to length of seta 6-I*: (0) shorter; (1) equal or longer. Seta 3-I is shorter than seta 6-I in some taxa, e.g. *Oc. (Och.) scapularis* (see Arnell, 1976: fig. 36). For examples of state (1), see Schick (1970: figs 15 and 31, '*Oc. (Pro.) terreus*' and '*Oc. (Pro.) homoeopus*' (Dyar)).

111. *Seta 3-I, development*: (0) single, rarely split apically; (1) branched. Seta 3-I is often single (rarely with apex split) in numerous taxa, e.g. *Abraedes*, *Aedes*, *Aztecaedes*, *Downsiomyia* (see Tanaka, 2002: fig. 8, *Do. nipponica* (LaCasse & Yamaguti)), *Finlaya* and '*Oc. (Protomacleaya)*'. See Belkin (1962: figs 210 and 217, *Ha. australis* and *Oc. (Geo.) longiforceps*) for examples of state (1).

112. *Seta 6-I, length relative to length of seta 7-I*: (0) equal or shorter; (1) longer. Seta 6-I is longer than seta 7-I in many Aedini (see Belkin, 1962: figs 217 and 270, *Oc. (Geo.) longiforceps* and *Oc. (Gli.) mcdonaldi*). It is shorter than or as long as seta 7-I in others, e.g. *Abraedes*, *Alanstonea*, *Ar. (Armigeres)*, *Aztecaedes*, *Fredwardsius*, *Gymnometopa*, *Haemagogus*, *Halaedes*, *Oc. (Ochlerotatus)* (some species), *Oc. (Rhinoskusea)*, *Opifex*, *Pa. argenteoventralis dunnii*, *Ps. (Psorophora)* (some species) (see Belkin et al., 1970: fig. 57, *Ps. (Pso.) ciliata*), some *Stegomyia*, *Udaya* and *Zeugnomyia*, as well as the outgroup species *Ma. titillans*.

113. *Seta 1-II, development*: (0)  $\leq 3$  branches (rarely 4-branched); (1)  $\geq 5$  branches. Reinert (1970) provided examples of state (0) (figs 11 and 12, *Di. franciscoi*, *Di. iyengari*, *Di. reginae* and *Di. whartoni*) and Belkin (1962) illustrated examples of state (1) (figs 217 and 281, *Oc. (Geo.) longiforceps* and *Ed. imprimens*).

114. *Seta 2-II, insertion relative to seta 1-II*: (0) mesal or directly anterior; (1) lateral. Seta 2-II is normally lateral to seta 1-II in Aedini (see Belkin, 1962: figs 210 and 297, *Ha. australis* and '*Ae. (Adm.) alboscuteellatus*'), however it is mesal to or anterior in line with seta 1-II (state 0) in other taxa, e.g. *Finlaya* and *Mo. pecuniosa* (see Reinert, 1993: fig. 7). See the information under character 12.

115. *Seta 2-II, length relative to length of seta 1-II*: (0) shorter; (1) equal or longer. Seta 2-II is normally shorter than seta 1-II in Aedini, e.g. *Mucidus* (see Tyson, 1970: figs 13–15) and *Psorophora*, however it is as long or longer than seta 1-II in some taxa, e.g. *Oc. (Rhinoskusea)*, *Sc. albolineata* (see Belkin, 1962: fig. 315) and *St. w-albus*.

116. *Seta 3-II, insertion relative to seta 2-II*: (0) mesal or directly posterior; (1) lateral. Examples of state (0) include species of *Aztecaedes* and *Kompia* (see Zavorstink, 1972: figs 31 and 36); examples of state (1) include species of *Abraedes* and *Zavortinkius* (see Zavorstink, 1972: fig. 33, *Ab. papago*; Reinert, 1999c: fig. 11, *Za. longipalpis*). See the information under character 12.

117. *Seta 3-II, development*: (0) single; (1) branched. See Belkin (1962) for examples of state (0) (fig. 230, *Ra. albilabris*) and state (1) (fig. 278, *Mu. (Pdo.) painei*).

118. *Seta 3-II, length relative to length of seta 6-II*: (0) equal or shorter; (1) longer. State (0) occurs in a number of aedine taxa, e.g. *Aedes*, *Ed. imprimens*, *Isoaedes*, *Ochlerotatus* (subgenera *Geoskusea* and *Levua*) and *Verrallina* (see Reinert, 1974: figs 37 and 47, *Ve. (Ver.) butleri* and *Ve. (Har.) yusafi*). Numerous taxa have seta 3-II longer than seta 6-II, e.g. *Abraedes*, *Aztecaedes*, *Gymnometopa*, *Haemagogus* and *Kenknightia* (see Reinert, 1990: figs 15 and 20, *Ke. dissimilis* and *Ke. luzonensis*). See character 119; seta 3-II is normally slender when it is short to moderately long and stout when it is long.

119. *Seta 3-II, thickness relative to seta 1-II*: (0) thinner; (1) as thick or thicker. The thickness of seta 3-II is determined by comparison with seta

1-II. See Belkin (1962) for illustrations of state (0) (fig. 210, *Ha. australis*) and state (1) (fig. 236, *Fl. bougainvillensis*).

120. *Seta 5-II, insertion relative to seta 4-II*: (0) lateral or directly posterior; (1) mesal. Seta 5-II is lateral to seta 4-II in most Aedini (occasionally at same level in some specimens) (see Belkin, 1962: fig. 233, *Pm. argyronotum*), however it is mesal in some taxa (see Belkin, 1962: fig. 207, *Op. (Opi.) fuscus*). This seta is normally lateral to seta 4-II, rarely positioned mesally, in '*Oc. (Pro.) hendersoni*'. See the information under character 12.

121. *Seta 5-II, length relative to length of seta 3-II*: (0) equal or shorter; (1) longer. Seta 5-II is shorter than or as long as seta 3-II in most aedine taxa, e.g. *Ayurakitia*, *Finlaya*, *Haemagogus* (see Arnell, 1973: figs 34 and 39, *Hg. (Hag.) equinus* and *Hg. (Hag.) splendens*) and *Op. (Opi.) fuscus*. Examples of taxa with seta 5-II longer than 3-II include species of *Halaedes* and *Rampamyia* (see Belkin, 1962: figs 226 and 230, *Ra. albilabris* and *Ra. notoscripta*).

122. *Seta 6-II, length relative to length of seta 7-II*: (0) equal or shorter; (1) longer. Seta 6-II is longer than seta 7-II in many Aedini (see Belkin, 1962: fig. 230, *Ra. albilabris*), however it is shorter in some taxa, e.g. *Op. (Opi.) fuscus* (see Belkin, 1962: fig. 207).

123. *Seta 3-III, length relative to length of seta 5-III*: (0) equal or shorter; (1) longer. Seta 3-III is noticeably longer than seta 5-III in most Aedini (see Belkin, 1962: fig. 207, *Op. (Opi.) fuscus*), however seta 3-III is shorter than seta 5-III in some taxa (see Belkin, 1962: fig. 210, *Ha. australis*).

124. *Seta 3-III, development*: (0) single; (1) branched. Seta 3-III is single in most taxa examined (see Belkin, 1962: fig. 230, *Ra. albilabris*). Seta 3-III is branched in several taxa, e.g. *Isoaedes*, *Kenknightia*, *Opifex* and *Oc. (Rhinokusea)* (see Reinert, 1976: figs 9–11).

125. *Seta 6-III, development*: (0) single; (1) branched. In some specimens of some species, e.g. *Co. (Alo.) banksi*, *Ke. harbachi* and '*Oc. (Pro.) galindoi*' (Schick), this seta is usually single but sometimes 2-branched, these are scored (0,1).

126. *Seta 2-V, insertion relative to seta 3-V*: (0) anterior; (1) posterior or directly mesal. Belkin (1962) provided illustrations of state (0) (fig. 236, *Fl. bougainvillensis*) and state (1) (fig. 217, *Oc. (Geo.) longiforceps*).

127. *Seta 5-V, length relative to median length of tergum VI*: (0) shorter; (1) equal or longer. See Belkin (1962) for a comparison of the two character states (fig. 313, *St. aegypti*, state 0; fig. 207, *Op. (Opi.) fuscus*, state 1).

128. *Seta 2-VI, insertion relative to seta 1-VI*: (0) mesal or directly anterior; (1) lateral. See examples in Belkin (1962: fig. 233, *Pm. argyronotum*, state 0; fig. 210, *Ha. australis*, state 1). See the information under character 12.

129. *Seta 3-VI, insertion relative to seta 1-VI*: (0) mesal or directly anterior; (1) lateral. Seta 3-VI is normally lateral to seta 1-VI in Aedini, e.g. *Bruceharrisonius* and *Tanakaius* (see Tanaka, 2002: figs 2 and 6, *Ta. togoi* and *Br. okinawanus* (Bohart)). However, it is positioned in line with or mesal to seta 1-VI (state 0) in other taxa, e.g. *Finlaya*, *Lu. fengi*, *Mc. (Cha.) wattensis*, *Mc. (Mac.) tremula*, *Op. (Opi.) fuscus* (see Belkin, 1962: fig. 207), *Ra. albilabris* and the non-aedine outgroup species *Cs. inornata* and *Cx. quinquefasciatus*. See the information under character 12.

130. *Seta 6-VII, insertion relative to seta 9-VII*: (0) anterior; (1) posterior or directly mesal. Seta 6-VII is inserted posterior (occasionally at the same level) to seta 9-VII in most Aedini, e.g. '*Oc. (Protomacleaya)*' (see illustrations in Schick, 1970 and Zavortink, 1972). It is anterior to seta 9-VII in some taxa, e.g. *Bruceharrisonius*, *Hi. gilli*, *Lu. fengi*, *Psorophora* (most species) (see Belkin *et al.*, 1970: figs 57, 59 and 66, *Ps. (Pso.) ciliata*, *Ps. (Jan.) ferox* and *Ps. (Gra.) jamaicensis*) and *Za. fulgens*. See the information under character 12.

131. *Seta 9-VII, length relative to length of seta 6-VII*: (0) equal or shorter; (1) longer. Seta 9-VII is normally longer than seta 6-VII (state 1) in Aedini, e.g. *Edwardsaedes*, *Georgecraigius*, *Halaedes*, *Oc. (Culicelsa)* (see Belkin *et al.*, 1970: figs 68 and 70, *Oc. taeniorhynchus* and *Oc. sollicitans*) and *Rampamyia*, but it is occasionally shorter than or as long as seta 6-VII, e.g. *Op. (Opi.) fuscus* (see Belkin, 1962: fig. 207). Seta 6-VII does not occur in pupae of *Ma. titillans*, therefore this character could not be scored for this species and is entered as missing (–) in the data matrix.

132. *Seta 9-VIII, insertion relative to posterolateral corner of segment*: (0) on corner; (1) slightly anterior or mesal; (2) noticeably anterior. Seta 9-VIII is inserted on the posterolateral corner of tergum VIII in many aedine taxa (see Schick, 1970: figs 11 and 15, '*Oc. (Pro.) thornstoni*' (Dyar & Knab) and '*Oc. (Pro.) terreus*'). See Berlin (1969: fig. 43, *Hw. sexlineata*)

for state (1). A few taxa have seta 9-VIII inserted noticeably anterior to the posterolateral corner of tergum VIII (state 2) (see Reinert, 1999c: fig. 11, *Za. longipalpis*).

133. *Seta 9-VIII, development*: (0) single or 2-branched; (1)  $\geq 3$  branches. Seta 9-VIII has three or more branches in most Aedini, e.g. *Finlaya* (see Belkin, 1962: figs 236 and 238, *Fl. bougainvillensis* and *Fl. burnetti*), *Fredwardsius*, *Mucidus*, *Rampomyia*, *Scutomyia* and *St. aegypti*, but it is single (occasionally two-branched) in some taxa, e.g. *Aedes*, *Macleaya* (subgenera *Chaetocruuiomyia* and *Macleaya*), *Molpemyia*, *Paraedes* (see Reinert, 1981: figs 17–21) and *Verrallina* (many species).

134. *Paddle, midrib, development*: (0) weak, terminating well before apex of paddle; (1) strong, extending to or near apex of paddle. Many aedine taxa have a well-developed midrib that extends to or near the apex of the paddle, e.g. *Aedes*, *Heizmannia*, *Howardina* (see Berlin, 1969: figs 12 and 17, *Hw. septemstriata* (Dyar & Knab) and *Hw. walkeri*) and *Ochlerotatus* (most species). The midrib, however, is weakly developed to indistinct in some taxa, e.g. *Udaya* and *Zeugomyia* (see Baisas & Feliciano, 1953: fig. 26, *Ze. fajardoii* Baisas & Feliciano and *Ze. aguilarii* Baisas & Feliciano). It is short and often restricted to about the basal 0.60 of the paddle in other taxa (state 0), e.g. *Aztecaedes*, *Jarnellius* (see Arnell & Nielsen, 1972: fig. 8, *Ja. (Jan.) varipalpus* and *Kompia*).

135. *Paddle, fringe of hair-like spicules*: (0) absent; (1) present. Many aedine taxa do not have a fringe of hair-like spicules on the paddle, e.g. *Aedes*, *Edwardsaedes*, *Mucidus*, *Ochlerotatus*, *Scutomyia*, *Stegomyia* (*St. aegypti* and the *Dendrophilus* Group) (see illustrations in Huang, 1997) and *Verrallina*. Reinert (2000b) listed the generic-level taxa of Aedini that have a fringe of hair-like spicules on the paddle. Examples of taxa with state (1) include *Abraedes*, *Armigeres*, *Belkinius*, *Lorrainea* and most *Stegomyia* (except as listed above). See Belkin (1962: figs 302, 327 and 356, *Lo. dasyorrhus*, *St. futunae* and *Ar. (Arm.) breinli*) for examples of state (1).

136. *Paddle, development of apical margin*: (0) rounded or straight (rarely slightly concave); (1) with moderately deep emargination distally; (2) with projection on mesal area at apex of midrib. The apical margin of the paddle is broadly or sharply rounded in most Aedini (see Belkin, 1962: figs 207 and 217, *Op. (Opi.) fuscus* and *Oc. (Geo.) longiforceps*), but it is sometimes flattened or slightly emarginate, e.g.

*Ja. (Jan.) varipalpus* and *Ja. (Jan.) deserticola* (Zavortink) (see Arnell & Nielsen, 1972: figs 8 and 10). The median, apical emargination is deep in some taxa, e.g. *Abraedes*, *Armigeres* (some species) (see Mattingly, 1971b: figs 32a and 32b, *Ar. (Arm.) subalbatus* and *Ar. (Arm.) malayi* (Theobald)) and the outgroup species *Ma. titillans*. Reinert (2000a: fig. 3, *Ay. griffithi*) illustrated state (2) and pointed out the uniqueness of *Ayurakitia* in which the outer part of the paddle is noticeably shorter than the inner part.

137. *Seta 1-Pa*: (0) absent; (1) present. State (1) is the normal condition in Aedini (see Belkin, 1962: figs 226 and 268, *Ra. notoscripta* and *Oc. (Emp.) vigilax*). Seta 1-Pa is absent in *Ma. titillans* (see Belkin *et al.*, 1970: fig. 51).

138. *Seta 1-Pa, ratio of length to length of paddle*: (0)  $\leq 0.33$ ; (1) 0.40–0.60; (2)  $\geq 0.80$ . *Downsiomyia* and *Finlaya* are examples of state (0) (see illustrations of *Finlaya*, as Kochi Group, in Belkin, 1962). *Bruceharrisonius greenii* (see Reinert, 2003: fig. 2E) and *Oc. (Lev.) geoskusea* are examples of state (1). *Tewarius agastyai*, *Te. reubenae* and *Er. quinquevittatus* (see Edwards, 1941: fig. 162) are examples of state (2). Species without seta 1-Pa are coded (-). See the information under character 137.

139. *Seta 1-Pa, development*: (0) single (rarely 2-branched); (1)  $\geq 3$  branches. See Reinert (1990: figs 15–23, *Kenknightia*) for state (0) and Reinert (1976c: figs 9–11, *Oc. (Rhinoskusea)* and Marks (1949: fig. 7, *Oc. theobaldi*) for state (1). Some species show an overlap between the two character states, e.g. *Do. leonis* (2 or 3 branches) and *Ps. (Jan.) ferox* (2 or 3 branches) and are scored (0,1). However, most specimens of these species have three or more branches. Species without seta 1-Pa are coded (-). See the information under character 137.

140. *Seta 2-Pa*: (0) absent; (1) present. Absence of seta 2-Pa (see Arnell, 1973: figs 34 and 40, *Hg. (Hag.) equinus* and *Hg. (Hag.) splendens*) is the usual condition in Aedini, however this seta is present in subgenera *Grabhamia* (except *Ps. (Gra.) infinis* (Dyar & Knab)) and *Psorophora* of *Psorophora* (see Belkin *et al.*, 1970: figs 57 and 64–66), *Ta. savoryi* (rarely absent on one side of a few specimens) (see Tanaka, 2002: fig. 3) and the outgroup species *Cx. (Cux.) quinquefasciatus*. One of six pupal exuviae of *Gc. (Lew.) fluviatilis* examined has two setae on one paddle and two setae and a setal alveolus on the other. This specimen is considered an anomaly.

## ADULTS (FEMALES EXCEPT WHERE OTHERWISE NOTED)

141. *Head, erect scales*: (0) absent; (1) present. Erect scales are absent in *Op. (Opi.) fuscus* (see Belkin, 1968: fig. 18), which has numerous setae instead.

142. *Head, position of erect scales*: (0) restricted to occiput; (1) on occiput and vertex. Harbach & Kitching (1998) defined the boundaries of the dorsal surface of the head for interpreting the extent of erect scales '... when erect scales are arranged in a more-or-less single transverse row or narrow band at the back of the head they are considered to be restricted to the occiput. When they are more numerous and cover more of the dorsal surface of the head, they are regarded as extending to the vertex, i.e. they are not restricted to the occiput'. See Tanaka *et al.* (1979) for examples of state (0) (figs 230 and 248, *St. riversi* and *Ar. (Arm.) subalbatus*) and state (1) (figs 220 and 241, *Ta. togoi* and *Ed. imprimens*). In some aedine species, several semierect, narrow, forked scales (often posterior to the ocular setae) are present on the vertex in addition to the erect scales on the occiput, and these are scored (1). Species without erect scales are coded (-). See the information under character 141.

143. *Head, decumbent scales of vertex*: (0) all broad; (1) all narrow; (2) both broad and narrow. Harbach & Knight (1980) illustrated examples of scales that are narrow and broad. See Tanaka *et al.* (1979) for examples of state (0) (fig. 222, *Hk. (Yam.) seoulensis*) and state (1) (fig. 221, *Ta. savoryi*). In species with both broad and narrow scales on the vertex, the narrow scales are usually on the median area and may be restricted to a double row along the coronal suture (see Tanaka *et al.*, 1979: fig. 228, '*Oc. (Fin.) oreophilus*'). In *Scutomyia*, a patch of narrow scales occurs on the anterior median area.

144. *Head, ocular line width*: (0) narrow; (1) broad. The ocular line is interpreted here as the area anterior to the ocular setae and posterior to the dorsal margin of the eye. For examples of a narrow ocular line see Tanaka *et al.* (1979: figs 220 and 222, *Ta. togoi* and *Hk. (Yam.) seoulensis*); for an example of broad scales see Reinert (1990: fig. 3, *Ke. harbachi*). The ocular line of *Cs. inornata* is moderate in width, and is scored as (0).

145. *Head, ocular scales*: (0) all narrow; (1) all broad; (2) both narrow and broad.

146. *Eyes, immediately above antennal pedicels*: (0) contiguous; (1) narrowly to moderately separated; (2)

broadly to very broadly separated. The distance separating the eyes is determined on the area immediately above the antennal pedicels and is measured in numbers of eye facets (diameter). Species with eyes that touch or are separated by a distance less than or equal to one eye facet are considered contiguous and are scored (0), e.g. *Ph. gubernatoris* and *Ph. lophoven-tralis*; those separated by 2–4 (rarely 5) facets are scored (1), e.g. *Da. geniculata* and *Da. echinus*; and those separated by 6 or more facets are scored (2), e.g. *Op. (Opi.) fuscus*. Scales protruding from the median, anterior area of the vertex or upper part of the interocular space may obscure this area, and in some cases, e.g. *Howardina*, the scales must be removed to determine the distance between the eyes. Gutsevich (1974a, b, 1975a, b) used the diameter of eye facets compared to the distance between the eyes as a means of distinguishing several genera and subgenera, however he used a different criterion than the number of facets used here.

147. *Interocular space, scales*: (0) absent; (1) present. Subgenera *Geoskusea*, *Levua* and *Rhinoskusea* of *Ochlerotatus* have the eyes contiguous for nearly the entire mesal length and the interocular space is reduced to a very small triangle that is apparently without scales. Scales are present in most Aedini. See the information under character 148.

148. *Interocular space, scales*: (0) all narrow; (1) all broad; (2) both narrow and broad. The interocular space is defined here as the area between the compound eyes extending dorsad from the postfrontal suture to a point level with the dorsal margins of the eyes. Most taxa examined have narrow scales on this area. Broad scales occur in a number of taxa, e.g. *Abraedes*, *Downsiomyia*, *Gymnometopa*, *Haemagogus*, *Kenknightia*, *Kompia*, *Stegomyia*, *Zavortinkius* and *Ps. (Jan.) ferox*. *Opifex (Opi.) fuscus* has only a few scattered small, broad scales on this area. Both narrow and broad scales occur in a few species, e.g. *Mc. (Cha.) wattensis*. Species without interocular scales are coded (-). See the information under character 147.

149. *Interocular space, setae*: (0) absent; (1) present. Setae are normally present on this area in Aedini and the outgroup species. They are absent in *Ayurakitia*, *Gymnometopa*, *Kompia* and *Udaya*.

150. *Interocular space, setae*: (0)  $\leq 5$ ; (1)  $\geq 6$ . Many aedine taxa have fewer than five setae on the interocular space, e.g. *Ab. papago* and *Fl. kochi*, whereas other taxa have six or more, often numerous, setae on this area, e.g. *Oc. dorsalis*. Taxa without interocular setae, see character 149, are coded (-).



151. *Antennal pedicel, vestiture on mesal surface*: (0) absent; (1) present. The presence of scales, setae or both is the usual condition in Aedini, but a few species lack vestiture on the mesal surface of the pedicel, e.g. *Vansomerenis*.

152. *Antennal pedicel, mesal surface, vestiture, composition*: (0) few to numerous scattered scales (not overlapping to only slightly overlapping and not silvery) and/or setae; (1) patch of broad, overlapping, silvery scales. State (0) occurs in most Aedini and the outgroup species. State (1) occurs in several taxa, e.g. *Abraedes*, *Albuginosus*, *Aztecaedes*, *Bothaella*, *Gymnometopa*, *Kompia*, *Rampamyia*, *Scutomyia*, *Stegomyia* and *Zeugomyia*. In taxa that exhibit state (0), the mesal surface of the pedicel has few to numerous, small to large, scattered to slightly overlapping, pale (white, cream-coloured, golden brown, etc.) or dark scales and/or setae (see Tanaka *et al.*, 1979: fig. 222, *Hk. (Yam.) seoulensis*), whereas taxa that exhibit state (1) have a moderately large to large patch of tightly overlapping, silvery scales (see Tanaka *et al.*, 1979: fig. 234, *St. aegypti*). Species without vestiture on the mesal surface of the pedicel, see character 151, are coded (-).

153. *Antennal pedicel, lateral surface, scales*: (0) absent; (1) present. The outer surface of the antennal pedicel is bare (see Tanaka *et al.*, 1979: fig. 228, '*Oc. (Fin.) oreophilus*') in most Aedini. Scales are present on this area in some taxa, e.g. *Alanstonea*, *Fredwardsius* and *Stegomyia* (see Huang, 1977b: fig. 2, *Fr. vittatus* and *St. aegypti*), *Oc. (Rusticoidus)*, *Ochlerotatus* (some species) (see Tanaka *et al.*, 1979: fig. 212, *Oc. dorsalis*) and the outgroup species *Ma. titillans*. *Armigeres (Arm.) subalbatus* has a patch of broad scales on the mesal surface that extend onto the dorsal and ventral surfaces but not onto the lateral surface.

154. *Apical two flagellomeres, length compared to length of other flagellomeres* (males): (0) disproportionately longer; (1) about same length. Antennae with the two distal flagellomeres approximately equal in length and much longer than the proximal flagellomeres is the usual condition in Aedini (see Tanaka *et al.*, 1979: figs 222 and 223, *Hk. (Yam.) seoulensis* and *Br. alektorovi*). The two apical flagellomeres are approximately the same length as the other flagellomeres in both subgenera of *Opifex* (see Belkin, 1968: figs 2 and 19, *Op. (Opi.) fuscus* and *Op. (Not.) chathamicus*).

155. *Antenna, flagellar whorls, development* (males): (0) few short setae, dispersed more or less around flagellomeres; (1) several moderately long to long

setae, directed more or less dorsally and ventrally and several laterally; (2) numerous long setae, normally directed dorsally and ventrally. Antennal whorls comprised of numerous long setae normally directed dorsally and ventrally is the usual condition in Aedini (see Reinert, 1973a: figs 1, 2 and 5, '*Ae. (Adm.) alboscuteclatus*', '*Ae. (Adm.) caecus*' and '*Ae. (Adm.) mediolineatus*'). Also see Mattingly (1970a: fig. 1) for examples of state (1) (*Hz. (Hez.) scintillans*) and state (2) (*Hz. (Mat.) achaetae*). *Opifex* is notable in having only a few short setae on each flagellomere (state 0) (see Belkin, 1968: figs 2 and 19, *Op. (Opi.) fuscus* and *Op. (Not.) chathamicus*). *Belkinius*, *Bothaella*, *Hz. (Heizmannia)*, *Indusius*, *Leptosomatomyia*, *Oc. (Geo.) longiforceps*, *Ochlerotatus* (subgenera *Levua* and *Rhinokusea*) (see Reinert, 1976c: fig. 2, *Oc. (Rhi.) longirostris*), *Paraedes*, *Verrallina* and *Zeugomyia* have several setae that are moderately long to long and normally directed dorsally and ventrally (state 1).

156. *Maxillary palpus, pale scales*: (0) absent; (1) present. See Tanaka *et al.* (1979) for examples of state (0) (figs 222 and 226, *Hk. (Yam.) seoulensis* and *Do. nipponica*) and state (1) (fig. 234, *St. aegypti*).

157. *Maxillary palpomeres, development* (males): (0) 5, palpomeres 2 and 3 fused/ankylosed; (1) 4, palpomere 5 absent or vestigial; (2) 3, palpomere 4 absent or vestigial; (3) 2, palpomere 3 absent or vestigial. Taxa exhibiting state (0) (see Tanaka *et al.*, 1979: figs 234 and 248, *St. aegypti* and *Ar. (Arm.) subalbatus*) have the integument with a paler, somewhat distinct ring where palpomeres 2 and 3 are fused/ankylosed whereas no such area is apparent in taxa that exhibit state (1). An example of state (1) is *Ed. imprimens* (see Reinert, 1976b: fig. 6), state (2) is *Ae. esoensis* (see Tanaka *et al.*, 1979: fig. 242) and state (3) is *Ze. gracilis*. There is no way of knowing whether palpomere 2 of males with short palpi actually consists of palpomeres 2 and 3 that are completely and unrecognizably fused.

158. *Maxillary palpomeres, position of palpomeres 4 and/or 5 relative to palpomere 3* (males): (0) down-turned; (1) up-turned; (2) nearly straight. State (0) normally includes both palpomeres 4 and 5 (see Tanaka *et al.*, 1979: fig. 213, *Oc. excrucians*), but in a few taxa only palpomere 5 is down-turned. Up-turned palpomeres 4 and 5 occur in some taxa, e.g. *Gymnometopa*, *Psorophora*, *Stegomyia* (see Tanaka *et al.*, 1979: fig. 234, *St. aegypti*) and the non-aedine outgroup species *Cx. quinquefasciatus*. Palpomeres 4 and 5 are nearly straight with palpomere 3 in some other taxa, e.g. *Bruceharrisonius*, *Isoaedes*, *Oc. (Geoskusea)* (see Tanaka *et al.*, 1979:

fig. 239, *Oc. (Geo.) baisasi*) and *Scutomyia*. Species without palpomeres 4 and 5, e.g. *Aedes*, are coded (-).

159. *Maxillary palpus, palpomere 3, ratio of length to length of proboscis* (males): (0)  $\leq 0.14$ ; (1)  $\geq 0.21$ . State (0) occurs in some taxa, e.g. *Aedes* and *Ochlerotatus* (subgenera *Levua* and *Rhinoskusea*) (see Reinert, 1976c: fig. 2, *Oc. (Rhi.) longirostris*). Palpomere 3 is long in many Aedini, e.g. *Aztecaedes*, *Kompia* and *Ochlerotatus* (see Tanaka *et al.*, 1979: figs 212 and 213, *Oc. dorsalis* and *Oc. excrucians*). Species without palpomere 3, see character 157, are coded (-).

160. *Maxillary palpus, palpomere 5, ratio of length to length of palpomere 4* (males): (0)  $\leq 0.55$ ; (1)  $\geq 0.66$ . Palpomere 5 is long in most species of Aedini (see Reinert, 1973a: figs 11 and 13, 'Ae. (Adm.) punctifemoris' and 'Ae. (Adm.) taeniorhynchoides'; Mattingly, 1971b: fig. 12b, *Ar. (Arm.) subalbatus*). Palpomere 5 is short in a few taxa, e.g. *Ia. cavaticus* (see Reinert, 1979: fig. 1), *Mc. (Mac.) tremula* and the non-aedine outgroup species *Or. signifera*. Species without palpomeres 4 and/or 5 are scored (-). See the information under character 157.

161. *Maxillary palpus, ratio of length to length of proboscis* (males): (0)  $\leq 0.27$ ; (1) 0.48–0.80; (2)  $\geq 0.84$ . Short maxillary palpi are found in males of several aedine taxa, e.g. *Aedes*, 'Ae. (Cancraedes)', *Belkinus*, *Bothaella*, *Christophersiomyia*, *Heizmannia*, *Huaedes*, *Leptosomatomyia*, *Oc. (Rhinoskusea)* (see Reinert, 1976c: fig. 2, *Oc. (Rhi.) longirostris*), *Op. (Nothoskusea)*, *Paraedes*, *Verrallina* and *Zeugnomyia*. The maxillary palpi are moderately long in some species, e.g. *Scutomyia albolineata* (see Huang, 1979: fig. 6) and long, often as long as or longer than the proboscis, in others (see Tanaka *et al.*, 1979: figs 212, 213 and 222, *Oc. dorsalis*, *Oc. excrucians* and *Hk. (Yam.) seoulensis*).

162. *Maxillary palpus, setae on palpomeres 3 (distally) and 4* (males): (0) absent or few, short to moderately long; (1) moderate to numerous, long. Numerous long setae are present on the ventral surface of palpomere 4 and distally on the ventral surface of palpomere 3 in a number of aedine taxa, e.g. *Mucidus* (see Tyson, 1970: fig. 6, *Mu. (Pdo.) quasiferinus*), *Ochlerotatus* and 'Ae. (Aedimorphus)' (see Tanaka *et al.*, 1979: figs 213, 215, 237 and 238, *Oc. excrucians*, *Oc. sticticus*, 'Ae. (Adm.) alboscute-latus' and 'Ae. (Adm.) vexans vexans'), whereas some taxa possess moderate numbers of long setae on these palpomeres, all are scored (1). Setae are absent or only a few short to moderately long ones

are present in other taxa, see Tanaka *et al.*, 1979: figs 234, 239 and 243, *St. aegypti*, *Oc. (Geo.) baisasi* and *Ae. yamadai*; Edwards, 1941: fig. 68, *Er. quinquevittatus*. Taxa without palpomere 5 and/or palpomere 4 and/or 3, e.g. *Aedes*, *Opifex* and *Oc. (Rhinoskusea)*, are coded (-). See the information under character 157.

163. *Proboscis, length relative to length of forefemur*: (0) shorter; (1) equal or longer. The proboscis is longer than, or occasionally equal to, the length of the forefemur in most aedine taxa, e.g. *Bruceharrisonius*, *Downsiomyia*, *Haemagogus* (see Arnell, 1973: fig. 38, *Hg. (Hag.) splendens*) and *Ochlerotatus* (most species), but it is shorter than the forefemur in a few taxa, e.g. *Fl. kochi*, *Mu. (Pdo.) quadripunctis* and *Za. longipalpis*.

164. *Proboscis, pale scales*: (0) absent; (1) present. The proboscis may be entirely dark-scaled (see Tanaka *et al.*, 1979: figs 226 and 232, *Do. nipponica* and *St. albopicta*) or have pale scales intermixed or forming patches or a band (see Tanaka *et al.*, 1979: figs 212 and 238, *Oc. dorsalis* and 'Ae. (Adm.) vexans nipponii').

165. *Proboscis, pale-scaled band near midlength*: (0) absent; (1) present. Most aedine taxa do not have a pale-scaled band near the middle of the proboscis, e.g. *Ae. esoensis* (see Tanaka *et al.*, 1979: fig. 242), *Db. rubrithorax* (see Russell, 1996: 81), *Oc. (Geo.) baisasi*, *Hg. (Hag.) equinus* and *St. aegypti*. Other taxa have a white-scaled, complete band, e.g. *Fl. kochi* (see Russell, 1996: 61), *Ra. notoscripta*, *Oc. (Cul.) mitchellae* and *Oc. (Cul.) taeniorhynchus* (see Carpenter & LaCasse, 1955: pl. 86). *Ochlerotatus (Chs.) fulvus* and subspecies *pallens* have the proboscis golden-scaled except for the dark-scaled distal area and are scored (1).

166. *Antepnота*: (0) approximated; (1) widely separated. The antepnота are widely separated in most Aedini (see Tanaka *et al.*, 1979: fig. 212, *Oc. dorsalis*) but nearly touch one another dorsally in certain taxa, e.g. *Hg. (Hag.) equinus*, *Hg. (Hag.) splendens* and *Hs. (Hez.) lii* Wu (see Tanaka *et al.*, 1979: fig. 211). The antepnота are not touching in *Hs. (Mattinglyia)* but are noticeably closer together and are coded (0).

167. *Antepnотal scales*: (0) absent; (1) present. Most species of Aedini have scales on the antepnотum (see Tanaka *et al.*, 1979: fig. 218, *Hl. koreica*), but a few taxa do not, e.g. *Ochlerotatus* subgenera *Geoskusea* and *Rhinoskusea* (see Reinert, 1976c: fig. 2, *Oc. (Rhi.) longirostris*).

168. *Anteprenotal scales*: (0) all narrow; (1) all broad; (2) both narrow and broad. See Tanaka *et al.* (1979) for examples of state (0) (fig. 216, *Oc. punctor*), state (1) (fig. 210, *Hz. (Hez.) kana* Tanaka, Mizusawa & Saugstad) and state (2) (fig. 216, *Oc. intrudens*).

169. *Anterior acrostichal setae*: (0) absent; (1) present. Anterior acrostichal setae are defined as those on the acrostichal area cephalad of the scutal angle; those caudad of this point are the posterior acrostichal setae. See Arnell (1976) for examples of state (0) (fig. 35, *Oc. (Och.) scapularis*) and state (1) (fig. 42, *Oc. obturbator* (Dyar & Knab)). Setae on the anterior promontory (the broad, median area of the mesonotum at the anterior end of the acrostichal area that projects more or less cephalad over the cervix) should not be confused with setae on the anterior end of the acrostichal area. Arnell (1973: 8) reported the presence of minute dorsocentral and acrostichal setae (visible only in slide preparations) in *Haemagogus*. These setae were not seen in pinned specimens of *Hg. equinus* and *Hg. splendens*, which are scored as (0).

170. *Posterior acrostichal setae*: (0) absent; (1) present. See Arnell (1976) for an example of state (0) (fig. 42, *Oc. obturbator*) and Zavortink (1972) for an example of state (1) (fig. 42, *Ja. (Lew.) muelleri*). Also see the information under character 169.

171. *Anterior dorsocentral setae*: (0) absent; (1) present. The dorsocentral area is defined as the longitudinal area on either side of the acrostichal area extending caudally from the antedorsocentral area (see Reinert, 1999c) to the prescutellar area. Setae on the area cephalad of the juncture of the prescutal suture are referred to as 'anterior dorsocentral setae' and those caudad as 'posterior dorsocentral setae'. See Arnell (1976) for an example of state (0) (fig. 35, *Oc. (Och.) scapularis*) and Zavortink (1972) for an example of state (1) (fig. 42, *Ja. (Lew.) muelleri*). Also see the information under character 169.

172. *Posterior dorsocentral setae*: (0) absent; (1) present. See Mattingly (1970c) for an example of state (0) (fig. 11, *Hz. (Hez.) complex*) and Zavortink (1972) for an example of state (1) (fig. 42, *Ja. (Lew.) muelleri*). Also see the information under character 171.

173. *Scutal scales*: (0) all narrow; (1) all broad; (2) both narrow and broad. The scutum (including the anterior promontory and antedorsocentral areas) of most aedine taxa is covered with narrow scales. Broad scutal scaling occurs in some Aedini, e.g. *Hg. (Hag) splendens* (see Arnell, 1973: fig. 38). Taxa with broad scales on the anterior promontory (e.g. *Ud. argyrurus* and *Ud. lucaris*) and/or supraalar area

(anterior to the base of the wing), and narrow scales elsewhere on the scutum, are scored as state (2).

174. *Scutum, erect twisted scales*: (0) absent; (1) present. Most taxa of Aedini do not have erect twisted scales. Erect twisted scales are present on the scutum and other structures, e.g. anteprenotum and scutellum, in species of *Mu. (Mucidus)* (see Tyson, 1970: fig. 2, *Mu. laniger*).

175. *Scutal scales, colour*: (0) all dark; (1) both pale and dark; (2) all pale. The scutum of many aedine taxa has both pale and dark scales (see Arnell, 1976: fig. 35, *Oc. (Och.) scapularis*). *Udaya argyrurus* and *Ud. lucaris* have a few broad, white scales on the anterior promontory and the anterior margin of the antedorsocentral areas whereas the rest of the scutum has narrow, dark scales (scored 1). *Ochlerotatus (Geo.) baisasi* and *Oc. (Geo.) longiforceps* have a few narrow, white scales on the anterior promontory and antedorsocentral areas that contrast with the narrow, dark scales on the remainder of the scutum (scored 1). Also, see the information under character 173. *Ochlerotatus caspius* has a contrasting pattern of golden and white scales and is scored (2). A stripe or variable arrangement or random mixture of pale and dark scales on the anterior part of the acrostichal and dorsocentral areas (state 1) is found in some aedine taxa, e.g. *Oc. (Gil.) aculeatus*, *Oc. cantans* and *Oc. (Buv.) edgari*.

176. *Combined anterior acrostichal and anterior dorsocentral areas, large patch of pale scales covering anterior  $\geq 0.7$* : (0) absent; (1) present. Females exhibiting state (1) have the pale-scaled patch completely covering the entire or at least the anterior 0.7 of the combined anterior acrostichal and anterior dorsocentral areas and often all or much of the scutal fossal area. This pale-scaled patch contrasts with darker scales elsewhere on the scutum (see Barraud, 1923: figs 13 and 17–19, *Ph. deccana* (Barraud), *Ph. cacharana* (Barraud), *Ph. lophoventralis* and *Ph. cogilli* (Edwards)). Species with only pale scales covering the entire scutum (see character 175) are coded (0) since they do not form a distinct contrasting patch on the combined anterior acrostichal and anterior dorsocentral areas.

177. *Anterior acrostichal area, pale-scaled stripe*: (0) absent; (1) present. When present, the pale-scaled stripe normally consists of narrow scales, but these are broad in some species, e.g. *Mo. pecuniosa* (see Reinert, 1993: fig. 3), *Za. fulgens* and *Za. longipalpis* (see Reinert, 1999c: fig. 1). The pale-scaled stripe is normally narrow as in '*Oc. (Fin.) oreophilus*' but may be moderate in width and slightly separated by the

acrostichal setae as in *Ta. togoi* (see Tanaka *et al.*, 1979: figs 228 and 220, respectively). In *St. aegypti*, a narrow white-scaled stripe occurs on either side of the scutum on the outer edge of the acrostichal area at the interface with the dorsocentral area (see Tanaka *et al.*, 1979: fig. 234). Belkin *et al.* (1970) referred to this stripe as the 'outer acrostichal line'. It is included here as an acrostichal stripe. Female paratypes of '*Oc. (Fin.) candidoscutellum*' have the acrostichal, dorsocentral, scutal fossal, prescutellar and supraalar areas with indistinct, narrow stripes of whitish scales on a background of golden-brown scales; hence, a pale-scaled stripe is scored as present in this species. Also see the information under characters 169 and 175.

178. *Posterior acrostichal area, pale-scaled stripe*: (0) absent; (1) present. See Tanaka *et al.* (1979) for illustrations of state (0) (fig. 222, *Hk. (Yam.) seoulensis*) and state (1) (fig. 228, '*Oc. (Fin.) oreophilus*'). Also see the information under characters 169, 175 and 177.

179. *Anterior dorsocentral area, pale-scaled stripe*: (0) absent; (1) present. A stripe normally extends over the central part of the dorsocentral area (see Tanaka *et al.*, 1979: fig. 217, *Hl. japonica japonica*), however it may be on the 'inner dorsocentral area' (see Berlin, 1969: figs 8 and 9) as in *Ab. papago* and many species of *Howardina*. See character 177 for information concerning '*Oc. (Fin.) candidoscutellum*'. Also see the information under character 171.

180. *Posterior dorsocentral area, pale-scaled stripe*: (0) absent; (1) present. Tanaka *et al.* (1979) illustrated state (0) (fig. 227, *Do. nishikawai*) and state (1) (fig. 228, '*Oc. (Fin.) oreophilus*'). Also see the information under characters 171 and 179.

181. *Scutal fossal scales*: (0) sparse; (1) dense. Most aedine taxa have uniformly dense narrow or broad scales covering the scutal fossa. The scutal fossa has bare areas or sparse, normally narrow scales in a few taxa, e.g. *Oc. (Chs.) bimaculatus* (Coquillett), *Oc. (Chs.) fulvus pallens*, *Ps. (Pso.) ciliata* and *Ps. (Pso.) howardii*.

182. *Scutal fossal scales, colour*: (0) all dark; (1) contrasting pale scales in large patch; (2) contrasting lines or small patches of pale scales on lateral and/or mesal and/or posterior margins; (3) indefinite arrangement of pale and darker scales. Species with the scutal fossa entirely or nearly entirely covered with pale scales are scored (1).

183. *Prescutellar area, median and/or posterior parts, scales*: (0) absent; (1) present. Numerous species have scales on the lateral and anterior

margins of the prescutellar area, but the median and posterior areas are bare (see Reinert, 1973c: fig. 2, *Bo. helenae*). *Stegomyia desmotes* and *St. gardnerii gardnerii* have only a very narrow, median bare stripe on the prescutellar area (scored 0). This area in *Hl. jugraensis* Leicester (see Knight 1968: fig. 1), *Hl. rizali* (Banks) and *Hl. sherki* (Knight) has a median, longitudinal, narrow, pale-scaled stripe, and the scales mesad of the prescutellar setae are dark. Some other taxa exhibit state (1), e.g. *Aztecaedes*, *Hg. (Haemagogus)* (see Arnell, 1973: fig. 38, *Hg. (Hag.) splendens*), *Mu. (Mucidus)*, *Ochlerotatus* (some species), *Oc. (Rhinoskusea)*, *Oc. (Rusticoidus)*, *Psorophora* (some species) and *Hw. walkeri*.

184. *Prescutellar setae*: (0) absent; (1) present. Prescutellar setae are normally present in Aedini, but are absent in some species, e.g. *As. brevitibia*, *Pa. argenteoventralis dunni* and *Hs. (Heizmannia)*.

185. *Prescutellar setae on each side of thorax*: (0)  $\leq 5$ ; (1)  $\geq 6$ . Taxa exhibiting state (1) normally have 10 or more setae on each side of the prescutellar space (see Reinert, 1976b: fig. 6, *Ed. imprimens*), but some have as few as six setae on each side. Some species have five or fewer setae on each side (see Reinert, 1990: fig. 1, *Ke. dissimilis*). Species without prescutellar setae are coded (-). See the information under character 184.

186. *Prescutellar area, pale scales on outer margin mesal to setae*: (0) absent; (1) present. Many aedine species have a narrow to moderately wide stripe of pale scales mesal to the prescutellar setae (state 1) (see Tanaka *et al.*, 1979: figs 217, 219 and 220, *Hl. japonica japonica*, *Co. (Col.) hatorii* and *Ta. togoi*) but other species have dark scales on this area (state 0) (see Tanaka *et al.*, 1979: fig. 229, *Ph. watasei* (Yamada)). Also see the information under character 183.

187. *Antealar area, scales on anterior part*: (0) absent; (1) present. The part of the antealar area anterior to the forward edge of the paratergite may lack scales, e.g. *Az. ramirezi* (see Zavortink, 1972: fig. 35), *Co. (Alo.) banksi* and *Co. (Alo.) pseudotaeniatus*, or bear scales. See the information under character 188.

188. *Antealar area, scales on anterior part, colour*: (0) all dark; (1) all pale; (2) both dark and pale. When present, scales on the anterior part of the antealar area may be dark (see Tanaka *et al.*, 1979: fig. 239, *Oc. (Geo.) baisasi*) or pale (see Tanaka *et al.*, 1979: fig. 222, *Hk. (Yam.) seoulensis*) or occasionally both dark and pale. Species without scales on the anterior part of the antealar area are coded (-). See the information under character 187.

189. *Supraalar area, pale scales*: (0) absent; (1) present. The supraalar area may be entirely dark-scaled (see Tanaka *et al.*, 1979: fig. 227, *Do. nishikawai*), bear a longitudinal pale-scaled patch (see Tanaka *et al.*, 1979: fig. 217, *Hl. japonica japonica*) or have a transverse pale-scaled patch/stripe (see Tanaka *et al.*, 1979: fig. 229, *Ph. watasei*; Barraud, 1923: figs 11–13 and 17, *Ph. gubernatoris*, *Ph. deccana* and *Ph. cacharana*).
190. *Anterior supraalar-posterior antealar area, transverse patch of pale scales*: (0) absent; (1) present. Some taxa, e.g. *Phagomyia* (see Barraud, 1923: figs 11–15 and 27, *Ph. gubernatoris*) possess a transverse patch or stripe of pale scales extending from the lateral margin of the scutum at the anterior supraalar-posterior antealar area mesally to or near the posterior dorsocentral area.
191. *Scutellum, scales on midlobe*: (0) all narrow; (1) all broad; (2) both narrow and broad. See Reinert (1973a: figs 5 and 6, '*Ae. (Adm.) mediolineatus*' and '*Ae. (Adm.) nigrostriatus*' (Barraud)) for examples of the scutellum with narrow scales on all lobes. Huang (1977: figs 1, 9 and 17, *St. edwardsi*, *St. annandalei* and *St. gardnerii gardnerii*; 1979: figs 6 and 20, *Sc. albolineata* and *Sc. laffooni* (Knight & Rozeboom)) provided examples of state (1).
192. *Scutellum, scales on lateral lobes*: (0) all narrow; (1) all broad; (2) both narrow and broad. See the information under characters 174 and 191.
193. *Paratergal scales*: (0) absent; (1) present. The paratergite may be bare as in *Hl. japonica japonica* and *Oc. (Geo.) baisasi* (see Tanaka *et al.* 1979: figs 217 and 239) or have several to numerous scales as in *Hk. (Yam.) seoulensis* and *St. aegypti* (see Tanaka *et al.*, 1979: figs 222 and 234). A few species, e.g. *Ve. (Nma.) indica*, normally have a bare paratergite but some specimens possess a few scales on this area. These species are coded (0,1).
194. *Parascutellar scales*: (0) absent; (1) present. Reinert (1999b) first noted the presence of parascutellar scales in an aedine, i.e. in *Oc. refiki*, the type species of subgenus *Rusticoidus*. Scales on this area also occur in other species of subgenus *Rusticoidus* and a few other species of *Ochlerotatus*.
195. *Mesopostnotal scales*: (0) absent; (1) present. Harrison & Bickley (1990) reviewed the occurrence of setae and scales on the mesopostnotum in Culicidae. They indicated that setae or scales or both occur in three tribes: Aedini, Culicini and Sabethini. Reinert (2001b) provided data on the mesopostnotal vestiture in species of *Ochlerotatus*. See Reinert (1999c: fig. 2, *Za. huangae* (Reinert) and *Za. monetus* (Edwards)) for examples of state (1).
196. *Mesopostnotal setae*: (0) absent; (1) present. Mattingly (1970c: figs 2 and 21, *Hz. (Hez.) aureochata* (Leicester) and *Hz. (Hez.) indica* (Theobald)) provided examples of state (1). See discussion under character 195.
197. *Postpronotal scales*: (0) absent; (1) present. Broad, narrow or both broad and narrow scales are normally present on the postpronotum in Aedini (see the information under character 198). Postpronotal scales are, however, absent in some taxa, e.g. *Ayurakitia*, *Bothaella* (see Reinert, 1973c: fig. 2, *Bo. helenae*), *Hw. walkeri*, *Oc. (Chs.) fulvus pallens*, *Oc. (Rhinoskusea)*, *Ps. (Pso.) ciliata* and *Udaya*.
198. *Postpronotal scales*: (0) all narrow; (1) all moderately broad to broad; (2) both narrow and moderately broad to broad. *Aedes esoensis* is an example of a species that exhibits state (0) (see Tanaka *et al.*, 1979: fig. 242). Tanaka *et al.* (1979: fig. 229, *Ph. watasei*) provided an example of state (1). Taxa with state (2) normally have narrow scales dorsally and a patch of broad scales ventrally on the postpronotum (see Wood *et al.*, 1979: pls 31 and 34, *Oc. impiger* and *Oc. intrudens*). Species without scales on the postpronotum, see character 197, are coded (-).
199. *Prepiracular setae*: (0) absent; (1) present. Prepiracular setae are normally absent in aedines, however they are present in *Psorophora* (see Wood *et al.*, 1979: pls 71 and 72, *Ps. (Gra.) columbiae* and *Ps. (Jan.) ferox*) and the outgroup species *Cs. inornata*.
200. *Postpiracular setae*: (0) absent; (1) present. Postpiracular setae are normally present in Aedini. They are, however, absent in some taxa, e.g. *Ar. (Leicesteria)*, *Ayurakitia*, *Heizmannia* (except in *Hg. (Mat.) catesi*), *Hg. (Haemagogus)* (many species) (see Arnell, 1973: figs 18 and 27, *Hg. (Hag.) janthinomys* and *Hg. (Hag.) panarchys* Dyar), *Ko. purpureipes*, *Stegomyia* (few species) and *Ze. gracilis*. These setae are absent in the outgroup species except *Ma. titillans*.
201. *Postpiracular scales*: (0) absent; (1) present. See Tanaka *et al.* (1979: fig. 220, *Ta. togoi*) for an example of state (1) and Arnell (1976: fig. 35, *Oc. (Och.) scapularis*) for an example of state (0).
202. *Hypostigmal scales*: (0) absent; (1) present. Scales on the hypostigmal area should not be con-

fused with those on the dorsal part of the subspiracular area when two patches are present on the latter, one immediately dorsal to the other. Scales are normally absent on the hypostigmal area of Aedini (see Zavortink, 1972: fig. 5, '*Oc. (Pro.) brelandi*'). They are present in some taxa, e.g. *Aztecaedes*, *Mc. (Chaetocruimyia)*, *Mu. (Mucidus)*, some *Ochlerotatus* (see Wood *et al.*, 1979: pls 15, 23 and 44, *Oc. campestris*, *Oc. dorsalis* and *Oc. riparius*), *Oc. (Rusticoidus)*, *Pseudarmigeres* and *Psorophora* (subgenera *Janthinosoma* and *Psorophora*). In some *Ar. (Leicesteria)* a group of long, broad scales on the lower posterior area of the postpronotum extends posteriorly over much of the lower hypostigmal area (coded 0), for example in *Ar. (Lei.) longipalpis* scales had to be partially removed from a specimen to determine their points of attachment.

203. *Subspiracular scales*: (0) absent; (1) present. The subspiracular area is bare in several aedine taxa, e.g. *Aedes*, '*Ae. (Cancraedes)*', *Ayurakitia*, *Bothaella*, *Downsiomyia*, *Isoaedes*, *Kenknightia*, *Lorrainea*, *Oc. (Geoskusea)*, *Oc. (Levua)*, *Oc. (Rhinoskusea)*, *Opifex*, *Paraedes*, *Ps. (Grabhamia)*, *Scutumyia*, *Udaya*, *Verrallina*, *Zavortinkius* and some species, e.g. '*Ae. (Adm.) domesticus*', *Hl. chrysolineata*, *Hw. walkeri*, *Oc. (Pcx.) atlanticus*, *Oc. (Chs.) fulvus pallens*, *Ps. (Pso.) howardii* and *St. futunae*. One or two patches of subspiracular scales are present in several taxa, e.g. many *Stegomyia* (see Huang, 1977: figs 4F, 17A and 32C, *St. seampi* (Huang), *St. desmotes* and *St. w-albus*), many '*Ae. (Aedimorphus)*', *Mu. (Mucidus)* and many *Ochlerotatus*.

204. *Upper proepisternal setae*: (0) 1–4; (1) 5–19; (2)  $\geq 20$ . After examination of most species of Aedini, generic-level taxa were found to possess numbers of setae in one of the three states. Some specimens of a few species have a slight overlap (usually of one seta) of the states (0,1) or (1,2), e.g. *Hl. chrysolineata*, *Ia. cavaticus*, *Ko. purpureipes*, *Oc. (Geo.) longiforceps* and *Ta. savoryi*, whereas most specimens of these species exhibit a single character state. A few upper proepisternal setae occur in some aedine taxa (state 0), e.g. *Bothaella* (see Reinert, 1973c: fig. 2, *Bo. helenae*). A moderate number (state 1) of these setae occur in several species, e.g. *Do. nipponica* and *Do. nishikawai* (see Tanaka *et al.*, 1979: figs 226 and 227), and they are numerous (state 2) in many species of *Ochlerotatus* (see Tanaka *et al.*, 1979: fig. 216, *Oc. punctor*).

205. *Upper proepisternal scales*: (0) absent; (1) present. Species of Aedini normally have scales on the upper proepisternum (see Tanaka *et al.*, 1979: figs 217 and 236, *Hl. japonica japonica* and *St. chemulpoensis*) but these are noticeably absent in *Oc. (Chs.) fulvus*

*pallens* and subgenera *Geoskusea*, *Levua* and *Rhinoskusea* (see Reinert, 1976c: fig. 2, *Oc. (Rhi.) longirostris*) of *Ochlerotatus*.

206. *Lower proepisternal scales*: (0) absent; (1) present. When scales are present on the lower proepisternum they usually cover all or much of the surface and are normally broad and silvery or white. Scales are present in a number of taxa, e.g. *Abraedes*, *Haemagogus*, *Ja. (Lew.) muelleri*, *Kompia*, *Oc. communis*, *Oc. (Och.) infirmatus*, *Oc. (Och.) scapularis*, '*Oc. (Pro.) burgeri*', '*Oc. (Pro.) terreus*', *Oc. (Rusticoidus)* (2 species), *Ps. (Jan.) ferox*, *Scutumyia*, *Stegomyia* and *Zavortinkius*. '*Aedes (Adm.) vexans vexans*' has several narrow and broad scales on the lateral margins of the lower proepisternum (see Reinert, 1973a).

207. *Upper mesokatepisternal setae*: (0) absent; (1) present. One or more upper mesokatepisternal setae are usually present in aedine species (see Tanaka *et al.*, 1979: figs 212 and 220, *Oc. dorsalis* and *Ta. togoi*). However, these setae are absent in some taxa, e.g. *Alanstonea*, *Ayurakitia*, *Eretmapodites*, *Hg. (Haemagogus)* (see Arnell, 1973, fig. 38, *Hg. (Hag.) splendens*), *Heizmannia*, *Huaedes* and *Udaya*. These setae are usually present but are absent in some specimens of a few species, e.g. *Ve. (Har.) yusafi*. The upper mesokatepisternum, and other areas of the thoracic pleura, are covered in scales in many species that lack these setae.

208. *Mesokatepisternal scales*: (0) in one large patch; (1) in two patches; (2) in three patches. See Wood *et al.* (1979) for examples of state (0) (pl. 15, *Oc. campestris*), state (1) (pl. 16, *Oc. canadensis canadensis*) and state (2) (pl. 34, *Oc. intrudens*).

209. *Upper prealar setae*: (0)  $\leq 20$ ; (1)  $\geq 21$ . Prealar setae occur on the upper prealar area (prealar knob) in Aedini. See Reinert (1972b: fig. 2, *Ay. peytoni*) for an example of state (0) and Tanaka *et al.* (1979: fig. 216, *Oc. punctor*) for state (1). A few specimens of some species exhibit a slight overlap of one or two setae between the two states, and are scored (0,1).

210. *Upper prealar scales*: (0) absent; (1) present. Scales on the upper prealar area (see Reinert, 1973a: figs 5 and 11, '*Ae. (Adm.) medilineatus*' and '*Ae. (Adm.) punctifemoris*') are usually intermixed with the prealar setae but some taxa only have several scales attached to the lower area of the knob and may be continuous with the scale patch on the lower prealar area. Upper prealar scales are absent in other taxa, e.g. *Paraedes barraudi* (see Reinert, 1981: fig. 1). See the information under character 209.

211. *Lower prealar scales*: (0) absent; (1) present. Scales on the lower prealar area (below knob) occur in a small to moderately large patch (see Tanaka *et al.*, 1979: figs 217, 220 and 222, *Hl. japonica japonica*, *Ta. togoi* and *Hk. (Yam.) seoulensis*). Lower prealar scales are absent in some species (see Tanaka *et al.*, 1979: fig. 239, *Oc. (Geo.) baisasi*). Also see the information under characters 209 and 210.

212. *Mesepimeral scales*: (0) absent; (1) present. Scales are normally present (see Tanaka *et al.*, 1979: figs 217 and 218, *Hl. japonica japonica* and *Hl. koreica*) on the mesepimeron of aedine species. However, they are absent in some taxa, e.g. *Ochlerotatus* (subgenera *Levua* and *Rhinoskusea*) (see Reinert, 1976c: fig. 2, *Oc. (Rhi.) longirostris*) and *Zeugomyia*.

213. *Mesepimeral scales*: (0) in one patch; (1) in two patches; (2) in three patches. See Wood *et al.* (1979) for examples of state (0) (pls 15 and 16, *Oc. campestris* and *Oc. canadensis canadensis*) and state (1) (pl. 46, *Ja. (Jar.) sierrensis*). Taxa without scales on the mesepimeron are coded (-). See the information under character 212.

214. *Lower anterior mesepimeral setae*: (0) absent; (1) present. Well-developed setae on the lower anterior area of the mesepimeron are found in species of a number of taxa, e.g. *Armigeres*, *Ayurakitia*, *Bothaella*, *Christophersomyia*, *Fredwardsius*, *Halaedes*, *Huaedes*, *Isoaedes*, *Leptosomatomyia*, *Oc. (Rusticoidus)*, *Psorophora*, *Skusea*, *Zeugomyia* and the outgroup species *Cs. inornata*, *Cx. quinquefasciatus* and *Ma. titillans*. See illustrations of this character in Tanaka *et al.* (1979): setae absent (fig. 242, *Ae. esoensis*) and setae present (fig. 216, *Oc. punctor*).

215. *Mesepimeral fine setae*: (0) absent; (1) present. Several to numerous short, fine setae are located ventral and/or posterior to the scale-patch on the mesepimeron in *Oc. (Geoskusea)* (see Mattingly, 1959: fig. 2C, *Oc. (Geo.) kabaenensis* (Brugl)) and subgenera *Neomacleaya* and *Verrallina* of *Verrallina* (Barraud, 1934; Reinert, 1974, 1984, 1999d).

216. *Metamer, vestiture*: (0) absent; (1) present. The metamer is bare in most Aedini. See character 217 for taxa with vestiture on the metamer. A few species, e.g. *Az. ramirezi* and *Mo. pecuniosa*, have the metamer bare, but rarely a specimen has a few scales, coded (0). *Fredwardsius vittatus* normally possesses scales on the metamer but occasionally these are absent (rubbed off?) and is coded (1).

217. *Metamer, vestiture*: (0) scales; (1) scales and setae. Scales are present in some taxa, e.g. *Ar. (Leicesteria)*, *Da. echinus*, *Ochlerotatus* (several species) (see Wood *et al.*, 1979: pls 18, 20 and 23, *Oc. cataphylla* (Dyar), *Oc. communis* and *Oc. dorsalis*), *Oc. (Rusticoidus)*, *St. desmotes*, *St. gardnerii gardnerii*, *St. unilineata*, *St. w-albus* and the outgroup species *Cs. inornata*. Species of *Oc. (Geoskusea)* have several pale scales and short, fine setae on the metamer (see Mattingly, 1959: fig. 2C, *Oc. (Geo.) kabaenensis*). Taxa without scales or setae on the metamer are coded (-). See the information under character 216.

218. *Upper calypter, setae or hair-like scales*: (0) 0–3; (1) numerous,  $\geq 7$ . Setae or hair-like scales are normally present and numerous (12–40) in females of Aedini. Some species, e.g. *Oc. spilotus*, have over 50 setae/scales on the upper calypter whereas some *Stegomyia* have 7–10 setae/scales. Setae/scales are, however, usually absent in species of *Udaya* and *Zeugomyia*, but one to three are sometimes present in some species. *Udaya lucaris* is unusual in having 0–6, very rarely 7, setae/scales on the upper calypter (coded 0). Dyar & Shannon (1924) and later Edwards (1929) and Harbach & Kitching (1998) pointed out the usefulness of this character in Culicidae.

219. *Upper calypter, setae or hair-like scales* (males): (0) 0–3; (1) numerous,  $\geq 7$ . The presence of several to numerous setae or hair-like scales along the posterior margin of the upper calypter is the usual condition of aedine males. Many species of *Ochlerotatus* have 30 or more setae/scales on the upper calypter, however some species of *Stegomyia* possess 7–10 setae/scales. Some taxa, e.g. *Belkinus*, '*Ae. (Cancraedes)*', *Paraedes*, *Oc. (Rhinoskusea)*, *Udaya* and *Zeugomyia*, have these setae/scales absent or reduced to only one to three. Males of *St. desmotes* examined possess 3–5 setae on the upper calypter and are coded (0).

220. *Alula, marginal scales*: (0) absent; (1) present. Mattingly (1957, 1958, 1959) pointed out the value of the varied development of scales on the alula (also see characters 221 and 222). Scales are present on the alula of most Aedini. These scales are absent in a few taxa, e.g. *Ps. (Gra.) columbiae* and *Ps. (Gra.) jamaicensis*. A few species, e.g. *Hg. (Hag.) splendens*, normally have several marginal scales but rarely a specimen has these scales absent (rubbed off?), coded (1).

221. *Alula, marginal scales*: (0) narrow; (1) broad. See Harbach & Kitching (1998) for illustrations of state (0) (fig. 12E) and state (1) (fig. 12D). Taxa

without marginal scales are coded (-). See the information under character 220.

222. *Alula, dorsal broad scales*: (0) absent; (1) present. These scales are absent in most Aedini. Moderately broad or broad scales anterior to the margin are present in several taxa, e.g. 'Ae. (*Canraedes*)', *Alanstonea*, *Diceromyia* (many species), *Eretmapodites* (see Harbach & Kitching, 1998: fig. 12D, *Er. silvestris* Ingram & de Meillon), *Gymnometopa*, *Heizmannia*, *Lorrainea* and *Udaya*.

223. *Remigium, dorsal setae*: (0) absent; (1) present. Several taxa lack dorsal remigial setae, e.g. *Abraedes*, *Georgecraigius* and *Rampamyia*. Few to several, short to long setae are present in other taxa, e.g. *Collessius* (see Tanaka *et al.*, 1979: fig. 219, *Co. (Col.) hatorii*), *Ochlerotatus* (most species) and *Paraedes*. In some species, short setae may be partially or completely hidden beneath numerous scales on the remigium. In *Oc. (Rhi.) longirostris* these setae are normally present but are very rarely absent (rubbed off?) and are coded (1).

224. *Remigium, insertion of dorsal setae*: (0) distally; (1) proximally. Very long, blunt-tipped setae arising dorsally near the base of the remigium (state 1) are characteristic of *Mc. (Chaetocruiomylia)* (see Marks, 1962: fig. 1C, *Mc. (Cha.) humeralis* (Edwards)), except *Mc. (Cha.) elchoensis*, in which they are absent (see Marks, 1962, 1964a). When present in other taxa these setae are located on the distal part of the remigium. Also see the information under character 223. Species without setae dorsally on the remigium are coded (-).

225. *Remigium, ventral setae*: (0) absent; (1) present. Within Aedini, only *Opifex* (both subgenera) have setae on the ventral surface of the remigium. These setae are also characteristic of *Culiseta* (see Harbach & Kitching, 1998: fig. 12C, *Cs. impatiens* (Walker)).

226. *Costal scales*: (0) all dark; (1) one pale-scaled patch at or near base; (2)  $\geq 3$  pale-scaled patches; (3) pale and dark scales intermixed for all or most of length, not forming defined pattern. Most aedine species have the costa entirely dark-scaled (state 0) (see Tanaka *et al.*, 1979: fig. 217, *Hl. japonica japonica*) or have a small to large patch of pale scales at the base (state 1) (see Tanaka *et al.*, 1979: fig. 222, *Hk. (Yam.) seoulensis*). Some species may have the basal pale patch reduced to only 2–4 pale scales. A few species, e.g. *Co. (Alo.) banksi* and *Co. (Alo.) pseudo-taeniatus*, have a small dark-scaled patch at the base of the costa and a white-scaled patch near the base on the anterior surface (scored as state 1). Three or more

white-scaled patches (state 2) are typical of *Finlaya* (see Russell, 1996: 61, *Fl. kochi*). Pale and dark scales are intermixed along the entire length of the costa (state 3) and do not form a defined pattern in some species, e.g. *Oc. grossbecki* (see Yamaguti & LaCasse, 1951: pl. XXXV), *Oc. (Cul.) sollicitans*, *Ps. (Gra.) jamaicensis*, *Ps. (Pso.) ciliata* and the outgroup species *Cs. inornata*, *Ma. titillans* and *Or. signifera*.

227. *Dark pigmentation around radiomedial crossvein and proximal segment of media<sub>3+4</sub>*: (0) absent; (1) present. Tyson (1970: figs 1–5 and 7) illustrated the two darkly pigmented areas of wings of several species of *Mucidus* (subgenera *Mucidus* and *Paradomyia*). *Ochlerotatus (Phl.) flavifrons* possesses a single, large, lightly pigmented, oval area near midlength of the wing, but this is not homologous with the darkly pigmented areas occurring in *Mucidus*, and is scored (0).

228. *Vein R<sub>2</sub>, length relative to length of R<sub>2+3</sub>*: (0) shorter; (1) equal or longer. State (1) is the normal condition in Aedini (see Carpenter & LaCasse, 1955: pls 46 and 47, *Oc. (Pcx.) atlanticus* and *Oc. aurifer*). This vein, however, is shorter than R<sub>2+3</sub> in *Belkinus* and *Zeugomyia*.

229. *Anal vein, point of termination*: (0) approximately in line with intersection of mediocubital crossvein and cubitus; (1) noticeably distad of this point. Termination of the anal vein beyond the intersection of the mediocubital crossvein and the cubitus (see Tanaka *et al.*, 1979: figs 212 and 220, *Oc. dorsalis* and *Ta. togoi*), with the distal portion normally nearly straight or gently curved, is the usual condition in Aedini. Termination near the intersection, with the distal part sharply curved caudally, occurs in some taxa, e.g. 'Ae. (*Canraedes*)', *Belkinus* and *Zeugomyia* (see examples in Mattingly, 1958: fig. 1).

230. *Wing, fringe scales, colour*: (0) uniform; (1) dark with patches of pale scales. Long, fusiform, fringe scales occur in a row perpendicular to the posterior margin of the wing. Harbach & Knight (1980: fig. 19d) illustrated the fringe scales and dorsal tertiary fringe scales. Uniformly coloured fringe scales is the usual condition in species of Aedini. A fringe consisting of patches of dark and pale scales occurs in *Mucidus (Mucidus)* and *Finlaya* (see Tyson, 1970: figs 1–3, 5 and 7, *Mucidus* species; Russell, 1996: 61, *Fl. kochi*).

231. *Wing, dorsal tertiary fringe scales on proximal 0.50*: (0) absent; (1) present. Reinert (2007) provided information on the presence/absence of these scales in females and males of 345 species of Culicidae. Dorsal



tertiary fringe scales of females are normally present and are short, narrow to moderately broad scales inserted on the dorsal surface parallel or at a small angle to the posterior margin of the wing above the long, fusiform, fringe scales. Females of *Pseudarmigeres* have sparse dorsal tertiary fringe scales on the basal 0.50 (state 1) and are sometimes rubbed off. These scales are noticeably absent on the proximal 0.50 of the posterior margin of the wing in some taxa, e.g. *Mu.* (*Pardomyia*), *Oc.* (*Chrysoconops*) and *Ps.* (*Janthinosoma* and *Psorophora*). Carpenter & LaCasse (1955) illustrated state (0) (pl. 62, *Oc.* (*Chs.*) *fulvus pallens*) and state (1) (pl. 64, *Oc.* *hexodontus*). See the information under character 230.

232. *Wing, dorsal tertiary fringe scales on proximal 0.50* (males): (0) absent; (1) present. Dorsal tertiary fringe scales in males of Aedini are absent on the proximal 0.50 of the wing margin in many taxa. See the information under character 231.

233. *Wing, dorsal tertiary fringe scales, colour*: (0) uniform; (1) intermixed or patches of pale and dark. See Carpenter & LaCasse (1955) for examples of state (0) (pl. 64, *Oc.* *hexodontus*) and state (1) (pl. 63, *Oc.* *grossbecki*). Species with scales absent from the proximal 0.50 of wings of females normally possess scales on the distal part. See the information under characters 230 and 231.

234. *Anteprocoxal scales*: (0) absent; (1) present. Scales are normally absent from the anteprocoxal membrane in Aedini. However, broad and silvery or white scales are present in some taxa, e.g. *Alanstonea*, *Ar.* (*Leicesteria*), *Ochlerotatus* (few species), *Oc.* (*Rusticoidus*), *Pseudarmigeres* and *Ps.* (*Jan.*) *ferox*.

235. *Postprocoxal scales*: (0) absent; (1) present. Scales are absent from the postprocoxal membrane in many species of Aedini. They are present in others, e.g. *Abraedes*, *Ar.* (*Leicesteria*), *Christophersiomyia*, *Diceromyia* (many species), *Fredwardsius*, *Gymnometopa*, *Hg.* (*Haemagogus*), *Huaedes*, *Hs.* (*Heizmannia*) (many species), *Ochlerotatus* (several species, see Wood *et al.* 1979: pls 12, 18 and 23, *Oc.* *aloponotum* (Dyar), *Oc.* *cataphylla* and *Oc.* *dorsalis*), *Oc.* (*Rusticoidus*), *Pseudarmigeres* and *Psorophora* (several species).

236. *Hindcoxa, base relative to dorsal margin of mesomerion*: (0) well below; (1) more or less at same level. Most species of Aedini have the base of the hindcoxa well below the dorsal margin of the mesomerion (see Tanaka *et al.*, 1979: figs 212 and 226, *Oc.* *dorsalis* and *Do.* *nipponica*). It is more or less at the

same level with or slightly above the mesomerion in some taxa, e.g. *Alanstonea*, *Armigeres*, *Belkinus*, *Hg.* (*Haemagogus*) (see Arnell, 173: fig. 38, *Hg.* (*Hag.*) *splendens*), *Heizmannia*, *Leptosomatomyia*, *Mc.* (*Chaetocruomyia*), *Pseudarmigeres*, *Scutomyia*, *St.* *desmotes*, *Udaya* and *Zeugomyia*.

237. *Fore-, mid- and hindfemora, complete subapical, pale-scaled bands*: (0) absent; (1) present. In Aedini, the fore-, mid- and hindfemora normally do not have a subapical band. A distinct subapical, pale-scaled band occurs on all three femora in *Finlaya*, *Fredwardsius* (see Mattingly, 1965: fig. 5A, *Fr.* *vittatus*), *Huaedes*, *Mucidus* and *Ps.* (*Grabhamia*). Incomplete subapical pale-scaled bands occur in *Db.* *alboannulatus*; hence this species is scored (0).

238. *Midfemur, median pale-scaled stripe from base to or near apex on anterior surface*: (0) absent; (1) present. Most aedine species do not have a median pale-scaled stripe on the anterior surface of the midfemur (see Tanaka *et al.*, 1979: fig. 223, *Br.* *alektorovi*). This feature is present in *Collessius* (subgenera *Alloeomyia* and *Collessius*), *Gy.* *mediovittata*, *Rampamyia* and *St.* *aegypti* (see Tanaka *et al.*, 1979: fig. 234). This stripe is sometimes incomplete in some specimens of *Gy.* *mediovittata* and *St.* *aegypti*, but they are scored (1). Other species have a pale-scaled stripe on the ventral margin of the anterior surface (scored 0).

239. *Hindfemur, pale scales dorsally and/or anteriorly at apex*: (0) absent; (1) present. The apices of the hindfemora in some species of Aedini have dark scales on the dorsal and anterior areas, e.g. *Hk.* (*Yam.*) *seoulensis* and '*Oc.* (*Fin.*)' *crossi* (see examples in Tanaka *et al.*, 1979: figs 222, 226 and 227, *Hk.* (*Yam.*) *seoulensis*, *Do.* *nipponica* and *Do.* *nishikawai*). A few species possess a subapical pale-scaled area with a very narrow band or fringe of dark scales at the apex, e.g. *Hk.* (*Hpk.*) *embuensis*, *Hk.* (*Hpk.*) *ingrami*, *Hl.* *chrysolineata* and *Hl.* *japonica japonica* (see Tanaka *et al.*, 1979: fig. 217). These species are scored (0). Many species of Aedini have a narrow to wide band of pale scales at the apex of the hindfemur, e.g. *Ta.* *savoryi* and *Ta.* *togoi* (see Tanaka *et al.*, 1979: fig. 220).

240. *Hindtibia, scales, colour*: (0) dark only; (1) dark with pale-scaled areas. The hindtibia may be entirely dark-scaled (state 0), or dark-scaled with pale scales intermixed, forming an anterior and/or posterior stripe, a narrow or broad basal, median or apical spot(s) or band(s) (state 1) (see LaCasse & Yamaguti, 1950: pl. 34, *St.* *chemulpoensis*; Bañez & Jueco, 1966: pl. 1, *Fl.* *poicilia*; Russell, 1996: 61, *Fl.* *kochi*).

241. *Hindtarsomere 1, basal pale scales*: (0) absent; (1) present. The basal part of hindtarsomere 1 may be dark-scaled (state 0) (see Tanaka *et al.*, 1979: fig. 226, *Do. nipponica*) or have pale scales forming a narrow to wide band (see LaCasse & Yamaguti, 1950: pl. 34, *St. chemulpoensis*) or small spot on the dorsal, ventral or posterior surface (state 1).

242. *Hindtarsomere 1, one or more median pale-scaled bands*: (0) absent; (1) present. The median area of hindtarsomere 1 may be entirely dark-scaled (state 0) (see Tanaka *et al.*, 1979: fig. 227, *Do. nishikawai*) or have one or more pale-scaled bands (rarely reduced to dorsal pale-scaled spots) (state 1) as in *Finlaya* (see Bañez & Jueco, 1966: pl. 1, *Fl. poicilia*; Russell, 1996: 61, *Fl. kochi*). A submedian white-scaled band occurs in *Ab. papago* (scored 1).

243. *Hindtarsomere 1, apical pale scales*: (0) absent; (1) present. See Zavortink (1972) for examples of state (0) (fig. 42, *Ja. (Lew.) muelleri*) and state (1) (fig. 48, *Gc. (Gec.) atropalpus*).

244. *Hindtarsomere 2, basal pale scales*: (0) absent; (1) present. See the information under character 241.

245. *Hindtarsomere 2, apical pale scales*: (0) absent; (1) present. See the information under character 243.

246. *Foreungues, development*: (0) both simple; (1) one simple, one toothed; (2) both toothed. Both foreungues bearing a short or long tooth (state 2) is the usual condition in females of Aedini (see Tanaka *et al.*, 1979: figs 219 and 220, *Co. (Col.) hatorii* and *Ta. togoi*). Females with both foreungues simple (state 0) are found in many taxa, e.g. *Abraedes*, '*Ae. (Cancraedes)*', *Howardina* (see Berlin, 1969: fig. 16, *Hw. walkerii*), *Huaedes*, *Hz. (Heizmannia)*, *Leptosomatomyia*, *Lorrainea*, *Macleaya*, *Ochlerotatus* (subgenera *Geoskusea*, *Levua* and *Rhinoskusea*), *Ps. (Grabhamia)*, *Scutomyia*, *Skusea*, *Ud. argyrurus* and *Ze. gracilis*. State (1), one unguis simple and the other toothed, occurs in the outgroup species *Cx. quinquefasciatus*.

247. *Foreungues, development (males)*: (0) both simple; (1) larger one simple, smaller one toothed; (2) larger one with one tooth, smaller one simple; (3) larger one with two teeth, smaller one simple; (4) both toothed, larger one with one tooth; (5) both toothed, larger one with two teeth. Both foreungues are simple (state 0) in some aedine taxa, e.g. *Alanstonea*, *Belkinus* (see Reinert, 1982: fig. 2, *Be. aurotaeniatus*), *Eretmapodites*, *Indusius*, *Leptosomatomyia*, *Lorrainea*, *Op. (Opifex)* and *Ze. gracilis*. See Huang (1990: fig. 3, *St. africana*) for example of state (1) and Reinert

(1972b: fig. 3, *Ay. griffithi*) for illustration of state (2). When both unguis are toothed, the larger one may possess one tooth (state 4) (see Wood *et al.*, 1979: pls 30 and 31, *Oc. hexodontus* and *Oc. impiger*) or two teeth (state 5) (see Wood *et al.*, 1979: pls 38 and 47, *Oc. (Cul.) nigromaculis* (Ludlow) and *Oc. (Cul.) sollicitans*). *Mansonia titillans* and *Or. signifera* have state (3).

248. *Midungues, development (males)*: (0) both simple; (1) larger one simple, smaller one toothed; (2) larger one with one tooth, smaller one simple; (3) larger one with two teeth, smaller one simple; (4) both toothed, larger one with one tooth; (5) both toothed, larger one with two teeth. See Huang (2004) for examples of state (0) (fig. 3D, *St. aegypti*), state (1) (fig. 11E, *St. ealaensis* (Huang)), state (2) (fig. 7D, *St. grantii* Theobald) and state (4) (fig. 6D, *St. unilineata*). Wood *et al.* (1979: pl. 38, *Oc. (Cul.) nigromaculis*) illustrated state (5). State (3) occurs in *Ma. titillans* and *Or. signifera*.

249. *Hindungues, development*: (0) both simple; (1) one simple, one toothed; (2) both toothed. Females of many taxa have simple hindungues (state 0) (see Reinert, 1972b: fig. 3, *Ay. griffithi*) whereas others have both hindungues toothed (state 2), e.g. *Aedes*, *Christophersomyia*, *Edwardsaedes*, *Halaedes*, *Mu. (Mucidus)*, *Ochlerotatus* (see plates in Wood *et al.*, 1979), *Oc. (Rusticoides)*, *Opifex*, *Psorophora* (subgenera *Janthinosoma* and *Psorophora*), *Tanakaius*, *Ve. (Harbachius)* and *Zavortinkius*. Most species that have toothed hindungues in females also have them toothed in the males (see character 250).

250. *Hindungues, development (males)*: (0) both simple; (1) one simple, one toothed; (2) both toothed. Males of many species have both hindungues simple (state 0) whereas others have both toothed (state 2), e.g. *Christophersomyia*, *Edwardsaedes*, *Halaedes*, *Mu. (Mucidus)*, *Ochlerotatus* (many species), *Op. (Not.) chathamius*, *Ps. (Jan.) ferox*, *Ps. (Pso.) ciliata*, *Tanakaius* and *Zavortinkius*. State (1), one hindunguis simple and the other toothed, occurs in a few species, e.g. *Oc. (Gli.) mcdonaldii*. See the information under character 249.

251. *Abdominal tergum I, laterotergite, scales*: (0) absent; (1) present. Most Aedini have numerous, or at least a few, scales on the laterotergite of abdominal segment I (see Tanaka *et al.*, 1979: figs 236 and 245, *St. chemulpoensis* and *Ve. (Har.) nobukonis*). These scales are absent in some taxa, e.g. *Gc. (Gec.) atropalpus*, *Gc. (Gec.) epactius*, '*Oc. (Fin.)*

*candidoscutellum*, *Oc.* (*Geoskusea*), *Oc.* (*Och.*) *infirmatus*, *Oc.* (*Och.*) *scapularis*, *Opifex*, *Ps.* (*Pso.*) *ciliata* and the four outgroup species.

252. *Abdominal tergum III, median dorsobasal pale-scaled area*: (0) absent; (1) present. Basal, pale-scaled bands or patches are present dorsally on the median area of tergum III of a number of taxa (see Tanaka *et al.*, 1979: figs 215 and 242, *Oc. sticticus* and *Ae. esoensis*) but the dorsobasal area is dark-scaled in other taxa (see their figures 221 and 224, *Ta. savoryi* and *Br. okinawanus*).

253. *Abdominal tergum III, median dorsoapical pale-scaled area*: (0) absent; (1) present. See Carpenter & LaCasse (1955: pls 75 and 76, *Oc. pionips* and *Oc. pullatus*) for state (0) and their plates 82 and 85 (*Oc. spencerii spencerii* and *Oc. stimulans*) for state (1). Species with tergum III entirely pale-scaled (see Carpenter & LaCasse, 1955: pl. 61, *Oc. flavescens*) are scored (1).

254. *Abdominal terga, lateral setae* (males): (0) relatively short to moderately long; (1) long. Setae that are coded state (0) are noticeably shorter than the dorsal width of the tergum whereas those coded as state (1) are as long or nearly as long as the dorsal width of the tergum. The lateral setae on the abdominal terga of males are few in number and relatively short in some taxa (state 0), e.g. *Bruceharrisonius*, *Hg. (Conopostegus)*, *Hg. (Hag.) splendens*, *Howardina*, *Isoaedes*, *Kenknightsia*, *Op. (Opi.) fuscus* (see Belkin, 1968: fig. 2), *Oc. (Geoskusea)*, *Oc. (Rhinoskusea)*, *Scutomyia*, *Stegomyia*, *Tanakaius* and *Zavorinkius*, whereas these setae are numerous and relatively short to moderately long in other taxa (state 0), e.g. *Downsiomyia*, *Finlaya*, *Mc. (Mac.) tremula* and *Mo. pecuniosa* (see Reinert, 1993: fig. 3). The setae are numerous and long (state 1) in many taxa, e.g. *Aedes*, '*Ae. (Aedimorphus)*' (most species) (see Reinert, 1973a: figs 2 and 5, '*Ae. (Adm.) caecus*' and '*Ae. (Adm.) mediolineatus*'), *Albuginosus*, *Edwardsaedes*, *Halaedes*, *Mu. (Mucidus)*, *Neomelaniconion*, *Ochlerotatus* (most species), '*Oc. (Protomacleaya)*' (most species) and *Oc. (Pseudoskusea)*.

255. *Abdominal segment VII, cross-section shape*: (0) laterally compressed; (1) dorsoventrally flattened; (2) cylindrical. Abdominal segment VII (and often segment VIII) of dead, dried females has a distinctive shape when viewed transversely. The cylindrical shape (state 2) occurs in *Psorophora* and the outgroup species *Ma. titillans*. See Tanaka *et al.* (1979: fig. 229, *Ph. watasei*) for state (0), their figure 212 (*Oc. dorsalis*) for state (1) and Ross (1947: fig. 184, *Ps. (Pso.) ciliata*) for state (2).

#### FEMALE GENITALIA

The series of papers on the comparative anatomy of female genital structures of Aedini by Reinert (2000c, d, e, f, g, 2001c, d, e, f, 2002b, c, d, e, 2008a, b, c, d, e, f, g, h, i, j, k, l) should be consulted for illustrations and descriptions.

256. *Intersegmental membrane between segments VII and VIII*: (0) short to intermediate; (1) long to very long. Taxa with intersegmental membranes separating segments VII and VIII that allow 50 percent or less of tergum VIII to be retracted into segment VII are considered short to intermediate (state 0) whereas those allowing 65 percent or more retraction are scored long to very long (state 1). The very long intersegmental membrane in *Psorophora* allows for complete or nearly complete retraction of segment VIII into segment VII (see Carpenter & LaCasse, 1955: pls 35 and 36, *Ps. (Jan.) ferox* and *Ps. (Jan.) horrida* (Dyar & Knab)), whereas taxa with short intersegmental membranes do not allow retraction or only a slight retraction of segment VIII (see Carpenter & LaCasse, 1955: pl. 97, '*Oc. (Pro.) zoosophus*').

257. *Tergum VIII, development*: (0) mostly membranous with heavily sclerotized, rod-shaped structures laterally on each side; (1) entirely sclerotized, rarely with few small, non-sclerotized areas on distal, lateral and proximal areas, without rod-shaped structures laterally on each side. *Psorophora* have tergum VIII, as well as sternum VIII (see character 263), nearly completely membranous except for small scattered, sclerotized, island-like areas usually bearing setae and a rod-shaped structure laterally on each side (state 0) (see Reinert, 2000d: figs 1–3, *Ps. (Gra.) jamaicensis*, *Ps. (Jan.) discrucians* (Walker) and *Ps. (Pso.) ciliata*). Species of *Oc. (Culicelsa)* (see Reinert, 2002e: fig. 28, *Oc. (Cul.) sollicitans*) have moderately large non-sclerotized areas on the proximal part except *Oc. taeniorhynchus*, which has the distal, lateral and proximal margins non-sclerotized (coded 1). Most Aedini have tergum VIII, as well as sternum VIII, entirely sclerotized (see figures in Reinert, 2000g, 2001d, 2002e). Tergum VIII of the outgroup species *Ma. titillans* has distal and lateral sclerotized areas and a large basomesal membranous area (scored 1).

258. *Tergum VIII, posterior margin*: (0) convex; (1) straight; (2) concave. See Reinert (2002e) for examples of state (0) (fig. 6, *Fl. kochi*) and state (1) (fig. 14, *Oc. (Lev.) geoskusea*). Reinert (2000g: fig. 4, *St. desmotes*) provided an example of tergum VIII with a concave posterior margin (state 2).

259. *Tergum VIII*, length relative to width: (0) shorter; (1) longer; (2) equal. The length of tergum VIII is defined by Reinert (2000c) as 'the distance measured to the apex along a perpendicular line drawn from a straight line across the base of the sclerotized and pigmented area of tergum VIII' and the width as 'the distance measured along a straight line across the widest part of the sclerotized and pigmented area of tergum VIII'. Tergum VIII of numerous aedine taxa is wider than long (see Reinert, 2002e: figs 1 and 8, *Mc. (Cha.) spinosipes* Edwards and *Do. nivea*). Tergum VIII that is longer than the width occurs in several taxa (see Reinert, 2002e: figs 10, 17 and 18, *Oc. (Geo.) fimbripes*, *Mu. (Muc.) alternans* and *Mu. (Pdo.) aurantius aurantius*).

260. *Tergum VIII*, moderately long to long seta(e) on lateral margins of proximal 0.40: (0) absent; (1) present. Some taxa have a relatively long and narrow tergum VIII that bears one or more moderately long to long setae, in addition to short setae, laterally especially on the proximal area (see Reinert, 2002e: figs 10 and 23, *Oc. (Geo.) fimbripes* (Edwards) and *Oc. caballus*).

261. *Tergum VIII*, insertion of setae: (0) on distal 0.60 or less; (1) on distal 0.70 or more. Many taxa have most of the surface of tergum VIII ( $\geq$  distal 0.70) covered with setae, e.g. *Aedes*, 'Ae. (*Aedimorphus*)' (most species) (see Reinert, 2000g: fig. 2, 'Ae. (*Adm.*) domesticus), 'Ae. (*Canraedes*)', *Bruceharrisonius*, *Christophersomyia*, *Edwardsaedes*, *Fredwardsius*, *Halaedes*, *Kompia*, *Mucidus*, *Neomelaniconion*, *Ochlerotatus s.l.* (most species), *Ochlerotatus* (subgenera *Geoskusea*, *Levua*, *Pseudoskusea*, *Rhinoskusea* and *Rusticoidus*), *Paraedes*, *St. aegypti*, *Ta. togoi* and *Ve. (Har.) yusafi*. Other taxa have few to several setae on the distal 0.60 or less of tergum VIII, e.g. *Belkinius*, *Bothaella* (see Reinert, 2000g: fig. 14, *Bo. helenae*), *Finlaya*, *Macleaya*, *Scutomyia* and *Skusea*.

262. *Tergum VIII*, scales: (0) absent, occasionally with 1–3 adventitious scales; (1) present,  $\geq$  14 scales. Tergum VIII lacks scales, or a few adventitious scales are present (state 0), in some aedine taxa, e.g. 'Ae. (*Adm.*) alboscuteclatus', 'Ae. (*Can.*) cancricomis', *Fr. vittatus*, *In. pulverulentus*, *Ja. (Jan.) deserticola*, *Mu. (Mucidus)*, *Oc. (Och.) infirmatus*, *Oc. (Och.) scapularis* (see Reinert, 2002e: fig. 26), *Ochlerotatus* (subgenera *Geoskusea*, *Levua*, *Pseudoskusea* and *Rhinoskusea*), *Psorophora*, *Rampamyia* and the outgroup species *Ma. titillans*. Specimens of *Be. aurotaeniatus* normally have two or three scales on tergum VIII but one possessed six scales (scored 0). Other aedines have a moderate number to numerous scales (state 1) (some species with scales nearly covering the tergum), espe-

cially on the distal part, e.g. *Ar. (Arm.) subalbatus*, *As. brevitibia*, *Br. greenii*, *Di. furcifer*, *Er. quinquevittatus*, *Fl. kochi*, *Hg. (Hag.) splendens*, *St. desmotes* and *Ud. argyrurus* (see Reinert, 2000e: fig. 1).

263. *Sternum VIII*, development: (0) mostly membranous; (1) mostly membranous, but with heavily sclerotized, rod-shaped structures laterally on each side; (2) mostly sclerotized with a narrow, median, longitudinal, non-sclerotized area; (3) entirely sclerotized. Sternum VIII is mostly membranous (state 0) in some aedine species (see Reinert, 2002e: fig. 28, *Oc. (Cul.) sollicitans*), also see the information under character 257. Species of all subgenera of *Psorophora* have a nearly entirely membranous sternum VIII with small, scattered, sclerotized, island-like areas and heavily pigmented, rod-like structures on each side (state 1) (see Reinert, 2000d: figs 1–3, *Ps. (Gra.) jamaicensis*, *Ps. (Jan.) discrucians* and *Ps. (Pso.) ciliata*). A sclerotized sternum VIII with a median, longitudinal, non-sclerotized area (state 2) is found in some species, e.g. *Oc. caballus* (see Reinert, 2002e: fig. 23) and *Hg. (Con.) leucocelaenus* (see Reinert, 2002c: fig. 1). The median, non-sclerotized area may extend from approximately proximal 0.30 to the entire length of sternum VIII. Sternum VIII is entirely sclerotized (state 3) in most aedine taxa (see Reinert, 2002c: figs 4 and 71, *Br. greenii* and *Mo. purpurea*).

264. *Sternum VIII*, posterior margin: (0) gently rounded; (1) more or less straight; (2) more or less uniformly sloping cephalad from apicolateral corners to midline; (3) median emargination separating broadly rounded lateral lobes; (4) median emargination separating sublateral lobes. See Reinert (2002e) for examples of state (0) (figs 10 and 20, *Oc. (Geo.) fimbripes* and *Oc. intrudens*), state (1) (fig. 6, *Fl. kochi*), state (2) (figs 32 and 33, '*Oc. (Pro.) kompi*' and '*Oc. (Pro.) terreus*'), state (3) (figs 17 and 24, *Mu. (Muc.) alternans* and *Oc. (Chs.) fulvus pallens*) and state (4) (fig. 9, *Pm. papuensis*).

265. *Sternum VIII*, seta 2-S, insertion relative to seta 1-S: (0) noticeably posterior; (1) lateral at or near same level as seta 1-S. See Reinert (2000c) for a description of seta 2-S in Aedini. Reinert (2000g) illustrated examples of state (0) (figs 12 and 16, *Al. marshallii* and *Cr. thomsoni*) and state (1) (figs 23 and 33, *In. pulverulentus* and *Sk. pemaensis*). A number of taxa have numerous long setae along the median area that do not appear to be in a distinct pattern. Since these setae are arranged in a longitudinal pattern, they are scored as state (0).

266. *Sternum VIII*, scales: (0) absent, occasionally with 1–3 adventitious scales; (1) present,  $\geq$  10 scales,

often covering much of surface. Some species of Aedini have no scales on sternum VIII, e.g. 'Ae. (Adm.)' *alboscuteclatus*, 'Ae. (Can.)' *cancricomes* and *Fr. vittatus* (see Reinert, 2000g: figs 9, 15 and 21), however some specimens occasionally have 1–3 scales scattered over the surface (see Reinert, 2002e: figs 3 and 23, *Da. geniculata* and *Oc. caballus*). *Collessius* (*Col.*) *macfarlanei* has no scales or rarely one or two, but the sternum has numerous short lanceolate setae interspersed with slender setae (scored 0). Most aedine species have several scales (see Reinert, 2002e: fig. 47, *Ko. purpureipes*) or even more numerous scales covering most of the surface of the sternum (see Reinert, 2002e: figs 4 and 6, *Br. greenii* and *Fl. kochi*). A few specimens of some species exhibit a slight overlap between states.

267. *Tergum IX*, width/length ratio: (0)  $\geq 2.0$ ; (1)  $\leq 1.8$ . Reinert (2000c) defined tergum IX width as 'the distance measured along a straight line across the widest part of the sclerotized and pigmented area of tergum IX' and tergum IX length as 'the distance measured to the apex along a perpendicular line drawn from a straight line across the base of the sclerotized and pigmented area of tergum IX'. Reinert (2008a) defined tergum IX width/length ratio as 'width measured along straight line across widest part of sclerotized and pigmented area of tergum IX divided by distance measured to apex along a perpendicular line drawn from a straight line across base of sclerotized and pigmented area of tergum IX'. Few aedines have a wide and relatively short tergum IX (state 0), e.g. *As. brevitibia*, *Belkinus* (see Reinert, 1982: fig. 3, *Be. aurotaeniatus*), *Co. (Alloeomyia)* and *Georgecraigius*. The outgroup taxa, *Cx. quinquefasciatus*, *Ma. titillans* (see Gerry, 1932: figs 28 and 40) and *Cs. inornata* (see Rees & Onishi, 1951: fig. 35) exhibit state (0). Most aedine taxa exhibit state (1) (see Reinert, 2000g: figs 16, 20 and 21, *Cr. thomsoni*, *Ed. imprimens* and *Fr. vittatus*).

268. *Tergum IX*, development: (0) single sclerite, usually with small to deep emargination on posterior margin; (1) two sclerites connected by membrane. Tergum IX of most aedine species is a single sclerite (state 0), e.g. *Aedes* (see Reinert, 2000g: fig. 1, *Ae. cinereus*), *Alanstonea*, *Belkinus*, *Bothaella*, *Christophersomyia*, *Diceromyia*, *Finlaya*, *Leptosomatomyia*, *Macleaya*, *Psorophora*, *Skusea*, *Verrallina* and *Zeugomyia*. This sclerite may be entirely sclerotized or have a narrow mesal connection between the lateral parts, and it may be darkly pigmented or have the mesal area slightly paler. Two lateral sclerites connected by membrane (state 1) are found in a few taxa, e.g. *Eretmapodites* (see Reinert, 2001f: figs 1 and 2, *Er. quinquevittatus* and *Er. chrysogaster*),

*Georgecraigius* (both subgenera), *Kenknightia*, *Opifex* (both subgenera) and *Udaya*.

269. *Tergum IX*, setae: (0) absent; (1) present. Setae are normally present on tergum IX in Aedini, but some species have no setae on the tergum, e.g. *Gc. (Gec.) atropalpus*, *Hg. (Con.) leucoclaenus*, *Pm. argyronotum* and the outgroup species *Ma. (Man.) titillans*. A few species, e.g. *Hw. walkeri*, normally have tergum IX without setae and are coded (0). One to three setae are normally present on one of the short, wide lobes of tergum IX in *Er. quinquevittatus*, but the other lobe often has the setae reduced in number or absent, coded (1).

270. *Tergum IX*, insertion of setae: (0) on distal area; (1) on distal and much of median areas. Most aedine taxa have setae distally on tergum IX, e.g. *Fl. kochi* (see Reinert, 2002e: fig. 6), but these setae occur distally and along much of the median area in *Pso. raphora* (see Reinert, 2000d: figs 1–3). Species without setae on tergum IX are coded (–). See the information under character 269.

271. *Postgenital lobe*, posterior margin: (0) rounded; (1) straight; (2) emarginate. See Reinert (2002e) for examples of state (0) (figs 31–35, 'Oc. (Protomacleaya)' and figs 8 and 19, *Do. nivea* and *Op. (Not.) chathamicus*), state (1) (fig. 43, *Hw. fulvithorax*) and state (2) (figs 4 and 25, *Br. greenii* and *Oc. grossbecki*).

272. *Postgenital lobe*, ratio of ventral width at distal 0.20 to cercus width at midlength: (0)  $\leq 0.65$ ; (1)  $\geq 0.66$ . The ratio is determined by dividing the width of the postgenital lobe at the distal 0.20 of its ventral length by the width of the cercus at 0.50 of its dorsal length. See Reinert (2000c) for definitions of 'cercus length' and 'ventral postgenital lobe length'.

273. *Postgenital lobe*, ventral index: (0) 0.47–1.64; (1) 1.65–2.81; (2) 2.90–4.32. The postgenital lobe ventral index is determined by dividing the ventral length by the ventral width at the distal 0.20 (Reinert, 2008a). The postgenital lobe is relatively short and wide in taxa that exhibit state (0) (see Reinert, 2001e: fig. 4, *Ve. (Ver.) carmenti*). It is moderately long and moderately wide in those taxa that exhibit state (1) (see Reinert, 2000g: figs 1 and 2, *Ae. cinereus* and 'Ae. (Adm.)' *domesticus*), and it is noticeably long and narrow in those that exhibit state (2) (see Reinert, 2002e: figs 34 and 39, 'Oc. (Pro.)' *triseriatus* and *Za. longipalpis*). See information included in character 272.

274. *Postgenital lobe*, insertion of ventral setae: (0) on distal area; (1) on median area; (2) on entire surface.

The presence of setae on the distal part (state 0) of the postgenital lobe is the usual condition in Aedini (see Reinert, 2002e: figs 3, 4 and 6, *Da. geniculata*, *Br. greenii* and *Fl. kochi*). Setae on the median area (state 1) are characteristic of *Fredwardsius* (see Reinert, 2000g: fig. 21, *Fr. vittatus*). *Opifex (Opi.) fuscus* (see Reinert, 2001d: fig. 1) has numerous setae covering the entire ventral surface (state 2) of the postgenital lobe.

275. *Upper vaginal sclerite*: (0) absent; (1) present. This structure is absent in a number of aedine taxa, e.g. *Aztecaedes*, *Kompia*, *Haemagogus* (see Reinert, 2002c: figs 1 and 2, *Hg. (Con.) leucocelaenus* and *Hg. (Hag.) splendens*), *Ochlerotatus* (subgenera *Chrysoconops*, *Culicelsa*, *Rhinoskusea* and *Rusticoidus*), *Psorophora*, *Skusea* and *Tanakaius*. An upper vaginal sclerite is present in many other taxa, e.g. *Aedes*, *Albuginosus*, *Armigeres*, *Edwardsaedes*, *Indusius*, *Isoaedes*, *Leptosomatomyia*, *Neomelaniconion*, *Stegomyia* (see Reinert, 2000g: figs 34 and 35, *St. aegypti* and *St. africana*), *Udaya* and *Zeugomyia*. The sclerite may be small and restricted to the inner margin of the upper vaginal lip, or extend as a well-developed plate mesally on the upper vaginal wall (see Reinert, 2001e: figs 1–3, *Ve. (Har.) yusafi*, *Ve. (Nma.) indica* and *Ve. (Ver.) butleri*). An upper vaginal sclerite is present in the four outgroup species.

276. *Lower vaginal sclerite*: (0) absent; (1) present. Absence of the lower vaginal sclerite (see illustrations in Reinert, 2000b) is the normal condition in Aedini, however it is well developed in *Verrallina* (Reinert, 1999d; 2001e: figs 1–3, *Ve. (Har.) yusafi*, *Ve. (Nma.) indica* and *Ve. (Ver.) butleri*). The outgroup species *Cx. quinquefasciatus* has a well-developed, horse shoe-shaped, lower vaginal sclerite on the median area of the vaginal wall between the inner margins of the lower vaginal lip. This structure in *Culex* has been frequently misinterpreted in the literature.

277. *Insula, development*: (0) tongue-like; (1) lip-like; (2) weakly/poorly developed or absent. Species in the *Aedes* group of genera have a tongue-like (lingulate) insula (see Reinert, 2000g: figs 1, 14, 17 and 24, *Ae. cinereus*, *Bo. helenae*, *Di. furcifer* and *Ia. cavaticus*) that distinguish them from species of the *Ochlerotatus* group of genera that have a lip-like insula (see Reinert, 2002e: figs 8, 9 and 26, *Do. nivea*, *Pm. papuensis* and *Oc. (Och.) scapularis*). Species of subgenera *Neomacleaya* and *Verrallina* of *Verrallina* have an ill-defined insula, whereas the insula is absent in species of subgenus *Harbachius*. See Reinert (1999d) for illustrations and a discussion of the insula in *Verrallina*.

278. *Insular setae*: (0) absent; (1) present. Insular setae are absent in many taxa, e.g. *Aedes*, *Alanstonea*, *Albuginosus* (see Reinert, 2000g: fig. 12, *Al. marshallii*), *Armigeres*, *Edwardsaedes*, *Scutomyia*, *Stegomyia*, *Udaya* and *Zeugomyia*. Many other taxa have insular setae, e.g. *Abraedes*, *Bruceharrisonius*, *Finlaya*, *Haemagogus*, *Kenknightsia*, *Kompia*, *Mucidus*, *Ochlerotatus*, *Psorophora* and *Zavortinkius*.

279. *Insula, insertion of setae*: (0) in lateral patches; (1) in median patch. Insular setae are well developed in lateral patches (state 0) in many taxa, e.g. *Downsiomyia*, *Finlaya*, *Howardina*, *Mucidus*, *Ochlerotatus*, ‘*Oc. (Protomacleaya)*’ (see Reinert, 2002e: figs 33 and 34, ‘*Oc. (Pro.) terreus*’ and ‘*Oc. (Pro.) triseriatus*’), *Opifex* and the outgroup taxa *Ma. titillans* and *Or. signifera*. Setae are present in a median patch (state 1) in *Haemagogus*, *Hz. (Heizmannia)* and the outgroup taxa *Cs. inornata* and *Cx. quinquefasciatus*. The setae are very short in species of subgenus *Heizmannia* of *Heizmannia* (see Reinert, 2002b) and are long and well developed in the other taxa (Reinert, 2002e). Insular setae are absent in *Hz. (Matinglyia)* and numerous other genera of Aedini, but one or more small tuberculi with or without a tiny spicule may be present. Species without insular setae are coded (–). See the information under character 278.

280. *Cercus index*: (0)  $\leq 2.88$ ; (1) 2.94–4.06; (2)  $\geq 4.21$ . Reinert (2000c) defined the cercus index as the ‘ratio of cercus length to cercus width’. Cercus length is measured on the dorsal surface and the width is measured at midlength of the cercus.

281. *Cercal scales*: (0) absent; (1) present. Cercal scales are absent in a number of taxa, e.g. *Psorophora* (see Reinert, 2000d: figs 1–3, *Ps. (Gra.) jamaicensis*, *Ps. (Jan.) discrucians* and *Ps. (Pso.) ciliata*), *Ud. argyrurus* and *Ze. gracilis*. Other taxa have several to numerous cercal scales, e.g. *Armigeres* (see Reinert, 2002d: figs 1 and 2, *Ar. (Arm.) subalbatus* and *Ar. (Lei.) longipalpis*), *Di. furcifer*, *Oc. (Rusticoidus)*, *Oc. grossbecki* and *St. desmotes*. Some specimens of a few species have one adventitious scale on one cercus; hence these species are scored (0).

282. *Cercus, distal part*: (0) sharply oblique; (1) gently oblique; (2) moderately to broadly rounded; (3) narrowly rounded; (4) truncate. Examples of the distal part of the cercus are illustrated in Reinert (2002e), i.e. state (0) (fig. 15, *Mc. (Mac.) tremula*), state (1) (fig. 34, ‘*Oc. (Pro.) triseriatus*’), state (2) (fig. 6, *Fl. kochi*) and state (3) (fig. 14, *Oc. (Lev.) geoskusea*). See Reinert (2002c: fig. 1, *Hg. (Con.) leucocelaenus*) for state (4). Some species of ‘*Ae. (Aedimorphus)*’ have the distal part of the cercus moderately to

broadly rounded (see Reinert, 2000g, figs 4 and 8, 'Ae. (Adm.) mediolineatus and 'Ae. (Adm.) punctifemoris' and are scored (2).

283. *Cercus/dorsal postgenital lobe index*: (0)  $\leq 3.20$ ; (1) 3.24–4.78; (2)  $\geq 4.90$ . Reinert (2000b) defined the cercus/dorsal postgenital lobe index as the 'ratio of the dorsal cercus length to the dorsal postgenital lobe length'. See Reinert (2000c) for definitions of measurements for the cercus and postgenital lobe.

284. *Accessory spermathecae*: (0) absent; (1) present. All species of Aedini have a large spermathecal capsule (primary) and most have two additional smaller spermathecal capsules (accessory). Reinert (2000g) provided examples of state (0) (fig. 65, 'Ae. (Adm.) argenteopunctatus) with a single primary spermathecal capsule and state (1) (figs 33 and 34, *Sk. pambaensis* and *St. aegypti*) with a primary and two accessory spermathecal capsules.

285. *Accessory spermathecae, development*: (0) two very small (rudimentary); (1) two large. Presence of two very small accessory spermathecal capsules that appear to be rudimentary are found in some species, e.g. 'Ae. (Adm.) alboscutellatus, 'Ae. (Adm.) culicinus and 'Ae. (Adm.) lowisii (Theobald) (see Reinert, 1973a: figs 18, 20 and 21). Examples of species with two large accessory spermathecal capsules are *Da. geniculata* and *Br. greenii* (see Reinert, 2002e: figs 3 and 4). See the information under character 284. Species with a single primary spermathecal capsule are coded (–).

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286. *Tergum IX, posterior margin*: (0) two small, relatively narrow lobes; (1) two moderately broad to broad lobes. See examples of state (0) in Tanaka *et al.* (1979: fig. 93, *Oc. intrudens* and *Oc. diantaeus*) and Belkin (1962: figs 327 and 333, *St. futunae* and *St. hoguei*) and state (1) in Reinert (1973a: figs 34 and 41, 'Ae. (Adm.) alboscutellatus and 'Ae. (Adm.) pallidostriatus) and Zavortink (1972: figs 46 and 49, *Gc. (Gec.) epactius* and *Gc. (Gec.) atropalpus*).

287. *Tergum IX, position of lateral lobes on posterior margin*: (0) close together; (1) widely separated. Belkin (1962: figs 267 and 270, *Oc. (Emp.) vigilax* and *Oc. (Gli.) mcdonaldii*) illustrated state (0). Small, widely separated lobes (state 2) are characteristic of some *Stegomyia*, e.g. see Huang, 1977a: fig. 14, *St. desmotes* (lobes separated by more or less flattened area) and fig. 1, *St. edwardsi* (lobes separated by broadly convex area). Also, see the information under character 286.

288. *Tergum IX, setae*: (0) absent; (1) present. Few aedine taxa have no setae on tergum IX (see Zavortink, 1972: figs 46 and 49, *Gc. (Gec.) epactius* and *Gc. (Gec.) atropalpus*; Reinert, 1974: figs 27, 30 and 35, *Ve. (Ver.) carmentis*, *Ve. (Nma.) indicus* and *Ve. (Har.) yusafi*). Most taxa have a few to numerous setae. *Isoaedes cavaticus* possesses both long and short, slender setae on broadly rounded lobes (see Reinert, 1979: fig. 3). In specimens of *Oc. (Rhi.) wardi* these setae are normally absent or rarely a specimen with a few short, fine setae on one lobe of tergum IX (coded 0).

289. *Tergum IX, setae*: (0) all slender; (1) some or all stout. Taxa with stout setae normally have some or all of the setae somewhat flattened. See Reinert (1973c: figs 8 and 9, *Bo. helenae* and *Bo. eldridgei*) for examples of state (0) and Wood *et al.* (1979: pls 30 and 42, *Oc. hexodontus* and *Oc. punctor*) for state (1). Some species possess setae on tergum IX that are moderately thickened, e.g. 'Oc. (Protomacleaya)', these are coded (1). Species without setae on tergum IX, e.g. *Gc. (Gec.) atropalpus* and *Oc. (Rhi.) longirostris*, are coded (–). See the information under character 288.

290. *Sternum IX, vestiture*: (0) absent; (1) present. Setae, and sometimes scales, are present on sternum IX in most Aedini (see Reinert, 1981: fig. 3, *Pr. barraudi*; Reinert, 1990: fig. 12, *Ke. dissimilis*) but are absent in some, e.g. *Ar. (Leicesteria)*, *Fredwardsius*, *Indusius*, *Isoaedes*, *Leptosomatomyia*, *Skusea* and *Stegomyia* (see Huang, 1979: fig. 1, *St. aegypti*). Setae are normally absent (very rarely a few present) on sternum IX of *Ma. (Man.) titillans* and *Or. signifera*, and are coded (0).

291. *Sternum IX, vestiture*: (0) setae; (1) setae and scales. Setae occur on sternum IX in many aedine taxa (see Reinert, 1973a: figs 34–36, 'Ae. (Adm.) alboscutellatus, 'Ae. (Adm.) caecus and 'Ae. (Adm.) culicinus). Setae and few to several scales are present in some taxa, e.g. *Hs. (Heizmannia)* (see Mattingly, 1970c: figs 15, 20 and 36, *Hs. covelli* Barraud, *Hs. funerea* (Leicester) and *Hs. reidi* Mattingly), *Ud. lucaris* and *Ze. gracilis*. Taxa without vestiture on sternum IX are coded (–). See the information under character 290.

292. *Gonocoxite, dorsomesal apical lobe*: (0) absent; (1) present. Examples of species without a lobe include *Ta. togoi*, *Ta. savoryi*, *Do. nipponica*, *Do. nishikawai* (Tanaka, Mizusawa & Saugstad), *St. riversi* and *St. galloisi* (see Tanaka *et al.*, 1979: figs 100, 109 and 115). An apical lobe is variously devel-

oped in most *Ochlerotatus* (see Wood *et al.*, 1979: pls 12, 16, 21 and 40, *Oc. aloponotum*, *Oc. canadensis canadensis*, *Oc. decticus* and *Oc. (Rus.) provocans*). The dorsomesal surface of the gonocoxite of 'Ae. (*Canraedes*)' possess a slightly subapical, somewhat expanded area bearing an elongate projection with terminal spiniform(s). The mesoventral surface of this area also is connected to the dorsomesal area of the claspette by a narrow, sclerotized strip. Species of 'Ae. (*Canraedes*)' are coded (1) based on the unusual development of this area.

293. *Gonocoxite, dorsomesal basal lobe*: (0) absent; (1) present. See Belkin (1962: figs 226, 297 and 327, *Ra. notoscripta*, 'Ae. (*Adm.*) alboscuteclatus and *St. futunae*) for examples of species without a basal lobe (state 0) and his figures 266, 268 and 278 (*Oc. (Buv.) edgari*, *Oc. (Emp.) vigilax* and *Mu. (Pdo.) painei*) for examples of species with a basal lobe (state 1). Species of subgenus *Geoskusea* of *Ochlerotatus* lack a basomesal lobe on the dorsal surface of the gonocoxite, but most species (all except *Oc. (Geo.) longiforceps*) have a densely setose lobe on this surface at approximately midlength of the mesal margin (see Belkin, 1962: figs 214, 215, *Oc. (Geo.) becki* (Belkin), *Oc. (Geo.) daggyi* (Stone & Bohart) and *Oc. (Geo.) perryi* (Belkin); Tanaka *et al.*, 1979: fig. 127, *Oc. (Geo.) baisasi*), and are coded (0).

294. *Gonocoxite, scales*: (0) absent; (1) present. Numerous scales are usually present on the gonocoxite in Aedini (see Tanaka *et al.*, 1979: figs 78, 87, 100 and 109, *Hs. (Hez.) lii*, *Oc. punctator*, *Ta. savoryi*, *Do. nipponica* and *St. albopicta*) but are absent in a few species, e.g. *Op. (Opi.) fuscus* (see Belkin, 1962: fig. 207), *In. pulverulentus* (see Reinert, 1976b: fig. 4) and *Ps. (Pso.) ciliata*, as well as the outgroup species *Cs. inornata* and *Cx. quinquefasciatus*. Species of *Edwardsaedes* have only a few broad scales on the gonocoxite that are often dislodged in slide-mounted specimens (scored 1).

295. *Gonocoxite, mesal surface*: (0) entirely membranous; (1) partly or entirely sclerotized. The mesal surface of the gonocoxite is commonly membranous in Aedini (see Ross, 1947: figs 145a and 155a, *Oc. dorsalis* and *Oc. excrucians*). This area is partially or completely sclerotized in *Indusius* (see Reinert, 1976b: fig. 4, *In. pulverulentus*), *Neomelaniconion*, *Oc. (Rhinoskusea)*, *Psorophora*, *Skusea*, *Udaya*, *Verrallina* (subgenera *Harbachius* and *Neomacleaya*) (see Reinert, 1974: fig. 35, *Ve. (Har.) yusafi*) and *Zeugnomyia*. State (1) also occurs in the outgroup species *Cs. inornata*, *Cx. quinquefasciatus* and *Or. signifera*.

296. *Gonocoxite, seta(e) on basomesal area of dorsal surface*: (0) absent; (1) present. This area of the gonocoxite is bare in some species, e.g. *Oc. (Geo.) baisasi* (see Tanaka *et al.*, 1979: fig. 127).

297. *Gonocoxite, setal development on basomesal area of dorsal surface*: (0) all slender; (1) one or more stout or flattened. For examples of state (0), see illustrations of '*Oc. (Protomacleaya)*' in Zavortink (1972). For an example of state (1), see Wood *et al.* (1979: pl. 20, *Oc. communis*). Species without setae on the basomesal area of the dorsal surface are coded (-). See the information under character 296.

298. *Gonocoxite, lateral setae*: (0) mostly short; (1) mostly long. Setae on the lateral surface of the gonocoxite are mostly short in *Indusius*, *Mc. (Macleaya)*, *Oc. (Levua)*, *Op. (Opifex)* and *Skusea*. Most of the lateral setae are long in most taxa of Aedini. See illustrations in Belkin (1962: fig. 207, *Op. (Opi.) fuscus*) for state 0 and his figure 297 ('Ae. (*Adm.*) alboscuteclatus') for state (1).

299. *Gonocoxite, few to several short blunt-tipped spiniforms in a row on mesal area of ventral surface*: (0) absent; (1) present. McIntosh (1971: figs 6–12, *Neomelaniconion* species) illustrated state (1).

300. *Gonocoxite, row or patch of long moderately broad to broad scales on mesal area of ventral surface*: (0) absent; (1) present. See Belkin (1962: figs 242 and 248, *Fl. franclemonti* and *Fl. fuscitarsis* (Belkin)) and Zavortink (1972: figs 55 and 60, *Hg. (Con.) leucotaeniatus* and *Hg. (Con.) leucocelaenus*) for examples of state (1).

301. *Gonocoxite, row or patch of long narrow lanceolate setae on mesal area of ventral surface*: (0) absent; (1) present. Belkin (1962, figs 226 and 230, *Ra. notoscripta* and *Ra. albilabris*) provided illustrations of state (1).

302. *Gonostylus, attachment to gonocoxite*: (0) apical; (1) subapical. Most species of Aedini have the gonostylus attached to the apex of the gonocoxite (state 0) (see Belkin, 1962: figs 217, 250, 268 and 321, *Oc. (Geo.) longiforceps*, *Fl. hollingsheadi* (Belkin), *Oc. (Emp.) vigilax* and *St. albopicta*) but some taxa have it attached subapically (state 1), e.g. *Aedes*, 'Ae. (*Canraedes*)', *Indusius*, *Neomelaniconion*, *Op. (Opi.) fuscus*, *Skusea* and *Ve. (Harbachius)*. The gonostylus is also attached subapically in some species of *Diceromyia*, *Lorrainea*, *Paraedes*, *Stegomyia* (Africanus Group) and most species of *Ve. (Neomacleaya)*. See Tanaka *et al.* (1979) for examples of state (1) (figs 130, 133, 136 and 140, *Ne. lineatopenne*, *Ae. esoensis*, *Ae.*



*yamadai*, *Ae. sasai* Tanaka, Mizusawa & Saugstad, *Ve. (Har.) nobukonis* and *Ve. (Nma.) atrisimilis* (Tanaka & Mizusawa)).

303. *Gonostylus*, proximal part: (0) narrow; (1) broad. The width of the basal apodeme is disregarded when measuring the width of the proximal part of the gonostylus. See Belkin (1962) for examples of state (0) (figs 268 and 276, *Oc. (Emp.) vigilax* and *Mu. (Muc.) alternans*) and state (1) (figs 207 and 273, *Op. (Opi.) fuscus* and *Oc. (Lev.) geoskusea*).

304. *Gonostylus*, median part: (0) noticeably narrower than proximal part; (1) slightly narrower to slightly broader than proximal part; (2) noticeably broader than proximal part. Taxa with the middle part much narrower than the proximal part (state 0) are illustrated by Wood *et al.* (1979: pl. 19, *Ae. cinereus*) and Tanaka *et al.* (1979: fig. 133, *Ae. esoensis* and *Ae. yamadai*). Species that have the middle part slightly narrower to slightly wider than the proximal part (state 1) are illustrated by Wood *et al.* (1979: pls 13, 14, 16 and 22, *Gc. (Gec.) atropalpus*, *Oc. aurifer*, *Oc. canadensis canadensis* and *Oc. diantaeus*). See Edwards (1941: fig. 62, *Ne. palpale*, *Ne. taeniarostre* (Theobald) and *Ne. bolense* (Edwards)) and Belkin *et al.* (1970: figs 59 and 66, *Ps. (Jan.) ferox* and *Ps. (Gra.) jamaicensis*) for species in which the median part is noticeably broader (state 2) than the proximal part.

305. *Gonostylus*, distal part: (0) narrower than proximal part; (1) slightly broader than proximal part; (2) much broader than proximal part. The distal part of the gonostylus is narrower than the proximal part (state 0) in most *Ochlerotatus* (see Wood *et al.*, 1979: pls 14, 15, 16 and 17, *Oc. aurifer*, *Oc. campestris*, *Oc. canadensis canadensis* and *Oc. cantator*; Jupp, 1996: fig. 29, *Albuginosus* species). Many species of *Stegomyia* have the distal part somewhat broader than the proximal part (state 1) (see Belkin, 1962: figs 321, 323 and 327, *St. albopicta*, *St. aobae* (Belkin) and *St. futunae*). A number of species of '*Ae. (Aedimorphus)*' have the distal part much broader than the proximal part (state 2) (see Reinert, 1973a: figs 34, 36 and 38, '*Ae. (Adm.) alboscuteclatus*', '*Ae. (Adm.) culicinus*' and '*Ae. (Adm.) mediolineatus*').

306. *Gonostylus*, elongate lobe on lateral surface: (0) absent; (1) present. See the discussion under character 307.

307. *Gonostylus*, insertion of elongate lobe on lateral surface: (0) on median part; (1) on distal part. A narrow, elongate lobe on the median part of the lateral surface of the gonostylus is illustrated in

Reinert (1973a: figs 41 and 46, '*Ae. (Adm.) pallidostriatus*' and '*Ae. (Adm.) taeniorhynchoides*') and Tewari & Hiriyani (1992: figs 3 and 8, *Te. agastyai* and *Te. reubenae*) and a lobe on the distal part in Reinert (1973a: figs 35 and 40, '*Ae. (Adm.) caecus*' and '*Ae. (Adm.) orbitae*'). Taxa without an elongate lobe on the lateral surface of the gonostylus (see character 306) are coded (-).

308. *Gonostylus*, moderately broad to broad lobe on median part of lateral surface: (0) absent; (1) present. See Mattingly (1970: figs 12 and 40, *Hs. (Hez.) complex* and *Hs. (Hez.) scintillans*) and Reinert (1972b: figs 6 and 7, *Ay. peytoni* and *Ay. griffithi*) for examples of species that bear a moderately broad and broad lobe on the median part of the lateral surface.

309. *Gonostylus*, horn-like projection on distal part of lateral surface: (0) absent; (1) present. See Reinert (1973a: figs 34, 36 and 42, '*Ae. (Adm.) alboscuteclatus*', '*Ae. (Adm.) culicinus*' and '*Ae. (Adm.) pampangensis*') for examples of species with a horn-like projection borne distally on the lateral surface of the gonostylus.

310. *Gonostylus*, seta(e) on distal 0.33: (0) absent; (1) present. Most aedine taxa have one or more setae on the distal 0.33 of the gonostylus in addition to the gonostylar claw(s). These may be minute to moderately long. See Tanaka *et al.* (1979: figs 112 and 130, *Ph. watasei* and *Ne. lineatopenne*) for examples of state (0) and their figures 81, 109 and 124 (*Oc. dorsalis*, *Oc. excrucians*, *Do. nipponica*, *Do. nishikawai*, *St. chemulpoensis* and '*Ae. (Adm.) alboscuteclatus*') for examples of state (1).

311. *Gonostylus*, scales: (0) absent; (1) present. Scales are usually absent from the gonostylus of Aedini, but they are present in some taxa, e.g. *As. brevitibia*, *Ar. (Lei.) magnus* (Theobald), *Ar. (Lei.) cingulatus* (Leicester), *Ar. (Lei.) omissus* (Edwards) (see Thurman, 1959: figs 41, 46 and 47), *Eretmapodites* (see illustrations in Service, 1990), *Lorrainea*, *Stegomyia* (some species, e.g. *St. chemulpoensis*, *St. mediopunctata* and *St. perplexa*) and *Ud. lucaris*.

312. *Gonostylar claw(s)*: (0) absent; (1) present. A few aedine taxa do not have a gonostylar claw, i.e. *Aedes* (see Tanaka *et al.*, 1979: fig. 133, *Ae. esoensis* and *Ae. yamadai*), *Belkinius* (see Reinert, 1982: fig. 2, *Be. aurotaeniatatus*), *Edwardsaedes* (see Reinert, 1976b: fig. 8, *Ed. imprimens*), *Indusius* (see Reinert, 1976b: fig. 4, *In. pulverulentus*), *Paraedes* (see Reinert, 1981: figs 3–9) and *Verrallina* (see Reinert, 1999d: figs 6–9). See character 313 for reference to taxa with one or more gonostylar claws.

313. *Gonostylar claw(s), number*: (0) one; (1) two; (2) three or more. Most species of Aedini have a single gonostylar claw (see Belkin, 1962: figs 210, 235, 268 and 321, *Ha. australis*, *Fl. samoana* Grünberg, *Oc. (Emp.) vigilax* and *St. albopicta*). Belkin (1962) provided illustrations of taxa with two gonostylar claws (fig. 273, *Oc. (Lev.) geoskusea*) and with three or more gonostylar claws (fig. 356, *Ar. (Arm.) breinli*). Some species of *Stegomyia* (see Bohart, 1957: figs 5M, 5N and 5P, *St. agrihanensis* (Bohart), *St. saipanensis* and *St. rotana*) have two gonostylar claws. *Pseudarmigères* have a single gonostylar claw near midlength of the gonostylus, plus numerous stout spicules that are similar in shape to the gonostylar claw on the mesal margin of the gonostylus distal to the claw (state 0) (see Jupp, 1996: fig. 41, *Pa. natalensis* (Edwards)). Taxa without a gonostylar claw are coded (-). See the information under character 312.

314. *Most proximal gonostylar claw, insertion on gonostylus*: (0) at or near apex; (1) subapical, some distance from apex; (2) near midlength. See Belkin (1962) for examples of state (0) (fig. 226, *Ra. notoscripta*), state (1) (figs 297 and 299, '*Ae. (Adm.) albocutellatus*' and '*Ae. (Adm.) vexans*' (= *nocturnus* Theobald) and state (2) (fig. 315, *Sc. albolineata*). State (2) is also characteristic of the Afrotropical genus *Albuginosus* (see Reinert, 1986: fig. 2, *Al. marshallii*) and *Pa. natalensis*. In species with more than one gonostylar claw (see character 313) the most proximal claw is used for measurements and descriptions. Taxa without a gonostylar claw are coded (-), see character 312.

315. *Most proximal gonostylar claw, ratio of length to length of gonostylus*: (0)  $\leq 0.35$ ; (1)  $\geq 0.39$ . The length of the gonostylar claw is determined by dividing its length by the length of the gonostylus. Belkin (1962) illustrated examples of a short gonostylar claw (figs 210, 266, 276 and 313, *Ha. australis*, *Oc. (Buw.) edgari*, *Mu. (Muc.) alternans* and *St. aegypti*) and a moderately long to long one (figs 230, 248 and 254, *Ra. albilabris*, *Fl. fuscitarsis* and *Fl. neogeorgiana*). Taxa without a gonostylar claw are coded (-), see character 312. Also see the information under character 313.

316. *Most proximal gonostylar claw, development*: (0) relatively narrow spiniform; (1) moderately broad spiniform; (2) short, claw-like spiniform; (3) flattened, relatively broad, somewhat leaf-like structure. Many aedines exhibit state (0), e.g. *Finlaya*, *Halaedes* (see Belkin, 1962: figs 210 and 254, *Ha. australis* and *Fl. neogeorgiana* (Belkin)), *Ochlerotatus* (most species), *Patmarksia*, *Rampamyia* and some *Stegomyia*. *Scutomyia* (see figures in Huang, 1979) have a single,

moderately broad, stout, bluntly pointed or bluntly rounded spiniform (state 1) inserted some distance from the apex. *Ochlerotatus (Lev.) geoskusea* (see Belkin, 1962: fig. 273) and *Cs. (Cus.) inornata* are examples of state (2). *Diceromyia scanloni* (see Reinert, 1970: fig. 9) and '*Ae. (Adm.) fitchii*' Ingram & de Meillon (see McIntosh, 1975: fig. 21) are examples of state (3). Taxa without a gonostylar claw are coded (-), see character 312. Also see the information under character 313.

317. *Most proximal gonostylar claw, apex*: (0) acute; (1) bluntly pointed; (2) truncate, rarely rounded but nearly truncate. Huang (1977a: fig. 14C, *St. desmotes*) provided an example of state (0). Species with state (1) have the apex bluntly pointed to bluntly rounded (see Belkin, 1962: figs 315 and 356, *Sc. albolineata* and *Ar. (Arm.) breinli*). Tanaka *et al.* (1979: figs 81 and 115, *Oc. dorsalis*, *Oc. excrucians*, *St. riversi* and *St. galloisi*) illustrated examples of a narrow, truncated apex (state 2). '*Ochlerotatus (Fin.) biocellatus*' has a moderately long, slender gonostylar claw with the distal part forked into two attenuate branches (scored 0). Taxa without a gonostylar claw are coded (-), see character 312. Also see the information under character 316.

318. *Gonostylus/gonocoxite index*: (0)  $\leq 0.26$ ; (1) 0.30–0.40; (2) 0.42–0.71; (3)  $\geq 0.73$ . Reinert (1990) defined the gonostylus/gonocoxite index as the 'ratio determined by dividing the gonostylus length by the gonocoxite length'. He also defined the length of the gonostylus as the 'absolute length of gonostylus, minus gonostylar claw, measured from the tip of the basal apodeme to the apex' and the length of the gonocoxite as the 'length measured along a straight line from the tip of the dorsal attachment of gonocoxite (dga of Knight and Harrison, 1988) to the apex'. See examples of state (0) in Mattingly (1958: fig. 20a, '*Ae. (Can.) masculinus*'), state (1) in (Tanaka *et al.*, 1979: fig. 130, *Ne. lineatopenne*), state (2) in Zavor tink (1972: figs 31 and 36, *Ko. purpureipes* and *Az. ramirezi*) and state (3) in Reinert (1973c: figs 8–10, *Bothaella*).

319. *Claspette*: (0) absent; (1) present. Reinert (1999c, 2000b) discussed the homology of the claspette and basal mesal lobe in Aedini. The claspette is absent in the outgroup species *Cx. quinquefasciatus*. In this species the lobe with modified setae that arises from the mesal area of the dorsal surface of the gonocoxite is not homologous with the claspette in Aedini, which arises from the basosternal portion of the mesal surface of the gonocoxite and is connected mesally with its mate by a spiculate, more-or-less narrow, somewhat trough-like aedeagal guide. Aedine species

have the claspette variously developed, see the information under character 320.

320. *Claspette, development*: (0) single basal setose plaque, columnar lobe absent; (1) single columnar lobe; (2) two basal lobes, columnar lobe absent; (3) two basal lobes, one columnar. The claspette in Aedini is connected mesally with its mate by a median, spiculate, aedeagal guide. A claspette developed as a basal setose plaque may be modified differently in various taxa. State (0) varies from a small, short, narrow, inconspicuous strip extending laterally onto the basosternal area of the mesal surface of the gonocoxite and bears one or a few very short, slender setae (e.g. *Oc. (Geoskusea)* and *Oc. (Pseudoskusea)*) to a moderately large structure with numerous flattened setae (see Belkin, 1962: fig. 210, *Ha. australis*), however this state is represented in many taxa by a small to large, more-or-less oblong structure bearing few to numerous, relatively short, slender setae (see Reinert, 1973a: fig. 34, '*Ae. (Adm.) alboscuteallatus*'; Huang, 1990: fig. 10, *St. africana*). Wood *et al.* (1979) illustrated a claspette with a single short to long, columnar lobe (state 1) (pls 15, 20 and 25, *Oc. campestris*, *Oc. communis* and *Oc. excrucians*). Taxa with state (2) have the claspette developed as two lobes which are not columnar and bear various setae and or spiniforms, e.g. species examined of *Eretmapodites*, *Hz. (Heizmannia)* (see Mattingly, 1970), *Lorrainea* and *Oc. (Rhinoskusea)*. *Paraedes* is included as state (2), even though one lobe is columnar, because the development of the stem and filament is different from other taxa that exhibit state (3) (see Reinert, 1981: figs 3 and 8, *Pr. barraudi* and *Pr. ostentatio*). Some species of *Stegomyia*, e.g. *St. craggi*, *St. desmotes* and *St. w-albus* (see Huang, 1977a: figs 11, 14 and 33) have the claspette somewhat bilobed but the development is different than other taxa with state (2) and are more similar to other species of *Stegomyia*, and are therefore coded (0). State (3) is characteristic of *Bruceharrisonius* (see Reinert, 2003: fig. 2A, *Br. greenii*) and some *Ochlerotatus* (see Belkin *et al.*, 1970: fig. 71, *Oc. (Pcx.) pertinax*).

321. *Claspette, subapical thumb-like projection on columnar stem*: (0) absent; (1) present. Wood *et al.* (1979) illustrated a claspette with a single short to long, columnar lobe without a thumb-like projection (state 0) (pls 15, 20 and 25, *Oc. campestris*, *Oc. communis* and *Oc. excrucians*) and a similar claspette but with a subapical thumb-like projection (state 1) normally bearing a seta (pls 22 and 51, *Oc. diantaeus* and *Oc. thibaulti*). Taxa without a columnar stem are coded (-). Also see the information under character 320.

322. *Claspette, ratio of columnar stem length to length of aedeagus*: (0)  $\leq 0.85$ ; (1)  $\geq 0.90$ . Reinert (1990, 1999c) defined the measurements of the length of the claspette stem (=basal mesal lobe) as the 'length measured along a straight line from the most basal portion of the lateral lobe to the apex of the stem, minus the claspette filament' and the length of the aedeagus as the 'length measured along a straight line from the base to the apex'. Taxa without a columnar stem are coded (-). Also see the information under character 320.

323. *Claspette, vestiture*: (0) one or more slender or stout, simple seta(e); (1) one stout spiniform, elliptical or circular in cross section; (2) one moderately wide to wide, normally elongate, flattened structure; (3) one short, broad, convoluted/twisted structure; (4)  $\geq 3$  moderately long, stout, bluntly pointed, spiculate setae; (5)  $\geq 3$  long, more or less flattened spiniforms. State (0) includes a claspette with one or more simple setae that may be slender and or stout (see Harbach & Knight, 1980: figs 81a and 81b). Tanaka *et al.* (1979: figs 118, 127 and 133, *St. albopicta*, '*Ae. (Adm.) vexans nipponii*' and *Ae. yamadai*) and Berlin (1969: figs 17 and 43, *Hw. walkeri* and *Hw. sexlineata*) provided examples of state (0). *Bothaella eldridgei* possesses a long, more or less lanceolate seta in addition to numerous short, simple setae (scored 0). Examples of a claspette filament are illustrated for state (1) by Zavortink (1972: figs 6 and 11, '*Oc. (Pro.) brelandi*' and '*Oc. (Pro.) zoosophus*'), state (2) by Arnell (1976: figs 6 and 30, *Oc. (Och.) incomptus* (Arnell) and *Oc. (Och.) infirmatus*) and Lu & Ji (1997: fig. 31, *Lu. fengi*), state (3) by Wood *et al.* (1979: pl. 51, *Oc. thibaulti*) and state (4) by Belkin *et al.* (1970: figs 59 and 66, *Ps. (Jan.) ferox* and *Ps. (Gra.) jamaicensis*). *Psorophora (Jan.) ferox* possesses a short, broad, convoluted structure in addition to the moderately long, stout, bluntly pointed, spiculate setae (scored 3,4). The complex claspette of '*Ae. (Canraedes)*' species possesses several long, dark, more or less flattened spiniforms and is scored (5). *Skusea pambaensis* has the claspette developed as a narrow, sclerotized strip extending from the aedeagal guide caudally along the mesal margin of the gonocoxite to approximately the apex where it expands and bears 7 or 8, long, dark, somewhat flattened spiniforms (scored 5).

324. *Claspette filament, distinct transverse striations*: (0) absent; (1) present. In most species of Aedini, the claspette filament (see Harbach & Knight, 1980) does not have transverse striations. The claspette filament of *Finlaya* is long, foliform and with a membrane-like sheath or flap that is annulated transversely on approximately the middle third. The sheath is absent in several species of '*Oc. (Finlaya)*' but the filament

has several transverse striations near midlength. These are scored (1). The filament in *Oc. (Rusticoides)* has transverse striations but it is shorter, broader and thicker (scored 1) (see Gutsevich, Monchadskii & Stakel'berg, 1974: figs 133 and 135; Mohrig, 1969: figs 63 and 64, *Oc. (Rus.) rusticus* and *Oc. (Rus.) refiki*) and Wood *et al.* (1979: pl. 40, *Oc. (Rus.) provocans* (Walker)). This character is coded (–) for *Cx. quinquefasciatus*. Also see the information under characters 319 and 323.

325. *Aedeagus, development*: (0) single tube-like, scoop-like or trough-like structure; (1) comprised of two lateral plates (aedeagal sclerites). Reinert (2000b) illustrated and described the forms of the aedeagus, i.e. state (0) (figs 2A and 2C, *Az. ramirezi* and *Oc. (Och.) scapularis*) and state (1) (figs 2E, 2F, 2I and 2J, 'Ae. (Adm.) mediolineatus', 'Ae. (Adm.) stenoetrus' (Edwards) and *Ia. cavaticus*). When the aedeagus is divided into two lateral plates each plate normally bears several stout lateral or apical teeth, or both, and the plates are usually not, or are only weakly, fused apically. Species of *Christophersiomyia* appear to have two lateral plates with the distal parts strongly curved mesally and fused at the apex, and without teeth (except *Cr. gombakensis*, which has two or three short, stout teeth laterally). Species of *Bothaella* have the distal part of the lateral plates curved mesally and fused at the apex, and each plate bears three to eight short or long teeth (teeth weakly developed in *Bo. helenae*). Some species of *Lorrainea* appear to have the aedeagus divided into two lateral plates, with the apices lightly fused and slightly extended posteriorly. In some taxa, e.g. *Alanstonea*, *Diceromyia* and *Isoaedes*, the aedeagus has numerous long, stout, curved teeth laterally and apically, but the apices of the lateral plates appear to be strongly fused. In the monobasic *Indusius*, the aedeagus is unknown since the only slide-mounted specimen of *In. pulverulentus* in existence is badly damaged and several structures are missing (see Reinert, 1976b). Species of *Ochlerotatus* have the aedeagus simple and tube-like, scoop-like or trough-like. Mohrig (1969) provided illustrations and a discussion of the simple form of aedeagus (state 0) for a number of Palaearctic species of *Ochlerotatus*, including subgenus *Rusticoides*, and Wood *et al.* (1979) illustrated this form of aedeagus for numerous species of Nearctic *Ochlerotatus*.

326. *Aedeagus, width*: (0) widest in distal 0.33; (1) widest in proximal 0.67. Reinert (1990) defined the aedeagus width as 'width measured at the widest point'. Zavortink (1972) provided illustrations of state (0) (figs 33 and 39, *Ab. papago* and *Gy. mediovitata*). See Wood *et al.* (1979: pls 41 and 54, *Oc. pullatus* and

*Oc. (Och.) trivittatus* (Coquillett) and Arnell (1976: fig. 30, *Oc. (Och.) infirmatus*) for examples of state (1).

327. *Aedeagal teeth*: (0) absent; (1) present. See examples in Belkin (1962: figs 226 and 287, *Ra. notoscripta* and *Ve. (Ver.) carmentis*) for state (0). Teeth in state (1) may be small and short (see Reinert, 1973c: fig. 8, *Bo. helenae*) to long and well developed (see Belkin, 1962: figs 297 and 315 ('Ae. (Adm.)' *alboscutellatus* and *Sc. albolineata*) for state (1). Also see the information for character 325.

328. *Aedeagal teeth, position*: (0) on distal  $\leq 0.55$ ; (1) on distal  $\geq 0.68$ . Belkin (1962: figs 315 and 314, *St. aegypti* and *Sc. albolineata*) illustrated state (0) and Edwards (1941: figs 66a and 66c, *Pa. argenteoventralis* (Theobald) and *Pa. kummi* (Edwards)) illustrated state (1). Also see the information under character 327.

329. *Aedeagus, small distal spicules*: (0) absent; (1) present. Most aedine species do not have spicules on the distal part of the aedeagus. A number of species of *Ochlerotatus* have tiny to small spicules on the distal area, especially species with the apex concave. Examples of state (1) are provided by Colless (1958: fig. 5, *Downsiomyia* species) and Mohrig (1969: fig. 57, *Oc. (Rus.) refiki* and *Oc. (Rus.) rusticus*).

330. *Opisthophallus and prosophallus*: (0) absent; (1) present. *Verrallina* and *Cx. quinquefasciatus* possess an opisthophallus and a prosophallus. See Reinert (1974, 1999d) for a discussion and illustrations of these structures in *Verrallina*.

331. *Opisthophallus, development*: (0) narrow with median area somewhat expanded, projecting nearly straight between basal pieces; (1) moderately broad to broad, projecting caudally between basal pieces. The opisthophallus is moderately broad to broad in *Verrallina*, especially the lateral parts, and projects caudally with the basolateral margins connected to the basal pieces of the gonocoxites. It is narrow in *Cx. quinquefasciatus*, the median area is somewhat expanded and it extends nearly straight between the basal pieces. Taxa without an opisthophallus are coded (–). See the information under character 330.

332. *Proctiger, sternal arm*: (0) absent; (1) present. The proctiger lacks a sternal arm in species of *Psorophora* and *Howardina* (see illustrations in Belkin *et al.* (1970) and many other Aedini. See Huang (1990, 1997) for illustrations of species of *Stegomyia* (Africanus and Dendrophilus Groups) that have a proctiger with well-developed sternal arms. *Neomelanimonion lineatopenne* possesses a small lobe on the

basomesal area of the proctiger (coded 1). Species of *Edwardsaedes* have the distal 0.50 of the paraproct developed as a dark, stout, curved, claw-like structure with a moderately pigmented, moderately broad, flattened structure near the base that is the dorsal cercal plate and not a sternal arm of the proctiger, and are scored (0).

333. *Proctiger, cercal setae*: (0) absent; (1) present. Cercal setae are absent from a number of taxa, e.g. *Aedes*, *Neomelanicton*, *Stegomyia* and *Verrallina*, as pointed out by Reinert (2000b), except for a few species of Edwards' (1932) Group C of '*Ae. (Aedimorphus)*', e.g. *Ae. apicoannulatus*, *Ae. argenteopunctatus*, *Ae. irritans*, *Ae. minutus* (Theobald), *Ae. punctothoracis* (Theobald) and *Ae. simulans*. Two other species, *Di. kanarensis* (Edwards) (see Tewari *et al.*, 1990) and *St. calceata* (see Huang, 1981), have a few long to very long, stout setae on the cercus, but because of their highly unusual development and location compared to other Culicidae they are considered a departure from normal. Cercal setae are present in a number of other taxa, e.g. *Downsiomyia*, *Finlaya* and *Ochlerotatus*, and are minute and uniform in length, except *Op. (Opi.) fuscus* in which the cercal setae are of two types, minute and some larger, longer ones (see Belkin, 1962: fig. 207).

334. *Proctiger, apical teeth on paraproct*: (0) absent; (1) present. See examples of state (0) in Belkin *et al.* (1970: figs 70 and 71, *Oc. (Cul.) sollicitans* and *Oc. (Pcx.) pertinax*) and state (1) in their figures 57, 59 and 66 (*Ps. (Pso.) ciliata*, *Ps. (Jan.) ferox* and *Ps. (Gra.) jamaicensis*) and figure 33 (*Cx. quinquefasciatus*).

335. *Paraproct, subapical small knob-like or thumb-like process*: (0) absent; (1) present. Reinert (1973: figs 34 and 35, '*Ae. (Adm.) alboscuteclatus*' and '*Ae. (Adm.) caecus*') illustrated examples of state (1).

#### BIOLOGY

336. *Habitat of immature stages*: (0) fresh-water ground pools; (1) brackish-water ground and rock pools; (2) fresh-water rock pools; (3) fresh-water containers (phytotelmata, small artificial containers, rock holes); (4) crab holes. Numerous habitats of immature stages of Culicidae are described and illustrated in Laird (1988). Descriptions of habitats of immature stages are also provided by other authors, e.g. Bates (1949), Hopkins (1936, 1952) and Colless (1957). The female selects the habitat in which the immature stages develop when she deposits her eggs. Only primary types of habitats are included here. Atypical habitats are not included. Belkin (1962) classified mosquitoes into two principal groups based on

the habitat requirements of the immature states, i.e. species that inhabit ground-water habitats and those that inhabit plant-container habitats. He considered the former as undoubtedly ancestral and the latter derived. Reinert (2002a) indicated that aedine species with a well-developed ventral brush normally inhabit ground-water habitats, and the strong development of the brush seems to be the ancestral condition. By contrast, species with a weakly developed ventral brush inhabit plant containers, and the weaker brush seems to be the more derived condition.

#### PHYLOGENETIC ANALYSIS

In our previous two studies on the phylogeny of Aedini (Reinert *et al.*, 2006, 2008), we analyzed the data using only implied weights, implemented by PIWE version 3.0 (for Windows) (Goloboff, 1997), with the default concavity constant of that program,  $K = 3$ . However, Goloboff (1993) had already questioned whether the same  $K$  value should be applied to data sets with small and large numbers of taxa. More recently, in a justification of differential weighting in analyses of morphological characters, Goloboff *et al.* (2008) noted that for large data sets, in which many, if not most, characters have large numbers of extra steps when fitted onto the optimal cladogram, the weighting strength of low  $K$  values can be far from moderate. This is because the cost of adding the last extra steps to such characters is so small that the weighting almost completely eliminates them from the analysis. Given the large number of taxa in the present study, Pablo Goloboff (personal communication) suggested that we investigate  $K$  values in the range of 7–12. However, only values of  $K$  ranging from 1 to 6 can be applied in PIWE and thus all analyses were performed using TNT version 1.1 (Goloboff *et al.*, 2003b), in which any value of  $K$  can be applied.

In TNT, we used the 'New Technology search' option, undertaking sectorial searches, the ratchet, tree drifting and tree fusing. For the ratchet, upweighting and downweighting probabilities were set to 5% and the number of replicates to 2000. The number of cycles of tree drifting was set to 50. Analyses were terminated once the most parsimonious cladogram (MPC) had been found 10 times. All other parameters were left at their default settings. Under 'Settings', the General RAM was set to 50 Mb and the maximum number of trees to be held to 10000. Cladograms were rooted between *Culiseta* and the remaining taxa. The analyses with the length ratio characters treated as ordered were undertaken with the same search parameters.

In our previous studies, we assessed clade support using Bremer support (Bremer, 1994) and relative Bremer support (Goloboff & Farris, 2001), which

measure the amount of evidence in favour of a group and the ratio of the amounts of favourable and contradictory evidence, respectively. However, the number of slightly suboptimal cladograms is so great that no meaningful Bremer support values could be obtained before the memory limits of the programs were reached and the present data set is so large that undertaking anticonstraint tree analysis to assess the group support for each clade individually was impractical. We therefore applied the parsimony jackknife (Farris *et al.*, 1996) as an alternative means of assessing clade support. However, Goloboff *et al.* (2003a) pointed out that when characters are differentially weighted, as they are in the present analysis, group support can be over- or under-estimated due to inequalities in the way the characters are resampled. This problem can be corrected by making the probability of increasing the weight of a character equal to the probability of decreasing it, a method they called symmetric resampling. We applied symmetric resampling, as implemented in TNT, to our data and recorded both the absolute frequencies of group occurrence and the frequency differences ('Groups present/Contradicted' or GC values; Goloboff *et al.*, 2003a). The analyses calculated the supports for the groups present on the MPC, 10000 replicates undertaken using the same New Technology search parameters given above, with the change probability left at the default value of 33 and groups with values less than 1 collapsed.

Illustrated cladograms were prepared as described by Reinert *et al.* (2006).

## RESULTS AND DISCUSSION

Analyses of the entire data set under implied weights with values of  $K$  ranging from 7 to 12 each produced a single MPC. However, it should be noted that whereas PIWE calculates weights using integer arithmetic and reports fits to one decimal place, TNT uses floating point arithmetic and reports fits to five decimal places. With this level of precision, TNT is highly unlikely to find more than one optimal cladogram and thus it is particularly important to pay attention to the group supports.

The MPCs obtained with  $K$  values of 7 to 9 were identical, the only difference being the values of the fits (202.55111, 194.67821 and 187.51606, respectively), and that for  $K = 10$  (fit = 180.97426) differed only in small changes in the relationships within one subclade of *Ochlerotatus*. Values of  $K > 10$  produced large changes in the relationships among the taxa, as did values of  $K < 7$  (results not shown). Thus the range of  $K = 7-10$  seems to represent a 'plateau of stability' within which the fittest tree is essentially unaffected by changes in  $K$ . Hence, we will restrict

subsequent discussion to the MPC obtained from the  $K = 9$  analysis (CI = 0.06, RI = 0.65). This MPC is shown in Figs 1A,B and 2A–J. In Fig. 1, symmetrical resampling supports are shown above the branches, as both absolute frequencies and frequency difference (GC) values, separated by '/', and jackknife (JK) values are shown below the branches. All three support values show similar patterns of support among the various clades. Thus, as the GC method outperforms the other two, especially in regard to its ability to discriminate support for poorly supported groups (Goloboff *et al.*, 2003a), we will report in detail only on these. It should be noted that the GC and jackknife values in Fig. 1 placed in square brackets are negative values resulting from constraining the analyses to use the groups in the MPC. They can be interpreted as equivalent to zero support for the groups concerned. Unambiguous character changes are mapped on the MPC in Fig. 2.

As in our previous studies (Reinert *et al.*, 2004, 2006, 2008), Aedini is recovered as monophyletic but the relationships among the non-aedine outgroup taxa have reverted back to those found in the first two papers, i.e. *Culiseta* + (*Culex* + (*Orthopodomyia* + (*Mansonia* + Aedini))), rather than having *Orthopodomyia* and *Mansonia* as sister genera. The first clade to branch from the main stem is again *Psorophora*, within which the three subgenera are all recovered as monophyletic. This is again followed by *Mucidus* + *Pardomyia* (the latter reinstated to subgeneric rank by Reinert, 2006b, an action that is strongly supported in the present analysis). At the next level, there is a division into two very large clades.

The first of these very large clades is itself divided into two large clades (Figs 1A, 2A–E). One subclade (Figs 1A, 2A) includes the large genus *Ochlerotatus* in a sister-group relationship with a much smaller clade comprising *Acartomyia* stat. nov. + (*Jarnellius* + (*Halaedes* + *Opifex*)). Reinert *et al.* (2008) included two subgenera in *Jarnellius*, the second being *Ja. (Lewnielsenius)*, the genus itself being paraphyletic relative to a group comprising *Abraedes*, *Aztecaedes*, *Gymnometopa* and *Kompia*. In the present analysis, the two subgenera of *Jarnellius* are widely separated and, consequently, *Lewnielsenius* stat. nov. is recognized as a separate genus (see below). Within *Ochlerotatus* (Figs 1A, 2B–C), many of the branches have very poor or no support. *Ochlerotatus theobaldi* is sister to the remaining taxa. Next to branch off is a clade comprised of *Oc. calumnior* plus a clade that includes subgenera *Pseudoskusea* + (*Culicelsa* + (*Buwirilia* + *Empihals*)). This is followed by a clade comprised of *Oc. andersoni* + *Oc. nivalis*, *Oc. sticticus*, *Oc. punctor* and *Oc. (Woodius)* subgen. nov.; then by *Oc. (Culicada)* stat. nov. The next clade to branch off within *Ochlerotatus* consists of two species unplaced

to subgenus, *Oc. aurifer* and *Oc. thibaulti*, in a sister-group relationship with a clade comprised of *Oc. (Gilesia) + (Oc. (Ochlerotatus) + (Oc. (Protoculex) + Oc. (Chrysoconops))*). The terminal clade in *Ochlerotatus* (Figs 1A, 2C) consists of *Oc. (Pholeomyia)* in a sister-group relationship with a large number of species, most of which are unplaced to subgenus, in a largely poorly supported set of relationships. However, within this clade there are several small groups with moderate to high support: *Oc. excrucians + Oc. fitchii*, *Oc. communis + Oc. pionips*, *Oc. flavescens + Oc. (Rusticoidus)*, *Oc. (Juppius)* subgen. nov. + *Oc. (Lepidokeneon)* subgen. nov. and *Oc. spencerii spencerii + Oc. impiger*.

Within the second subclade (Figs 1A, 2D–E), the first group to branch off comprises (*Himalaius + Bruceharrisonius*) + (*Vansomerenis + (Zavortinkius + Kenknightia)*). This is followed by five species of uncertain generic and subgeneric placement: ‘*Oc. (Fin.) biocellatus + (Oc. (Fin.) crossi*, and ‘*Oc. (Fin.) candidoscutellum + (Oc. (Fin.) keefei*, and ‘*Oc. (Pro.) knabi*. The remaining taxa are then divided into two large clades. Within the first, *Rampamyia + (Molpemyia + (Luius + Macleaya))* are sister to the remaining taxa, which are divided into two further clades comprising *Dobrotworskyius + (Patmarksia + Georgecraigius)*, and *Tanakaius + (Hulecoeteomyia + (Gilesius + Collessius))*. The two subgenera of *Collessius*, *Co. (Alloeomyia)* and *Co. (Collessius)*, are reciprocally monophyletic. Within the second (Figs 1A, 2E), the first five groups to branch off include eight species currently placed in ‘*Oc. (Protomacleaya)*’ and ‘*Oc. (Fin.) oreophilus* in a sister-group relationship with *Jihlienius + Phagomyia*. All of these relationships are very weakly supported except for the monophyly of *Phagomyia*. Beyond these, *Hopkinsius* (with its two monophyletic subgenera, *Hopkinsius* and *Yamada*), is first to branch off, followed by *Dahlia*. The terminal group consists of two clades

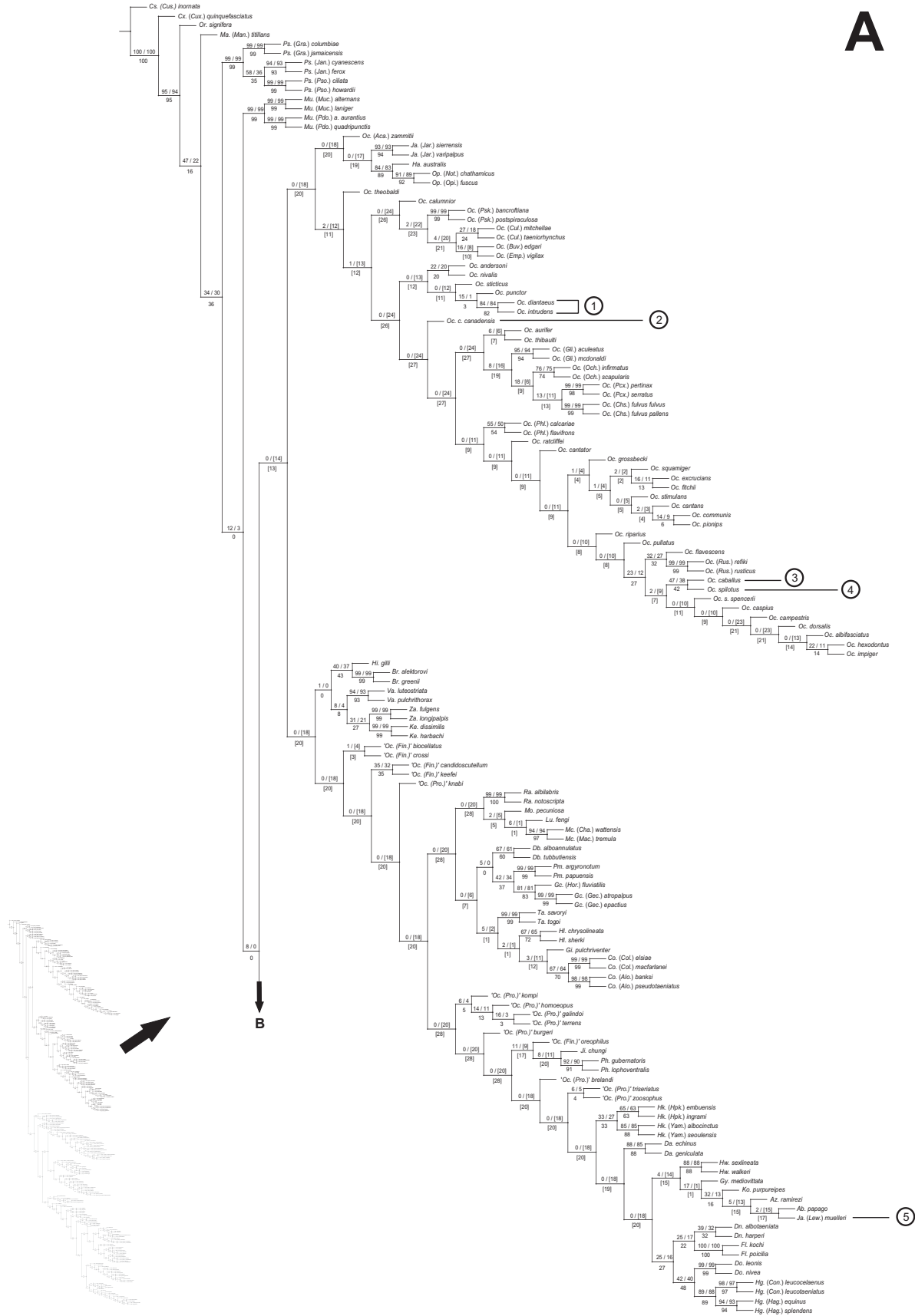
of genera: *Howardina + (Gymnometopa + (Kompia + (Aztecaedes + (Abraedes + Lewnielsenius stat. nov.))*), and (*Finlaya + Danielsia*) + (*Downsiomyia + Haemagogus*). The two subgenera of *Haemagogus*, *Conopostegus* and *Haemagogus*, are reciprocally monophyletic.

In the second very large clade (Figs 1B, 2F–J), the first clade to branch off comprises *Sallumia* stat. nov. + (*Geoskusea* stat. nov. + (*Levua* stat. nov. + *Rhinoskusea* stat. nov.)), followed by the genus pair, *Elpeytonius* gen. nov. + *Catageiomyia* stat. nov. The remaining taxa are then split into two large clades. Within the first, the large genus *Aedimorphus* stat. nov. is sister to a number of genera, which are disposed between two further clades (Figs 1B, 2G). One comprises *Polyleptiomyia* stat. nov. + (*Bifidistylus* gen. nov. + (*Albuginosus + (Tewarius + (Christophersomyia + (Huaedes + Leptosomatomyia))*))). The present results confirm the decision by Reinert (2006a) to propose *Tewarius* as a genus for four species originally placed in *Aedes (Diceromyia)*. The second comprises *Neomelaniconion + (Edwardsaedes + (Aedes + (Paraedes + Verrallina))*). Within *Verrallina*, subgenera *Harbachius* and *Neomacleaya* are recovered as monophyletic but subgenus *Verrallina* is paraphyletic with respect to *Neomacleaya*.

Within the second large clade (Figs 1B, 2H–J), the first group to branch off comprises *Skusea + (Indusius + Cancraedes stat. nov.)*, followed by *Fredwardsius*, *Isoaedes* and *Borichinda*, each on a separate branch. Next come three successive small clades: *Diceromyia + Ayurakitia*, *Dendroskusea* stat. nov., and *Scutomyia + (Catatassomyia stat. nov. + Bothaella)*. At the next split, *Stegomyia* forms the sister-group of a clade comprising the remaining genera. Within the latter (Figs 1B, 2I), *Cornetius* stat. nov. branches off first. A clade comprising *Petermattinglyius* gen. nov. + (*Alanstonea + Pseudarmigeres + Heizmannia*) is sister to another comprising

**Figure 1A,B.** Symmetrical resampling support and jackknife values for each clade of the single most parsimonious cladogram (Fit = 187.51606) obtained from analysis of the data (Appendix 1) under implied weights ( $K = 9$ ). Values for absolute frequencies (left of slash) and the frequency difference (GC, right of slash) are shown above the branches and jackknife (JK) support values are shown below the branches. Values placed in square brackets are negative values resulting from constraining the analyses to use the groups in the MPC. They can be interpreted as equivalent to zero support for the groups concerned. Circled numbers adjacent to terminal groups indicate revised and newly established generic-level taxa: 1, *Ochlerotatus* subgenus *Woodius* subgen. nov.; 2, *Culicada* stat. nov.; 3, *Ochlerotatus* subgenus *Juppius* subgen. nov.; 4, *Ochlerotatus* subgenus *Lepidokeneon* subgen. nov.; 5, *Lewnielsenius* stat. nov.; 6, *Sallumia* stat. nov.; 7, *Geoskusea* stat. nov.; 8, *Levua* stat. nov.; 9, *Rhinoskusea* stat. nov.; 10, *Elpeytonius* gen. nov.; 11, *Catageiomyia* stat. nov.; 12, *Aedimorphus* stat. nov.; 13, *Polyleptiomyia* stat. nov.; 14, *Bifidistylus* gen. nov.; 15, *Cancraedes* stat. nov.; 16, *Dendroskusea* stat. nov.; 17, *Catatassomyia* stat. nov.; 18, *Cornetius* stat. nov.; 19, *Petermattinglyius* gen. nov.; 20, *Stegomyia* subgenus *Mukwaya* subgen. nov.; 21, *Stegomyia* subgenus *Actinothrix* subgen. nov.; 22, *Stegomyia* subgenus *Zoromorphus* subgen. nov.; 23, *Stegomyia* subgenus *Bohartius* subgen. nov.; 24, *Stegomyia* subgenus *Xyele* subgen. nov.; 25, *Stegomyia* subgenus *Heteraspidion* subgen. nov.; 26, *Stegomyia* subgenus *Huangmyia* subgen. nov.

A





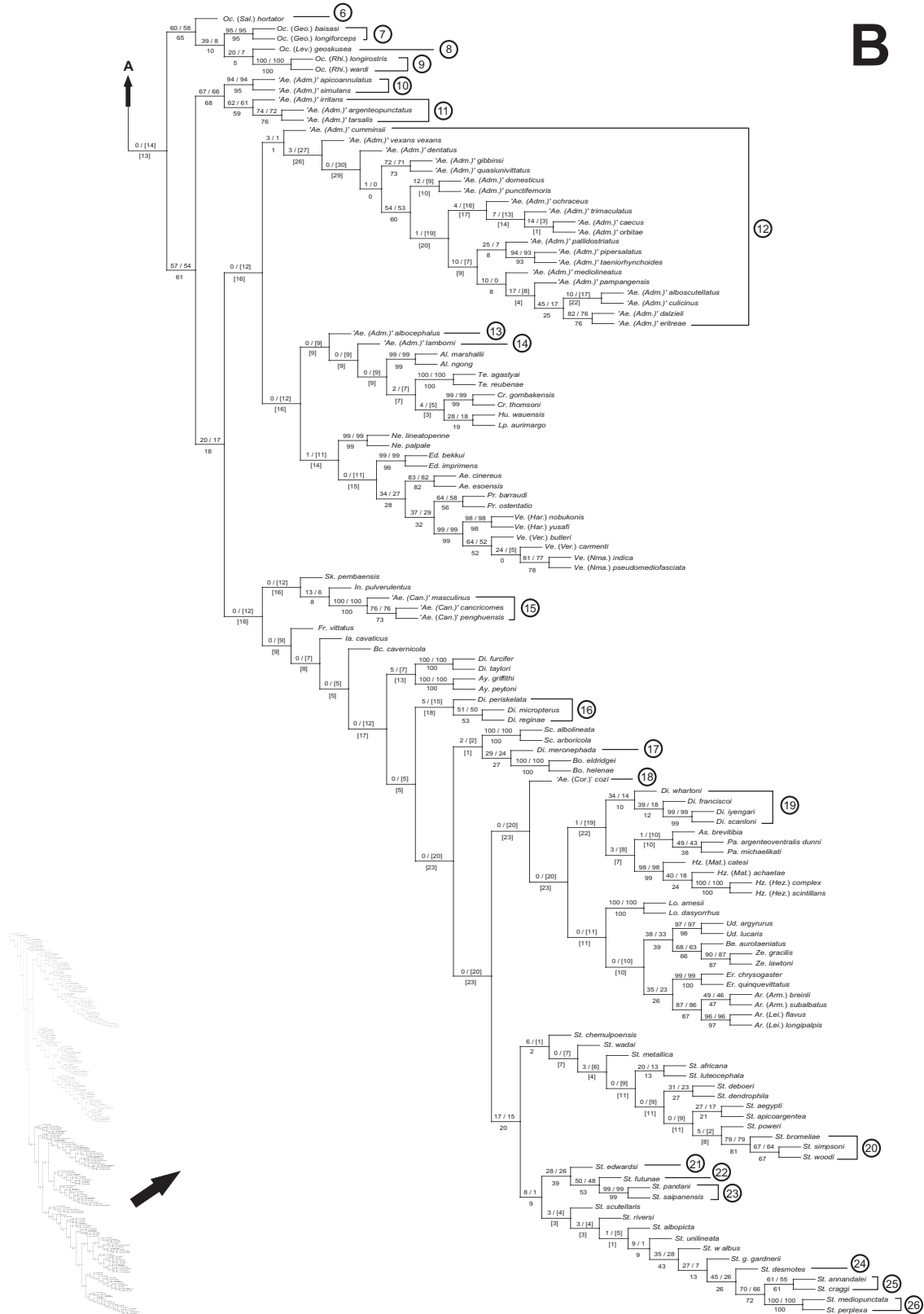
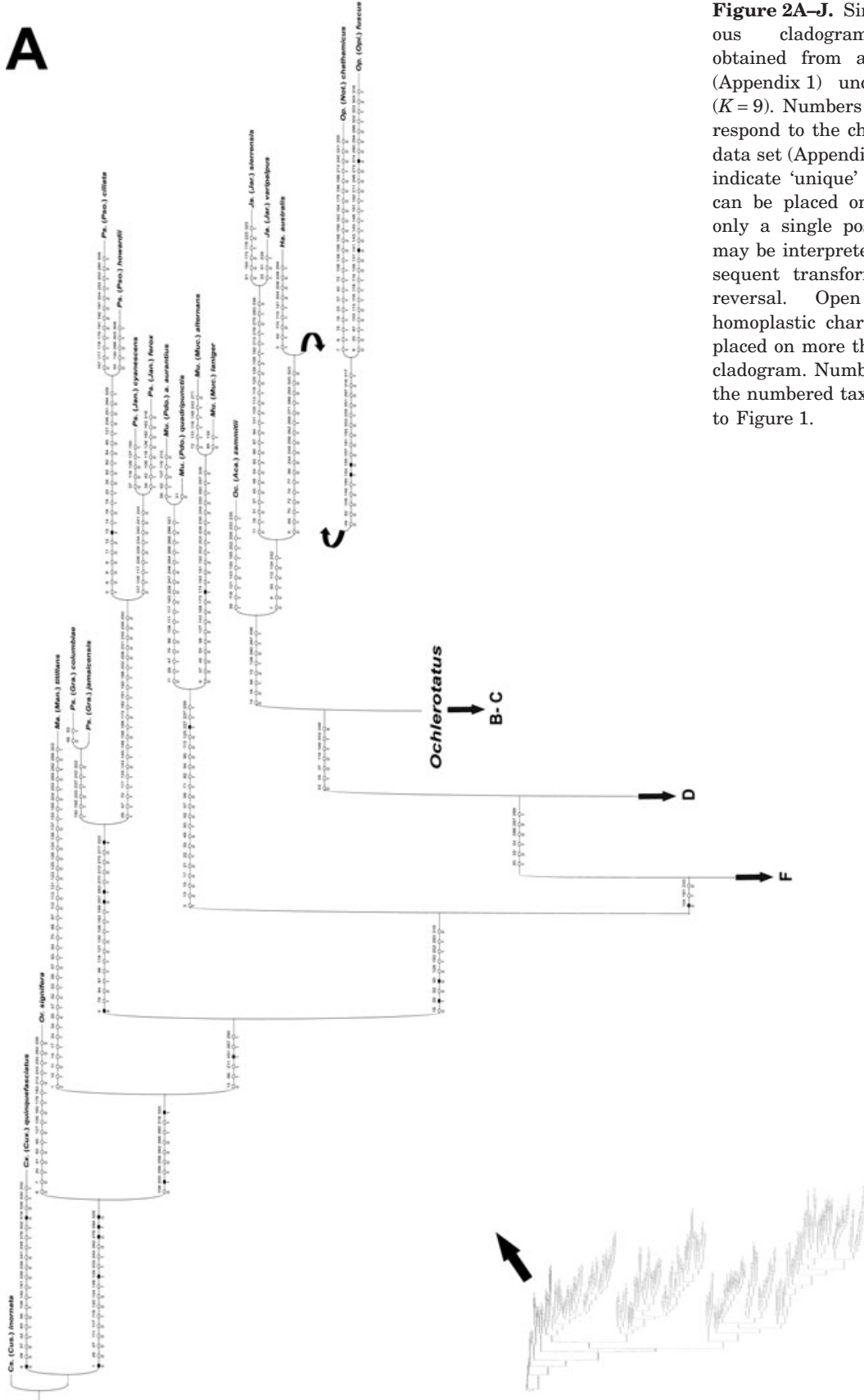
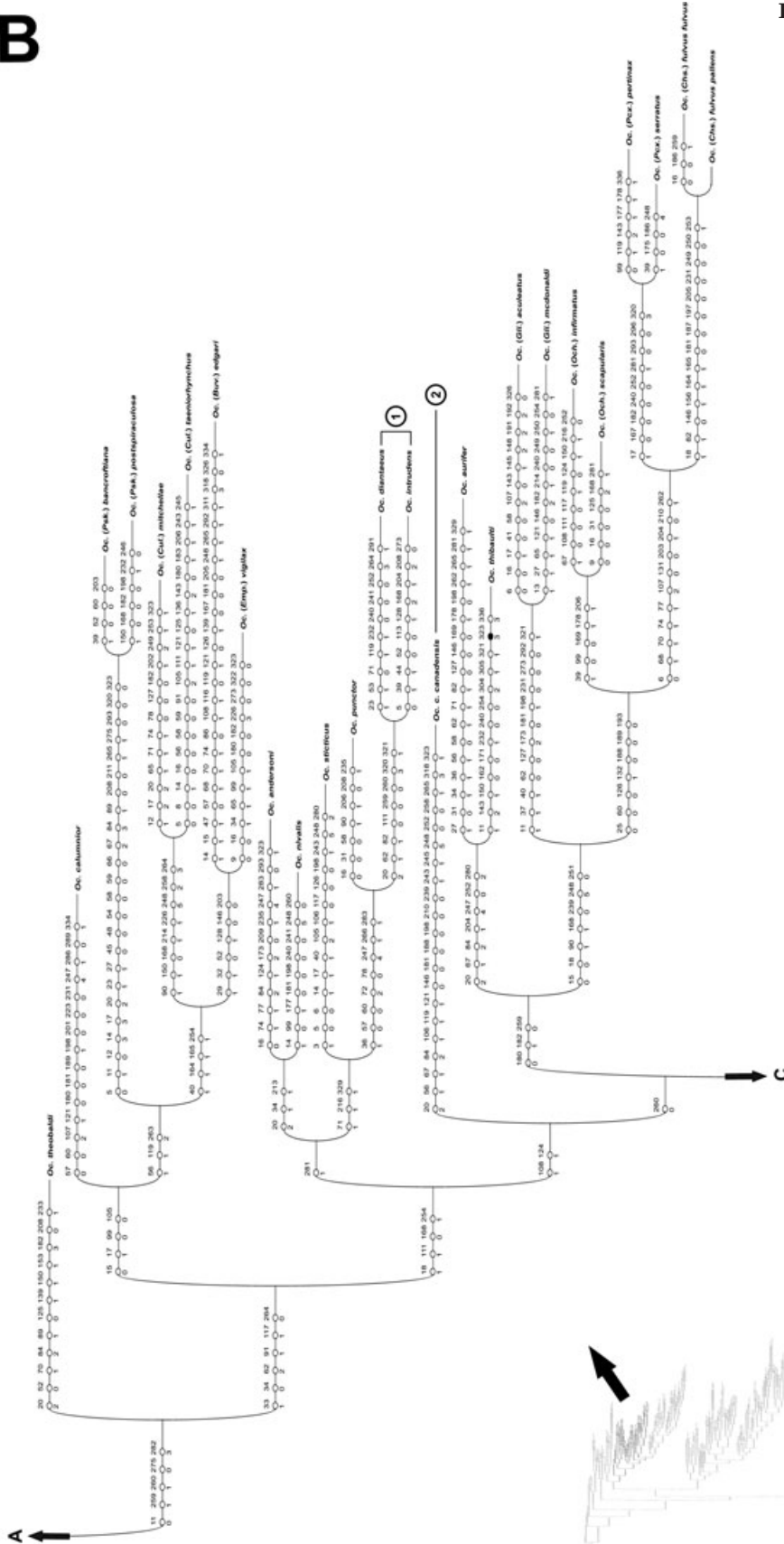


Figure 1. Continued



**Figure 2A–J.** Single most parsimonious cladogram (Fit = 187.51606) obtained from analysis of the data (Appendix 1) under implied weights ( $K = 9$ ). Numbers on the branches correspond to the characters listed in the data set (Appendix 1). Darkened circles indicate ‘unique’ character states that can be placed onto the cladogram in only a single position, although they may be interpreted as undergoing subsequent transformation or secondary reversal. Open circles represent homoplastic character states that are placed on more than one branch of the cladogram. Numbers in circles refer to the numbered taxa listed in the legend to Figure 1.

**B**



**Figure 2. Continued**

C

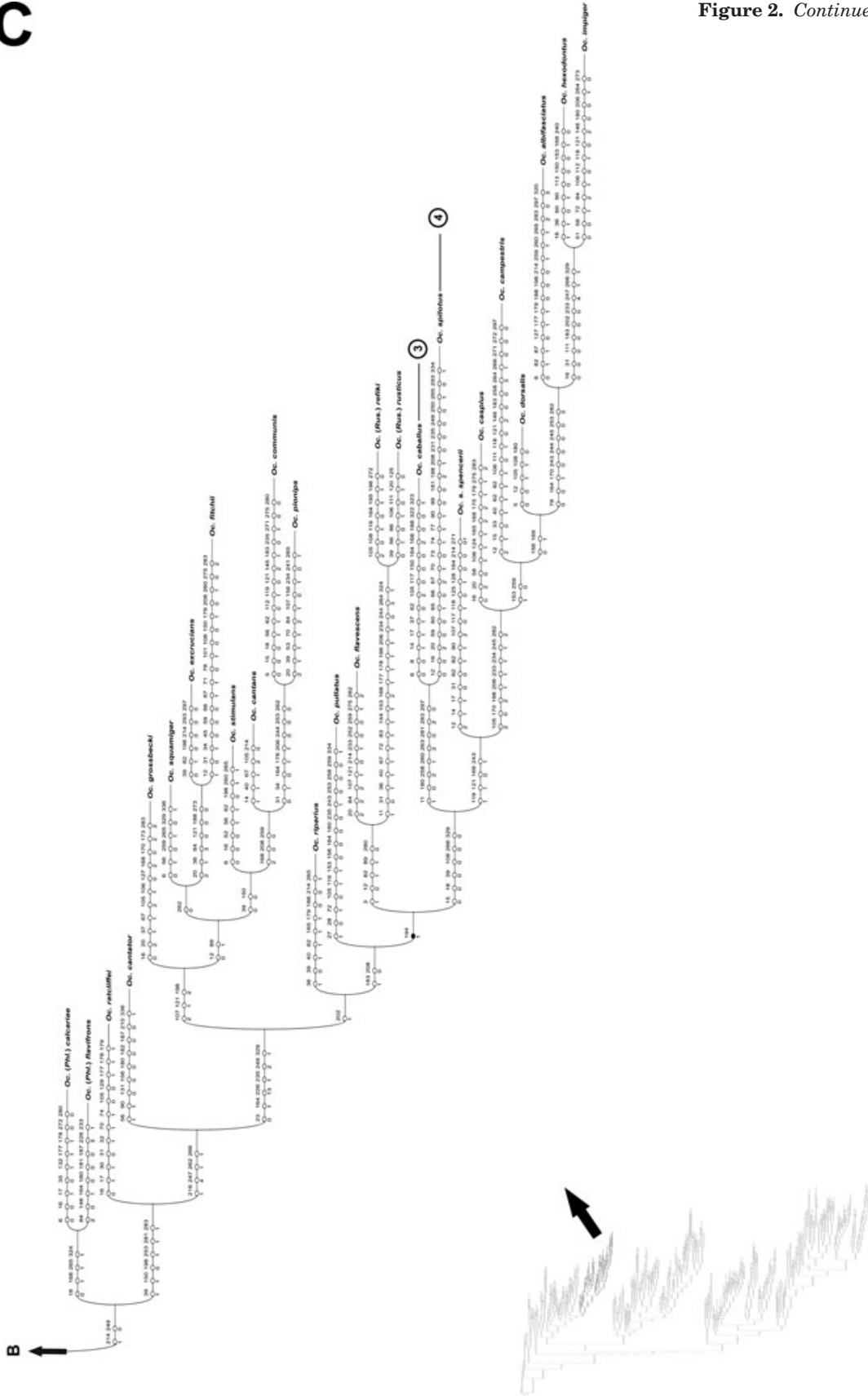
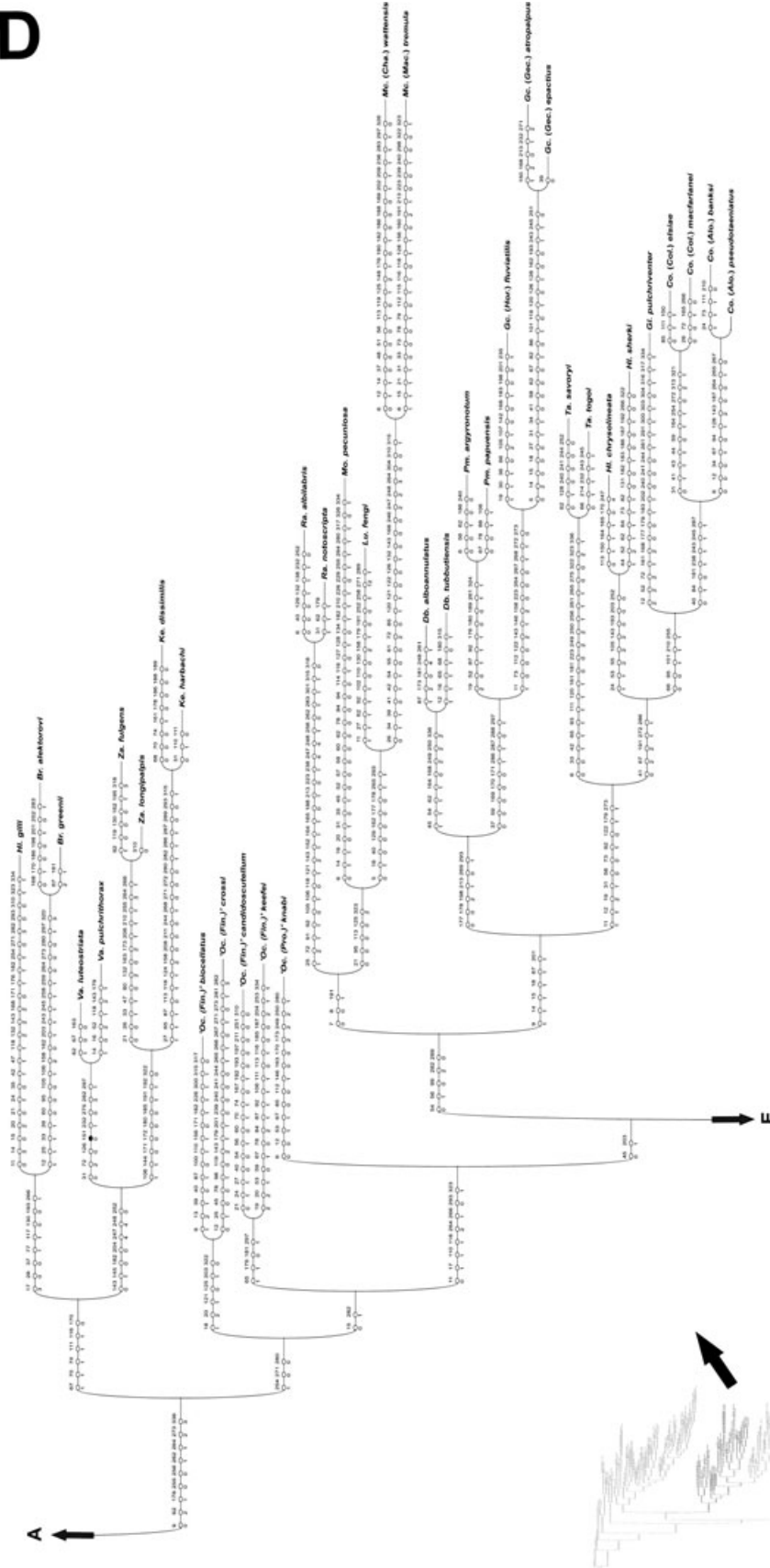


Figure 2. Continued

**D**



**Figure 2.** *Continued*

**E**

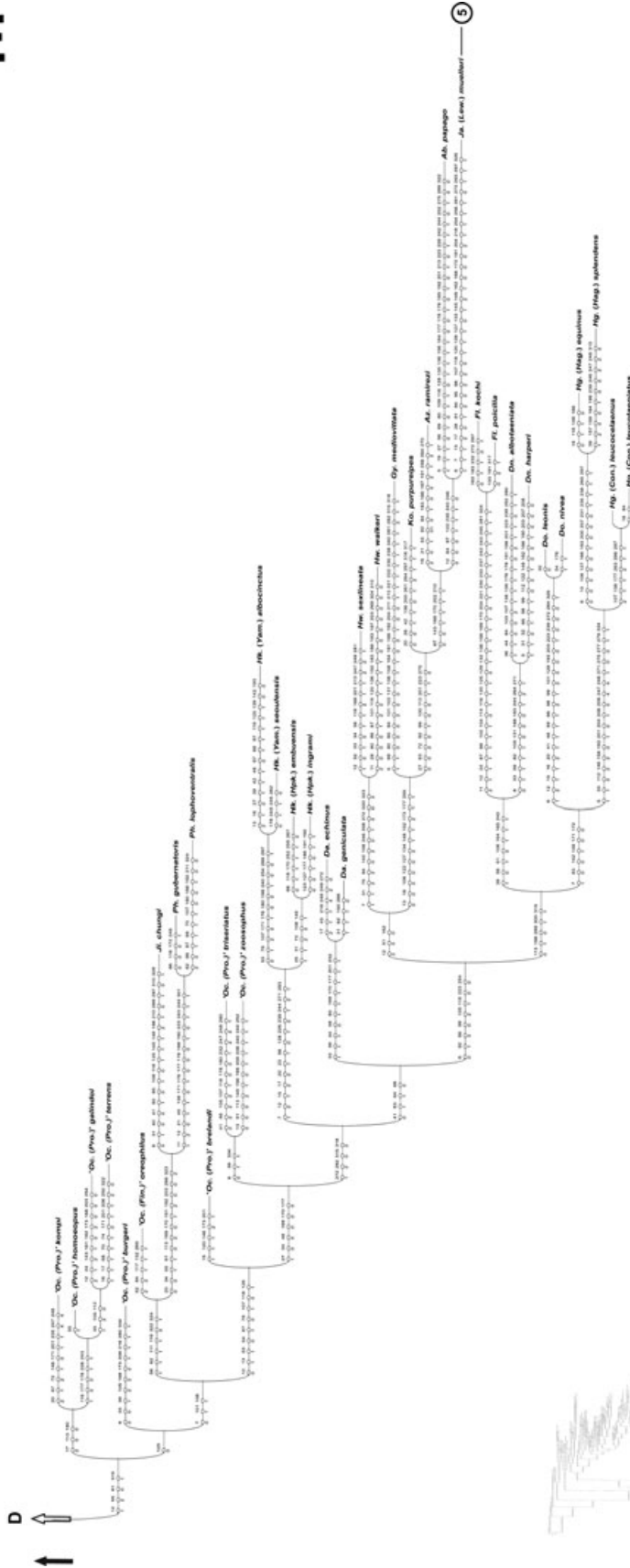


Figure 2. Continued

**F**

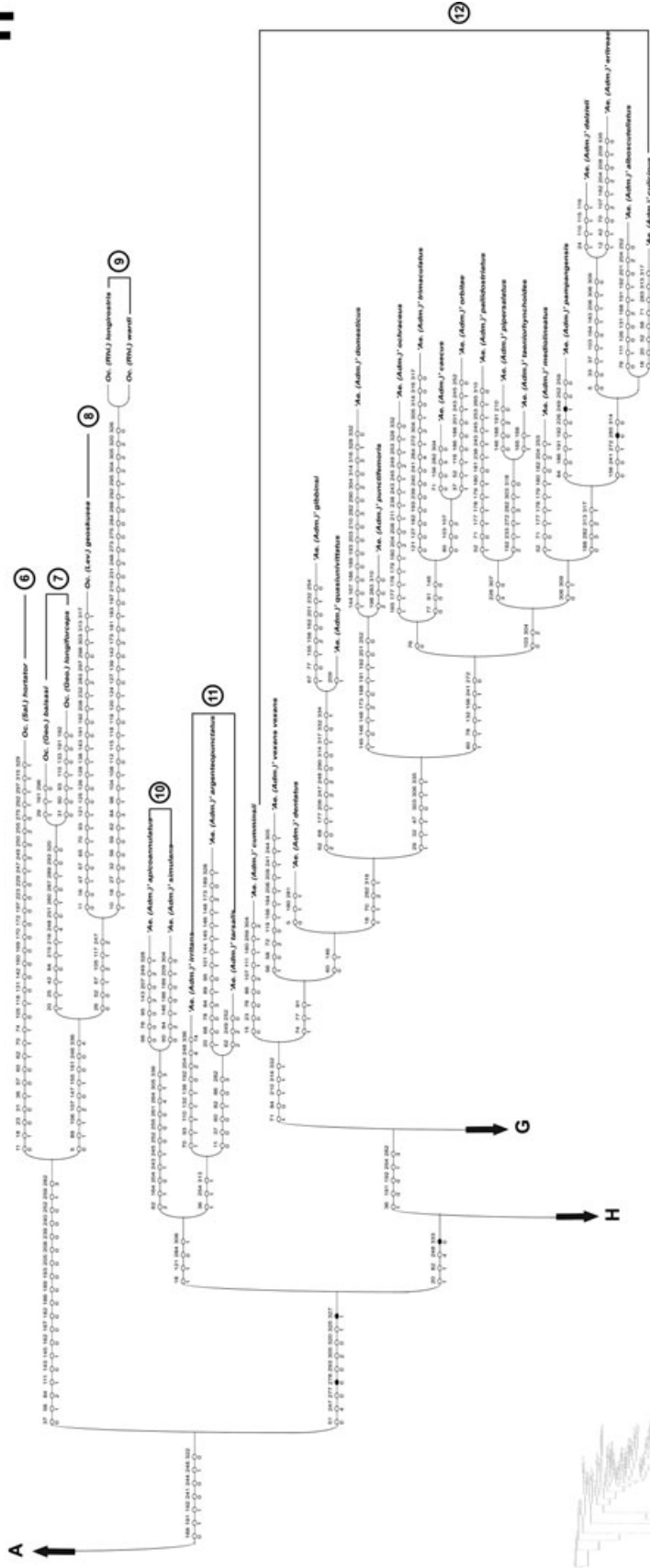
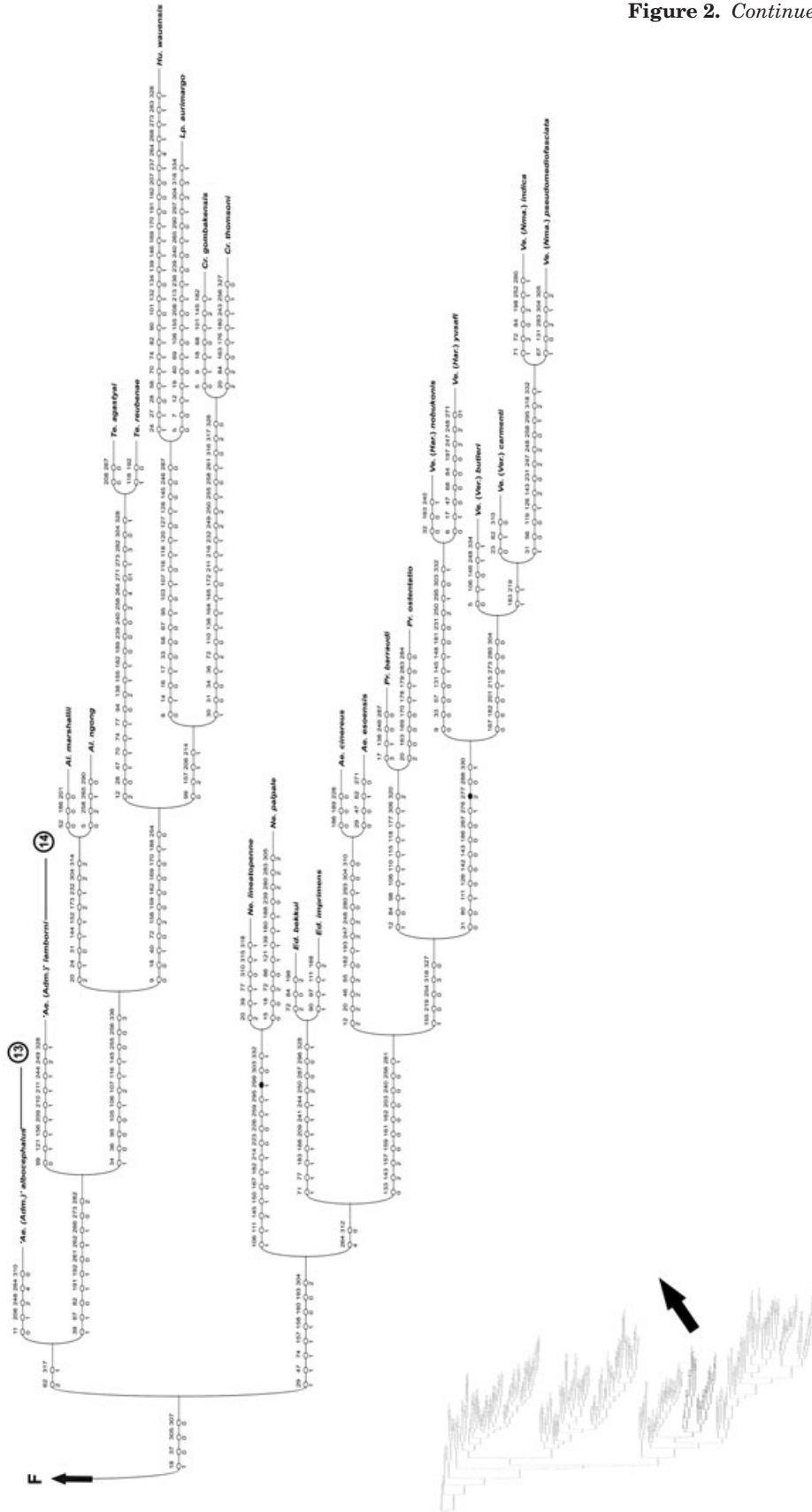


Figure 2. *Continued*

G

Figure 2. Continued





H

Figure 2. Continued

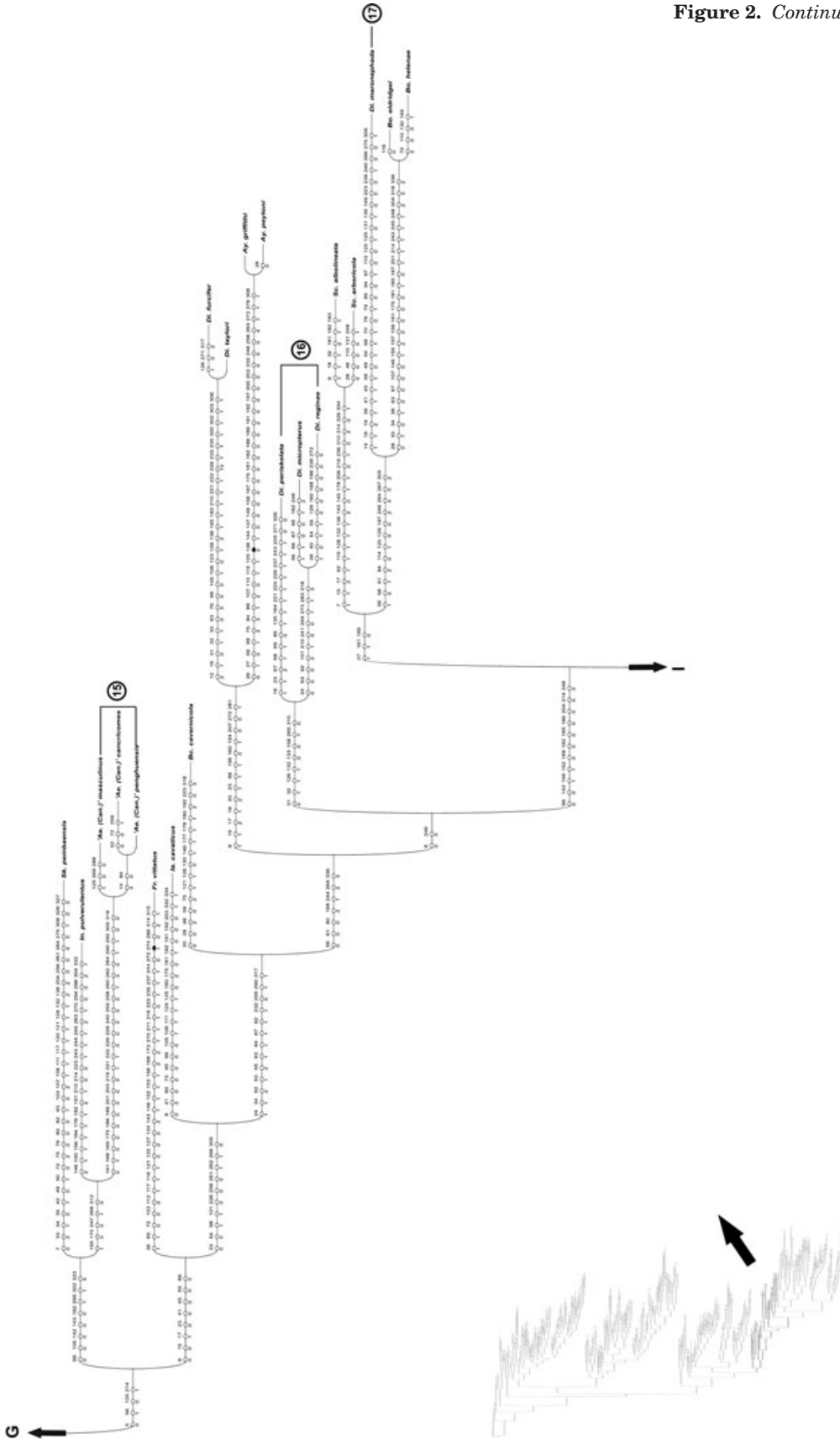
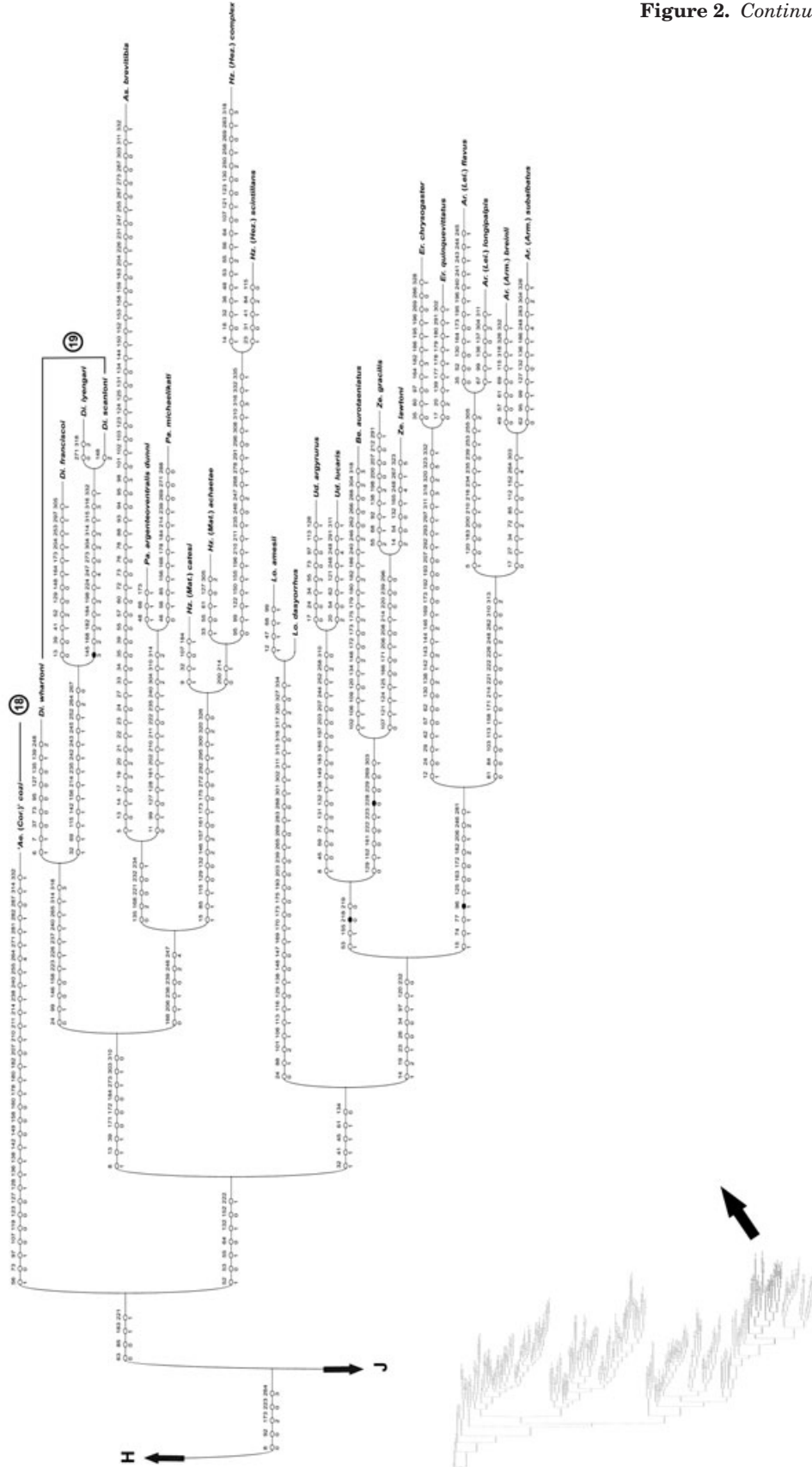


Figure 2. Continued



J

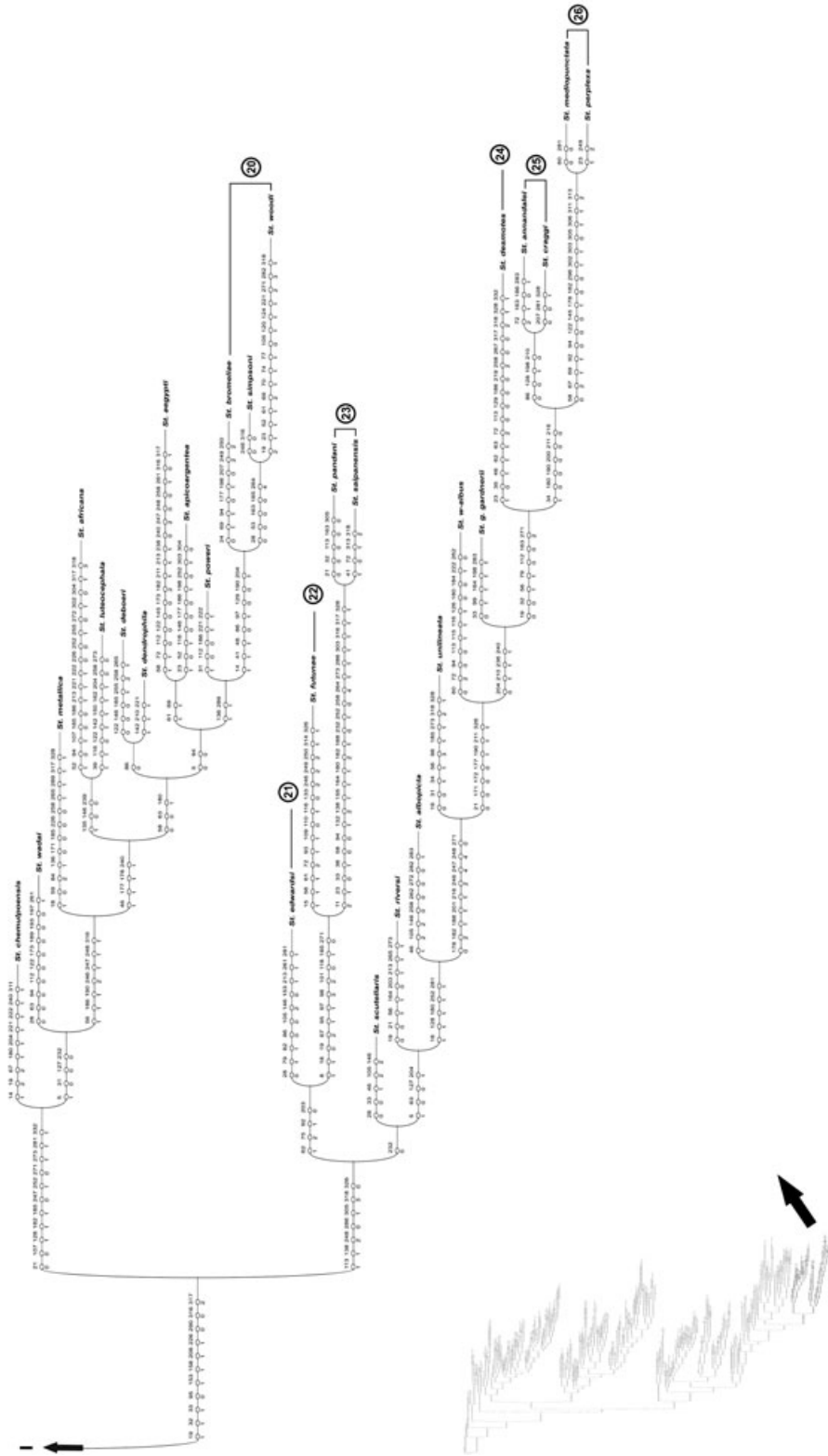


Figure 2. Continued

*Lorrainea* + (((*Udaya* + (*Belkinus* + *Zeugomyia*)) + (*Eretmapodites* + *Armigeres*)). Within *Heizmannia*, subgenus *Mattinglyia* is paraphyletic relative to subgenus *Heizmannia*, whereas in *Armigeres*, subgenera *Armigeres* and *Leicesteria* are reciprocally monophyletic. Within the new genus *Petermattinglyius*, a second subgenus, *Aglaonotus* subgen. nov., is recognized for *Pe. whartoni*.

The species of *Stegomyia* (Figs 1B, 2J) are divided into two clades, neither of which is well supported. Within the first clade, all the branches along the main stem are very poorly supported. The species pairs *St. africana* + *St. luteocephala*, *St. deboeri* + *St. dendrophila*, and *St. aegypti* + *St. apicoargentea* have moderate support, and the terminal group of three species, *St. bromeliae* + (*St. simpsoni* + *St. woodi*), is strongly supported and described below as *Stegomyia* (*Mukwaya*) subgen. nov. Within the second clade, the first group to branch off the main stem has moderate support and comprises *Stegomyia* (*Actinothrix*) subgen. nov. + *Stegomyia* (*Zoromorphus*) subgen. nov. + *Stegomyia* (*Bohartius*) subgen. nov. The branch supports along the main stem of the other clade are generally poorly to moderately supported. Only the terminal group and its subclades, comprising *Stegomyia* (*Xyele*) subgen. nov. + (*Stegomyia* (*Heteraspidion*) subgen. nov.) + *Stegomyia* (*Huangmyia*) subgen. nov.), have GC values exceeding 40.

The analyses with the 14 length ratio characters treated as ordered using values of  $K = 7-12$  produced somewhat different patterns of relationships (not shown) to those found when these characters are treated as unordered. Nevertheless, under all these values of  $K$ , every genus and subgenus mentioned above was recovered as monophyletic, with the sole exception of *Dendroskusea* stat. nov., the three species of which formed a paraphyletic series with respect to a larger clade variously comprising *Stegomyia* and its relatives. Consequently, ordering the length ratio characters has minimal impact on the integrity of the genera and subgenera we recognize here. Furthermore, although it seems intuitively sensible to treat lengths as ordered sequences, so that given three observed lengths of, say, 6 cm, 9 cm and 12 cm, it is reasonable that a change from 6 cm to 12 cm should 'go via' a length of 9 cm, and thus take two steps, it is also feasible for a genetic change to result in a direct doubling of the length from 6 cm to 12 cm, without any intervening 9 cm length being involved, and thus take a single step. As we have no evidence for or against either scenario, we do not consider that ordering the length ratio characters is justifiable and thus prefer not to make this assumption. Consequently, all subsequent discussion is based on the analyses conducted with all multistate characters treated as unordered.

#### COMPARISON WITH REINERT *ET AL.* (2004, 2006, 2008)

A comparison of the present results with those obtained previously (Reinert *et al.*, 2004, 2006, 2008) is again revealing with regard to the stability of the patterns of relationships obtained despite differences in the taxa and characters included in these analyses. We have again recovered as monophyletic groups all those taxa, for which two or more species are included, that were treated by Reinert *et al.* (2004, 2006, 2008) as genera, with two exceptions that will be discussed further below. Thus, the monophyly of the following genera and subgenera is corroborated: *Aedes*, *Albuginosus*, *Armigeres* (and its two subgenera), *Ayurakitia*, *Bothaella*, *Bruceharrisonius*, *Christophersiomyia*, *Collessius* (and its two subgenera), *Dahlia*, *Danielsia*, *Dobrotworskyius*, *Downsiomyia*, *Edwardsaedes*, *Finlaya*, *Georgecraigius* (and subgenus *Georgecraigius*), *Eretmapodites*, *Geoskusea*, *Gilesius*, *Haemagogus* (and its two subgenera), *Heizmannia* (and subgenus *Heizmannia*), *Hopkinsius* (and its two subgenera), *Howardina*, *Hulecoeteomyia*, *Jarnellius*, *Kenknightsia*, *Lorrainea*, *Macleaya*, *Mucidus* (and its two subgenera), *Neomelaniconion*, *Ochlerotatus* (subgenera *Chrysoconops*, *Culicelsa*, *Gilesia*, *Pholeomyia*, *Protoculex*, *Rusticoidus* and *Pseudoskusea*), *Opifex*, *Paraedes*, *Patmarksia*, *Phagomyia*, *Pseudarmigeres*, *Rhinoskusea*, *Psorophora* (and its three subgenera), *Rampamyia*, *Scutumyia*, *Stegomyia*, *Tanakaius*, *Udaya*, *Vansomerenis*, *Verrallina* (and subgenera *Harbachius* and *Neomacleaya*), *Zavortinkius* and *Zeugomyia*. In addition, as noted above, the monophyly of *Tewarius*, newly added to the current data set, is confirmed. Reinert *et al.* (2004) found that *Heizmannia* subgenus *Mattinglyia* was paraphyletic with respect to *Heizmannia* (*Heizmannia*), a relationship that was also found in the present study (Figs 1B, 2I). In contrast, whereas Reinert *et al.* (2004) recovered all three subgenera of *Verrallina* as monophyletic taxa, here *Verrallina* (*Verrallina*) is paraphyletic with respect to *Verrallina* (*Neomacleaya*). Finally, Reinert *et al.* (2008) found that *Jarnellius* was paraphyletic, with the nominotypical subgenus being sister to a clade comprising *Jarnellius* (*Lewnielsenius*) + (*Abraedes* + (*Aztecaedes* + (*Gymnometopa* + *Kompia*))). In the present study, the latter five taxa (with *Lewnielsenius* stat. nov. raised to genus) remain together as a clade (Figs 1A, 2E), albeit with different internal relationships (see below), whereas *Jarnellius* s.s. moves to a position in the clade that also includes *Acartomyia*, *Halaedes*, *Opifex* and *Ochlerotatus* (also see below).

With regard to intergeneric relationships, many of those found previously are also recovered in the present study. As noted above, Aedini itself is

monophyletic, and the relationships among the four outgroup taxa are the same as those found by Reinert *et al.* (2004, 2006; but not 2008). The next two branch points, involving *Psorophora*, *Mucidus* (subgenera *Mucidus* + *Pardomyia*), and the remaining taxa (Figs 1A, 2A) are identical to those found by Reinert *et al.* (2008), except for a rearrangement among the subgenera of *Psorophora*, in which subgenera *Psorophora* and *Janthinosoma* are sisters, rather than subgenera *Psorophora* and *Grabhamia*. Following these are two branch points subtending three large clades that correspond in general terms to the foci of the three previous studies. Thus, the first clade is mostly comprised of *Ochlerotatus* (Figs 1A, 2A–C), the next consists of *Finlaya* and its relatives (Figs 1A, 2D–E), and the third includes *Aedes*, *Aedimorphus*, *Stegomyia* and their relatives (Figs 1B, 2F–J). Consequently, the relationships within each of these three major groups will be compared with the previous study for which they served as a focus.

The first clade (Figs 1A, 2A–C) consists of the large genus *Ochlerotatus* in a sister-group relationship with the aforementioned clade: *Acartomyia* + (*Jarnellius* + (*Halaedes* + *Opifex*)). In the analysis of Reinert *et al.* (2008), which focused on this group of genera, *Acartomyia* [represented by '*Oc. (Och.) zammitii*'] was the sister of *Ochlerotatus*. *Halaedes* + *Opifex* together were sister to all the remaining taxa, and *Jarnellius* s.s. was very distantly placed within this group. Reinert *et al.* (2008) also found *Geoskusea*, *Levua* and *Rhinuskusea* deeply nested within *Ochlerotatus*, and were thus compelled to treat them as subgenera thereof. In the present analysis, these three taxa are placed, together with *Sallumia*, in a clade that is sister to that including *Aedes*, *Aedimorphus* and *Stegomyia* (Figs 1B, 2F). In contrast to the findings of Reinert *et al.* (2008), *Geoskusea* is here recovered as monophyletic and the relationships of these three reinstated genera reflect the results of Reinert *et al.* (2004, 2006). Within *Ochlerotatus* (Figs 1A, 2B–C), although the previously recognized subgenera are all recovered as monophyletic, there is much conflict between the present results and those of Reinert *et al.* (2008). In particular, the basal lineages, which in Reinert *et al.* (2008: fig. 1A) were either poorly supported or involved in a six-way polytomy, show considerable rearrangement in the present results, where they are also poorly supported for the most part. The exception is the *Oc. ratcliffei* – *Oc. impiger* clade (Figs 1A, 2C), which includes the same taxa as the comparable clade in Reinert *et al.* (2008: fig. 1A), except for the loss of *Oc. andersoni* and gain of *Oc. fitchii*. Within this clade, the subclade comprised of *Oc. flavescens* – *Oc. impiger* also contains the same set of taxa as before, although their interrelationships are again much changed compared to those in Reinert

*et al.* (2008). However, these changes are perhaps to be expected given the poor support for most branches within *Ochlerotatus*, and further work will be required before a robust internal phylogeny of the genus is achieved.

The second clade (Figs 1A, 2D–E) comprises those taxa that in the results of Reinert *et al.* (2006, 2008) formed a paraphyletic series between the *Ochlerotatus* group and the *Aedes-Isoaedes-Scutomyia-Stegomyia* group. However, its support in the present study is very low and its monophyly must remain questionable. Nevertheless, within this clade, numerous subclades are recovered that were also recovered in the analyses of Reinert *et al.* (2006, 2008), and even the branching sequence is similar. First to branch off in the present analysis is a clade comprised of *Himalaius* + *Bruceharrisonius* and *Vansomerenis* + (*Zavortinkius* + *Kenknightia*), followed by two pairs of species of uncertain generic assignment, '*Oc. (Fin.) biocellatus*' + '*Oc. (Fin.) crossi*', and '*Oc. (Fin.) candidoscutellum*' + '*Oc. (Fin.) keefei*' (Figs 1A, 2D). In the results of Reinert *et al.* (2006, 2008), these four groups were arranged in a paraphyletic series (with *Hopkinsius* included with '*Oc. (Fin.) biocellatus*' and '*Oc. (Fin.) crossi*' in the results of Reinert *et al.*, 2006; also see below). The pattern of relationships within the first large subclade (Figs 1A, 2D, *Ra. albilabris* – *Co. pseudotaeniatus*) closely resembles those found by Reinert *et al.* (2008), but with the inclusion of a group comprising *Dobrotworskyius*, *Patmarksia* and *Georgecraigius*, and the exclusion of *Finlaya*. In contrast, the pattern seen in the second large subclade (Figs 1A, 2E) more closely resembles the topology found by Reinert *et al.* (2006), but for the addition of *Hopkinsius* (not considered by them) and the subclade comprising *Gymnometopa* + (*Kompia* + (*Aztecaedes* + (*Abraedes* + *Lewnielsenius* stat. nov.))). This clade also includes numerous taxa of uncertain generic placement currently placed in '*Ochlerotatus (Protomacleaya)*' and '*Ochlerotatus (Finlaya)*', the relationships of which remain obscure.

In the present study, we greatly increased our sampling of the *Aedes* Group of genera (subgenera of *Aedes sensu* Reinert, 2000b). Reinert *et al.* (2006) and Reinert *et al.* (2008) only included the same seven taxa to represent this group, namely the two species of *Aedes* and *Scutomyia* included in the present study, the sole species of *Isoaedes* and two species of *Stegomyia*, *St. aegypti* and *St. africana*. Thus, a comparison with their results in regard to these taxa is not meaningful. In contrast, Reinert *et al.* (2004) included 41 species from this group, representing 22 genera, and thus a limited comparison is possible. In the present analysis, we increased our sampling of *Aedimorphus* from four species to 27, *Diceromyia* from two species to 10 and *Stegomyia* from six to 28. We

also added representatives of the recently described genera *Tewarius* (2 species) and *Borichinda* (1 species), two additional species of *Canraedes* stat. nov. and the single species of *Cornetius* stat. nov. We greatly increased our representation of this group to 117 taxa, thus it is not surprising that few of the intergeneric and intrageneric relationships found by Reinert *et al.* (2004) were recovered in the present analysis (although we would reiterate that all the genera themselves are recovered as monophyletic). Although not all the species previously placed in *Aedimorphus* form a single clade in the present study (we separate some as genera *Catageiomyia* stat. nov., *Elpeytonius* gen. nov., *Bifidistylus* gen. nov. and *Polyleptomyia* stat. nov.), the four species analyzed by Reinert *et al.* (2004) do fall within a monophyletic *Aedimorphus* s.s. (Figs 1B, 2F), which they did not in their analysis. The relationships among the six previously analyzed species of *Stegomyia* are also different (Figs 1B, 2J), with the exception of the pairing of *St. albopicta* and *St. desmotes* (making due allowance for the species added to the present analysis). The clade comprised of *Aedes*, *Paraedes* and *Verrallina* is recovered (Figs 1B, 2G), though *Paraedes* is now the sister-genus of *Verrallina*, rather than *Aedes*, as found by Reinert *et al.* (2004). *Pseudarmigeres* and *Heizmannia* remain very closely related, although *Alanstonea* is also now included as the sister of the former genus (Figs 1B, 2I). Finally, the sister-group association of *Belkinius* and *Zeugnomyia* is recovered here, and *Armigeres* remains closely associated with this pair, although *Eretmapodites* and *Udaya* are also included in the clade (Figs 1B, 2I).

#### CLASSIFICATION OF EVALUATED TAXA

Our decision to recognize new generic-level taxa, or to resurrect available names for such groups, is based on the topology of the most parsimonious cladogram and the principle of equivalent rank, taking into account the branch support and the number and nature of the characters that support the branches. Specifically, generic-level taxa are recognized for clades that are supported by GC (frequency difference) values  $\geq 40$ , or slightly lower values in a few cases where numerous characters support the group. In general, the data for the largest genera are insufficient to resolve all of the internal relationships; consequently, some species are assigned to subgenera and others are left unassigned. Since monobasic taxa and those represented by a single species in the analysis do not receive GC values (these are technically undefined rather than zero), practical consideration had to be given to the number and quality of the supporting characters and are used to determine taxonomic rank.

As is usually the case with generic-level groups of Aedini, most genera and subgenera are polythetic taxa, i.e. they are not diagnosed by unique characters but by *unique combinations* of characters. Hence, although the individual characters may be independently derived elsewhere, they do not occur in the same combination in any other group.

Most of the species groups within genus *Ochlerotatus* are indistinct. Whereas species within species groups are morphologically similar to one another, there is little evidence of clear gaps between most of the groups. The general lack of distinct clustering (Figs 1A, 2B–C) reflects the difficulty of classifying *Ochlerotatus* based on morphological data. Even so, the character data supporting four additional clades are sufficiently strong to recognize them as subgenera.

*Ochlerotatus* subgenus *Woodius* (Figs 1A, 2B) is proposed for *Oc. diantaeus* and *Oc. intrudens*, two morphologically distinct species (JK 82; GC 84) that are widely distributed in northern areas of the Holarctic Region. *Woodius* is diagnosed by a unique combination of eight homoplastic characters (Fig. 2B). The subgenus is fully described in the 'New Generic-Level Taxa' section.

*Ochlerotatus canadensis* is a morphologically variable but strongly differentiated Nearctic species without obvious affinities. It was regarded originally as a member of Group E (*dorsalis* group) of Edwards (1932). Based on the structure of the male genitalia, Nielsen (1955) concluded that *canadensis* was distinct enough to have a separate group designation. Rohlf (1963), however, concluded that *canadensis* was closer to the *communis* group based on numerical taxonomic analyses of morphological data and transferred the species to that group. Eight years later, Lunt & Nielsen (1971b) observed that thoracic setal characters elucidated by Lunt & Nielsen (1971a) did not support the placement of *canadensis* in the *communis* group and recommended that it be placed in a group by itself. Rohlf (1977) analyzed the thoracic setal data of Lunt & Nielsen (1971a) using cluster analysis and non-metric multidimensional scaling analyses and concluded that *canadensis* was sufficiently different to warrant its placement in a separate group. In an analysis of 18S rDNA sequences by Shepard *et al.* (2006), *canadensis* was placed in a sister relationship with '*Oc. (Pro.) triseriatus*, an unnatural relationship based on extensive morphological differences that may have resulted from only 21 aedine species being included in the analysis. Because the affinities of *canadensis* were not resolved in our previous cladistic analysis of *Ochlerotatus* (Reinert *et al.*, 2008), it was retained as an unplaced member of the genus. However, as *canadensis* is diagnosed by a unique combination of 21 homoplastic characters in the

present analysis (Fig. 2B), we have chosen to resurrect *Culicada* Felt for this monobasic lineage. *Ochlerotatus canadensis* is the originally designated type of this generic-level taxon. Two subspecies of *canadensis*, the nominotypical form and *mathesoni* Middlekauff, are currently recognized (Appendix 2).

The clade comprised of *Juppius* + *Lepidokeneon* is not strongly supported by jackknife (42) and GC (38) values, and it is diagnosed by a combination of eight homoplastic characters (Fig. 2C). However, the terminal taxa are diagnosed by unique combinations of 14 and 24 characters, respectively, and are otherwise distinct elements within genus *Ochlerotatus* (see the New Generic-Level Taxa section). Technically, a single terminal has an undefined GC rather than a zero GC; hence, the two subgenera are established on the number and quality of their diagnostic characters. The adults of species included in subgenus *Juppius* are medium-size mosquitoes whereas those included in subgenus *Lepidokeneon* are quite large, and they exhibit notable anatomical differences, especially in the male genitalia. Significant differences also exist in the fourth-instar larvae and pupae. Furthermore, the two groups are geographically isolated: species of subgenus *Juppius* occur in eastern Africa (Ethiopia and Sudan to South Africa), with an extension into southwestern Asia to Iran, and those of subgenus *Lepidokeneon* occur in Australia. *Lepidokeneon* comprises the species included in the Stricklandi Section of *Ochlerotatus* (see Lee *et al.*, 1984).

*Lewnielsenius* was established as a subgenus of genus *Jarnellius* because the only included species, *Aedes (Heteronychia) muelleri* Dyar, was distinguished from other species of *Jarnellius* by a combination of 16 homoplastic characters (Reinert *et al.*, 2006). In the present study, *muelleri* is sister with *Abraedes* and diagnosed by an extensive combination of 30 homoplastic characters (Fig. 2E). *Lewnielsenius* is obviously not closely related to species of *Jarnellius sensu stricto*. In as much as most of the other groups that comprise the clade shown in Fig. 2E have generic rank, *Lewnielsenius* is herein recognized as a genus based on the degree of morphological distinction and the principle of equivalent rank.

We previously proposed *Sallumia* as a subgenus of *Ochlerotatus* for two Neotropical species, *Oc. hortator* and (provisionally) *Oc. perventor* (Cerqueira & Costa), based on a combination of 23 homoplastic characters that diagnosed and distinguished the former species from a lineage consisting of *Geoskusea*, *Levua* and *Rhinoskusea* (Reinert *et al.*, 2008: fig. 2B). With the inclusion of additional taxa and character data, *Oc. hortator* is strongly supported (GC 58; JK 65) as the sister of that lineage (Figs 1B, 2F) in a clade that is not associated with species of *Ochlerotatus*. *Sallumia* is diagnosed by an extensive combination of 30

homoplastic characters. Likewise, although the monophyly of *Levua* is not established, it is diagnosed by a unique combination of 23 homoplastic characters. In addition to being diagnosed by many homoplastic characters, the data strongly support the monophyly of *Geoskusea* (GC 95; JK 95; 13 characters) and *Rhinoskusea* (GC 100; JK 100; 37 characters). Although Reinert *et al.* (2008) recognized the four taxa as subgenera because they fell within a clade of *Ochlerotatus* species, they are herein reinstated to generic rank based on the new hypothesis of phylogenetic relationships, the principle of equivalent rank, strong character support and their independence from *Ochlerotatus sensu stricto*.

The sister group of *Sallumia* + (*Geoskusea*, *Levua*, *Rhinoskusea*) has a well-supported basal clade (GC 66; JK 68) comprised of five species of '*Aedes (Aedimorphus)*' that are split into two well-defined monophyletic taxa. The monophyly of the first taxon, *apicoannulatus* + *simulans*, is strongly supported (GC 94; JK 95) by a combination of 11 homoplastic characters and the second, *irritans* – *tarsalis*, is reasonably well supported (GC 61; JK 59) by three homoplastic characters (Fig. 2F). Based on the degree of morphological distinctness and position relative to other clades in the cladogram, the two groups are ranked as genera. This first is formally named and described as *Elpeytonius* in the New Generic-Level Taxa section. It only includes the two species included in the analyses. *Catageiomyia* Theobald is resurrected from synonymy with *Aedimorphus* for the clade comprised of *irritans* – *tarsalis*. In addition to the three species included in the analysis (*irritans*, *argenteopunctatus* and *tarsalis*), *Catageiomyia* includes 25 other species (see Appendix 2). The two genera are distinct elements of the Afrotropical aedine fauna.

The sister group to *Elpeytonius* + *Catageiomyia* is split into two large clades (Figs 1B, 2F–J). Within the first, genus *Aedimorphus* (Figs 1B, 2F) is sister to a number of genera that are also divided between two clades (Figs 1B, 2G). The second large clade (Figs 1B, 2H–J) includes five historically recognized genera (*Armigeres*, *Eretmapodites*, *Heizmannia*, *Udaya*, *Zeugomyia*) and taxa previously included in the composite genus *Aedes (sensu Reinert, 2000b)*. As is generally true among higher-level taxa of Culicidae, the relationships of these major clades are weakly supported. This, however, is not surprising since to date neither morphological nor molecular data have satisfactorily resolved deeper relationships among culicine genera (see review of Harbach, 2007).

'*Aedimorphus*' *sensu auctorum* includes 102 species, seven with a subspecies in addition to the nominotypical form (Reinert *et al.*, 2006). As traditionally defined (Knight & Stone, 1977), 15 nominal taxa are

considered to be synonyms of 'Aedimorphus'. Two of these nominal taxa, *Catageomyia* (see above) and *Polyleptomyia* (see below), are removed from synonymy herein for 28 and 2 species, respectively (Appendix 2), that are clearly unrelated to other species traditionally placed in 'Aedimorphus'. As a result of recognizing two new genera, *Elpeytonius* (see above) and *Bifidistylus* (see below), for four species of 'Aedimorphus' *sensu auctorum*, genus *Aedimorphus*, as defined herein, includes 68 species. Because the majority of internal relationships are weakly supported (Fig. 1B), and because specimens of many of the 68 species were unavailable for study, especially from Africa, we are reluctant to propose subgeneric status for the three strongly supported monophyletic terminal taxa of the clade (*gibbinsi* + *quasiunivittatus*, *pipersalatus* + *taeniorhynchoides* and *dalzieli* + *eritreae*). Further study is needed to determine whether *Aedimorphus* is a monophyletic group or a polyphyletic assemblage. Thirteen nominal taxa remain in synonymy for monophyletic groups within our redefined concept of *Aedimorphus* that may require generic-level recognition in the future.

The sister to *Aedimorphus* (Figs 1B, 2G) is comprised of a pair of weakly supported clades, each consisting of a pectinate series of taxa that, with the exception of 'Ae. (Adm.) *albocephalus*' and 'Ae. (Adm.) *lamborni*', are well-defined genera. As alluded to above, the two 'Ae. (Aedimorphus)' species exhibit morphological distinctions that clearly indicate they are unrelated to species of *Aedimorphus sensu stricto*. Although weakly supported, the cladistic analysis places them in a phylogenetic relationship with respect to a clade comprised of *Albuginosus* + (*Tewarius* + (*Christophersomyia* + (*Huaedes* + *Leptosomatomyia*))), with *albocephalus* basal to *lamborni*. Although the internal branches of the clade are weakly supported and only 5 and 9 homoplastic characters diagnose the *albocephalus* and *lamborni* branches, respectively, the two species exhibit clear distinctions from one another and other species that comprise the generic groups within the clade. For this reason, the two branches should in principle have the same (equivalent) rank as the other terminal taxa of the clade, and so we have chosen to resurrect the generic name *Polyleptomyia* Theobald from synonymy with *Aedimorphus* for the *albocephalus* branch and to establish genus *Bifidistylus* for the *lamborni* branch. Theobald (1905) introduced *Polyleptomyia* as a new monobasic genus for *albocephala* (ending agrees in gender with *Polyleptomyia*), which he originally named *Stegomyia albocephalus* two years earlier (Theobald, 1903b). Based on the paucity of relevant information, *gandarai* (da Cunha Ramos, Capela & Ribeiro) is also included in this genus.

*Bifidistylus* includes two species, *lamborni* and *boneti* (Gil Collado) with its two subspecies, *boneti boneti* and *boneti kumbae* (Chwatt). Despite the low number of characters that diagnose the two genera, characters of the females and the male and female genitalia that are not included in the analysis indicate that they are monophyletic groups.

The sister to the *Polyleptomyia* – *Leptosomatomyia* clade (Figs 1B, 2G) includes five well-defined genera that are very strongly supported (Fig. 1B), which further corroborates their elevation to generic rank based on the results of our first study (Reinert *et al.*, 2004). With regard to these genera, the only difference noted in the present analysis is the topology of relationships within genus *Verrallina*. Whereas the three subgenera of *Verrallina* were monophyletic in our first study, subgenus *Verrallina* is now paraphyletic with respect to subgenus *Neomacleaya*, which is undoubtedly due to the inclusion of a greater number of characters and taxa in the present analysis. Despite this, we are convinced that the recognition of three subgenera is appropriate.

As noted above, the large clade shown in Figs 1B and 2H–J is comprised of taxa that were previously included in the composite genus *Aedes* (*sensu* Reinert, 2000b) and five historically recognized genera, *Armigeres*, *Eretmapodites*, *Heizmannia*, *Udaya* and *Zeugomyia*. In the first clade to branch off (Figs 1B, 2H), *Skusea* and *Indusius* have a paraphyletic relationship with respect to *Canraedes*, the monophyly of which is fully supported (JK 100; GC 100) by an extensive combination of 23 homoplastic characters. Based on the exceptional degree of character support and the principle of equivalent rank, we have no hesitation in recognizing *Canraedes* as a genus. *Canraedes masculinus*, the only species of the group included in our first study, was strongly supported as the sister to *Lorrainea* + (*Udaya* + (*Alanstonea* + *Eretmapodites*)) (Reinert *et al.*, 2004: fig. 4B), but its affinities have changed due to the inclusion of additional characters and taxa in the analysis.

*Dendroskusea* Edwards is resurrected from synonymy with *Diceromyia* for the clade comprised of *periskelata*, *micropterus* and *reginae* (Figs 1B, 2H). Although this clade is diagnosed by a combination of only eight homoplastic characters in the absence of JK and GC support (and is also the only genus not recovered as monophyletic when the length ratio characters are treated as ordered), the three species seem to comprise a homogeneous group that is clearly unrelated to members of genus *Diceromyia*. The pairing of *micropterus* and *reginae* is fairly well supported (GC 50; JK 53; Fig. 1B) by a combination of 10 homoplastic characters (Fig. 2H). *Dendroskusea* was originally proposed by Edwards (1929a) as a subgenus of *Aedes* for six nominal species: *Aedes*



*iyengari* Edwards, *Ae. punctipes* Edwards and *Ae. punctissimus* Barraud (a synonym of *iyengari*), which are now recognized as members of genus *Petermattinglyius* (see below), and the three species included in the present study. *Culex micropterus* Giles is the type species of *Dendroskusea* by original designation (Edwards, 1929a). Based on the paucity of relevant information, two nominal species, *Ae. kanarensis* Edwards and *Ae. ramachandrai* Reuben are provisionally placed in the genus pending further study.

Dyar & Shannon (1925) introduced *Catatassomyia* as a new monobasic genus for *meronephada*, which they also recognized as new. Twenty-eight homoplastic characters diagnose this clade (Fig. 2H). Based on this unique combination of characters and other distinguishing features not included in the analysis, we choose to reinstate *Catatassomyia* as a genus. The only other option is to recognize *Catatassomyia* as a subgenus of *Bothaella*; however, in the absence of morphological evidence and support (GC 24; JK 27) for a relationship with *Bothaella*, *Catatassomyia* must be afforded equivalent rank. Based on the taxonomic history of *meronephada*, it is obvious that this species was never properly placed at generic level. Edwards (1929b) transferred *meronephada* to *Aedes* (*Stegomyia*) and placed *Catatassomyia* in synonymy with that taxon. Edwards (1932) divided subgenus *Stegomyia* into four groups and placed *meronephada* in Group B (*w-alba*-group). Mattingly (1965) divided Group B into three subgroups and assigned *meronephada* to a monobasic subgroup (B2, *meronephada* subgroup) based on characters indicative of an affinity with species of *Aedes* (*Aedimorphus*). The species remained in *Aedes* (*Stegomyia*) until Huang (1978) transferred it to *Aedes* (*Diceromyia*) based on 'a closer resemblance' to species of that group 'than to any other subgenus of *Aedes*'. The results of the present study indicate that *meronephada* is not closely related to either *Aedimorphus*, *Diceromyia* or *Stegomyia*.

Huang (2005) established *Cornetius* as a monobasic subgenus for *Aedes cozi*, which was originally described as a species of *Aedes* (*Stegomyia*) by Cornet (1973). Based on a study of the adult and immature stages, Huang (2005) found that *cozi* is 'very distinct' from all traditionally recognized subgenera of *Aedes* [Huang did not accept the reclassification of *Aedini* proposed by Reinert *et al.*, 2004], which is clearly corroborated by the 31 homoplastic characters that diagnose *Cornetius* (Fig. 2I). Based on this unique combination of characters, the absence of evidence of affinities with other taxa and the principle of equivalent rank, *Cornetius* is elevated to generic rank.

The monophyly of the clade comprised of *whartoni* – *scanloni* (Figs 1B, 2I) is not strongly supported (GC

14; JK 10), but it is a distinct group that is diagnosed by a combination of 11 homoplastic characters and a number of features that were not included in the analysis (see description in the New Generic-Level Taxa section); hence, the reason we have chosen to establish genus *Petermattinglyius* for this lineage. In addition to the four species included in the analysis (*whartoni*, *franciscoi*, *iyengari* and *scanloni*), this taxon also includes the allied nominal species *Aedes punctipes* Edwards (see Appendix 2). These species occur in the Oriental Region. Two of the five species, *punctipes* and *iyengari*, were originally placed in *Aedes* subgenus *Skusea* (Edwards, 1921, 1923b, respectively) and later transferred to *Aedes* subgenus *Dendroskusea* (Edwards, 1929a). A few years later, Edwards (1932) synonymized subgenus *Dendroskusea* with subgenus *Diceromyia* and transferred the African and Oriental species of subgenus *Skusea* to the composite subgenus, which he divided into groups A (African species) and B (Oriental species). From that point on, *Diceromyia* remained a dumping ground for a morphologically diverse collection of species with ambiguous affinities (Mattingly, 1959: 38).

As noted above, the species of *Stegomyia* included in the analysis are divided between two clades (Figs 1B, 2J) that are weakly supported (GC 15; JK 20; Fig. 1B) by a combination of 11 homoplastic characters. Because this study was seriously handicapped by the unavailability of numerous important species, especially from the Afrotropical, Australasian and Oriental Regions, it is not possible to know whether the relationships recovered in the analysis are natural or, indeed, whether the genus is truly monophyletic. For this reason, the present treatment and classification of *Stegomyia* is regarded as preliminary.

It is unfortunate that the type species of *Stegomyia* is *St. aegypti* because this species, and the closely allied *St. mascarensis* (MacGregor), are radically different from other species currently included in the genus. Based on this morphological disparity, there is no doubt that the pairing of *aegypti* with *apicoargentea* in the present analysis (Figs 1B, 2J) is an erroneous relationship engendered by the relative paucity of *Stegomyia* species available for study. As a number of species included in the analysis comprise well-supported monophyletic clades or morphologically distinct terminal branches that merit subgeneric rank, it is necessary to recognize the nominotypical subgenus of *Stegomyia* based on the 17 homoplastic characters that diagnose the type species. As a foundation for establishing a natural classification for all species currently included in *Stegomyia*, the nominotypical subgenus is here restricted to the 'aegypti group' of Huang (2004), which is defined by the holomorphology of *aegypti* and *mascarensis* (Appendix 2).

The male genitalia of *aegypti* and *mascarensis* are extremely similar but differ significantly from those of other *Stegomyia* species. A diagnosis of subgenus *Stegomyia* based on adult morphology is provided by Huang (2004: 15, as the *aegypti* group of *Aedes* subgenus *Stegomyia*).

In addition to the nominotypical subgenus, the first of the two clades that comprise genus *Stegomyia* (Figs 1B, 2J) includes a strongly supported terminal group (GC 79; JK 81: Fig. 1B) that we choose to recognize as subgenus *Mukwaya*. This subgenus is equivalent to the *simpsoni* group of Huang (2004), which includes eight species (Appendix 2) in the Afrotropical Region. A diagnosis of subgenus *Mukwaya* based on adult morphology is provided by Huang (2004: 17, as the *simpsoni* group of *Aedes* subgenus *Stegomyia*).

The second clade of genus *Stegomyia* is split into two subclades, the first of which includes subgenera *Actinothrix*, *Zoromorphus* and *Bohartius* arrayed in a cascading series of relationships. The subclade as a whole is not strongly supported (GC 26; JK 39: Fig. 1B), but the diagnostic characters and zoogeographic distributions of the three groups strongly support their subgeneric status. *Actinothrix* is established as a subgenus for *Stegomyia edwardsi* Barraud, a distinct species described from the Andaman Islands that is diagnosed by a combination of 10 homoplastic characters (Fig. 2J). Edwards (1932) placed *edwardsi* in Group B (*w-alba*-group) and Belkin (1962) introduced a new group (*edwardsi* group) for this species and two South Pacific species, *tulagiensis* Edwards and *robinsoni* Belkin. Huang (1977a) also included *seampi* Huang in the *edwardsi* group.

*Zoromorphus* is a monobasic subgenus, diagnosed by a unique combination of 14 homoplastic characters (Fig. 2J). The type species, *St. futunae*, was described as a 'very clearly marked endemic species' of the Horne Islands of Australia (Belkin, 1962). *Stegomyia futunae* was originally included among species of the *scutellaris* group, Group C, of Edwards (1932).

The sister-group relationship of subgenus *Zoromorphus* with subgenus *Bohartius* is moderately supported (GC 48; JK 53: Fig. 1B) by a combination of 11 homoplastic characters (Fig. 2J). Subgenus *Bohartius* is proposed for five species (Appendix 2) that are endemic to the Mariana Islands in the western Pacific Ocean. *Bohartius* is equivalent to Group F (*pandani* group) of Bohart (1957). The monophyly of the subgenus is strongly supported (GC 99; JK 99: Fig. 1B) by an extensive combination of 23 homoplastic characters (Fig. 2J).

Branch supports along the stem of the other subclade are generally weak to moderate. Only the terminal taxa (Figs 1B, 2J), i.e. *Xyele*, *Heteraspidion* and

*Huangmyia*, have sufficient character support and other attributes to warrant subgeneric status. *Xyele* is established as a monobasic subgenus for *St. desmotes* based on a unique combination of 16 homoplastic characters and equivalent rank relative to other subgeneric groups. *Stegomyia desmotes*, a disparate species traditionally included in Group B (*w-alba*-group) of Edwards (1932), is widely distributed in the Oriental Region. Huang (1977a) established the monobasic *desmotes* subgroup for this species based on distinctive morphological features of the larval, pupal and adult stages, including the female genitalia. The description of the *desmotes* subgroup (Huang, 1977a: 25–26) provides an adequate description of subgenus *Xyele*.

The monophyly of *Heteraspidion* is strongly supported (GC 55; JK 61: Fig. 1B) by only four homoplastic characters (Fig. 2J). The subgenus is established for the two Oriental species (*annandalei* and *craggi*) that were included in the analysis. These two species were also traditionally placed in Group B (*w-alba*-group) of Edwards (1932). Huang (1977a) placed these two species in a separate subgroup, the polythetic *annandalei* subgroup, based on a unique combination of characters. Huang's (1977a: 25–26) characterization of the subgroup also applies to subgenus *Heteraspidion*. Additional morphological features of the subgenus are contained in Appendix 1.

Subgenus *Huangmyia* is undoubtedly monophyletic. It is fully supported (GC 100; JK 100) by a unique combination of 16 homoplastic characters (Figs 1B, 2J). In addition to the two species included in the analysis (*mediopunctata* and *perplexa*), the subgenus also includes the nominal species *St. malikuli* (Huang). Edwards (1932) included *St. mediopunctata* in his Group C (*scutellaris* group). Knight & Hurlbut (1949) subdivided the *scutellaris* group into three subgroups, one of which, Subgroup III, was established for *St. mediopunctata* (the *mediopunctatus* subgroup of *Aedes* subgenus *Stegomyia*). Huang (1973), based on 'strikingly differentiated characters', followed Mattingly (1965) in placing the subgroup within the *w-albus* group of Edwards (1932). Subgenus *Huangmyia*, which includes the species that Huang (1973) included in the *mediopunctatus* subgroup of *Aedes* (*Stegomyia*), is a morphologically distinct group within genus *Stegomyia*.

Finally, it is necessary to address the status of '*Ochlerotatus* (*Protomacleaya*)'. When Zavortink (1972) removed *Protomacleaya* from *Aedes* (*Finlaya*), he stated: 'Although the subgenus is quite diverse, is defined mainly on negative characters, and many of the included species depart from the "normal" in 1 or more characteristics of 1 or more stages, it is, I believe, natural because of the basically similar male genitalia of virtually all species.' As repeatedly shown

in our studies (Reinert *et al.*, 2004, 2006, 2008 and the present study), '*Oc. (Protomacleaya)*' is a polyphyletic assemblage. Ultimately, the group may be split up into monophyletic taxa and classified accordingly. However, the criteria for doing so are not explicitly clear, and until the affinities of all members of the group are known, '*Ochlerotatus (Protomacleaya)*' *sensu auctorum* is retained pending further phylogenetic analysis.

### CONCLUDING COMMENTS

We fully realize that our proposed changes to the traditional classification of tribe Aedini, and to the historical broad concept of genus *Aedes* in particular, has not been accepted in some areas, principally due to an inexplicable phobia of nomenclatural change. In response to this, we must ask: What good is it to build a classification if the monophyletic lineages of equivalent rank are not denoted by unique names? Black (2004) pointed out that characters used to place species into broad taxonomic categories for convenience of identification usually do not reflect evolutionary relationships, and as noted by Harbach (2007) the acceptance of broad genus-group concepts for reasons of convenience is phylogenetically unsupportable. The rank of taxonomic groups should be gauged relative to relationships with other groups. If the degree of morphological distinction that separates the 12 traditionally recognized genera of Aedini (Knight & Stone, 1977) is accepted as a measure of generic separation, then the many monophyletic groups of Aedini that exhibit an equal or greater degree of anatomical differentiation should be ranked accordingly. This is aptly demonstrated by our series of studies (Reinert *et al.*, 2004, 2006, 2008 and the present study), which have resulted in the formal recognition herein of 80 genera and 48 subgenera within tribe Aedini. Based on the limited number of species of some genera available for study, including *Eretmapodites*, *Howardina*, *Neomelaniconion* and *Zeugomyia*, and especially *Aedimorphus*, *Ochlerotatus* and *Stegomyia*, it is likely that additional generic-level taxa (principally subgenera) will be recognized as a result of future studies.

### NEW GENERIC-LEVEL TAXA

The new generic-level taxa recognized in the present study are described below. References are provided for those taxa that were previously well defined and illustrated as informal taxonomic groups, e.g. species groups and subgroup. The following abbreviations are used in the descriptions: ♀ = female, ♀g = female

genitalia, ♂ = male, ♂g = male genitalia, P = pupa and L = fourth-instar larva. The taxa are listed in alphabetical order.

#### *BIFIDISTYLUS* REINERT, HARBACH & KITCHING, GEN. NOV.

*Type species: Aedes (Aedimorphus) lamborni* Edwards, 1923.

#### *Females*

*Head:* Vertex with narrow, curved, decumbent scales; occiput and vertex with numerous long, erect, forked scales; ocular line narrow, with narrow, curved scales; eyes above antennal pedicels contiguous or separated by less than diameter of 1 ocular facet; antennal pedicel with several small, broad, white scales and few short, slender setae on mesal surface; clypeus bare; maxillary palpus dark-scaled with apex white-scaled, longer than forefemur.

*Thorax:* Scutum covered with narrow, curved, dark and pale scales except for bare, median part of prescutellar area, with small group of broad, white scales on prescutellar area mesal to setae on each side; scutellum with broad, silvery scales on all lobes; acrostichal (anterior and posterior), dorsocentral (anterior and posterior) and prescutellar setae well developed; paratergite with broad, white scales; antepronota widely separated, with narrow, curved pale scales, several setae; postpronotum with narrow, curved scales, several posterior setae; postspiracular area with broad, white scales, several setae; subspiracular area with elongate patch of broad, white scales; upper proepisternum with broad, white scales, numerous setae, lower proepisternal area bare; prealar area with few broad, white scales and several setae on upper area, lower area with patch of broad, white scales; mesokatepisternum with moderately large upper and small lower posterior patches of broad, white scales, few upper and several lower posterior setae; mesepimeron with patch of broad, white scales on upper and extending over middle areas, upper setae present, lower setae absent.

*Wing:* Dark-scaled with small pale-scaled patch at base of costa dorsally, pale-scaled area larger on ventral surface; upper calypter with numerous setae on margin; alula with narrow, dark scales on posterior margin; dorsal tertiary fringe scales dark; remigium with 1 or 2 setae distally on dorsal surface.

*Legs:* Ante- and postprocoxal membranes bare; hindfemur with white scales at apex; hindtibia dark-scaled with white-scaled apical band; hindtarsus dark-scaled, hindtarsomeres 1–4 with white-scaled,

apical bands, hindtarsomeres 2–4 with white-scaled, basal bands, hindtarsomere 5 white-scaled; fore-, mid- and hindungues equal, each with 1 tooth.

*Abdomen:* Tergum I with patch of broad, white scales on laterotergite; terga II–VI with dorsobasal, pale-scaled areas.

*Genitalia:* Tergum VIII moderately pigmented, width greater than length, numerous broad scales covering distal area and few scattered scales on proximal area, short setae on approximately distal 0.40, apex flat with several moderately long to long, stout and few short, slender setae; sternum VIII moderately pigmented with heavily pigmented band on distal margin, width greater than length, apex with moderate, median emargination separating somewhat flattened, broadly rounded lobes, numerous broad scales on approximately distal 0.80, seta 2-S inserted posterior to seta 1-S; terga IX comprised of 2 moderately pigmented, lateral sclerites separated by membrane mesally, each sclerite with apex broadly rounded and bearing 5–13 short, slender setae; postgenital lobe moderately long, moderately wide, apex with moderate, median emargination, several setae on distal area; upper vaginal sclerite moderately pigmented, moderately large; without lower vaginal sclerite; insula tongue-like, without setae; cercus moderately long, moderately wide, apex broadly rounded with few short and few moderately long setae, numerous short setae on much of dorsal surface, numerous broad scales (*Bf. lamborni*) or scales absent (*Bf. boneti kumbae* (Chwatt)); 3 spermathecal capsules, spherical, 1 large and 2 slightly smaller.

#### *Males*

*Head:* Antennae with distal 2 flagellomeres disproportionately long, remainder of flagellomeres short with numerous long setae directed primarily dorsally and ventrally; maxillary palpus with 5 palpomeres, slightly shorter than proboscis, palpomeres 4 and 5 downturned, palpomeres 4 and 5 and distal part of 3 with numerous long setae lateroventrally.

*Legs:* Fore- and midungues unequal, each with 1 tooth; hindungues equal, simple.

*Abdomen:* Terga with numerous long, slightly curved setae laterally.

*Genitalia:* Tergum IX moderately pigmented, posterior margin with moderate-sized, rounded lobe on each side of relatively narrow, median area, each lobe bearing several slender setae; gonocoxite moderately long, moderately wide, dorsal surface with numerous moderately long, slender setae on mesal area, lateral

surface with moderate number of long, stout setae, ventral surface with several short, slender setae on mesal area and several long, stout setae on approximately distal 0.25, numerous broad scales on lateral and ventral surfaces, mesal surface membranous; gonostylus attached at apex of gonocoxite, approximately 0.50 length of gonocoxite, proximal part moderately broad, bifurcated slightly proximal to midlength, outer lobe longer with short subapical seta and somewhat broader than inner lobe which bears 1 short, flattened, bluntly pointed, gonostylar claw at apex; aedeagus comprised of 2 darkly pigmented, lateral sclerites, each with few elongate teeth on approximately distal 0.50, dorsal flap covering sclerites and with proximal part broadly rounded; phallosome with short, narrow, basal piece; proctiger relatively long, with distal part darkly pigmented and pointed, without cercal setae or basal lobe; claspette comprised of small, somewhat rounded, basal plaque bearing few short, slender setae proximally and several short, stout setae distally; sternum IX with 1–4 short setae on median, posterior area.

#### *Pupae*

*Trumpet:* Moderately long; moderately wide distally; tracheoid area weakly developed at base.

*Cephalothorax:* Setae 1,3-CT similarly developed; 4,5-CT branched, similar in length; 10,12-CT branched; 11-CT normally single, longer than 10,12-CT.

*Abdomen:* Seta 3-I long, stout, single, longer than 6,7-I; 1-II with numerous slender branches; 2-II inserted lateral to 1,3-II; 3-II,III long, stout, single; 3-III longer than 5-III; 5-V longer than median, dorsal length of terga VI; 6-VII inserted posterior and slightly mesal to 9-VII, 9-VII branched, longer than 6-VII; 9-VIII with 3–5 branches.

*Paddle:* Apical margin rounded; midrib extends to near apex of paddle; without hair-like spicules on margins; seta 1-Pa short, single or 2-branched.

#### *Fourth-instar larvae*

*Head:* Seta 1-C slender, single; 4-C short, with 4 or 5 slender branches, inserted mesal and slightly anterior or slightly posterior to 6-C; 5,6-C moderately long, stout, aciculate; 5-C with 8 or 9 branches, inserted posteromesal to 6,7-C; 6-C with 4 branches, close to 5-C, inserted mesal and slightly posterior to 7-C; 7-C moderately long, with 10 or 11 aciculate branches; 12-C short, branched, inserted mesal to 13-C; 13-C with 2–5 branches, longer than 12-C; 14-C single; 19-C absent; antenna moderately long, with spicules, seta 1-A with 4–7 branches.

*Thorax*: Setae 1–3-P not inserted on common setal support plate, 1-P > 2-P > 3-P length; 5,6-P long, single, 5-P longer than 6,7-P; 7-P long, with 2 or 3 branches; 4-M short, with 2 or 3 branches; 5,7-M long, single, 5-M longer than 7-M; 2-T with 4 or 5 slender branches; 6-T single.

*Abdomen*: Seta 6-I–VI long, stout, with 2 branches; 7-I long, stout, with 2 or 3 branches; 12-I absent; 8-II branched; 1-VII very long, stout, single, noticeably longer than dorsal length of saddle; 2,4-VIII single; comb comprised of numerous scales in triangular patch; segment X with saddle incomplete ventrally, acus absent, seta 1-X short, single or 2-branched, inserted on saddle, 2-X moderately long, with 7–10 branches, 3-X long, single, ventral brush with several, long, multiple-branched setae, inserted on grid with both transverse and lateral bars, 1 (rarely 2) shorter, branched, precratal seta.

*Siphon*: Moderately long; acus absent; numerous pecten spines (evenly spaced on proximal 0.50 of siphon and proximal to seta 1-S in *Bf. lamborni*; distal spines wider spaced and extending to near apex of siphon, seta 1-S inserted within pecten in *Bf. boneti kumbae*).

#### Included species

*Bifidistylus boneti boneti* (Gil Collado), *Bf. boneti kumbae* and *Bf. lamborni*.

#### Distribution

Equatorial Guinea, Kenya, Malawi, Republic of Cameroon, Democratic Republic of Congo, Republic of South Africa and Zambia.

#### Bionomics

Larvae of *Bf. lamborni* were collected from a pool of foul water in a cavity in the top of a well-shaded rock on a river bank (Edwards, 1923a) and in a muddy pool used as a pig-wallow and rock-pools (Hopkins, 1936, 1952). Immature stages of *Bf. boneti kumbae* were taken from a rock-pool in a densely shaded stream (Chwatt, 1948; Hopkins, 1952). Females of *Bf. lamborni* were taken biting during the day in a forest (scarce), during the night (rare) and in the forest canopy (very rare) (Haddow *et al.*, 1952).

#### Discussion

The above generic description is based primarily on specimens examined of *Bf. lamborni* (♀, ♀g, ♂, ♂g, P and L) and *Bf. boneti kumbae* (♂, ♂g, P and L) and published information on *Bf. boneti boneti* (Gil Collado, 1936; Edwards, 1941). Pao & Knight (1970) described and illustrated the larval maxilla and man-

dible of *Bf. lamborni*. Additional descriptive information is provided in Appendix 1 for species included in the analysis.

#### Etymology

*Bifidistylus* is derived from the Latin adjective *bifidus*, -a, -um, meaning split into two parts, bifurcated, and *stilus* (masculine), meaning a Roman writing instrument. The name is masculine and refers to the bifurcated gonostylus of the male genitalia. Recommended abbreviation of *Bifidistylus* = *Bf.*

ELPEYTONIUS REINERT, HARBACH & KITCHING,  
GEN. NOV.

*Type species*: *Ochlerotatus apicoannulatus* Edwards, 1912 (*nom. nov.* for *Aedimorphus alboannulatus* Theobald, 1905).

#### Females

*Head*: Vertex with entire area covered with narrow, curved, decumbent scales or with few to several narrow scales on anterior, median area; occiput and vertex with numerous erect, forked scales; ocular line narrow, with narrow, pale scales; eyes above antennal pedicels touching or separated by diameter of 2 ocular facets; antennal pedicel with mesal surface bearing few short, slender setae, few small, broad, dark scales present or absent; clypeus bare; maxillary palpus dark-scaled; proboscis dark-scaled with narrow, complete or incomplete, pale-scaled band near midlength, proboscis longer than forefemur.

*Thorax*: Scutum covered with narrow, curved scales except bare prescutellar area; acrostichal (anterior and posterior) and dorsocentral (anterior and posterior) setae present; prescutellar area with 7–9 setae on each side; scutellum with broad, silvery scales on all lobes; paratergite with broad, pale scales; antepronota widely separated, with broad, silvery scales, several setae; postpronotum with narrow, curved, dark scales on upper area, posterior setae present; postspiracular area without scales, 3 or 4 setae present; scales absent on hypostigmal area, subspiracular area, lower proepisternum, lower and upper prealar areas and metameron; mesokatepisternum with small upper and small lower posterior patches of broad, pale scales, setae present; mesepimeron with small upper patch of pale scales, without lower setae.

*Wing*: Dark-scaled, with small pale-scaled patch at base of costa; upper calypter with several setae on margin; remigium with 1 or 2 short setae on dorsal surface distally; dorsal tertiary fringe scales dark.

*Legs:* Ante- and postprocoxal areas bare; hindfemur and hindtibia with pale scales at apex; hindtarsomeres 1–4 each dark-scaled with wide, apical, white-scaled band, tarsomere 5 entirely or nearly entirely white-scaled; fore- and midungues, equal, each with 1 tooth.

*Abdomen:* Tergum I with patch of broad, white scales on laterotergite; terga I–VI dark-scaled dorsally; segment VII laterally compressed.

*Genitalia:* Tergum VIII moderately pigmented, width greater than length, few scales on distal part; sternum VIII moderately pigmented, width greater than length, apex with moderate, median emargination separating small to moderate-sized, sublateral lobes, scales absent or few in number, seta 2-S inserted posterior to seta 1-S; tergum IX comprised of single, moderately pigmented sclerite, apex with small, median emargination separating small, rounded lobes, each with 2–4 short, slender setae; postgenital lobe moderately long, moderately wide, apex with moderate, median emargination, setae on distal part of ventral surface; upper vaginal sclerite moderately pigmented, small to moderate size; without lower vaginal sclerite; insula tongue-like, with 4–6 small tuberculi on distal area; cercus moderately long, moderately wide, apex broadly rounded, without scales; single large, spherical, spermathecal capsule.

#### *Males*

*Head:* Antenna with distal 2 flagellomeres disproportionately long, remainder of flagellomeres short with numerous long setae directed primarily dorsally and ventrally; maxillary palpus with 5 palpomeres, palpomeres 4 and 5 somewhat downturned, palpomeres 4 and 5 and distal part of 3 with several long setae lateroventrally.

*Legs:* Foreungues unequal, each with 1 tooth; midungues unequal, larger one simple, smaller one with 1 tooth; hindungues equal, both simple.

*Abdomen:* Terga with several moderately long setae laterally.

*Genitalia:* Tergum IX moderately pigmented and sclerotized, posterior margin with pair of moderately large, broadly rounded lobes each with 3–6 short, slender setae; gonocoxite moderately long, moderately wide, dorsal surface with several short and few moderately long, slender setae on mesal area, several long, stout setae on outer area and on lateral surface, broad scales on outer part of dorsal, lateral and ventral surfaces, mesal surface membranous; gono-

stylus attached at apex of gonocoxite, relatively long, approximately proximal 0.60 narrow, distal part broader with several minute, fine setae, terminal short, broad, leaf-like gonostylar claw attached to rounded apex, outer margin of approximately distal 0.30–0.40 with long, narrow, curved, finger-like lobe with minute seta near apex; aedeagus with 2 elongate, lateral sclerites each bearing few, elongate teeth on distal part, membrane-like dorsal flap covering lateral sclerites; proctiger moderately long, apex bluntly rounded, with 2 or 3 minute cercal setae; claspette developed as short, narrow, plaque bearing few short setae at base of gonocoxite; sternum IX moderately long, setae absent or with 3 or 4 short, slender setae on median, posterior area.

#### *Pupae*

*Trumpet:* Moderately long, narrow, darkly-pigmented; tracheoid area weakly developed at base.

*Cephalothorax:* Seta 1-CT with 3 branches, long but noticeably shorter than 3-CT; 5-CT longer than 4-CT; 7-CT longer than 6-CT; 11-CT single.

*Abdomen:* Seta 3-I very long, stout, single; 6-I longer than 7-I; 1-II multiple-branched, slender; 2-II, 3-II, III long, stout, single, 3-II inserted mesal or at same level anterior to 2-II; 6-II long, stout, single, longer than 3-II; 5-V longer than median, dorsal length of tergum VI; 9-VII branched, inserted anterior and lateral to and longer than 6-VII; 9-VIII with 6 or 7 stout, aciculate branches.

*Paddle:* Apical margin rounded; midrib extending to apex of paddle; without hair-like spicules on margins; seta 1-Pa short, with 2 or 3 branches.

#### *Fourth-instar larvae*

*Head:* Seta 1-C slender, single; 4-C short, with 3–9 very slender branches, inserted mesal and either slightly anterior or slightly posterior to 6-C; 5-C long, stout, with 7–10 aciculate branches, inserted posterior and mesal to 6,7-C; 6-C long, stout, with 4–6 aciculate branches, inserted close to 5-C; 7-C moderately long to long, stout, with 8–11 aciculate branches, inserted anterior and lateral to 6-C; 12-C inserted mesal to 13-C; 13-C with several relatively long branches, longer than 12-C; 14-C short, single or 2-forked; 19-C absent; antenna moderately long, narrow, with several spicules, seta 1-A with 3–6 branches.

*Thorax:* Setae 1–3-P not inserted on common setal support plate, 1-P > 2-P > 3-P length, 1,3-P branched, 2-P single; 5,7-P branched; 6-P single, longer than 5,7-P; 1,4-M and 1,2-T branched; 6-T single.

*Abdomen:* Seta 7-I long, stout, with 2 branches; 12-I absent; 1,5,8-II branched; 1-VII long; 1-VIII longer than 2-VIII; 2,4-VIII single; comb with numerous scales in patch; segment X with saddle incomplete ventrally, acus absent, seta 1-X single to 3-branched, inserted on saddle, 2-X with 3–5 moderately long branches, 3-X long, single, ventral brush with several, fan-like, multiple-branched setae attached to grid with both transverse and lateral bars, several shorter, branched, precratal setae.

*Siphon:* Acus present; pecten with several evenly spaced spines; seta 1-S with 2–5 branches, inserted distal to pecten.

#### *Included species*

*Elpeytonius apicoannulatus* and *El. simulans* (Newstead & Carter).

#### *Distribution*

Central African Republic, Ghana, Liberia, Republic of Cameroon, Democratic Republic of Congo, Nigeria, Sierra Leone, Sudan and Uganda.

#### *Bionomics*

Immature stages of *El. apicoannulatus* have been collected from rot-holes in mango, pawpaw, cotton and various other trees, dracaenas, stumps of banana plants and cut stems of bamboos (Evans, 1926) [we note that Hopkins (1936: 130, 1952: 170) apparently misinterpreted Evans' (1926) comments on habitats of this species] and tree-holes (Haddow *et al.*, 1952, Hopkins, 1936, 1952). *Elpeytonius simulans* have been collected from bamboo stumps (Kumm, 1931) and tree-holes (Haddow *et al.*, 1952; Hopkins, 1936, 1952). Females of *El. simulans* have been taken occasionally biting humans during the day in forests and plantations and rarely in forests during the night (Haddow *et al.*, 1952).

#### *Discussion*

Evans (1926) briefly described and partially illustrated the male genitalia and fourth-instar larva of *El. apicoannulatus* (description of larva was noted by Edwards, 1932: 167). Hopkins (1936, 1952) described and illustrated the fourth-instar larvae of *El. apicoannulatus* (utilized Evans' illustration) and *El. simulans*. Apparently, the description and illustration of the fourth-instar larva of *El. apicoannulatus* was not included in any of the Culicidae catalogs and supplements starting with Stone, Knight & Starcke (1959) to the present. Edwards (1941) provided brief descriptions of the female, male and pupa of *El. apicoannulatus* and illustrated the male genitalia. He briefly described the female and male of *El. simulans* and illustrated the adult female and male genitalia.

Pao & Knight (1970) described and illustrated the fourth-instar larval mouthparts of *El. simulans*. The above generic description of the pupae and fourth-instar larvae are based on specimens of *El. simulans* and the published partial descriptions and illustrations of both species. Additional descriptive information is provided in Appendix 1 for species included in the analysis.

#### *Etymology*

*Elpeytonius* is named in honour of Mr E. L. Peyton in recognition of his important contributions to the taxonomy and biology of Culicidae, for introducing the first author (JFR) to the exciting world of mosquito biosystematics over 45 years ago, and for steering the interests of the second author (REH) toward a career in mosquito taxonomy. The generic name is masculine, formed from his initials (E. L., which were indicated without corresponding names on his birth certificate), surname and the Latin suffix '-ius'. Recommended abbreviation = *El.*

#### OCHLEROTATUS SUBGENUS JUPPIUS REINERT, HARBACH & KITCHING, SUBGEN. NOV.

*Type species:* *Grabhamia caballa* Theobald, 1912.

#### *Females*

*Head:* Vertex covered with narrow, curved, decumbent scales; occiput and vertex with numerous long, erect, forked scales; ocular line narrow, with narrow, curved, pale scales; eyes above antennal pedicels separated by diameter of approximately 4 ocular facets; antennal pedicel with numerous small, broad, non-overlapping scales and few short, slender setae on mesal surface; clypeus bare; maxillary palpus dark-scaled, with or without few pale scales intermixed; proboscis dark-scaled, longer than forefemur.

*Thorax:* Scutum covered with narrow, curved pale and dark scales including most of median, prescutellar area; parascutellar area with 2–4 narrow, curved, pale scales; scutellum with narrow, curved scales on all lobes; acrostichal (anterior and posterior), dorso-central (anterior and posterior) and prescutellar areas with numerous dark setae; paratergite with broad, pale scales; antepronota widely separated, with narrow, curved, pale scales, several setae; postpronotum with narrow, curved scales dorsally and few somewhat broader scales ventrally, several posterior setae; hypostigmal area with broad, pale scales; postspiracular area with numerous broad, pale scales, few setae; subspiracular area with numerous broad, pale scales; upper proepisternum with broad, pale scales, numerous setae, lower area bare; prealar area with broad, pale scales on upper and lower areas,

several to numerous setae; mesokatepisternum with large upper and moderate lower posterior patches of broad, pale scales, several upper and numerous lower posterior setae; mesepimeron with large patch of broad, pale scales on upper area and extending over middle area, several upper setae, with 4 or 5 lower setae; metameron with several broad, pale scales.

*Wing:* Some veins with moderately broad scales, other veins with narrow scales, dark and pale scales intermixed on some or most veins (*Oc. caballus* and *Oc. chelli* Edwards) or dark-scaled (*Oc. juppi* (McIntosh)); costa with pale-scaled patch at base; upper calypter with numerous setae on margin; alula with dark scales on posterior margin; dorsal tertiary fringe scales narrow, dark; remigium with 1 or 2 setae distally on dorsal surface.

*Legs:* Anteprocoxal membrane bare; postprocoxal membrane with broad, pale scales; femora with numerous pale scales intermixed with dark-scaled areas, apices pale-scaled; tibiae with numerous pale scales intermixed with dark scales; tarsi dark-scaled with basal, pale-scaled bands on tarsomeres 1 and 2, and tarsomere 3 of mid- and hindtarsi; fore-, mid- and hindungues equal, each with 1 tooth.

*Abdomen:* Tergum I with patch of broad, pale scales on laterotergite; terga II–VI with dorsobasal pale-scaled patch expanded as complete or incomplete median, longitudinal stripe; segment VII dorsoventrally flattened.

*Genitalia:* Intersegmental membrane between segments VII and VIII very long; tergum VIII moderately pigmented with small non-pigmented notches on lateral and apical margins, length greater than width, without scales (1 adventitious scale in *Oc. juppi*), short setae on entire length, 2 or more long setae on lateral margins, apex flat with small, median emargination; sternum VIII moderately pigmented with narrow, median, non-pigmented strip, length greater than width, apical margin gently rounded, without scales (rarely with 1 adventitious scale), setae on nearly entire length, seta 2-S inserted slightly posterior to seta 1-S; tergum IX comprised of single moderately pigmented, moderately long sclerite, apex with shallow, median emargination separating rounded lobes, each bearing 4–8 short setae, 9–15 total setae; postgenital lobe moderately wide, dorsal length short, apex flat or with very shallow, median emargination, few setae on distal area; without upper and lower vaginal sclerites; insula lip-like, with 2 moderately long, slender setae in lateral patches, 4 total setae; cercus moderately pigmented, long, narrow, apex narrowly rounded, without scales (occa-

sionally 1 adventitious scale in *Oc. juppi*), numerous setae covering most of dorsal surface; 3 spermathecal capsules, spherical, 1 large and 2 slightly smaller.

#### *Males*

*Head:* Antennae with distal 2 flagellomeres disproportionately long, remainder of flagellomeres short with numerous long setae directed primarily dorsally and ventrally; maxillary palpus with 5 palpomeres, longer than proboscis, with palpomeres 4 and 5 downturned, palpomeres 4 and 5 and distal part of 3 with numerous long setae lateroventrally.

*Legs:* Fore- and midungues unequal, larger unguis with 2 teeth, smaller unguis with 1 tooth; hindungues equal, each with 1 tooth.

*Abdomen:* Terga with numerous long, curved setae laterally; tergum VIII with posterior margin flat.

*Genitalia:* Tergum IX moderately pigmented, posterior margin with darkly pigmented, short, narrow lobe on each side of midline bearing few short, stout, somewhat flattened setae and few short, slender setae; gonocoxite heavily pigmented, moderately long, moderately wide, dorsal surface with several short, slender setae on most of area and few long, stout setae on outer area, mesal area with small, apical lobe bearing few short, slender setae and small, basal lobe bearing few short, slender and 1 or 2 moderately long, slender setae, lateral surface with several long, stout setae, ventral surface with few moderately long, slender setae on proximal area and several long, stout setae on distal area, several broad scales on lateral and ventral surfaces, mesal surface membranous; gonostylus attached at apex of gonocoxite, long, approximately 0.70 length of gonocoxite, relatively narrow throughout length but median part slightly wider than proximal part, distal part curved mesally and narrower than proximal part, with 2 or 3 short, slender setae, gonostylar claw short, slender, apex truncate, attached at apex of gonostylus; aedeagus tube-like, lateral margins bowed outward, widest on middle 0.33, apex bluntly pointed; phallosome with basal piece short; proctiger relatively short, distal part darkly pigmented, with curved, pointed apex, 5–8 minute, cercal setae; claspette comprised of single, relatively short, slender stem bearing one, long, flattened, relatively narrow, claspette filament at apex, with distal part slightly curved; sternum IX moderately pigmented, moderately long, with several short and moderately long setae on median, posterior area.

#### *Pupae*

*Trumpet:* Relatively short; moderately wide distally; pinna moderately long; tracheoid area weakly developed at base.



*Cephalothorax*: Seta 1-CT longer than 3-CT, both branched; 4,5-CT similarly developed, branched; 6-CT much shorter than 7-CT; 11-CT single, longer than 10,12-CT.

*Abdomen*: Seta 6-I single or 2-branched, longer than 3,7-I; 1-II with few to several slender branches; 3-II moderately long, single (3-II,III with 3 branches in *Oc. juppi*, fig. 3 of McIntosh, 1973); 6-II single, longer than 3-II; 3-III single, noticeably longer than 5-III; 1-IV–VI long, moderately stout, with 2 or 3 branches; 5-IV,V with 2 very long branches, noticeably longer than median, dorsal length of following tergum; 6-VII shorter than and inserted posterior and slightly mesal to 9-VII; 9-VIII with 10–12 stout, lightly aciculate branches.

*Paddle*: Apical margin more or less flat, with minute spicules; without hair-like spicules on margins; midrib extends to apex of paddle; seta 1-Pa short, single (occasionally 2-branched).

#### *Fourth-instar larvae*

*Head*: Seta 1-C single, distal part attenuate; 4-C short, very slender, single or 2-branched, inserted mesal and in line with 6-C; 5-C long, stout, single, inserted posterior and mesal to 6,7-C; 6-C long, stout, single, inserted mesal and slightly posterior to 7-C; 7-C moderately long, moderately stout, with 4–7 aciculate branches; 12-C with 4 or 5 branches, inserted mesal to 13-C; 13-C single, longer than 12-C; 14-C single; 19-C absent; antenna relatively short, moderately pigmented, with few scattered, minute spicules, seta 1-A short, single or with 2 or 3 branches, tips not reaching apex of antenna.

*Thorax*: Setae 1–3-P not inserted on common setal support plate, 1-P > 2-P > 3-P length, 1,2-P single, 3-P short, with 2 or 3 branches; 4-P short, single or with 2 branches; 5-P moderately stout, long, single, longer than 6-P; 6-P long, normally 2-branched (rarely single); 7-P long, with 3 branches; 4-M branched; 2-T with 3 branches; 6-T single.

*Abdomen*: Seta 7-I with 2 or 3 slender branches, approximately 0.60 length of 6-I; 12-I present; 6-II with 2 branches, longer than 6-III; 8-II with 2 or 3 branches; 6-III,IV moderately long, moderately stout, with 2 branches; 1-VII short, with 2 slender branches, approximately 0.40 dorsal length of segment X; 12-VII single; 1-VIII with 5–7 branches; 2,4-VIII single; comb with several thorn-like scales in short curved row; segment X with saddle incomplete ventrally, acus present, seta 1-S short, single, inserted on saddle, 2-X moderately long, with several branches, 3-X long, single, ventral brush with numerous long,

branched setae inserted on grid with well developed transverse and lateral bars, with 2 (rarely 3) shorter, branched, precratal setae.

*Siphon*: Relatively short; acus present; pecten with several evenly spaced spines on approximately proximal 0.45 of siphon, distal 1 or 2 spines longer; seta 1-S with 4–6 short branches, inserted distal to pecten.

#### *Included species*

*Ochlerotatus caballus*, *Oc. chelli* and *Oc. juppi*.

#### *Distribution*

Aden, Eritrea, Ethiopia, Iran, Kenya, Lesotho, Namibia, Republic of South Africa, Sudan and Zimbabwe.

#### *Bionomics*

Hopkins (1936, 1952) provided a summary of the immature habitats of *Oc. caballus* to include a rock-pool, a stream, water-furrows and small or medium-sized depressions in the veldt, which were filled periodically by rain or irrigation water. The habitats usually contained vegetation. McIntosh (1973) reported the larvae of *Oc. juppi* occur in temporary ground pools in grassland. McIntosh (1973) indicated the females of *Oc. juppi* are highly anthropophilic and readily feed on larger domesticated animals and possibly also, to some extent, on birds, during the daytime but with peak feeding in the early part of the night. *Ochlerotatus caballus*, like the previous species, readily feed on humans and larger domesticated animals.

#### *Discussion*

Subgenus *Juppius* includes medium-sized mosquitoes. Confusion concerning the identity of *Oc. caballus* and *Oc. chelli* occurred until McIntosh (1973) evaluated the species included in this group. See McIntosh (1973) for descriptions, partial illustrations and a discussion of the species. Hopkins (1952) described the fourth-instar larva of *Oc. caballus* and Jupp (1996) provided partial illustrations of the adults of *Oc. caballus* and *Oc. juppi* and the male genitalia of the latter species. The adult habitus of the primarily African *Juppius* species share a number of characters with those of the Australian subgenus *Lepidokeneon*, however notable differences exist in adult characters, especially in the male genitalia, and fourth-instar larvae. Additional descriptive information is provided in Appendix 1 for species included in the analysis.

#### *Etymology*

*Juppius* is named in honour of Dr Peter G. Jupp in recognition of his important contributions to the tax-

onomy of mosquitoes of southern Africa and studies on mosquito-vectored pathogens. The subgeneric name is masculine, formed from his surname and the masculine Latin suffix '-ius'. Recommended subgeneric abbreviation = *Jup*.

*OCHLEROTATUS* SUBGENUS *LEPIDOKENEON* REINERT,  
HARBACH & KITCHING, SUBGEN. NOV.

*Type species: Aedes (Ochlerotatus) spilotus* Marks, 1963.

#### *Females*

*Head:* Vertex covered with narrow, curved, decumbent scales; occiput and vertex with numerous long, erect, forked scales; ocular line narrow, with narrow, curved pale and dark scales; eyes above antennal pedicels separated by diameter of 4 or 5 ocular facets; antennal pedicel with several small, broad, non-overlapping scales and few short, slender setae on mesal surface; clypeus bare; maxillary palpus dark-scaled normally with few pale scales intermixed; proboscis dark-scaled with numerous pale scales intermixed, longer than forefemur.

*Thorax:* Scutum covered with narrow, curved scales including transverse bar on median part of prescutellar area, background scales dark with pale scales intermixed or in small patches; parascutellar area with 2–4 narrow, curved, pale scales; scutellum with narrow, curved scales on all lobes; acrostichal (anterior and posterior), dorsocentral (anterior and posterior) and prescutellar areas with numerous dark setae; paratergite with moderately broad to broad, pale scales; antepnota widely separated, with numerous pale and dark scales, numerous setae; postpronotum with large patch of narrow, curved scales dorsally and small patch of broad scales ventrally, several posterior setae; hypostigmal area with broad, pale scales (few in *Oc. turneri* (Marks)); postspiracular area with numerous broad, and some relatively narrow, pale scales, several setae; subspiracular area with broad, pale scales; upper proepisternum with broad, pale scales, numerous setae, lower proepisternal area bare; prealar area with broad, pale scales on upper and lower areas, several setae; mesokatepisternum with large upper and moderate lower posterior patches of broad, pale scales, several upper and numerous lower posterior setae; mesepimeron with large patch of broad, pale scales on upper area and extending over middle area, patch may have partial break at midlength, numerous upper setae, without lower setae (Marks, 1963 indicated lower seta(e) present or absent in *Oc. stricklandi* Edwards);

metameron with few broad, pale scales and 1–3 short setae (Marks, 1963 indicated this area was bare in *Oc. turneri*).

*Wing:* All veins with broad dark and pale scales intermixed; costa with pale-scaled patch at base; upper calypter with numerous setae on margin; alula with dark scales on posterior margin; dorsal tertiary fringe scales moderately broad with intermixed pale and dark scales; remigium with 3 setae distally on dorsal surface.

*Legs:* Ante- and postprocoxal membranes bare; femora with numerous pale scales intermixed with dark-scaled areas, apices pale-scaled; tibiae with numerous pale scales intermixed with dark scales; tarsi with pale scales intermixed with dark scales, more numerous on tarsomeres 1 and 2 and fewer on distal tarsomeres (tarsomere 5 occasionally dark-scaled); fore- and midungues equal, each with 1 tooth; hindungues equal, both simple but with seta-like spine subbasally.

*Abdomen:* Tergum I with patch of broad, pale scales on laterotergite; segment VII dorsoventrally flattened.

*Genitalia:* Intersegmental membrane between segments VII and VIII very long; tergum VIII moderately pigmented, with small non-pigmented notches on lateral and apical margins, length greater than width, without scales, short setae on entire length, 2 or more long, slender setae on lateral margins, apex flat or with very shallow, median emargination; sternum VIII moderately pigmented with narrow, median, non-pigmented strip, length greater than width, apical margin gently rounded with median area slightly flattened, without scales, setae on entire length, seta 2-S inserted lateral to seta 1-S; tergum IX comprised of single, moderately pigmented sclerite, apex with moderate, median emargination separating rounded lobes each bearing 8–12 short setae, 20–21 total setae; postgenital lobe moderately wide, dorsal length short, apex with shallow, median emargination, few setae on distal area; without upper and lower vaginal sclerites; insula lip-like, with 2 moderately long, slender setae in lateral patches, 4 total setae; cercus moderately pigmented, long, narrow, apex narrowly rounded, without scales, numerous setae extending from near base to apex of dorsal surface; 3 spermathecal capsules, spherical, 1 large and 2 slightly smaller.

#### *Males*

*Head:* Antennae with distal 2 flagellomeres disproportionately long, remainder of flagellomeres short with numerous long setae directed primarily dorsally

and ventrally; maxillary palpus with 5 palpomeres, approximately equal to or slightly longer than proboscis, palpomeres 4 and 5 downturned, palpomeres 4 and 5 and distal part of 3 with numerous long setae lateroventrally.

*Legs:* Foreungues unequal, larger unguis with 2 teeth, smaller unguis with 1 tooth; midungues unequal, larger unguis with round swelling at midlength, smaller with 1 tooth; hindungues equal, with seta-like spine post-basally.

*Abdomen:* Terga with numerous long, curved setae laterally; posterior margin of tergum VIII with median lobe.

*Genitalia:* Tergum IX moderately pigmented, posterior margin with darkly pigmented, short, narrow lobe on each side of midline bearing few short, stout, somewhat flattened setae and 1 or 2 short, slender setae; gonocoxite moderately pigmented, relatively long, moderately wide, dorsal surface covered with numerous very short, slender setae, approximately distal 0.20 with few long, stout setae, mesal area with small, apical lobe bearing few very short, slender setae and several short, stout setae, without basal lobe, lateral surface with numerous long, stout and few moderately long setae, ventral surface with several moderately long setae on proximal area and few very long, stout setae on approximately distal 0.20, few short, slender setae on mesal area, several broad scales on dorsal and numerous scales on lateral and ventral surfaces, mesal surface membranous; gonostylus attached at apex of gonocoxite, long, approximately 0.66 length of gonocoxite, relatively narrow throughout length but median part slightly wider than proximal part, distal part curved mesally, narrower than proximal part and with 2–4 short, slender setae, gonostylar claw short, slender, apex truncate, attached at apex of gonostylus; aedeagus tube-like, elongate, sides approximately parallel but slightly wider on proximal 0.33, apex truncate; phallosome with basal piece short; proctiger relatively long, distal part darkly pigmented with several minute teeth at apex, 6 or 7 minute cercal setae; claspette comprised of single, short, slender, curved stem bearing one, apical, moderately long, flattened, moderately broad claspette filament with comb-like row of short spicules on outer margin, apex bluntly rounded; sternum IX moderately pigmented, moderately long, with several moderately long setae on median posterior area.

#### *Pupae*

*Trumpet:* Moderately long, moderately wide distally; pinna long; tracheoid area weakly developed at base.

*Cephalothorax:* Setae 1,2-CT similarly developed, branched; 4,5-CT similarly developed, branched; 6-CT much shorter than 7-CT; 11-CT single, longer than 10,12-CT.

*Abdomen:* Seta 6-I single, longer than 3,7-I; 1-II with multiple slender branches; 3-II moderately long, branched; 6-II long, single, noticeably longer than 3-II; 3-III single, longer than 5-III; 1-IV–VI moderately long, slender, with 3 branches; 5-IV,V single, very long, noticeably longer than median, dorsal length of following tergum; 6-VII shorter than and inserted posterior and slightly mesal to 9-VII; 9-VIII with 4–7 slender branches.

*Paddle:* Apical margin rounded, with tiny spicules; without hair-like spicules on margins; midrib extends to near apex of paddle; seta 1-Pa short, single.

#### *Fourth-instar larvae*

*Head:* Seta 1-C single, distal part attenuate; 4-C short, with 2–5 very slender branches, inserted anteromesal to 5,6-C; 5-C long, stout, single, inserted posteromesal to 6,7-C; 6-C long, stout, single, inserted anteromesal to 7-C; 7-C long, stout, with 4–7 aciculate branches; 12-C with 2 or 3 branches, inserted mesal to 13-C; 13-C with 2 or 3 branches (single on 1 side of 1 specimen), longer than 12-C; 14-C single; antenna moderately long, darkly pigmented, with numerous spicules, seta 1-A with 3–7 aciculate branches, tips not reaching apex of antenna.

*Thorax:* Setae 1–3-P not inserted on common setal support plate, 1-P > 2-P > 3-P length, 1-P stout, very long, single, 2-P single, 3-P single or occasionally 2-branched; 4-P long, single; 5-P very long, single, longer than 6-P; 6-P long, with 2 branches; 7-P very long, with 3 branches; 4-M branched; 2-T with 2 branches; 6-T single.

*Abdomen:* Seta 7-I long, stout, with aciculate branches; 12-I present; 6-II with 2 branches, shorter than 6-III; 8-II single; 6-III,IV long, stout, single; 1-VII very long, stout, single, noticeably longer than dorsal length of segment X; 12-VII branched; 1-VIII single; 2,4-VIII branched; comb with few long, stout scales in short, curved row; segment X with saddle large, complete on ventral surface, acus not seen, seta 1-X single, inserted on saddle, 2-X moderately long, with several branches, 3-X long, single, ventral brush with numerous long, multiple-branched setae inserted on grid with well developed transverse and lateral bars, without precratal setae.

*Siphon*: Moderately long; acus present; pecten with numerous, evenly spaced spines extending beyond midlength of siphon, few distal spines noticeably longer; seta 1-S with 4–7 aciculate branches, inserted distal to pecten.

#### Included species

*Ochlerotatus spilotus*, *Oc. stricklandi* and *Oc. turneri*.

#### Distribution

Australia.

#### Bionomics

Marks (1963), Dobrotworsky (1965) and Lee *et al.* (1984) provided summaries of the known bionomics of the included species. *Ochlerotatus spilotus* immature stages have been collected during September or October, mostly in roadside excavations or ditches and once in a waterhole in a watercourse. All habitats had greenish or cloudy water, with some emergent vegetation, and most were partly shaded. *Ochlerotatus stricklandi* immature stages have been collected from September to December, from temporary, fresh-water ground pools in areas of predominantly winter rainfall. Nothing is known about the bionomics of the immature stages of *Oc. turneri*. *Ochlerotatus spilotus* females have been collected biting humans and rabbits during the daytime and *Oc. stricklandi* and *Oc. turneri* females have been reported biting humans, the former species during the daytime.

#### Discussion

Adults of species included in subgenus *Lepidokeneon* are quite large. Species assigned to subgenus *Lepidokeneon* were previously placed in the Stricklandi Section of *Aedes* (*Ochlerotatus*) by Marks (1957, 1963), Dobrotworsky (1965) and Lee *et al.* (1984). The last two authors included a listing of literature associated with the species. See Marks (1963) for descriptions, illustrations and a discussion of all species assigned to the subgenus. Dobrotworsky (1965) included taxonomic information for *Oc. spilotus* and *Oc. stricklandi*. Additional morphological features are provided in Appendix 1 for species included in the analysis.

#### Etymology

*Lepidokeneon* is derived from the Greek nouns *lipis*, *-idos* (feminine), meaning scale, and *keneon* (masculine), meaning flank. The name is masculine and refers to the dense thoracic pleural scaling of the

adults (meaning scaled or scaly flank or side). The recommended abbreviation for subgenus *Lepidokeneon* = *Lpd.*

#### OCHLEROTATUS SUBGENUS WOODIUS REINERT, HARBACH AND KITCHING, SUBGEN. NOV.

*Type species*: *Aedes intrudens* Dyar, 1919.

#### Females

*Head*: Vertex covered with narrow, curved, decumbent scales; occiput and vertex with numerous, long, pale, erect, forked scales; ocular line with narrow, curved, pale scales; eyes above antennal pedicels separated by diameter of 3 or 4 ocular facets; antennal pedicel with few small, broad, non-overlapping scales and several short, slender setae on mesal surface; clypeus bare; maxillary palpus dark-scaled (occasionally with few pale scales intermixed in *Oc. intrudens*); proboscis dark-scaled, longer than forefemur.

*Thorax*: Scutum covered with narrow, curved scales except bare median, prescutellar area, both pale and dark scales present, pale scales covering scutal fossal, antear, much of supraalar, usually narrow stripe on acrostichal (anterior and posterior) and lateral margins of prescutellar areas; without parascutellar scales; scutellum with narrow, curved scales on all lobes; acrostichal (anterior and posterior), dorsocentral (anterior and posterior) and prescutellar areas with numerous setae; antepnota widely separated, with pale scales, several setae; postpronotum nearly covered with scales, narrow, curved on dorsal area and moderately broad to broad on ventral area, several posterior setae; postspiracular area with broad, pale scales, several setae; subspiracular area with elongate patch of broad, pale scales; upper proepisternum with broad, pale scales, numerous setae, lower proepisternum bare; prealar area with patch of broad, pale scales on lower area and extending onto lower part of upper area, numerous setae; mesokatepisternum with broad, pale scales in large upper and moderate lower posterior patches, patches connected or separated by narrow strip, several upper and numerous lower posterior setae; mesepimeron with large patch of broad, pale scales on upper and extending over middle areas, numerous upper setae, lower setae absent in *Oc. diantaeus* or absent to 1–4 setae in *Oc. intrudens*; metameron with several broad, pale scales.

*Wing*: Dark-scaled; upper calypter with numerous setae on margin; alula with dark scales on posterior margin; dorsal tertiary fringe scales dark; remigium with 1–3 setae distally on dorsal surface.

*Legs:* Ante- and postprocoxal membranes bare; femora with pale-scaled fringe at apex; tibiae with anterior surface dark-scaled; tarsi dark-scaled, unguis equal in size, each with 1 tooth.

*Abdomen:* Tergum I with patch of broad, pale scales on laterotergite; segment VII dorsoventrally flattened.

*Genitalia:* Intersegmental membrane between segments VII and VIII very long; tergum VIII moderately pigmented, width greater than length, without or with 1–7 scattered scales, short setae on approximately distal 0.90, apex flat to very gently concave; sternum VIII moderately pigmented, width greater than length, apical margin gently rounded or gently rounded with shallow, median emargination, moderate number of scales, setae on nearly entire area; tergum IX comprised of single moderately pigmented sclerite, apex with small, median emargination separating rounded lobes each bearing 4–9 short, slender setae, 9–17 total setae; postgenital lobe moderately wide, apex with small, median emargination, several setae on distal area; without upper and lower vaginal sclerites; insula lip-like, with 2 or 3 moderately long, slender setae in lateral patches, 4–6 total setae; cercus moderately pigmented, long, narrow, apex narrowly rounded, 1–3 scales, numerous setae extending from near base to apex of dorsal surface; 3 spermathecal capsules, spherical, 1 large and 2 slightly smaller.

#### *Males*

*Head:* Antenna with distal 2 flagellomeres disproportionately long, remainder of flagellomeres short with numerous long setae directed primarily dorsally and ventrally; maxillary palpus with 5 palpomeres, dark-scaled, equal to or longer than proboscis, palpomeres 4 and 5 slightly downturned, palpomeres 4 and 5 and distal part of 3 with moderate to numerous long setae lateroventrally.

*Legs:* Fore- and midungues unequal, each with 1 tooth; hindungues equal, each with 1 tooth.

*Abdomen:* Terga with moderate to numerous long, slightly curved setae laterally.

*Genitalia:* Tergum IX moderately to heavily pigmented, posterior margin with darkly pigmented, short, relatively narrow lobe on each side of midline bearing 5–9 short, stout, slightly curved setae; gonocoxite moderately to heavily pigmented, relatively long, moderately wide, dorsal surface with several short, slender setae on mesal area, several moderately long, slender setae on distal area and long, stout

setae on lateral area, mesal area with large, apical lobe bearing few short, slender setae, small, basal lobe bearing 1 moderately long, stout, somewhat flattened seta and few short, slender setae, lateral surface with several long, stout setae, ventral surface with several moderately long, slender setae on proximal area, distal area with few long, stout setae and patch of moderately long, lanceolate setae on mesal part, scales few on dorsal surface and numerous on lateral and ventral surfaces, mesal surface membranous; gonostylus attached at apex of gonocoxite, long, approximately 0.60–0.65 length of gonocoxite, relatively narrow throughout length but median part somewhat broader than proximal part, distal part curved mesally and narrower than proximal part, with 2–5 short, slender setae, gonostylar claw short, slender, apex truncate, attached at apex of gonostylus; aedeagus tube-like, moderately long, proximal 0.67 relatively wide, distal part relatively narrow; phallosome with basal piece short; proctiger moderately long, distal part darkly pigmented with curved, pointed apex, numerous minute, cercal setae; claspette comprised of 2 lobes, outer lobe moderately long, projecting along proximal part of mesal surface of gonocoxite and bearing 2 moderately long, darkly pigmented, moderately curved setae at apex, lobe connected at base to inner, moderately long, slender, columnar lobe with subapical area broader and bearing small, thumb-like projection with 1 short seta, claspette filament inserted at apex, short to moderately long, flattened, broad mesally; sternum IX moderately pigmented, moderately long, with several short to moderately long, slender setae on posterior area.

#### *Pupae*

*Trumpet:* Moderately long; relatively narrow distally; pinna short; tracheoid area weakly developed at base.

*Cephalothorax:* Setae 1,3-CT similarly developed, normally 2-branched; 4,5-CT similarly developed; 6-CT much shorter than 7-CT; 11-CT normally single (rarely 2-branched in *Oc. intrudens*).

*Abdomen:* Seta 6-I longer than 3,7-I; 1-II short, with few to several slender branches; 3-II relatively short, single or 2-branched, shorter than 6-II; 3-III moderately long, normally single, longer than 5-III; 1-IV,V moderately long, slender, single or with 2–4 branches; 5-IV,V single to 3-branched, longer than median, dorsal length of following tergum; 6-VII shorter than and inserted posterior and slightly mesal to 9-VII; 9-VIII with 3–9 (normally 3–5) branches with distal parts forked.

*Paddle*: Apical margin rounded; without hair-like spicules on margins; midrib extends to near apex of paddle; seta 1-Pa short, single (very rarely 2-branched).

#### *Fourth-instar larvae*

*Head*: Seta 1-C spiniform, apex bluntly pointed; 4-C short, with 3–6 very slender branches, inserted mesal and at same level or slightly posterior to 6-C; 5-C long, stout, with 3 or 4 aciculate branches, inserted posteromesal to 6,7-C; 6-C long, stout, with 2–4 aciculate branches, inserted posteromesal to 7-C; 7-C long, stout, with 4–6 (rarely 3) aciculate branches; 12-C short, branched, inserted mesal to 13-C; 13-C single in *Oc. intrudens* or with 2 or 3 branches in *Oc. diantaeus*, longer than 12-C; 14-C single; 19-C present; antenna moderately long (*Oc. intrudens*) to long (*Oc. diantaeus*), with numerous spicules, seta 1-A with 3–5 aciculate branches, tips not reaching apex of antenna.

*Thorax*: Setae 1–3-P not inserted on common setal support plate, 1-P > 2-P > 3-P, 1-P very long, single, 2-P short, single, 3-P short, with 2 or 3 branches; 4-P single (rarely 2-branched); 5,6-P long, single, 5-P longer than 6-P; 7-P long, with 2 or 3 branches; 4-M and 2-T branched; 6-T single.

*Abdomen*: Setae 6-I–V and 7-I long, stout, single; 12-I present; 6-II slightly shorter than 6-III; 8-II normally 2-branched (occasionally single); 1-VII branched, relatively short; 10,12-VII single; 1-VIII with 5–8 branches, noticeably longer than 2-VIII; 2,4-VIII single (2-VIII rarely 2-branched in *Oc. diantaeus*); comb with several scales in one curved or irregular row; segment X with saddle incomplete ventrally, acus present, seta 1-X single, inserted on saddle, 2-X moderately long, multiple-branched, 3-X long, single, ventral brush with numerous, long, branched setae inserted on grid with well developed transverse and lateral bars, with 3 or 4 shorter, branched, precratal setae.

*Siphon*: Moderately long; acus present; pecten with numerous spines, distal 2 or 3 spines longer and more widely spaced, seta 1-S inserted distal to pecten (rarely on level with last pecten spine in *Oc. intrudens*).

#### *Included species*

*Ochlerotatus diantaeus* Howard, Dyar & Knab and *Oc. intrudens*.

#### *Distribution*

Nearctic and Palearctic Regions.

#### *Bionomics*

Wood *et al.* (1979) reported that larvae of *Oc. intrudens* in Canada hatch from overwintering eggs

in April and inhabit temporary, woodland, snowmelt pools. Carpenter & LaCasse (1955) indicated larvae of this species occur in a variety of habitats, including woodland pools, open bogs and marshes, particularly in water from melting snow in the northern United States, whereas Natvig (1948) found the larval habitats in Norway to be principally shallow pools and water-filled ditches with bottoms covered with decaying pine needles located at the border of pine woodlands, and Gutsevich *et al.* (1974) reported similar habitats in Russia. Larvae of *Oc. diantaeus* in Canada were found in temporary spring pools in hardwood forests in which the water was usually stained dark brown by abundant leaf litter (Wood *et al.*, 1979), in the United States larvae were found mostly in shaded pools with cold water left from melting snow in dense forests (Carpenter & LaCasse, 1955), and in Russia Gutsevich *et al.* (1974) reported larval habitats as different types of temporary water bodies in forests formed from snowmelt, e.g. pits, ditches and puddles in shaded or open locations. Females of *Oc. intrudens* are persistent biters of humans during the day and night (Carpenter & LaCasse, 1955; Wood *et al.*, 1979). *Ochlerotatus diantaeus* females also feed on humans (Gutsevich *et al.*, 1974; Tanaka *et al.*, 1979; Becker *et al.*, 2003).

#### *Discussion*

Carpenter & LaCasse (1955), Wood *et al.* (1979) and Tanaka *et al.* (1979) included descriptions and illustrations of females, males, male genitalia and fourth-instar larvae of *Oc. diantaeus* and *Oc. intrudens*. Yamaguti & LaCasse (1951) and Reinert (2002e) provided a description and illustration of the female genitalia of *Oc. intrudens* and Darsie (1951) and Tanaka (1999) described and illustrated the pupa of this species. Kalpage & Brust (1968), Horsfall & Voorhees (1972) and Dahl (1997) described and illustrated the eggs of *Oc. diantaeus* and *Oc. intrudens*. Distribution maps for both species in Canada are found in Wood *et al.* (1979) and in the United States and Canada in Darsie & Ward (2005). Additional descriptive information is provided in Appendix 1 for species included in the analysis.

#### *Etymology*

*Woodius* is named in honour of Dr D. Monty Wood in recognition of his important contributions to the taxonomy of mosquitoes and other Diptera of North America, especially Canada. The subgeneric name is masculine, formed from his surname and the masculine Latin suffix '-ius'. Recommended subgeneric abbreviation = *Woo*.

*PETERMATTINGLYIUS* REINERT, HARBACH &  
KITCHING, GEN. NOV.

*Type species: Aedes (Skusea) iyengari* Edwards, 1923.

#### *Females*

*Head:* Vertex with broad, decumbent scales; occiput with number of short, erect forked scales; vertex normally with few semi-erect, forked scales posterior to ocular setae; ocular line narrow; eyes above antennal pedicels contiguous; antennal pedicel with few small, broad scales and short, slender setae on mesal surface; clypeus bare; maxillary palpus dark-scaled with pale scales distally (pale scales absent in *Pe. whartoni* (Mattingly) and *Pe. punctipes* (Edwards)); proboscis dark-scaled, longer than forefemur.

*Thorax:* Scutum with at least posterior 0.25 densely covered with broad scales including entire prescutellar area and extending anteriorly over supraalar area; scutellum entirely covered with broad, overlapping, dark scales; acrostichal (anterior and posterior) and dorsocentral (anterior and posterior) areas without setae; paratergite with pale scales; antepnota widely separated, with broad scales, some species also with narrow scales, setae present; postpronotum with broad scales, some species also with narrow scales, posterior setae present; postspiracular area without scales, setae present; subspiracular area with broad, pale scales; upper proepisternum with broad, pale scales and 3–6 setae, lower proepisternal area bare; prealar area with scales present or absent, setae present; mesokatepisternum with upper and lower posterior patches of broad, pale scales, upper and lower posterior setae present; mesepimeron with single large patch of broad, pale scales, upper and 2 or 3 lower setae present (lower setae absent in *Pe. whartoni*).

*Wing:* Dark-scaled, with pale-scaled patch at base of costa; upper calypter with several setae on margin; alula with row of dark scales on posterior margin and few moderately broad to broad, dark scales above marginal scales; dorsal tertiary fringe scales dark; remigium with 2 or 3 setae on dorsal surface distally.

*Legs:* Anteprocoxal membrane bare; postprocoxal membrane with broad, pale scales (absent in *Pe. whartoni*); femora with preapical, pale-scaled band and pale scales at apex; tibiae with several median, pale-scaled bands or spots (absent in *Pe. whartoni*); hindtarsus with tarsomere 1 with pale-scaled basal and apical spots and 2 median bands (median pale-scaled bands absent in *Pe. whartoni*); fore-, mid- and hindtarsus equal, simple.

*Abdomen:* Tergum I with dorsobasal, median, pale-scaled patch (absent in *Pe. whartoni*) and broad, pale scales on laterotergite; segment VII laterally compressed.

*Genitalia:* Tergum VIII moderately pigmented, with numerous broad scales, apex broadly rounded or flat; sternum VIII moderately pigmented, with numerous broad scales, apex sloping from apicolateral corners to midline (*Pe. whartoni* with moderately deep, median emargination separating broadly, rounded lobes), base nearly straight, seta 2-S inserted lateral to seta 1-S; tergum IX comprised of single, moderately pigmented sclerite, width greater than length, apex with median, emargination separating rounded lobe on each side, each bearing 1–6 short setae (rarely 1 lobe without setae); postgenital lobe with apex rounded or with shallow, median emargination, setae on distal part; upper vaginal sclerite moderately pigmented, moderately large; without lower vaginal sclerite; insula tongue-like, with 2–4 tuberculi on distal area, without setae; cercus moderately long, moderately wide, apex broadly rounded, without scales; 3 spermathecal capsules, 1 large and 2 slightly smaller.

#### *Males*

*Head:* Antenna with distal 2 flagellomeres disproportionately long, remainder of flagellomeres short with numerous long setae directed primarily dorsally and ventrally; maxillary palpus with 5 palpomeres, palpomeres 4 and 5 relatively short, slightly downturned, with only few short setae, palpomere 5 with pale scales at least basally (dark-scaled in *Pe. whartoni*); proboscis dark-scaled with narrow, pale-scaled band distal to midlength (entirely dark-scaled in *Pe. whartoni*).

*Legs:* Fore- and midtarsus unequal, larger unguis with one tooth (simple on midtarsus of *Pe. franciscoi* (Mattingly)); hindtarsus equal, simple.

*Abdomen:* Terga with few short setae laterally.

*Genitalia:* Tergum IX with posterior margin bearing pair of broadly rounded lobes each with 8–15 moderately long, slender setae; gonocoxite moderately long, relatively wide, numerous long setae on lateral surface and outer area of dorsal surface, numerous broad scales on lateral, ventral and outer areas of dorsal surface, dorsal surface with several short, moderately flattened setae on distal area of mesal margin (absent in *Pe. whartoni*), ventral surface with small patch of long setae on proximal area of mesal margin (less developed in *Pe. franciscoi*), gonostylus attached at apex of gonocoxite, relatively broad especially on distal part, single gonostylar claw attached pre-

apically on gonostylus; aedeagus comprised of 2 moderately long, lateral sclerites each with several elongate, lateral teeth extending from base to apex, with membranous, dorsal flap covering proximal part; proctiger relatively short, without cercal setae; claspette comprised of small, short, basal plaque bearing several short setae; sternum IX with one to several short to moderately long setae on posterior area.

#### *Pupae*

*Trumpet*: Relatively short, broad distally (long and narrow in *Pe. whartoni*); tracheoid area weakly developed at base.

*Cephalothorax*: Setae 1,3-CT similarly developed; 6-CT single, much shorter than 7-CT; 11-CT longer than 12-CT; 11,12-CT single.

*Abdomen*: Seta 1-II short, with 2 branches (rarely with 3 branches); 3-II,III long, single; 6-VII inserted mesal and posterior to 9-VII; 9-VIII with 2–5 branches, aciculate.

*Paddle*: Apical margin rounded or with very shallow, median emargination (broadly rounded in *Pe. whartoni*); midrib extends to or near apex of paddle; fringe of hair-like spicules on outer and inner margins (absent in *Pe. whartoni*); seta 1-Pa short, single (branched in *Pe. whartoni*).

#### *Fourth-instar larvae*

*Head*: Seta 1-C single, relatively slender; 4-C short to moderately long, with 12–19 branches, inserted mesal and slightly posterior to 6-C; 5-C long, single, inserted posterior to 4,6,7-C; 7-C moderately long, with 3–8 branches; 12-C branched, inserted mesal to 13-C; 13-C single, longer than 12-C; 14-C short, single; 19-C absent; antenna short, without spicules (long with few spicules in *Pe. whartoni*).

*Thorax*: Setae 1–3-P not inserted on common setal support plate, 1-P > 2-P > 3-P length; 5,7-P branched; 6-P single, longer than 5,7-P; 5-M single, noticeably longer than 6,7-M; 2,6-T single.

*Abdomen*: Seta 6-I–V with 2 long, stout, aciculate branches; 7-I long, single or 2-branched; 12-I absent; 8-II with 2 or 3 branches; 1-VII noticeably longer than dorsal length of saddle; 2,4-VIII single; segment X with saddle incomplete ventrally, acus absent, seta 1-X long, single, inserted on posteroventral area of saddle, 2-X long, single, 3-X moderately long, with 3–5 branches, ventral brush with several long setae with 2–4 branches, inserted on grid with transverse bars, 2 short, branched, precratal setae.

*Siphon*: Relatively short (long in *Pe. whartoni*), acus absent; pecten with several spines; seta 1-S single, inserted distal to pecten.

#### *Included species*

*Petermattinglyius franciscoi*, *Pe. iyengari*, *Pe. punctipes*, *Pe. scanloni* (Reinert) and *Pe. whartoni*.

#### *Distribution*

Bangladesh, India, Indonesia, Malaysia, Myanmar, Singapore and Thailand.

#### *Bionomics*

Immature stages are normally found in bamboo (pots, stumps, internodes, etc.) and occasionally in tree holes or holes in logs (Reinert, 1970). Females have been collected biting humans, in human-baited traps, in light traps and resting in houses.

#### *Discussion*

See Reinert (1970) for descriptions and illustrations (\*) of known stages for species of *Petermattinglyius*, i.e. *Pe. franciscoi* (♀\*, ♂\*, ♂g\*, P\*, L\*), *Pe. iyengari* (♀\*, ♂\*, ♂g\*, P\*, L\*), *Pe. scanloni* (♀\*, ♂\*, ♂g\*), and *Pe. whartoni* (♀\*, ♂\*, ♂g\*, P\*, L\*). The female of *Pe. punctipes* is described by Edwards (1921). Female genitalia of *Pe. franciscoi* and *Pe. iyengari* are partially described and illustrated by Mattingly (1959). Species of the genus are divided between two subgenera (see below). Additional descriptive information is provided in Appendix 1 for species included in the analysis.

#### *Etymology*

*Petermattinglyius* is named in honour of Dr Peter Frederick Mattingly in recognition of his many important contributions to the taxonomy of family Culicidae. The generic name is masculine, formed from his first name, surname and the Latin suffix '-ius'. Recommended abbreviation = *Pe.*

#### *PETERMATTINGLYIUS SUBGENUS AGLAONOTUS*

REINERT, HARBACH & KITCHING, SUBGEN. NOV.

*Type species*: *Aedes (Diceromyia) whartoni* Mattingly, 1965.

#### *Females*

*Head*: Maxillary palpus dark-scaled.

*Thorax*: Prealar knob without scales; mesepimeron without lower setae.

*Legs*: Postprocoxal membrane bare; tibiae without pale-scaled, median bands or spots; hindtarsomere 1 without pale-scaled, median bands.



*Abdomen:* Terga IV–VI with dorsal surface dark-scaled.

*Genitalia:* Posterior margin of sternum VIII with moderate, median emargination separating broadly rounded lobes; IX-Te index 0.72; Ce/dorsal PGL index 2.30.

#### *Males*

*Head:* Maxillary palpus and proboscis dark-scaled.

*Genitalia:* Dorsal surface of gonocoxite without short, moderately flattened setae on distal area of mesal surface; gonostylar claw relatively short.

#### *Pupae*

*Trumpet:* Long and narrow throughout length.

*Cephalothorax:* Setae 1,3,7,10-CT branched.

*Abdomen:* Seta 5-V shorter than median, dorsal length of tergum VI; 9-VIII with 5 branches.

*Paddle:* Without hair-like spicules on margins; seta 1-Pa branched.

#### *Fourth-instar larvae*

*Head:* Antenna long, with spicules.

*Abdomen:* Setae 7-I, 6-VI single.

*Siphon:* Relatively long.

#### *Included species*

*Petermattinglyius whartoni.*

#### *Distribution*

Malaysia and Thailand.

#### *Bionomics*

Immature stages have been collected from fresh, coloured water in large and small split bamboo, bamboo internodes, bamboo stumps and a bamboo cup, 1 to 2 m above ground, in mountain, hilly and valley terrain, in partial and heavy shade, in secondary rain forests and secondary bamboo groves and at an altitude of 100 to 1,600 m. One collection of larvae was taken from a hole in a log lying on the ground.

#### *Discussion*

Additional descriptive information is provided in Appendix 1 for the species included in the analysis.

#### *Etymology*

*Aglaonotus* is derived from the Greek *aglaos* (masculine adjective), meaning splendid, bright, beautiful,

noble, and *notos* (masculine noun), meaning back, ridge. The name is masculine and refers to the dark, shiny scaling of the scutum. Recommended abbreviation for subgenus *Aglaonotus* = *Agl.*

*PETERMATTINGLYIUS* SUBGENUS *PETERMATTINGLYIUS*  
REINERT, HARBACH & KITCHING, SUBGEN. NOV.

#### *Females*

*Head:* Maxillary palpus dark-scaled and normally with pale scales distally.

*Thorax:* Prealar knob with scales; mesepimeron with 2 or 3 lower setae.

*Legs:* Postprocoxal membrane with broad scales; tibiae with 3 or more pale-scaled, median bands or spots; hindtarsomeres 1 with 2 pale-scaled, median bands.

*Abdomen:* Terga IV–VI usually with pale-scaled patches on dorsal surface.

*Genitalia:* Sternum VIII with posterior margin sloping from apicolateral corners to midline; IX-Te index 0.26–0.50; Ce/dorsal PGL index 2.77–3.00.

#### *Males*

*Head:* Maxillary palpus with at least pale scales basally on palpomere 5; proboscis with narrow, pale-scaled band distal to midlength.

*Genitalia:* Dorsal surface of gonocoxite with several short, moderately flattened setae on distal part of mesal surface; gonostylar claw relatively long.

#### *Pupae*

*Trumpet:* Relatively short, broad distally.

*Cephalothorax:* Setae 1–3,7,10-CT single.

*Abdomen:* Seta 5-V longer than median, dorsal length of tergum VI; 9-VIII with 2 or 3 branches.

*Paddle:* With hair-like spicules on margins; seta 1-Pa single.

#### *Fourth-instar larvae*

*Head:* Antenna short, without spicules; seta 1-A short, single.

*Abdomen:* Setae 7-I and 6-VI branched.

*Siphon*: Relatively short.

*Included species*

*Petermattinglyius franciscoi*, *Pe. iyengari*, *Pe. punctipes* and *Pe. scanloni*.

*Distribution*

Bangladesh, India, Indonesia, Malaysia, Myanmar, Singapore and Thailand.

*Bionomics*

Immature stages have been collected from water in bamboo pots, bamboo stumps, tree holes, and hollow in a teak log (Reinert, 1970). Females have been collected in human-baited traps and also biting humans at an elevation of 300 m in forest fringe and scrub areas. Adults have been collected in light traps and resting in houses.

*Discussion*

Additional descriptive information is provided in Appendix 1 for species included in the analysis. Inclusion of *Pe. punctipes* is based on the published description of Edwards (1921). Recommended abbreviation = *Pet.*

STEGOMYIA THEOBALD SUBGENUS *ACTINOTHRIX*  
REINERT, HARBACH & KITCHING, SUBGEN. NOV.

*Type species*: *Stegomyia edwardsi* Barraud, 1923.

Subgenus *Actinothrix* includes the species placed in the Edwardsi Group of Belkin (1962: 445–446) and the Edwardsi Subgroup of Huang (1977a: 3–5). Taxonomic information in these two papers now forms the description of the subgenus. Additional character information in support of the subgenus is provided in Appendix 1. Barraud (1923, 1934) provided illustrations and brief descriptions of the male, male genitalia and female of the type species. Huang (1977a) included a more complete description of the male, male genitalia, female and female genitalia and Tewari *et al.* (2008) described and illustrated the pupa and fourth-instar larva of the type species. Information on distribution, bionomics and taxonomic discussion of species in the subgenus was provided by Belkin (1962) and Huang (1974, 1977a). See Belkin (1962) and Huang (1974) for descriptions and illustrations of the other species included in the subgenus. Belkin (1965) provided additional information on species included in the subgenus.

*Included species*

*Stegomyia edwardsi*, *St. robinsoni* (Belkin), *St. seampi* (Huang) and *St. tulagiensis* (Edwards).

*Etymology*

*Actinothrix* is derived from the Greek nouns *aktis*, *-inos* (feminine), meaning ray, beam, and *thrix* (femi-

nine), meaning hair. The name is feminine and refers to the unusual development of setae 1–3-P of the larvae (*vis-à-vis* setae like rays). Recommended abbreviation for subgenus *Actinothrix* = *Act.*

STEGOMYIA THEOBALD SUBGENUS *BOHARTIUS*  
REINERT, HARBACH & KITCHING, SUBGEN. NOV.

*Type species*: *Aedes (Stegomyia) pandani* Stone, 1939.

Subgenus *Bohartius* includes the species placed in the Pandani Subgroup of Bohart (1957). The subgroup was described on pages 33–34 and this taxonomic information now forms the description of the subgenus. Additional character information in support of the subgenus is included in the data matrix (Appendix 1) of the present study. Bohart (1957) provided a description of the type species of the subgenus including the male, male genitalia, female, pupa and fourth-instar larva, illustrations of the male genitalia, female, pupa and fourth-instar larva, and information on distribution and bionomics. Reinert (2000g) illustrated the female genitalia of *St. pandani* and provided a description of the female genitalia for the subgenus (as Pandani Assemblage). Bohart (1957) also included descriptions and illustrations of the other species included in the subgenus. Stone (1945) provided descriptive information for *St. pandani* and *St. saipanensis* (Stone).

*Included species*

*Stegomyia agrihanensis* (Bohart), *St. neopandani* (Bohart), *St. pandani*, *St. rotana* (Bohart & Ingram) and *St. saipanensis*.

*Etymology*

*Bohartius* is named in honour of Dr Richard M. Bohart in recognition of his important contributions to the taxonomy of mosquitoes, especially in the southwestern Pacific area and the western United States. The subgeneric name is masculine, formed from his surname and the masculine Latin suffix *-ius*. Recommended subgeneric abbreviation = *Boh.*

STEGOMYIA THEOBALD SUBGENUS *HETERASPIDION*  
REINERT, HARBACH & KITCHING, SUBGEN. NOV.

*Type species*: *Stegomyia annandalei* Theobald, 1910.

Subgenus *Heteraspidion* includes the species placed in the Annandalei Subgroup of Huang (1977a). Her description of the group on pages 15–17 now forms the description of the subgenus. Additional character information in support of the subgenus is provided in the data matrix (Appendix 1) of the present study. Huang (1977a) included a description of the type species of the subgenus, i.e. male, male genitalia, female, female genitalia, pupa and fourth-instar

larva, illustrations of the male, male genitalia, female genitalia, pupa and fourth-instar larva, and information on distribution, bionomics and a taxonomic discussion. Mattingly (1965) also provided information and illustrations on the type species. Matsuo *et al.* (1974b) described and illustrated the egg of *St. annandalei*. See Huang (1977a) for a description and illustrations of the other species included in the subgenus.

#### *Included species*

*Stegomyia annandalei* and *St. craggi* Barraud.

#### *Etymology*

*Heteraspidion* is derived from the Greek *heteros* (masculine adjective), meaning different, and *aspidion* (masculine noun), meaning little shield. The name is masculine and refers to the distinctive character of the scutellum, which has broad dark scales on the midlobe and broad white scales on the lateral lobes. Recommended abbreviation for *Heteraspidion* = *Het.*

#### STEGOMYIA THEOBALD SUBGENUS HUANGMYIA REINERT, HARBACH & KITCHING, SUBGEN. NOV.

*Type species: Stegomyia mediopunctata* Theobald, 1905.

Subgenus *Huangmyia* includes the species placed in the *Mediopunctatus* Subgroup of Huang (1977a). The subgroup was described on pages 31–32 and this taxonomic information now forms the description of the subgenus. Additional character information in support of the subgenus is provided in the data matrix (Appendix 1) of the present study. Huang (1977a) included a description of the type species of the subgenus, i.e. male, male genitalia, female, female genitalia, pupa and fourth-instar larva, illustrations of the male genitalia, female genitalia, pupa and fourth-instar larva, and information on distribution, bionomics and a taxonomic discussion. Huang (1977a) included descriptions and illustrations of the other species included in the subgenus and Mattingly (1965) provided information and illustrations of some species. Matsuo *et al.* (1974b) described and illustrated the egg of *St. perplexa* Leicester.

#### *Included species*

*Stegomyia malikuli* (Huang), *St. mediopunctata* and *St. perplexa*.

#### *Etymology*

*Huangmyia* is named in honour of Dr Yiau-Min Huang in recognition of her many important contributions to the taxonomy of the aedine genus *Stegomyia*. The subgeneric name is feminine, formed from her surname and the feminine Greek noun '-myia',

meaning 'fly'. Recommended subgeneric abbreviation = *Hua*. Note: *Hua*. was previously used for subgenus *Huaedes* Huang, which was elevated to generic-level by Reinert *et al.* (2004) and given the generic abbreviation *Hu*.

#### STEGOMYIA THEOBALD SUBGENUS MUKWAYA REINERT, HARBACH & KITCHING, SUBGEN. NOV.

*Type species: Stegomyia simpsoni* Theobald, 1905.

Subgenus *Mukwaya* includes the species placed in the *Simpsoni* Group of Huang (2004). The group was described on pages 14 and 17 and now forms the description of the subgenus. Huang (2004) included a list of the then known life stages that were described, illustrated and brief information on immature and female bionomics for species currently placed in subgenus *Mukwaya*. Partial illustrations for most known stages of included species, including the type species *St. simpsoni*, were also provided. Previously, Huang (1979, 1986) published information (as *simpsoni* complex) concerning species now included in the subgenus. Reinert (2000g) provided a description of the female genitalia of the *Simpsoni* Assemblage (=subgenus *Mukwaya*) and illustrated the female genitalia of *St. simpsoni*. Considerable important information concerning the type species ecology, behaviour, physiology, morphology, etc. was provided in a series of papers by Pajot (1975, 1976a, b, 1977). Edwards (1941) included descriptive information and some illustrations for *St. kivuensis* (Edwards), *St. simpsoni*, *St. subargentea* (Edwards) and *St. woodi* (Edwards). Hopkins (1952) described the fourth-instar larvae of *St. simpsoni*, *St. strelitziae* (Muspratt) and *St. subargentea*. See descriptions and/or illustrations in Mattingly (1971c), Hinton (1981) and Linley & Service (1994) for the egg of *St. woodi*. The present study includes taxonomic information (see Appendix 1) concerning known life stages of *St. bromeliae* Theobald, *St. simpsoni* and *St. woodi*. The works of Mattingly (1952, 1953) provide taxonomic information and distribution data for most species and that of Muspratt (1956) provides this information for species occurring in southern Africa.

#### *Included species*

*Stegomyia bromeliae*, *St. gandaensis* (Huang), *St. josiahae* (Huang), *St. kivuensis*, *St. lili* Theobald, *St. sampi* (Huang), *St. simpsoni*, *St. strelitziae*, *St. subargentea* and *St. woodi*.

#### *Etymology*

*Mukwaya* is named in honour of Dr Louis Godfrey Mukwaya in recognition of his many contributions to medical entomology and our knowledge of *St. simpsoni*. The subgeneric name is a masculine

patronymic formed from his surname. Recommended abbreviation for *Mukwaya* = *Muk*.

*STEGOMYIA* THEOBALD SUBGENUS *STEGOMYIA*

*Type species: Culex aegypti* Linnaeus, 1762 = *Culex fasciatus* Fabricius, 1805.

Subgenus *Stegomyia* of genus *Stegomyia* is herein restricted to the species included in the Aegypti Group of Huang (2004). Huang (2004) provided a diagnosis for the subgenus (as Aegypti Group) that included male and female characters (page 15), a key to adults (pages 22–24), a key to male genitalia (pages 30–31), partial illustrations of the adults (figs 1–3), and an illustration of the male genitalia of *St. aegypti* (fig. 35). Additional information on the type species of the subgenus, *St. aegypti*, is provided by Christophers (1960) (biology of the species), Ross & Horsfall (1965), Matsuo *et al.* (1974b) and Linley (1989) (description and illustration of the egg), Belkin (1962) (illustrations of male genitalia, pupa and fourth-instar larva), Mattingly (1965) (descriptions, illustrations and discussion of subspecies and varieties), Tanaka *et al.* (1979) (descriptions and illustrations of the female, male and genitalia, and fourth-instar larva), Huang (1979) (illustrations of the female genitalia, male and genitalia, pupa and fourth-instar larva), Reinert (2000g) (description and illustration of the female genitalia) and Appendix 1 of the present paper.

*Included species*

*Stegomyia aegypti aegypti*, *St. aegypti formosa* (Walker) and *St. mascarensis* (MacGregor).

*STEGOMYIA* THEOBALD SUBGENUS *XYELE* REINERT, HARBACH & KITCHING, SUBGEN. NOV.

*Type species: Stegomyia desmotes* Giles, 1904.

Subgenus *Xylele* includes the species placed in the Desmotes Subgroup of Huang (1977a). The subgroup was described on pages 25–26 and this taxonomic information now forms the description of the subgenus. Additional character information in support of the subgenus is provided in Appendix 1 of the present paper. Huang (1977a) included a description of the type species of the subgenus, i.e. male, male genitalia, female, female genitalia, pupa and fourth-instar larva, illustrations of the male, male genitalia, female, female genitalia, pupa and fourth-instar larva, and information on distribution, bionomics and a taxonomic discussion. Information and illustrations were also provided by Mattingly (1965). Reinert (2000g) illustrated the female genitalia of *St. desmotes* and provided a description of the female

genitalia for the subgenus (as Desmotes Assemblage). Matsuo *et al.* (1974) described and illustrated the egg.

*Included species*

*Stegomyia desmotes*.

*Etymology*

*Xylele* is derived from the Greek noun *xylele* (masculine) meaning a kind of dagger, a tool for scraping wood. The name is masculine and refers to the spike-like or dagger-like gonostylar claw of the male genitalia, which is unique among Oriental *Stegomyia*. Recommended abbreviation for *Xylele* = *Xyle*.

*STEGOMYIA* THEOBALD SUBGENUS *ZOROMORPHUS* REINERT, HARBACH & KITCHING, SUBGEN. NOV.

*Type species: Aedes (Stegomyia) futunae* Belkin, 1962.

Subgenus *Zoromorphus* includes a single species, *St. futunae*, described and illustrated by Belkin (1962: 455–456, female, male, male genitalia, pupa and fourth-instar larva; figs 327 and 328, male genitalia, pupa and fourth-instar larva). The description of the type species now forms the description of the subgenus. Additional character information in support of the subgenus is provided in Appendix 1 of the present paper. Belkin (1962) also provided information on distribution and bionomics, and a taxonomic discussion in which he stated ‘*A. futunae* is a very clearly marked species in all stages’.

*Included species*

*Stegomyia futunae*.

*Etymology*

*Zoromorphus* is Latinized from the Greek *zoros* (masculine adjective), meaning pure, sheer, and *morphe* (feminine noun), meaning form, figure, shape. The name is masculine and is in reference to its distinction as a monobasic lineage known only from the Horne Islands of the South Pacific. Recommended abbreviation for subgenus *Zoromorphus* = *Zor*.

ABBREVIATIONS OF AEDINE GENERA

Recommended two-letter abbreviations are noted below for all formally recognized genera of tribe Aedini.

*Abraedes* Zavortink = *Ab*.  
*Acartomyia* Theobald = *Ac*.  
*Aedes* Meigen = *Ae*.  
*Aedimorphus* Theobald = *Am*.  
*Alanstonea* Mattingly = *As*.  
*Albuginosus* Reinert = *Al*.  
*Armigeres* Theobald = *Ar*.  
*Ayurakitia* Thurman = *Ay*.

*Aztecaedes* Zavortink = *Az.*  
*Belkinius* Reinert = *Be.*  
*Bifidistylus* Reinert, Harbach & Kitching = *Bf.*  
*Borichinda* Harbach & Rattanarithikul = *Bc.*  
*Bothaella* Reinert = *Bo.*  
*Bruceharrisonius* Reinert = *Br.*  
*Cancraedes* Edwards = *Ca.*  
*Catageiomyia* Theobald = *Cg.*  
*Catatassomyia* Dyar & Shannon = *Ct.*  
*Christophersiomyia* Barraud = *Cr.*  
*Collessius* Reinert, Harbach & Kitching = *Co.*  
*Cornetius* Huang = *Cn.*  
*Dahlia* Reinert, Harbach & Kitching = *Da.*  
*Danielsia* Theobald = *Dn.*  
*Dendroskusea* Edwards = *Ds.*  
*Diceromyia* Theobald = *Di.*  
*Dobrotworskyius* Reinert, Harbach & Kitching = *Db.*  
*Downsiomyia* Vargas = *Do.*  
*Edwardsaedes* Belkin = *Ed.*  
*Elpeytonius* Reinert, Harbach & Kitching = *El.*  
*Eretmapodites* Theobald = *Er.*  
*Finlaya* Theobald = *Fl.*  
*Fredwardsius* Reinert = *Fr.*  
*Georgecraigius* Reinert, Harbach & Kitching = *Gc.*  
*Geoskusea* Edwards = *Ge.*  
*Gilesius* Reinert, Harbach & Kitching = *Gi.*  
*Gymnometopa* Coquillett = *Gy.*  
*Haemagogus* Williston = *Hg.*  
*Halaedes* Belkin = *Ha.*  
*Heizmannia* Ludlow = *Hs.*  
*Himalaius* Reinert, Harbach & Kitching = *Hi.*  
*Hopkinsius* Reinert, Harbach & Kitching = *Hk.*  
*Howardina* Theobald = *Hw.*  
*Huaedes* Huang = *Hu.*  
*Hulecoeteomyia* Theobald = *Hl.*  
*Indusius* Edwards = *In.*  
*Isoaedes* Reinert = *Ia.*  
*Jarnellius* Reinert, Harbach & Kitching = *Ja.*  
*Jihlienius* Reinert, Harbach & Kitching = *Ji.*  
*Kenknightia* Reinert = *Ke.*  
*Kompia* Aitken = *Ko.*  
*Leptosomatomyia* Theobald = *Lp.*  
*Levua* Stone & Bohart = *Le.*  
*Lewnielsenius* Reinert, Harbach & Kitching = *Ln.*  
*Lorrainea* Belkin = *Lo.*  
*Luius* Reinert, Harbach & Kitching = *Lu.*  
*Macleaya* Theobald = *Mc.*  
*Molpemyia* Theobald = *Mo.*  
*Mucidus* Theobald = *Mu.*  
*Neomelaniconion* Newstead = *Ne.*  
*Ochlerotatus* Lynch Arribálzaga = *Oc.*  
*Opifex* Hutton = *Op.*  
*Paraedes* Edwards = *Pr.*  
*Patmarksia* Reinert, Harbach & Kitching = *Pm.*  
*Petermattinglyius* Reinert, Harbach & Kitching = *Pe.*  
*Phagomyia* Theobald = *Ph.*

*Polyleptiomyia* Theobald = *Po.*  
*Pseudarmigeres* Stone & Knight = *Pa.*  
*Psorophora* Robineau-Desvoidy = *Ps.*  
*Rampamyia* Reinert, Harbach & Kitching = *Ra.*  
*Rhinoscusea* Edwards = *Rh.*  
*Sallumia* Reinert, Harbach & Kitching = *Sl.*  
*Scutomia* Theobald = *Sc.*  
*Skusea* Theobald = *Sk.*  
*Stegomyia* Theobald = *St.*  
*Tanakaius* Reinert, Harbach & Kitching = *Ta.*  
*Tewarius* Reinert = *Te.*  
*Udaya* Thurman = *Ud.*  
*Vansomerenis* Reinert, Harbach & Kitching = *Va.*  
*Verrallina* Theobald = *Ve.*  
*Zavortinkius* Reinert = *Za.*  
*Zeugnumyia* Leicester = *Ze.*

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix 1.** Data matrix for 270 taxa and 336 morphological characters used in the analysis. See text for explanation of coding. Polymorphisms are indicated as follow: A = 01, B = 02, C = 03, D = 04, E = 12, F = 13, G = 14, H = 23, I = 24, J = 34.

**Appendix 2.** Checklist and conspectus of reclassification of aedine taxa. With the new taxa proposed in the present study, 80 genera are recognized in tribe Aedini. As in our previous studies (Reinert *et al.*, 2004, 2006, 2008), some species cannot be assigned to generic-level taxa with confidence because of a lack of specimens for examination and/or inadequate published descriptions. Consequently, these species (followed by an asterisk (\*) in the list below) are only provisionally placed in the genera. As previously, where it is not possible to assign species to a genus formally recognized herein or by Reinert *et al.* (2004, 2006, 2008), they are retained in the old broad concept of the genus-level taxon in which they were previously placed. For example, some unassigned species previously placed in '*Ochlerotatus (Finlaya)*' and '*Ochlerotatus (Protomacleaya)*' are listed under these generic-level taxa of previous authors (*sensu auctorum*). The following checklist and conspectus includes all aedine species and subspecies recognized as valid on 5 November 2009. Where necessary, the terminations of species names have been changed to agree in gender with generic names in compliance with Articles 31.2 and 34.2 of the *International Code of Zoological Nomenclature* (International Commission on Zoological Nomenclature, 1999). The type species of each generic-level taxon is indicated by a dagger (†).

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