

Phylogeny and classification of Aedini (Diptera: Culicidae), based on morphological characters of all life stages

JOHN F. REINERT^{1*}, RALPH E. HARBACH² and IAN J. KITCHING²

¹Center for Medical, Agricultural and Veterinary Entomology, United States Department of Agriculture, Agricultural Research Service, 1600/1700 SW, 23rd Drive, Gainesville, FL 32608–1067, USA

²Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

Received December 2003; accepted for publication May 2004

Higher-level relationships within Aedini, the largest tribe of Culicidae, are explored using morphological characters of eggs, fourth-instar larvae, pupae, and adult females and males. In total, 172 characters were examined for 119 exemplar species representing the existing 12 genera and 56 subgenera recognized within the tribe. The data for immature and adult stages were analysed separately and in combination using equal (EW) and implied weighting (IW). Since the classification of Aedini is based mainly on adult morphology, we first tested whether adult data alone would support the existing classification. Overall, the results of these analyses did not reflect the generic classification of the tribe. The tribe as a whole was portrayed as a polyphyletic assemblage of *Aedes* and *Ochlerotatus* within which eight (EW) or seven (IW) other genera were embedded. Strict consensus trees (SCTs) derived from analyses of the immature stages data were almost completely unresolved. Combining the adult and immature stages data resulted in fewer most parsimonious cladograms (MPCs) and a more resolved SCT than was found when either of the two data subsets was analysed separately. However, the recovered relationships were still unsatisfactory. Except for the additional recovery of *Armigeres* as a monophyletic genus, the groups recovered in the EW analysis of the combined data were those found in the EW analysis of adult data. The IW analysis of the total data yielded eight MPCs consisting of three sets of two mutually exclusive topologies that occurred in all possible combinations. We carefully studied the different hypotheses of character transformation responsible for each of the alternative patterns of relationship but were unable to select one of the eight MPCs as a preferred cladogram. Overall, the relationships within the SCT of the eight MPCs were a significant improvement over those found by equal weighting. Aedini and all existing genera except *Ochlerotatus* and *Aedes* were recovered as monophyletic. *Ochlerotatus* formed a polyphyletic assemblage basal to *Aedes*. This group included *Haemagogus* and *Psorophora*, and also *Opifex* in a sister-group relationship with *Oc. (Not.) chathamicus*. *Aedes* was polyphyletic relative to seven other genera, *Armigeres*, *Ayurakitia*, *Eretmapodites*, *Heizmannia*, *Udaya*, *Verrallina* and *Zeugomyia*. With the exception of *Ae. (Aedimorphus)*, *Oc. (Finlaya)*, *Oc. (Ochlerotatus)* and *Oc. (Protomacleaya)*, all subgenera with two or more species included in the analysis were recovered as monophyletic. Rather than leave the generic classification of Aedini in its current chaotic state, we decided a reasonable and conservative compromise classification would be to recognize as genera those groups that are 'weighting independent', i.e. those that are common to the results of both the EW and IW analyses of the total data. The SCT of these combined analyses resulted in a topology of 29 clades, each comprising between two and nine taxa, and 30 taxa (including *Mansonia*) in an unresolved basal polytomy. In addition to ten genera (*Armigeres*, *Ayurakitia*, *Eretmapodites*, *Haemagogus*, *Heizmannia*, *Opifex*, *Psorophora*, *Udaya*, *Verrallina* and *Zeugomyia*), generic status is proposed for the following: (i) 32 existing subgenera of *Aedes* and *Ochlerotatus*, including nine monobasic subgenera within the basal polytomy, i.e. *Ae. (Belkinius)*, *Ae. (Fredwardsius)*, *Ae. (Indusius)*, *Ae. (Isoaedes)*, *Ae. (Leptosomatomyia)*, *Oc. (Abraedes)*, *Oc. (Aztecaedes)*, *Oc. (Gymnometopa)* and *Oc. (Kompia)*; (ii) three small subgenera within the basal polytomy that are undoubtedly monophyletic, i.e. *Ae. (Huaedes)*, *Ae. (Skusea)* and *Oc. (Levua)*, and (iii) another 20 subgenera that fall within the resolved part of the SCT, i.e. *Ae. (Aedes)*, *Ae. (Alanstonea)*, *Ae. (Albuginosus)*, *Ae. (Bothaella)*, *Ae. (Christophersomyia)*, *Ae. (Diceromyia)*, *Ae. (Edwardsaedes)*, *Ae. (Lorrainea)*, *Ae. (Neomelaniconion)*, *Ae. (Paraedes)*, *Ae. (Pseudarmigeres)*, *Ae. (Scutomomyia)*, *Ae. (Stegomyia)*, *Oc. (Geoskusea)*, *Oc. (Halaedes)*, *Oc. (Howardina)*, *Oc. (Kenknightia)*, *Oc. (Mucidus)*, *Oc. (Rhinoscusea)* and *Oc. (Zavortinkius)*. A clade consisting of *Oc. (Fin.) kochi*, *Oc. (Fin.) poicilius* and relatives is raised to generic rank as

*Corresponding author. E-mail: jreinert@gainesville.usda.ufl.edu

Finlaya, and *Downsiomyia* Vargas is reinstated from synonymy with *Finlaya* as the generic name for the clade comprising *Oc. (Fin.) leonis*, *Oc. (Fin.) niveus* and their relatives. Three other species of *Finlaya* – *Oc. (Fin.) chrysolineatus*, *Oc. (Fin.) geniculatus* and *Oc. (Fin.) macfarlanei* – fall within the basal polytomy and are treated as *Oc. (Finlaya) incertae sedis*. *Ochlerotatus* (*Ochlerotatus*) is divided into three lineages, two of which, *Oc. (Och.) atropalpus* and *Oc. (Och.) muelleri*, are part of the basal polytomy. The remaining seven taxa of *Oc. (Ochlerotatus)* analysed, including the type species, form a reasonably well-supported group that is regarded as *Ochlerotatus s.s.* *Ochlerotatus* (*Rusticoides*) is retained as a subgenus within *Ochlerotatus s.s.* *Ochlerotatus* (*Nothoskusea*) is recognized as a subgenus of *Opifex* based on two unique features that support their sister-group relationship. A new genus, ***Tanakaius* gen. nov.**, is proposed for *Oc. (Fin.) togoi* and the related species *Oc. (Fin.) savoryi*. The taxonomic status and generic placement of all currently valid species of Aedini are listed in an appendix. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, **142**, 289–368.

ADDITIONAL KEYWORDS: cladistics – mosquitoes – systematics – taxonomy.

INTRODUCTION

Numerous species of mosquitoes (Diptera: Culicidae) are pests or vectors of pathogens that cause disease in humans and domesticated animals. Despite their medical importance and long history of study, the taxonomy of mosquitoes is far from complete and the existing system of classification is not entirely natural. This is particularly true of the very large tribe Aedini, which includes c. 1200 species-level taxa (Knight & Stone, 1977; Knight, 1978; Ward, 1984, 1992; Gaffigan & Ward, 1985) classified in 12 genera (Appendix 1). Aedines are worldwide in distribution, but generic-level diversity is better represented in the Oriental and Australasian Regions. To avoid confusion, the classification of Aedini established by valid taxonomic acts prior to the present study (see Appendix 1) is referred to as the ‘existing’ classification and the included generic-level taxa are referred to as the ‘existing’ genera and subgenera.

Little attention has been given to Aedini (*sensu* Belkin, 1962; *Aedes* group of Edwards, 1932) as a whole and phylogenetic relationships within the tribe are poorly known, the most detailed study being that of Harbach & Kitching (1998). Their analysis, based on 73 morphological characters and nine of the existing genera, indicated that Aedini is a monophyletic assemblage in a paraphyletic relationship with *Mansoniini*. However, relationships among aedine genera were generally poorly resolved due in part to polymorphism introduced by the inclusion in *Aedes* of the more recently recognized genera *Ayurakitia* (see Reinert, 2000c), *Ochlerotatus* (see Reinert, 2000d) and *Verrallina* (see Reinert, 1999c).

Lunt & Nielsen (1968, 1971a, b) examined the number and arrangement of adult thoracic setae of 63 species of North American *Aedes* (mostly in genus *Ochlerotatus*) and proposed phylogenetic relationships and a classification of species groups and subgenera that generally agree with the existing classification.

Schultz *et al.* (1986) explored the evolutionary relationships of electromorphs of 14 North American species of *Ochlerotatus* (*Ochlerotatus*) and one species of *Aedes* (*Aedimorphus*) using phenetic and phylogenetic analyses. They suggested that *Culicelsa* Felt (currently a synonym of subgenus *Ochlerotatus*) comprises the most primitive species of *Aedes* examined and was ancestral to a lineage subsequently divided into subgenera *Aedimorphus* and *Ochlerotatus*.

Qu & Qian (1989, 1993) proposed a phylogeny for 38 genera of mosquitoes, including nine genera of Aedini (exemplar species not mentioned). Later, Harbach & Kitching (1998) re-analysed Qu & Qian’s data set and dismissed the phylogenetic relationships described by these authors because they were both nonparsimonious and very poorly resolved. Qu *et al.* (1994) provided an analysis of 14 subgenera (exemplar species not mentioned) of genus *Aedes* occurring in China based on 14 morphological traits observed in females (4), males (1), male genitalia (6) and larvae (3). Their preferred hypothesis of relationships divided the subgenera of *Aedes* into two groups. The first group included *Edwardsaedes*, *Heizmannia* (*Mattinglyia*) (as *Sinoaedes* Gong & Lu; see Reinert, 2000b), *Stegomyia*, *Neomelaniconion*, *Aedes* and *Aedimorphus*; the second included *Mucidus*, *Finlaya* + *Christophersiomyia*, *Ochlerotatus*, *Cancraedes* + *Ayurakitia* + *Verrallina*, and *Bothaella*.

Few molecular studies of Aedini have been published. Munstermann (1988) examined nine species of the *Annulipes* group of *Ochlerotatus* (*Ochlerotatus*) using seven diagnostic isoenzymes. Kumar *et al.* (1998) provided restriction maps of the rDNA cistron for seven species of *Aedes* (*Stegomyia*), two species of *Ochlerotatus* (*Ochlerotatus*), one species of *Ochlerotatus* (*Protomacleaya*) and one species in each of the nominotypical subgenera of *Armigeres* and *Haemagogus*. Although these studies treated only a few species representing few genera and subgenera, they generally appear to provide support for the existing classi-

fication of Aedini. However, the results of DNA studies by Wesson *et al.* (1992) and Besansky & Fahey (1997) lend support to Arnell's (1973) claim that *Haemagogus* are 'undoubtedly derived from the genus *Aedes*' (*Aedes* included *Ochlerotatus*). Wesson *et al.* suggested splitting *Aedes* into two genera, one of these supposedly containing *Haemagogus*, *Psorophora* and species related to *Aedes* (*Protomacleaya*) *triseriatus* (Say) (also see Munstermann & Conn, 1997 for a discussion of this study and additional information). Their study included only single species of *Haemagogus*, *Psorophora*, *Aedes* (*Aedimorphus*) and *Aedes* (*Protomacleaya*) and four species of *Aedes* (*Stegomyia*).

The aim of the present study was to determine the phylogenetic relationships of Aedini based on explicit cladistic methodology. The existing classification of Aedini is based principally on adult morphology, and no comprehensive attempt has been made to resolve higher-level relationships within the tribe. In recent decades, the classification of the tribe has changed through the synonymy of subgenera, removal of subgenera from synonymy, recognition of new subgenera and the restoration of subgenera to generic rank based on intuitive interpretation of morphology, with more emphasis in recent years placed on immature stages. In this paper, we present the results of comprehensive analyses of phylogenetic relationships among all existing genera, subgenera and major species groups within Aedini, and propose changes to the existing classification of the tribe that more accurately reflect purported natural affinities.

MATERIAL AND METHODS

TAXA EXAMINED

The study taxa comprised an ingroup of 119 species representing the 12 genera and 56 subgenera of Aedini (Appendix 1; see also for their authorship and geographical distribution), and included type species of most genus-group names (abbreviations for genera and subgenera follow Reinert, 2001a). However, we did not include type species if they had numerous missing life stages or inadequate specimens for detailed study. We also included several species from the largest subgenera to represent informal species groups, e.g. *Aedimorphus*, *Finlaya*, *Ochlerotatus* and *Stegomyia*. The outgroup taxa were representative species from four nonaedine genera: *Culex quinquefasciatus*, *Culiseta inornata*, *Mansonia titillans* and *Orthopodomyia signifera*. These were selected because Harbach & Kitching (1998) hypothesized that they are closely related to the Aedini.

Generally, we examined 3–6 specimens (range 1–20) of each life stage and structure for each species. However, only a single (damaged) life stage was

available for a few species, e.g. one pupal exuvia of *Ae. (Adm.) domesticus*, whereas for other species we were able to examine numerous perfect specimens, e.g. 20 females of *Oc. (Pro.) triseriatus*. We also studied individually reared, pin-mounted adults with associated slide-mounted fourth-instar larval and pupal exuviae where available. A phase contrast or differential interference contrast microscope with 400× magnification is needed to observe the very slender distal portions of many setae for the measurement of total length.

Specimens examined were from the following collections: National Museum of Natural History, Smithsonian Institution, Washington, DC; The Natural History Museum, London, UK; Department of Zoology and Entomology, University of Queensland, Brisbane, Australia; Florida State Collection of Arthropods, Division of Plant Industry, Gainesville, Florida; Laboratoire/Cellule Entomologie, EID Mediterranee, Montpellier, France; Bohart Museum, University of California, Davis, California; and the first author.

CHARACTER DESCRIPTIONS

The data (Appendix 2) comprise 172 characters from eggs (3), fourth-instar larvae (53), pupae (27), females (52), males (8), female genitalia (14) and male genitalia (15). Characters were derived from direct observations except where stages were unavailable or structures were missing from available specimens. We coded some such missing data from literature sources (e.g. characteristics of most eggs) or collection data sheets. Remaining missing data were denoted by a '?'. All multistate characters were treated as unordered. Polymorphic characters were explicitly coded as exhibiting only those states observed, i.e. disjunctive character state sets (e.g. 0, 2) were not converted to range.

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. We have reinterpreted the homologies of several structures from those used in some published works.

Anatomical nomenclature and chaetotaxy follow Harbach & Knight (1980, 1982) except for terms proposed by Reinert (1990, 1999b, 2000e, 2002a). Many structures and states of characters used in the present study are illustrated in these references. However, references to illustrations of some characters in other publications are cited in the explanations of characters below.

Eggs

1. *Deposition*: (0) laid singly; (1) laid in a raft; (2) laid in a mass. Numerous authors, e.g. Howard

- et al.* (1913, 1917), Edwards (1932, 1941), Ross (1947), Carpenter & LaCasse (1955), Belkin (1962), Ross & Horsfall (1965), Dobrotworsky (1965), Bohart & Washino (1978) and Clements (1999), routinely indicated that the eggs of genera *Aedes* and *Ochlerotatus* (as genus *Aedes*) are laid singly. However, egg deposition and morphology (also see characters 2 and 3) of numerous species of Aedini are unknown (see Appendix 2). Macdonald (1960) reviewed the unusual egg-laying habits of species of *Ar.* (*Leicesteria*) 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 container. Other species of the subgenus deposit their eggs in ribbons directly on the water surface. In general, *Ar.* (*Leicesteria*) eggs hatch about two days after being laid, which is somewhat similar to the egg rafts of most species of *Culex*. The eggs of species of subgenus *Armigeres* and other aedine genera, e.g. *Aedes*, *Ochlerotatus* and *Psorophora*, are laid singly, can withstand a period of dryness and will not hatch until they have been immersed in water.
2. *Shape*: (0) anterior end flattened, posterior end rounded; (1) both ends tapered; (2) anterior end elongate and narrow; (3) anterior end rounded, posterior end tapered. Various aedine eggs are illustrated in numerous articles, e.g. Howard *et al.* (1913), Ross & Horsfall (1965), Kalpage & Brust (1968), Mattingly (1970a), Moriya *et al.* (1973), Matsuo *et al.* (1974), Hinton (1981), Linley (1989), Linley & Chadee (1990, 1991) and Linley *et al.* (1991).
 3. *Outer chorion*: (0) pattern absent or weakly developed; (1) pattern well developed; (2) with spiny appearance, each cell with elongate anteriorly inclined tubercle. See literature cited for character 2.

Larvae (fourth-instar)

4. *Labiogula*: (0) short, length < width; (1) moderate to long, length \geq width. Labiogular width is measured from the outer margins of the posterior tentorial pits. The length is measured from the caudolateral angle of the dorsomentum to the posterior margin of the collar. See Belkin (1962: figs 303, 314) for examples of state (0) and his figures 277 and 298 for state (1).
5. *Antenna*: (0) short, ≤ 0.40 median length of dorsal apotome; (1) moderate to long, ≥ 0.42 median length of dorsal apotome. Antennal length is determined by dividing the antennal shaft

- length by the dorsal apotome median length (whole larva preferred). Antennae vary from short, e.g. *Ar.* (*Armigeres*), to very long, e.g. *Ps.* (*Janthinosoma*) (see Belkin *et al.*, 1970: fig. 60). See illustrations in Belkin (1962: figs 357 and 298, respectively) for states (0) and (1).
6. *Seta 1-A, development*: (0) single or 2-branched; (1) ≥ 3 branches. Most species of Aedini have seta 1-A single or multiple-branched. However, some species have this seta single or two-branched (state 0), and it is also two-branched in some specimens of a few species in which seta 1-A is multiple-branched, which is scored (0,1).
 7. *Seta 1-A, length*: (0) short, $\leq 3.0 \times$ antennal width at point of attachment; (1) longer, $\geq 3.1 \times$ antennal width at point of attachment. Seta 1-A is normally moderately long to long (state 1) in most Aedini, e.g. subgenera *Protomacleaya* (see figs in Zavortink, 1972) and *Zavortinkius* of *Ochlerotatus*, but is short in some taxa (state 0), e.g. *Armigeres*, *Opifex* and most *Ae.* (*Stegomyia*) (see figs in Belkin, 1962).
 8. *Setae 2,3-A, position*: (0) apical or nearly apical; (1) noticeably subapical. Except for *Oc.* (*Rhinoskusea*), setae 2- and 3-A are inserted apically or nearly apically on the antennae of Aedini. *Rhinoskusea* have these setae inserted noticeably subapical, as does the outgroup species *Ma. titillans*. Reinert (1976b: figs 12–14) illustrates the subapical condition (0).
 9. *Seta 1-C, development*: (0) spiniform; (1) single, thinner, distal part thin; (2) forked or branched, stout. Spiniform setae are stout, dark and have the apices relatively blunt, rarely thin. 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. Species of *Verrallina*, *Ae.* (*Aedes*) and *Oc.* (*Zav.*) *longipalpis* have seta 1-C long, somewhat stouter than normal and the apices are blunt or bluntly pointed; these are scored here as (1). In species where seta 1-C is branched, the seta has a dark, short and stout proximal area and two or three distal branches, e.g. the Kochi Group of *Oc.* (*Finlaya*) (some species with up to six branches, see Marks, 1947), *Oc.* (*Fin.*) *reinerti* (Rattananarithikul & Harrison) (two very stout branches) and *Oc.* (*How.*) *walkeri* (see Berlin, 1969 for illustration of state 2), whereas Bohart (1957) noted that this seta has 2–6 branches in *Ae.* (*Stg.*) *pandani* Stone.
 10. *Seta 4-C, position*: (0) anterior to seta 6-C; (1) at same level or posterior to seta 6-C. The position of seta 4-C appears to be constant in subgenera and genera for which the taxonomy is stable.

- However, both states occur in some of the larger subgenera, but in different species groups. See Belkin (1962) for illustrations of state (0) (his figs 218, 277) and state (1) (his figs 211, 298). See character 12 for comment.
11. *Seta 4-C, length*: (0) short; (1) moderate to long. The development of seta 4-C is consistent for subgenera and genera, with few exceptions.
 12. *Seta 6-C, position*: (0) anterior to seta 7-C; (1) at same level or posterior to seta 7-C. The positions of setae 6- and 7-C are determined on flattened head capsules, normally exuviae. If the head is not flattened, but turned downward anteriorly, these setae may appear to be positioned differently. This also applies to characters 10 and 13.
 13. *Seta 7-C, position*: (0) anterior to seta 5-C; (1) at approximately same level as seta 5-C; (2) posterior to seta 5-C. See character 12 for comment.
 14. *Seta 12-C, position*: (0) mesad of or at same level as seta 13-C; (1) laterad of seta 13-C. 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 a few species of Aedini is interpreted as seta 13-C.
 15. *Seta 13-C, development*: (0) single; (1) branched. Within subgenera and genera that are well defined, the branching of seta 13-C is fixed, with few exceptions.
 16. *Seta 19-C*: (0) absent; (1) present. Hochman & Reinert (1974) reported the occurrence of seta 18-C and the presence or absence of seta 19-C on the ventral cervical membrane of larvae belonging to 29 genera, 72 subgenera and 331 species of Culicidae. These setae vary in length from minute to relatively long, pale to dark, slender to rather stout and can be single or branched. See Hochman & Reinert for illustrated examples and a discussion about the occurrence of seta 19-C in the large and heterogeneous subgenera *Finlaya* and *Ochlerotatus* of *Ochlerotatus*, and its taxonomic importance and possible phylogenetic significance.
 17. *Ventromedian cervical sclerite*: (0) absent; (1) present. A small sclerite is present on the ventromedian area of the cervix in many aedine larvae. It was not observed in *Ae. (Can.) masculinus*, *Oc. (Cha.) wattensis*, *Oc. (Fin.) macfarlanei*, *Oc. (Kom.) purpureipes*, *Oc. (Lev.) geoskusea* (only three larvae available), *Oc. (Mac.) tremulus*, *Oc. (Och.) atlanticus* (apparently absent in some but present in other specimens), subgenera *Rhinokusea* and *Zavortinkius* of *Ochlerotatus*, *Armigeres*, *Ayurakitia*, *Eretmapodites*, *Psorophora*, *Udaya*, *Zeugomyia*, and the outgroup species. Reinert (1976c) provided a review and illustrations of the sclerite in Culicidae.
 18. *Setae 1-3-P*: (0) not attached to a common setal support plate; (1) two or three of these setae attached to a common setal support plate. All or occasionally only two of setae 1-3-P are attached to a common setal support plate in species of subgenera *Alanstonea*, *Bothaella*, *Huaedes* and *Scutomylia* of *Aedes*, *Ar. (Armigeres)*, *Abraedes*, most *Finlaya*, *Gymnometopa*, *Howardina*, *Kenknighthia*, *Pseudokusea* and *Rhinokusea* of *Ochlerotatus*, and *Ayurakitia*, *Haemagogus* and *Zeugomyia*. They are also attached to a common plate in *Oc. (Pro.) triseriatus* and the outgroup species *Cs. inornata* and *Cx. quinquefasciatus*.
 19. *Seta 1-P, length*: (0) \leq length of seta 2-P; (1) $>$ length of seta 2-P. Seta 1-P is normally longer than seta 2-P in Aedini, but it is shorter in subgenera *Bothaella* and *Huaedes* of *Aedes*, *Ae. (Scu.) arboricola*, the Kochi Group of *Oc. (Finlaya)*, *Oc. (How.) walkeri*, *Oc. (Och.) muelleri* and *Ayurakitia*.
 20. *Seta 3-P, length*: (0) $<$ length of seta 2-P; (1) \geq length of seta 2-P. Seta 3-P is normally shorter than seta 2-P, but it is noticeably longer in *Ae. (Christophersiomyia)* and the outgroup species *Cs. inornata*.
 21. *Seta 5-P, length*: (0) \leq length of seta 6-P; (1) $>$ length of seta 6-P. The length of seta 5-P in relation to that of seta 6-P is relatively consistent for the subgenera and smaller genera of Aedini.
 22. *Seta 5-P, development*: (0) single; (1) branched. The development of seta 5-P is fixed for subgenera, with few exceptions.
 23. *Seta 8-P, length*: (0) $\leq 1.2 \times$ length of seta 4-P; (1) $\geq 1.8 \times$ length of seta 4-P. Seta 8-P is noticeably shorter than or equal to the length of seta 4-P in all but a few species of *Ochlerotatus*, e.g. *Oc. (Och.) sollicitans* (Walker) and *Oc. (Rusticoidus)*.
 24. *Seta 13-P*: (0) absent; (1) present. Seta 13-P is present in only a few species of Aedini. It has been noted in members of the Sexlineatus Section and two species (Ioliota Group) of the Walkeri Section of *Oc. (Howardina)* (Berlin, 1969; Reinert, 2000d), species of *Ae. (Bothaella)* (Reinert, 1973b, 2000d) and four species of *Ae. (Stegomyia)*, i.e. *Ae. hoguei* Belkin, *Ae. robinsoni* Belkin, *Ae. tulagiensis* Edwards and *Ae. upolensis* Marks (Belkin, 1962; Reinert, 2000d). Harbach & Kitching (1998) noted the sporadic presence of seta 13-P in *Aedes* and *Psorophora*.
 25. *Seta 4-M, development*: (0) single; (1) branched. Seta 4-M is branched (rarely single) in subgen-

- era of Section I and single (rarely branched) in subgenera of Section II of *Ochlerotatus* (Reinert, 2000d).
26. *Seta 7-M, length*: (0) < length of seta 5-M; (1) ≥ length of seta 5-M. Seta 7-M is normally shorter than seta 5-M in most Aedini; however, it is longer in *Ae. (Skusea)*, subgenera *Chaetocruomyia*, *Geoskusea*, *Halaedes*, *Kompia* and *Macleaya* of *Ochlerotatus*, *Eretmapodites* and a few other species, e.g. *Ae. (Adm.) alboscutellatus*, *Ae. (Stg.) scutellaris*, *Oc. (Fin.) togoi*, *Ps. (Jan.) ferox* and the outgroup species *Cx. quinquefasciatus*.
 27. *Seta 2-T, development*: (0) single; (1) branched. Development of seta 2-T is fixed for subgenera, with few exceptions.
 28. *Seta 3-I, development*: (0) single; (1) branched. The development of seta 3-I is consistent for subgenera and genera, with few exceptions. Some specimens of a few species show an overlap of the two states.
 29. *Seta 7-I, length*: (0) < 0.45 length of seta 6-I; (1) ≥ 0.55 length of seta 6-I. Seta 7-I is normally moderately long to long (≥ 0.55 length of seta 6-I, see Belkin, 1962: fig. 303) in Aedini, but it is shorter (≤ 0.45 length of seta 6-I, see Belkin, 1962: fig. 357) in *Ae. (Adm.) mediolineatus*, *Ae. (Sku.) pambaensis*, *Ar. (Arm.) breinli*, *Oc. (Muc.) alternans*, *Oc. (Muc.) laniger*, *Oc. (Not.) chathamicus* and *Op. fuscus*.
 30. *Seta 7-I, development*: (0) single to 3-branched, normally stout; (1) ≥ 4 branches. Most aedine generic-level taxa have seta 7-I single to three-branched and relatively stout. However, it is thinner and with four or more branches in *Ae. (Adm.) mediolineatus*, *Ae. (Sku.) pambaensis*, *Ar. (Arm.) breinli* (most specimens), *Oc. (Muc.) idus*, *Ps. (Psorophora)* (occasionally three-branched in *Ps. howardii*) and *Opifex* (most specimens).
 31. *Seta 12-I*: (0) absent; (1) present. Seta 12-I is absent in *Aedes*, *Armigeres*, *Ayurakitia*, *Eretmapodites*, *Heizmannia*, *Udaya*, *Verrallina*, *Zeugomyia*, Section II of *Ochlerotatus* (see Reinert, 2000d) and *Oc. (Cha.) wattensis*. It is present in *Haemagogus*, *Opifex*, *Psorophora* and Section I of *Ochlerotatus*. In the case of Section I of *Ochlerotatus*, Reinert (2000d) noted six exceptions, i.e. *Oc. impiger daisetsuzanus* (Tanaka, Mizusawa & Saugstad), *Oc. laguna* (Arnell & Nielsen), *Oc. monticola* (Belkin & McDonald), *Oc. muelleri* and *Oc. varipalpus* (Coquillett), as well as *Oc. (Cha.) tulliae* (Taylor). Arnell (1973) and Harbach & Kitching (1998) noted that seta 12-I was normally present in *Haemagogus*, but absent in a few species.
 32. *Seta 6-II, development*: (0) single; (1) branched. Seta 6-II is normally branched in Aedini, but it is single in *Ae. (Alanstonea)* (see Ramalingam & Ramakrishnan, 1971: fig. 2), subgenera *Levua*, *Molpemyia* and *Mucidus* of *Ochlerotatus*, *Eretmapodites*, *Ve. (Harbachius)* and *Ar. (Arm.) breinli*.
 33. *Seta 7-II, development*: (0) similar to seta 7-I; (1) different from seta 7-I. The length, thickness and branching of seta 7-II are normally consistent in well-defined subgenera and genera of Aedini, but in some of the larger subgenera consistency occurs only at the species-group level. See Belkin (1962: fig. 208) for an example of state (0) and his fig. 218 for state (1).
 34. *Seta 8-II, development*: (0) single; (1) branched. Seta 8-II is normally either single or branched within a species but may show an overlap of the two states in some specimens. It is consistent in most aedine subgenera and/or genera that are well-defined. In some large subgenera, e.g. *Finlaya* and *Ochlerotatus*, the condition of seta 8-II is generally consistent at the species-group level.
 35. *Seta 3-V, length*: (0) ≤ 1.55 × length of seta 5-V; (1) ≥ 1.90 × length of seta 5-V. Seta 3-V is at least two times longer (often much longer) than seta 5-V in Section I of *Ochlerotatus* whereas it is shorter than or equal to 1.5 × the length of seta 5-V in Section II (Reinert, 2000d).
 36. *Seta 2-VII, development*: (0) single; (1) branched. Seta 2-VII is single in most Aedini. However, it is branched in *Ayurakitia*, *Haemagogus*, subgenera *Bothaella*, *Diceromyia* and *Scutomyia* of *Aedes*, *Ae. (Stg.) futunae*, subgenera *Aztecaedes*, *Gymnometopa*, *Howardina* and *Kompia* of *Ochlerotatus*, and several groups of *Oc. (Finlaya)*. Seta 2-VII is single or two-branched in *Ae. (Edw.) imprimens*, *Ae. (Psa.) agenteoventralis dunnii*, *Ae. (Stg.) albopictus*, *Ae. (Stg.) desmotes* and *Ae. (Stg.) scutellaris*.
 37. *Seta 3-VII, length*: (0) short to moderately long; (1) very long. Seta 3-VII is normally short to moderately long in Aedini, but it is very long in *Haemagogus* (see illustrations in Arnell, 1973), *Ae. (Psa.) agenteoventralis dunnii*, *Oc. (Fin.) togoi* and subgenera *Gymnometopa*, *Howardina* and *Pseudoskusea* of *Ochlerotatus*, and the outgroup species *Cs. inornata* and *Or. signifera*.
 38. *Seta 12-VII, position*: (0) anterior to seta 13-VII; (1) at approximately same level as seta 13-VII; (2) posterior to seta 13-VII. Seta 12-VII is posterior to seta 13-VII in most Aedini, anterior in some taxa, e.g. *Ae. (Scutomyia)*, some *Ae. (Stegomyia)*, *Hg. (Haemagogus)*, some *Oc. (Howardina)* and *Oc. (Kompia)*, and located at

- approximately the same level as seta 13-VII in the remainder of the species examined.
39. *Seta 12-VII, development*: (0) single; (1) branched. The development of seta 12-VII is consistent in subgenera/genera, with few exceptions.
 40. *Setae 1, 2-VIII*: (0) not attached to common setal support plate; (1) both attached to common setal support plate. Only a few of the species examined have setae 1, 2-VIII attached to a common setal support plate, i.e. *Ae. (Adm.) alboscuteclatus*, *Ae. (Adm.) vexans vexans*, *Ae. (Edw.) bekkui*, *Ae. (Edw.) imprimens*, *Ae. (Neo.) lineatopennis*, *Ae. (Neo.) palpalis*, *Ae. (Stg.) desmotes*, *Oc. (Muc.) alternans*, *Oc. (Muc.) laniger* and *Ve. (Nma.) indica*.
 41. *Seta 2-VIII, development*: (0) single; (1) branched. Seta 2-VIII is single and moderately long to long in many species of Aedini, but it is two- or three-branched in some species. This seta is very short, has multiple branches and is developed similar to seta 1-VIII in *Armigeres*. Also see the comment for character 42.
 42. *Seta 4-VIII, development*: (0) single; (1) branched. Seta 4-VIII is often single in Aedini, but it is branched in subgenera *Aedimorphus* and *Edwardsaedes* of *Aedes*, subgenera *Bruceharrisonius*, *Halaedes* and *Nothoskusea* of *Ochlerotatus*, *Armigeres*, *Eretmapodites*, *Opifex*, *Psorophora*, *Ae. (Neo.) lineatopennis*, *Oc. (Och.) atlanticus*, *Oc. (Och.) fulvus pallens* and the outgroup species *Ma. titillans*. Species with seta 4-VIII branched normally also have seta 2-VIII branched. A few species have some specimens with seta 4-VIII single and others two-branched.
 43. *Comb*: (0) few to several scales in 1 or 2 irregular rows; (1) numerous scales in a patch. The development of the comb is consistent for most subgenera of Aedini. However, in some subgenera, i.e. *Aedimorphus* and *Albuginosus* of *Aedes*, and *Finlaya*, *Howardina*, *Ochlerotatus* and *Protomacleaya* of *Ochlerotatus*, development of the comb is only homogeneous within species groups. Scales are in a patch in the outgroup species except *Ma. titillans*.
 44. *Comb plate*: (0) absent; (1) present. A comb plate is normally present in *Psorophora* (see Belkin *et al.*, 1970: fig. 67). It is also present in *Ae. (Stg.) annandalei* (Theobald), *Ae. (Stg.) craggi* (Barraud), *Ae. (Stg.) desmotes*, *Ae. (Stg.) maeheri* Bohart, *Ae. (Stg.) gurneyi* Stone & Bohart, *Ae. (Stg.) malikuli* Huang, *Ae. (Stg.) mediopunctatus* (Theobald), *Ae. (Stg.) perplexus* (Leicester), *Oc. (Fin.) dorseyi* (Knight), *Oc. (Cha.) elchoensis* (Taylor), *Oc. (Mac.) tremulus*, *Hg. (Hag.) capricornii* Lutz, *Hg. (Hag.) janthinomys* Dyar and usually in *Ae. (Scu.) arboricola*.
 45. *Siphon, acus*: (0) absent; (1) present. Many species of Aedini possess an attached or detached siphonal acus. However, an acus is absent in *Armigeres*, *Ayurakitia*, *Heizmannia*, *Opifex*, *Udaya*, *Zeugnomia*, subgenera *Alanstonea*, *Albuginosus*, *Christophersiomyia*, *Diceromyia*, *Huaedes*, *Leptosomatomyia*, *Lorrainea*, *Pseudarmigeres*, *Skusea* and *Stegomyia* of *Aedes*, *Abraedes*, *Chaetocruimyia*, *Gymnometopa*, *Halaedes*, *Macleaya*, *Molpemyia* and *Zavortinkius* of *Ochlerotatus*, *Er. quinquevittatus*, *Oc. (How.) walkerii* and the outgroup species *Ma. titillans* and *Or. signifera*.
 46. *Pecten*: (0) absent; (1) present, spines evenly spaced; (2) present, distal one or more spines more widely spaced. Pecten spines are reduced in number and are rarely absent on both sides of the siphon in *Eretmapodites* (see illustrations in Hopkins, 1952; Service, 1990). However, the larval stage is unknown for many species of this genus. Pecten spines are absent from larvae of *Armigeres* and the outgroup species *Ma. titillans* and *Or. signifera*. Reinert (1999c) noted that the distal one or more pecten spines are more widely spaced in *Verrallina*, some *Psorophora*, subgenera *Aedes*, *Aedimorphus* (see illustrations in Hopkins, 1952), *Edwardsaedes*, *Isoaedes* and *Neomelaniconion* of *Aedes*, *Oc. (Rusticoidus)*, many *Oc. (Ochlerotatus)* and some *Oc. (Mucidus)*. This condition also occurs in *Ae. (Can.) masculinus*, the Dendrophilus Group of subgenus *Stegomyia*, some specimens of *Ae. (Stg.) aegypti*, *Ae. (Huaedes)* and *Ae. (Paraedes)*.
 47. *Seta 1-S*: (0) one seta at base of siphon; (1) one seta some distance from base of siphon; (2) two or more setae some distance from base of siphon. Seta 1-S inserted ventroposteriorly some distance from the base of the siphon, and without accessory setae, is the usual condition in Aedini. *Aedes* (*Aedes*) and *Oc. (Rusticoidus)* possess accessory setae in addition to the nonbasal seta 1-S. Reinert (1999a, 2000d) discussed the presence of accessory setae in these two taxa and noted their occurrence in a few species of *Oc. (Ochlerotatus)*, i.e. *Oc. crinifer* (Theobald) (see Arnell, 1976), *Oc. hexodontus* (Dyar), *Oc. hokkaidensis* (Tanaka, Mizusawa & Saugstad) and *Oc. punctor* (Kirby) (see Tanaka *et al.*, 1979). Accessory setae on the siphon are typical of genus *Culex*. Seta 1-S positioned at the base of the siphon is characteristic of many species of *Culiseta* Felt.

48. *Seta 6-S, development*: (0) absent; (1) short; (2) long. Seta 6-S is normally short and somewhat curved or nearly straight in Aedini. However, it is long and nearly straight in *Psorophora*, *Ae. (Lorrainea)* and subgenera *Bruceharrisonius* and *Kenknightia* of *Ochlerotatus*. Seta 6-S is moderately long to long and is coded as long (2) in *Ps. (Jan.) ferox*. This seta is long in *Oc. (How.) walkeri*, very long in the Kochi Group of *Oc. (Finlaya)*, and long and aciculate in *Opifex*. Seta 6-S is absent from the modified siphon of *Ma. titillans*.
49. *Seta 8-S, length*: (0) short; (1) long. Seta 8-S is noticeably long in subgenera *Alanstonea* and *Lorrainea* of *Aedes*, subgenus *Bruceharrisonius* and the Kochi Group (see illustrations in Belkin, 1962) of subgenus *Finlaya* of *Ochlerotatus*, and the outgroup species *Ma. titillans*. It is short in other Aedini.
50. *Saddle, acus*: (0) absent; (1) present. A small acus on the lower anterior margin of the saddle is common in species of subgenera *Ochlerotatus* and *Rusticoidus* of *Ochlerotatus*, but it is also found in *Ae. (Adm.) vexans vexans*, *Oc. (Psk.) postspiraculosus* and the outgroup species *Cs. inornata*. The acus is absent in *Oc. (Och.) atropalpus* and *Oc. (Och.) muelleri*.
51. *Sclerotization of segment X*: (0) dorsal saddle; (1) completely encircles segment X. All species of Aedini have either a small or large dorsal saddle or sclerotization that completely encircles segment X. A saddle completely encircling segment X is found in *Ae. (Edw.) imprimens*, *Ae. (Huaedes)*, several species of *Oc. (Ochlerotatus)*, *Psorophora* and the outgroup species. See Reinert (2002a) for illustrations of different development of this character.
52. *Seta 1-X, position*: (0) inserted on saddle; (1) inserted ventral to saddle. Seta 1-X is inserted on the ventral or ventroposterior margin of the saddle in *Ae. (Lorrainea)*, *Opifex*, *Oc. (Geo.) baisasi*, *Oc. (Mac.) tremulus* and *Oc. (Och.) muelleri*, and is scored (0).
53. *Seta 3-X, development*: (0) single; (1) branched. Seta 3-X is normally single in Aedini, but it is branched in *Armigeres*, *Zeugomyia* and certain other species, e.g. *Ae. (Edw.) imprimens*, *Ae. (Stg.) futunae*, *Er. quinquevittatus*, *Oc. (Azt.) ramirezi*, *Oc. (Gym.) mediiovittatus*, *Oc. (How.) sexlineatus*, *Oc. (Kom.) purpureipes*, *Ud. lucaris* and the outgroup species *Cs. inornata* and *Ma. titillans*. Both states (0,1) occur in *Hs. (Mat.) achaetae* where the seta is single or two-branched.
54. *Sclerotization supporting seta 4-X (ventral bush)*: (0) absent; (1) grid with only transverse bars; (2) grid with both lateral and transverse bars; (3) boss. Reinert (2002a) conducted a comparative analysis of the ventral brush and its attachment to segment X in Aedini. Sclerotization supporting the ventral brush was divided into four types and 18 subtypes. The ancestral form of the ventral brush was hypothesized to have consisted of numerous, multiple-branched setae with short, stout stems attached to a well-developed grid consisting of both transverse and lateral grid bars. This brush also had numerous multiple-branched, precratal setae with short stems inserted on the ventral midline of a complete saddle. The derived condition was described as a brush comprised of few, simple, single setae on a poorly developed grid with only transverse grid bars. This brush lacked precratal setae, and the saddle was incomplete ventrally. Reinert further proposed that the condition in *Ae. (Christophersomyia)* could represent the most derived state because of the occurrence of a similar condition in most sabethine mosquitoes (see discussion in Harbach & Kitching, 1998). The ventral brush in sabethines, however, is normally represented by a single pair of setae (species of subgenus *Sabethinus* of *Sabethes* have an auxiliary pair of setae 4-X). The well-developed boss of *Oc. (Mol.) pecuniosus* (state 3) is shown in Reinert (1993: fig. 8).
55. *Precratal/preboss setae* (i.e. two or more setae anterior to grid/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 preboss seta whereas other species have a single precratal seta (these are scored as 0).
56. *Seta 4a-X of ventral brush*: (0) short; (1) long. Reinert (2002a), following Belkin (1962) and Knight & Laffoon (1971), defined seta 4-X as 'Any seta of the ventral brush, the variable number of paired or unpaired setae arising from the ventral longitudinal midline of abdominal segment X. The most caudal (posterior) seta is designated as seta 4a-X, the next cephalad (anterior) seta as 4b-X, and so on'. Seta 4a-X is normally long, rarely moderately long, and similar in length to seta 4b-X in Aedini. Subgenera *Abraedes*, *Aztec-aedes* and *Kompia* of *Ochlerotatus*, and *Oc. (Och.) muelleri*, have a short seta 4a-X (see illustrations in Zavortink, 1972).

Pupae

57. *Cephalothorax with clear unpigmented spots*: (0) absent; (1) present. Clear unpigmented areas of

- the cephalothorax (scutum and metanotum) of pupal exuviae are found in *Ae. (Blk.) aurotaeniatus* and members of the Kochi Group of *Oc. (Finlaya)* (see illustrations in Belkin, 1962). In the latter group, the abdomen of some species also has one or more clear unpigmented areas. A similar condition occurs in *Ae. (Ala.) brevitibia*. Belkin (1962) reported that in living pupae of the Kochi Group, which breed almost entirely in water in plant axils, these unpigmented areas are iridescent blue and are very similar to those found in pupae of many New World sabethines and species of *Cx. (Microculex)*, which also inhabit water held in leaf axils. Mattingly (1969) also reported 'Some South American sabethine and culicine pupae, occurring in bromeliad axils, are provided with luminescent integumentary patches which persist for some time after emergence of the adult'. Berlin's (1969) illustrations of the pupal metanotum of *Oc. (How.) inaequalis* (Grabham) and *Oc. (How.) stenei* (Thompson) show an unpigmented lateral spot. Unfortunately, no specimens of these species were available for examination and it is uncertain if these spots are similar to those reported above.
58. *Tracheoid area of trumpet*: (0) absent; (1) present at base, weakly developed; (2) present distal to base, well developed. The tracheoid area is usually weakly developed at the base of the trumpet in most genera and subgenera of Aedini, but it is absent in some genera and subgenera, e.g. *Armigeres*, subgenera *Alanstonea*, *Fredwardsius*, *Huaedes*, *Leptosomatomyia* and *Skusea* of *Aedes*, *Oc. (Gymnometopa)*, *Opifex*, most species of genus *Psorophora*, *Ae. (Adm.) alboscuteallatus* and the outgroup species *Cs. inornata* and *Or. signifera*. In subgenera *Mucidus* and *Rhinoskusea* of *Ochlerotatus*, the Kochi Group of *Oc. (Finlaya)* and the outgroup species *Cx. quinquefasciatus* and *Ma. titillans*, the tracheoid area is subbasal and well developed (see Belkin *et al.*, 1970: figs 33, 51).
 59. *Seta 1-CT, development*: (0) similar in development to seta 3-CT; (1) very strongly developed, considerably longer than seta 3-CT; (2) weakly developed, considerably shorter than seta 3-CT. With few exceptions, the development of seta 1-CT is constant within subgenera and smaller genera.
 60. *Seta 5-CT, length*: (0) $\leq 1.2 \times$ length of seta 4-CT; (1) $> 1.3 \times$ length of seta 4-CT. The length of seta 5-CT is normally consistent within subgenera of Aedini, but a few exceptions exist, especially in larger subgenera in which the condition appears to be constant within species groups.
 61. *Seta 7-CT, length*: (0) \leq length of seta 6-CT; (1) $1.2-5.0 \times$ length of seta 6-CT; (2) $\geq 6.0 \times$ length of seta 6-CT. Seta 7-CT is noticeably longer than seta 6-CT in most Aedini. However, it is shorter or equal in length to seta 6-CT in *Ae. (Bothaella)*, some *Stegomyia* of *Aedes*, *Ar. (Armigeres)*, *Eretmapodites*, many *Heizmannia* and *Zeugomyia*. See Belkin (1962: figs 356 and 210, respectively) for examples of states (0) and (1) and Reinert (2000c: fig. 3) for state (2).
 62. *Seta 11-CT, development*: (0) single; (1) branched. Some species, e.g. *Ae. (Bot.) eldridgei*, *Ae. (Bot.) helenae*, *Ae. (Isa.) cavaticus*, *Oc. (How.) walkeri*, *Oc. (Mol.) pecuniosus*, *Oc. (Och.) communis* and *Ps. (Gra.) columbiae*, show an overlap between the two alternatives in which seta 11-CT is single in some specimens but two-branched in others (scored 0,1).
 63. *Seta 13-CT*: (0) absent; (1) present. Seta 13-CT is present on the metanotum in *Ae. (Blk.) aurotaeniatus*, *Ae. (Stg.) futunae* and *Oc. (Abr.) papago*. In three paratypes of the latter species examined, a well-developed, two-branched seta is present on both sides of one exuviae, an alveolus is present on both sides of another, and the seta and alveolus are absent on the third. Reinert (1980, 2000d) provided a review of the occurrence of seta 13-CT in Culicidae and Aedini.
 64. *Seta 6-I, length*: (0) \leq length of seta 7-I; (1) $>$ length of seta 7-I. Seta 6-I is normally longer than seta 7-I in Aedini. It is shorter in *Ae. (Adm.) alboscuteallatus*, *Ae. (Psa.) argenteoventralis durni*, subgenera *Alanstonea*, *Fredwardsius* and some *Stegomyia* of *Aedes*, *Ar. (Armigeres)*, *Haemagogus*, subgenera *Abraedes*, *Aztecaedes*, *Gymnometopa*, *Halaedes*, *Macleaya*, *Nothoskusea*, *Rhinoskusea*, some *Finlaya* and some *Ochlerotatus* of *Ochlerotatus*, *Opifex*, *Ps. (Psorophora)*, *Udaya* and *Zeugomyia*, as well as the outgroup species *Ma. titillans*.
 65. *Seta 2-II, position*: (0) medial to or at same level as seta 1-II; (1) lateral to seta 1-II. Seta 2-II is normally lateral to seta 1-II in Aedini; however, it is medial to or at the same level as seta 1-II in a few species, e.g. *Ae. (Bot.) helenae*, the Kochi Group of *Oc. (Finlaya)* and *Oc. (Mol.) pecuniosus* (see Reinert, 1993: fig. 7).
 66. *Seta 2-II, length*: (0) $<$ length of seta 1-II; (1) \geq length of seta 1-II. Seta 2-II is normally shorter than seta 1-II in Aedini; however, it is as long or longer and often stouter than seta 1-II in some species.
 67. *Seta 3-II, position*: (0) medial to or at same level as seta 2-II; (1) lateral to seta 2-II. The position of seta 3-II, in relation to seta 2-II, is relatively constant in subgenera and smaller genera of

- Aedini. A few exceptions are usually correlated with species groups, e.g. in *Oc. (Finlaya)*.
68. *Seta 3-II, length:* (0) \leq length of seta 6-II; (1) $>$ length of seta 6-II. Length of seta 3-II is consistent for subgenera, with some exceptions.
 69. *Seta 3-III, development:* (0) single, stout; (1) branched, normally slender. Seta 3-III in some species, e.g. *Ae. (Lor.) amesii*, *Ae. (Scu.) arboricola*, *Ar. (Lei.) longipalpis*, *Oc. (Fin.) poicilius*, *Oc. (Fin.) togoi*, *Oc. (How.) walkeri* and *Oc. (Zav.) fulgens*, show an overlap where some specimens are single and others are two-branched, these are scored (0,1).
 70. *Seta 5-II, position:* (0) lateral to or at same level as seta 4-II; (1) medial to seta 4-II. Seta 5-II is normally longer than seta 4-II, hence their lengths can usually be used to determine their identities. Positions of seta 5-II are fixed for subgenera and smaller genera, with few exceptions.
 71. *Seta 6-II, length:* (0) \leq length of seta 7-II; (1) $>$ length of seta 7-II. Seta 6-II is normally longer than seta 7-II in Aedini; however, it is shorter in some subgenera, genera and species groups (see Appendix 2).
 72. *Seta 6-III, development:* (0) single; (1) branched. Species in most subgenera of Aedini are relatively consistent in having seta 6-III either single or branched. However, in some specimens of some species the seta usually exhibits one state but occasionally exhibits the other state, e.g. normally single but sometimes two-branched, these are scored (0,1).
 73. *Seta 6-VII, position:* (0) anterior to seta 9-VII; (1) posterior to or at same level as seta 9-VII. Seta 6-VII is usually inserted posterior to or occasionally at the same level mesad of seta 9-VII. Seta 6-VII is located anterior to seta 9-VII in *Ae. (Bot.) helenae*, *Ar. (Lei.) flavus*, *Er. chrysogaster*, *Er. quinquevittatus*, *Hs. (Hez.) complex*, *Oc. (Brh.) greenii*, *Oc. (Zav.) fulgens*, species of *Psorophora* (occasionally posterior in some specimens of *Ps. (Pso.) howardii*). See character 77 for the outgroup species *Ma. titillans*.
 74. *Seta 5-V, length:* (0) $<$ medial length of tergum VI; (1) \geq medial length of tergum VI. Seta 5-V is often single (rarely two-branched), very long, stout and longer than the tergum of the following segment in supraspecific groups of Aedini, but in some taxa it is branched, short to moderately long, slender and shorter than tergum VI. See Belkin (1962: figs 207, 281) for a comparison of the two character states.
 75. *Seta 2-VI, position:* (0) medial to or at same level as seta 1-VI; (1) lateral to seta 1-VI. The position of seta 2-VI, in relation to seta 1-VI, is normally consistent within most subgenera, smaller genera and species groups of the larger subgenera, e.g. *Finlaya* and *Ochlerotatus* of *Ochlerotatus*.
 76. *Seta 3-VI, position:* (0) medial to or at same level as seta 1-VI; (1) lateral to seta 1-VI. Seta 3-VI is normally laterad of seta 1-VI in Aedini. However, it is positioned at the same level or mesad of seta 1-VI in *Heizmannia*, *Opifex*, *Zeugomyia*, subgenera *Belkinius*, *Bothaella* and *Lorrainea* of *Aedes*, subgenera *Chaetocruomyia* and *Macleaya* of *Ochlerotatus*, the Kochi and Niveus Groups of *Oc. (Finlaya)*, and the outgroup species *Cs. inornata* and *Cx. quinquefasciatus*.
 77. *Seta 9-VII, length:* (0) \leq length of seta 6-VII; (1) $>$ length of seta 6-VII. Seta 9-VII is normally longer than seta 6-VII in Aedini, but it is occasionally shorter than or equal to the length of seta 6-VII. 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. This seta is also absent in *Ma. (Man.) dyari* Belkin, Heinemann & Page and *Ma. (Man.) flaveola* (Coquillett).
 78. *Seta 9-VIII, development:* (0) single or 2-branched; (1) \geq 3 branches. Seta 9-VIII normally has three or more branches in most Aedini, but it is single (occasionally two-branched) in some taxa, e.g. subgenera *Aedes* (see Tanaka, 2000: figs 1–3), *Paraedes* and several *Stegomyia* of *Aedes*, subgenera *Chaetocruomyia*, *Macleaya*, *Molpemyia* and some other species of *Ochlerotatus*, *Udaya* and *Verrallina*.
 79. *Paddle midrib:* (0) weakly developed, not reaching apex of paddle; (1) well developed, extending to or near apex of paddle. Most genera and subgenera of Aedini have the midrib of the paddle well developed and extending to or near the apex of the paddle. The midrib, however, is weakly developed and nearly indistinct in some genera, subgenera and species. See Baisas & Feliciano (1953: fig. 26) for state (0) in *Zeugomyia*.
 80. *Paddle, fringe of long hairlike spicules:* (0) absent; (1) present. Reinert (2000d) listed the genera and subgenera of Aedini with a fringe of hairlike spicules on the pupal paddle. These are present or absent in subgenera and genera, with few exceptions. Most species of *Ae. (Stegomyia)* have well-developed hairlike spicules on the paddle margin, but there are notable exceptions, e.g. *Ae. (Stg.) aegypti* and the *Dendrophilus* Group (see illustrations in Huang, 1997).
 81. *Paddle, apical margin:* (0) sharply or broadly rounded, flat or very slightly concave; (1) with well-developed emargination at or near apex of midrib; (2) with projection on mesal area at apex

of midrib. Reinert (2000c) 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. The median, apical emargination is deep in some *Armigeres* (see Mattingly, 1971: fig. 32a, b), *Eretmapodites*, subgenera *Abraedes*, *Aztecaedes*, *Halaedes*, *Kompia*, and a few other species of *Ochlerotatus*, and the outgroup species *Ma. titillans*.

82. *Seta 1-Pa, development*: (0) single, rarely 2-branched; (1) ≥ 3 branches. Several species show an overlap between the two character states, e.g. *Ae. (Ala.) brevitibia* (2 or 3 branches), *Ae. (Bot.) eldridgei* (2–5 branches), *Ae. (Neo.) palpalis* (2–4 branches), *Oc. (Fin.) leonis* (2 or 3 branches), *Ps. (Jan.) ferox* (2 or 3 branches) and *Cs. inornata* (2 or 3 branches); however, most specimens of these species have three or more branches, these are scored (0,1). Seta 1-Pa is absent in some species of both subgenera of *Armigeres*, and in the outgroup species *Ma. titillans*.
83. *Seta 2-Pa*: (0) absent; (1) present. Absence of seta 2-Pa is the normal condition in Aedini. However, seta 2-Pa is present in subgenera *Grabhamia* (except *Ps. infinis* (Dyar & Knab)) and *Psorophora* of *Psorophora* (see Belkin *et al.*, 1970: figs 57, 64–66) and the outgroup species *Cx. quinquefasciatus*.

Adults (females except where otherwise noted)

84. *Erect scales of head*: (0) absent; (1) restricted to occiput; (2) 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’. They also illustrated states (1) (their fig. 6B) and state (2) (their fig. 6A). Erect scales in Aedini are either restricted to the occiput or borne on both the occiput and vertex depending on the subgenus or genus. In some species, several semierect, narrow, forked scales similar to erect scales on the occiput occur on the vertex (often posterior to the ocular setae) and these are scored (2). They are absent in *Opifex*; however, numerous short, curved, dark setae occur on the occiput and vertex.
85. *Decumbent scales of vertex*: (0) broad; (1) narrow; (2) both broad and narrow. 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. In *Ae. (Scutomyia)* a patch of narrow scales occurs on the anterior median area.
86. *Ocular line*: (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. The ocular line of *Cs. inornata* is moderate in width and is here scored as (0).
87. *Ocular scales*: (0) absent; (1) narrow; (2) broad; (3) both narrow and broad. In *Hs. (Hez.) complex*, *Hs. (Hez.) scintillans*, *Hs. (Mat.) achatae* and *Hs. (Mat.) catesi*, the ocular line is very narrow and the ocular setae are positioned far forward, very near the posterior margins of the eyes. The ocular line in these species does not bear scales, but some broad scales extend from the vertex anteriorly to the eye margins. Therefore, this character is coded (0) in these species. Scales are also absent in *Ae. (Can.) masculinus*.
88. *Eyes, immediately above antennal pedicels*: (0) contiguous; (1) narrowly to moderately separated; (2) broadly to very broadly separated. The distance between the eyes (measured in number of eye facets) is determined on the area immediately above the antennal pedicels. Scales protruding from the median anterior area of the vertex or upper part of the interocular space may obscure this area. In some cases, the scales must be removed to determine the distance between the eyes, e.g. species of *Oc. (Howardina)*. The eyes of Aedini vary from being contiguous to very broadly separated depending on the subgenus or genus. 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. Species with the eyes that touch or are separated by less than or equal to one eye facet immediately above the antennal pedicels are scored (0), those separated by 2–4 (rarely five) facets are scored (1) and those separated by six or more facets are scored (2). *Eretmapodites* have the eyes very widely separated (9–13 facets).
89. *Interocular setae*: (0) absent; (1) present. 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. Setae are normally present on this area in Aedini and the outgroup species. They are absent in *Ayurakitia*,

- subgenera *Gymnometopa* and *Kompia* of *Ochlerotatus*, and *Udaya*.
90. *Interocular space, scales*: (0) absent; (1) narrow; (2) broad; (3) both narrow and broad. The interocular space is reduced to a very small triangle and is apparently without scales in subgenera *Canraedes* and *Lorrainea* of *Aedes* and *Geoskusea*, *Levua* and *Rhinoskusea* of *Ochlerotatus*, and is scored (0). In these subgenera, the eyes are contiguous for nearly the entire mesal length resulting in a very small interocular space. *Aedes* (*Adm.*) *domesticus* has narrow and a few somewhat broader scales and is scored (1). *Opifex fuscus* has only a few scattered small broad scales. *Aedes* (*Alb.*) *marshallii*, *Oc.* (*Cha.*) *wattensis* and *Ve.* (*Har.*) *nobokonis* have narrow scales laterally and a few broad scales medially, and are scored (3).
 91. *Antennal pedicel, mesal surface*: (0) with scattered scales and/or setae; (1) with patch of broad, overlapping, silvery scales. State (0) is found in most Aedini and the outgroup species. State (1) is found in subgenera *Albuginosus*, *Bothaella*, *Scutomyia* and *Stegomyia* of *Aedes*, subgenera *Abraedes*, *Aztecaedes*, *Gymnometopa* and *Kompia* of *Ochlerotatus*, and *Zeugomyia*. In 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. 237), whereas in state (1) a moderately large to large patch of tightly overlapping, silvery scales is present (see Tanaka *et al.*, 1979: fig. 234).
 92. *Antennal pedicel, lateral surface*: (0) bare; (1) with scales. The outer surface of the antennal pedicel is bare in most Aedini. Scales are present on this area in subgenera *Alanstonea*, *Fredwardsius* and *Stegomyia* of *Aedes*, *Oc.* (*Rusticoidus*), *Oc.* (*Och.*) *dorsalis*, *Oc.* (*Och.*) *sollicitans* 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. See Huang (1977a: fig. 2B, D) for examples of state (1).
 93. *Apical flagellomeres (males)*: (0) both apical flagellomeres disproportionately long compared with other flagellomeres; (1) these flagellomeres not disproportionately long in comparison with others. Two distal flagellomeres approximately equal in length and much longer than the proximal flagellomeres is the usual condition in Aedini. However, the two apical flagellomeres are approximately the same length as the others in *Oc.* (*Nothoskusea*) and *Opifex* (see Belkin, 1968: figs 2, 19).
 94. *Antenna, development of flagellar whorls (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; (2) numerous long setae, directed normally dorsally and ventrally. Antennal whorls comprised of numerous long setae directed normally dorsally and ventrally is the usual condition in Aedini. *Ochlerotatus* (*Not.*) *chathamicus* and *Op. fuscus* are notable in having only a few short setae on each flagellomere (see illustrations in Belkin, 1968). Subgenera *Belkinus*, *Bothaella*, *Indusius*, *Leptosomatomyia* and *Paraedes* of *Aedes*, *Oc.* (*Geo.*) *longiforceps* and subgenera *Levua* and *Rhinoskusea* of *Ochlerotatus*, *Hz.* (*Heizmannia*), *Verrallina* and *Zeugomyia* have several setae that are moderately long to long and normally directed dorsally and ventrally. See Mattingly (1970b: fig. 1) for examples of states (1) and (2).
 95. *Maxillary palpomeres (males)*: (0) five, palpomeres 2 and 3 fused/ankylosed; (1) four, fifth absent or vestigial; (2) three, fourth absent or vestigial; (3) two, third absent or vestigial. In state (0), palpomeres 2 and 3 are fused/ankylosed with a paler, somewhat distinct ring at the fusion/ankylosis whereas no such area is apparent in the other states. Very short palpi are found in males of the following Aedini: subgenera *Aedes*, *Belkinus*, *Bothaella*, *Canraedes*, *Christophersiomyia*, *Huaedes*, *Leptosomatomyia*, *Paraedes* and most species of *Geoskusea* of *Aedes*, a few species of *Haemagogus*, *Heizmannia*, subgenera *Nothoskusea* and *Rhinoskusea* of *Ochlerotatus*, *Verrallina* and *Zeugomyia* (Reinert, 2000d). 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. The number of palpomeres is consistent for subgenera and genera, with very few exceptions, e.g. *Oc.* (*Geo.*) *baisasi* and *Oc.* (*Geo.*) *longiforceps*.
 96. *Anteppronota*: (0) approximated; (1) more widely separated. The anteppronota are nearly touching dorsally in *Hg.* (*Hag.*) *equinus*, *Hg.* (*Hag.*) *splendens*, *Hz.* (*Hez.*) *complex* and *Hz.* (*Hez.*) *scintillans*. These structures are somewhat more separated but still close together in *Hz.* (*Mat.*) *achaetae*, *Hz.* (*Mat.*) *catesi*, *Ae.* (*Psa.*) *argenteoventralis dunnii*, *Ae.* (*Psa.*) *michaelikati* and *Ar.* (*Arm.*) *breinli*.
 97. *Acrostichal setae*: (0) absent; (1) present. Setae are either present or absent on the acrostichal area depending on the subgenus or genus of

- Aedini. Harbach & Knight (1980) defined the acrostichal area as 'The median longitudinal area of the scutum from the anterior promontory to the prescutellar space; bearing the acrostichal setae'. 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 the presence or absence of setae on the anterior end of the acrostichal area. Among *Ae. (Bothaella)*, these setae are absent in *Ae. eldridgei*, whereas they are absent or reduced to 2–4 on the anterior area in some specimens of *Ae. helenae* (scored 0,1).
98. *Dorsocentral setae*: (0) absent; (1) present. Setae are normally present on the dorsocentral area (as defined by Reinert, 1999b) of Aedini, at least a few on the anterior part, posterior part or both. However, these setae are absent in *Ae. (Stg.) demotes* and subgenera *Alanstonea*, *Christophersomyia* and *Pseudarmigeres* of *Aedes*, the Niveus Group of subgenus *Finlaya* and subgenera *Kenknightia* and *Zavortinkius* of *Ochlerotatus*, *Armigeres*, *Haemagogus* and *Heizmannia*.
 99. *Prescutellar area, median and/or posterior parts*: (0) bare; (1) with scales and/or setae. Numerous species have several to a moderate number of scales on the lateral and anterior margins of the prescutellar area, but the median and posterior areas are bare (state 0). This area in other species has scales or scales and setae on the median and/or posterior parts (state 1). Unfortunately, this area is often partially rubbed in specimens and it is difficult to determine the extent of scaling. Therefore, nearly perfect specimens are required to score this character.
 100. *Prescutellar setae*: (0) absent; (1) present. Prescutellar setae are normally present in Aedini, but are absent in *Ae. (Ala.) brevitibia*, *Ae. (Psa.) argenteoventralis dunni* and the nominotypical subgenera of *Haemagogus* and *Heizmannia*. They are either present or absent in specimens of *H. (Mat.) achaetae*.
 101. *Scutellum, scales on midlobe*: (0) narrow; (1) broad; (2) both narrow and broad. The state of scales on the midlobe of the scutellum is relatively consistent for subgenera, but some exceptions occur, which are usually in the larger subgenera and appear to characterize species groups. For *Oc. (Mucidus)*, see discussion of character 102.
 102. *Scutellum, scales on lateral lobes*: (0) narrow; (1) broad. The median as well as the lateral lobes of *Oc. (Muc.) alternans* and *Oc. (Muc.) laniger* bear several narrow and a few moderately broad, decumbent, falcate scales and numerous long, twisted, erect scales. These are scored as (0). Long, twisted, erect scales are also present on other body areas of these species, e.g. head, thorax, abdomen, etc. (see illustrations in Tyson, 1970).
 103. *Paratergal scales*: (0) absent; (1) present. A few species, e.g. *Ae. (Edw.) imprimens* and *Ve. (Nma.) indica*, normally have the paratergite bare but occasionally a specimen will possess a few scales on this area. These species are coded as polymorphic (0,1).
 104. *Parascutellar scales*: (0) absent; (1) present. Reinert (1999a) 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 *Rusticoidus* and a few species of *Oc. (Ochlerotatus)*.
 105. *Anteprenotal scales*: (0) absent; (1) present. The presence of scales on the anteprenotum is normally consistent in subgenera of Aedini. Some species differ from the norm, but the scales are usually consistently present or absent in species groups. When present, scales may be narrow, broad or both narrow and broad.
 106. *Postpronotal scales*: (0) absent; (1) present. The postpronotum normally bears narrow, broad or both narrow and broad scales in Aedini. Postpronotal scales are, however, absent in *Ae. (Bothaella)* (see Reinert, 1973b: fig. 2), *Oc. (How.) walkeri*, *Oc. (Och.) fulvus pallens*, *Ps. (Pso.) ciliata*, *Oc. (Rhinoskusea)*, *Ayurakitia* and *Udaya*. One specimen of *Ve. (Har.) yusafi* examined had one broad, white scale whereas other specimens had no scales.
 107. *Prespiracular setae*: (0) absent; (1) present. Prespiracular setae are characteristic of *Psorophora*. These setae are also found in the outgroup species *Cs. inornata*.
 108. *Postspiracular setae*: (0) absent; (1) present. Postspiracular setae are normally present in Aedini. They are, however, absent in *Ze. gracilis*, *Oc. (Kom.) purpureipes*, *Ar. (Leicesteria)*, *Ayurakitia*, *Eretmapodites*, *Haemagogus (Haemagogus)* (see illustrations in Arnell, 1973) and *Heizmannia* (except in *H. (Mat.) catesi*). Their absence in *Oc. (Kom.) purpureipes* is unique among species of *Ochlerotatus*. These setae are absent in the outgroup species except *Ma. titillans*.
 109. *Postspiracular scales*: (0) absent; (1) present. The presence or absence of scales on the postspiracular area is normally fixed for subgenera and smaller genera of Aedini, and for species groups within larger subgenera.
 110. *Hypostigmal scales*: (0) absent; (1) present. Hypostigmal scales are normally absent in

- Aedini. They are present, however, in *Ae.* (*Pseudarmigeres*), subgenera *Aztecaedes*, *Chaetocruomyia*, *Mucidus*, *Rusticoidus* and some *Ochlerotatus* of *Ochlerotatus*, subgenera *Janthinosa* and *Psorophora* of *Psorophora*, and *Ar.* (*Lei.*) *longipalpis*.
111. *Subspiracular area*: (0) bare; (1) with scales and/or setae. The subspiracular area is bare in subgenera *Aedes*, *Bothaella*, *Canraedes*, *Isoaedes*, *Lorrainea*, *Paraedes* and *Scutomyia* of *Aedes*, the Niveus Group of *Oc.* (*Finlaya*), subgenera *Geoskusea*, *Kenknightsia*, *Levua*, *Nothoskusea*, *Rhinuskusea* and *Zavortinkius* of *Ochlerotatus*, *Ps.* (*Grabhamia*), *Ayurakitia*, *Opifex*, *Udaya*, *Verrallina* and some other species, e.g. *Ae.* (*Adm.*) *domesticus*, *Ae.* (*Stg.*) *futunae*, *Oc.* (*Fin.*) *chrysolineatus*, *Oc.* (*How.*) *walkeri*, *Oc.* (*Och.*) *atlanticus*, *Oc.* (*Och.*) *fulvus pallens* and *Ps.* (*Pso.*) *howardii*. Short fine setae are present on the subspiracular area in *Ae.* (*Adm.*) *alboscuteallatus* (see Reinert, 1973a: fig. 1), scales and setae are present in *Oc.* (*Och.*) *varipalpus* (Coquillett) (see Arnell & Nielsen, 1972: fig. 7), and scales or setae and scales are present in *Ps.* (*Pso.*) *ciliata*.
 112. *Upper proepisternal setae*: (0) 1–4; (1) 5–19; (2) ≥ 20 . A few species examined have an overlapping condition, e.g. *Hs.* (*Mat.*) *catesi* has 4–5 setae (these are coded 0,1).
 113. *Upper proepisternum, scales*: (0) absent; (1) present. Species of Aedini normally have scales on the upper proepisternum but these are noticeably absent in *Oc.* (*Och.*) *fulvus pallens*, *Ae.* (*Canraedes*) and subgenera *Geoskusea*, *Levua* and *Rhinuskusea* of *Ochlerotatus*.
 114. *Lower proepisternum, 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. *Aedes* (*Adm.*) *vexans vexans* has several narrow and broad scales on the lateral margins of the lower proepisternum (see Reinert, 1973a: fig. 5).
 115. *Upper mesokatepisternal setae*: (0) absent; (1) present. One or more upper mesokatepisternal setae are usually present in Aedini. However, setae are absent in subgenera *Alanstonea*, *Diceromyia* (some species), *Huaedes*, *Pseudarmigeres* (some species) and *Scutomyia* of *Aedes*, *Ayurakitia*, *Eretmapodites*, *Hg.* (*Haemagogus*), *Heizmannia*, *Oc.* (*Mucidus*), *Udaya* and some *Zeugomyia*. Occasionally, a specimen of some species, e.g. *Ve.* (*Har.*) *yusafi*, lacks these setae. Many species without these setae have this area, as well as other pleural areas, covered in scales.
 116. *Prealar setae*: (0) ≤ 20 ; (1) ≥ 21 . Some species exhibit a slight overlap in the two character states, these are coded (0,1).
 117. *Lower prealar area, scales*: (0) absent; (1) present. Scales occurring in a patch on the posterior mesanepisternum ventrad of the prealar knob are the lower prealar scales. Presence or absence of a patch of scales on the lower prealar area is consistent for subgenera and genera, with very few exceptions. See Tanaka *et al.* (1979: fig. 248) for state (0) and their figure 212 for state (1).
 118. *Upper prealar area, scales*: (0) absent; (1) present. Scales on the prealar knob (upper prealar area) vary from narrow and curved, e.g. *Ae.* (*Adm.*) *mediolineatus* and *Ae.* (*Adm.*) *vexans vexans*, to broad and flat, e.g. *Hg.* (*Con.*) *leucocelaenus* and *Hg.* (*Con.*) *leucotaeniatus*. Some species, e.g. *Oc.* (*Och.*) *atlanticus* and *Oc.* (*Och.*) *scapularis* (see Arnell, 1976: fig. 35), have a few to several broad scales on the ventral area of the knob that are contiguous with the scales on the lower prealar area.
 119. *Mesepimeron, scales*: (0) absent; (1) present. Scales are normally present on the mesepimeron in Aedini. They are, however, absent in *Ae.* (*Canraedes*), subgenera *Levua* and *Rhinuskusea* of *Ochlerotatus*, and *Zeugomyia*.
 120. *Lower anterior mesepimeral setae*: (0) absent; (1) present. Well-developed setae on the lower anterior area of the mesepimeron are found in species of the following genera and subgenera (see Reinert, 2000a): subgenera *Bothaella*, *Canraedes*, *Christophersiomyia*, *Fredwardsius*, *Huaedes*, *Isoaedes*, *Leptosomatomyia*, *Pseudarmigeres*, *Skusea*, *Stegomyia* (the Edwardsi Group), *Diceromyia* (some species) and *Neomelaniconion* (many species) of *Aedes*, subgenera *Halaedes*, *Mucidus*, *Rusticoidus*, *Finlaya* (a few species) and *Ochlerotatus* (several species) of *Ochlerotatus*, *Armigeres*, *Ayurakitia*, most *Heizmannia*, *Opifex*, *Psorophora* and *Zeugomyia*.
 121. *Mesepimeron, fine setae on ventral, posterior or both areas*: (0) absent; (1) present. Several to numerous short, fine setae are located ventral, posterior or both to the scale-patch on the mesepimeron in *Oc.* (*Geoskusea*) (see Mattingly, 1959: fig. 2C) and subgenera *Neomacleaya* and *Verrallina* of *Verrallina* (Barraud, 1934; Reinert, 1974, 1984, 1999c).
 122. *Metameron*: (0) bare; (1) with scales; (2) with setae. The metameron is bare in most Aedini. Scales are present in several *Oc.* (*Ochlerotatus*) (see Wood *et al.*, 1979: figs 18, 20, 23), some other subgenera, e.g. *Oc.* (*Rusticoidus*) and *Ar.* (*Leicesteria*), and a few other species. Species

- of *Oc.* (*Geoskusea*) are unique among Aedini in having short, fine setae on the metameron (see Mattingly, 1959: fig. 2C).
123. *Upper calypter, setae or hairlike scales*: (0) absent or reduced to 1–3; (1) present, several or numerous. Setae or hairlike scales are normally present in females of Aedini. 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 0–7 setae/scales on the upper calypter. Dyar & Shannon (1924) first and later Edwards (1929) and Harbach & Kitching (1998) pointed out the usefulness of this character in Culicidae.
124. *Upper calypter, setae or hairlike scales (males)*: (0) absent or reduced to 1–3; (1) present, several to numerous. The presence of several to numerous setae or hairlike scales along the posterior margin of the upper calypter is the usual condition of aedine males. However, in subgenera *Belkinus*, *Canraedes* and *Paraedes* of *Aedes*, *Oc.* (*Rhinoskusea*), *Udaya* and *Zeugomyia* these setae or scales are absent or reduced to only one to three. In *Oc.* (*Rhi.*) *wardi*, the range is 3–5, an overlap of the two alternatives (scored 0,1).
125. *Alula, marginal scales*: (0) absent; (1) narrow; (2) broad. Mattingly (1957, 1958, 1959) pointed out the value of the varied development of scales on the alula (also see character 126). The presence of narrow scales on the margin of the alula is the usual condition in Aedini.
126. *Alula, dorsal moderately broad or broad scales*: (0) absent; (1) present. Scales are absent from the dorsal surface of the alula in most Aedini. Moderately broad or broad scales are present in subgenera *Alanstonea*, *Canraedes*, many *Diceromyia* and *Lorrainea* of *Aedes*, *Eretmapodites*, *Heizmannia*, *Oc.* (*Gymnometopa*) and *Udaya*. See Harbach & Kitching (1998: fig. 12D) for an illustration of state (1) in *Eretmapodites*.
127. *Remigial setae, dorsal*: (0) absent; (1) present, distal; (2) present, proximal. Very long, blunt-tipped setae arising dorsally from near the base of the remigium are characteristic of *Oc.* (*Chaetocruomyia*) (see Marks, 1962: fig. 1C), except *Oc. elchoensis* (Taylor), in which they are absent (see Marks, 1962, 1964). Within Aedini, the presence or absence of setae dorsally on the remigium is normally fixed in subgenera or genera, with few exceptions. Short setae may be partially or completely hidden beneath numerous scales on the remigium in some species.
128. *Remigial setae, ventral*: (0) absent; (1) present. Only the two monobasic taxa of Aedini, *Oc.* (*Nothoskusea*) and *Opifex*, have setae on the ventral surface of the remigium. These setae are also characteristic of genus *Culiseta* (see Harbach & Kitching, 1998: fig. 12C).
129. *Anal vein of wing*: (0) ending approximately at intersection of mcu and cubitus; (1) ending noticeably distal to intersection of mcu and cubitus. Termination of the anal vein beyond the intersection of the mediocubital crossvein and the cubitus, with the distal portion normally nearly straight or gently curved, is the usual condition in Aedini. Termination near the intersection of mcu and the cubitus, with the distal part sharply curved, is found in specimens examined of subgenera *Belkinus* and *Canraedes* of *Aedes*, *Oc.* (*Rhinoskusea*) and *Zeugomyia*.
130. *Vein R₂, length*: (0) <length of vein R₂₊₃; (1) ≥ length of vein R₂₊₃. Vein R₂ longer than vein R₂₊₃ is the normal condition in Aedini. This vein, however, is shorter than R₂₊₃ in *Ae.* (*Blk.*) *aurotaeniatatus* and *Zeugomyia*.
131. *Anteprocoxal scales*: (0) absent; (1) present. Scales are normally absent from the anteprocoxal membrane of Aedini. However, broad and silvery or white scales are normally present in subgenera *Alanstonea* and *Pseudarmigeres* of *Aedes*, *Ar.* (*Leicesteria*), *Oc.* (*Rusticoides*), *Oc.* (*Och.*) *dorsalis* and *Ps.* (*Jan.*) *ferox*.
132. *Postprocoxal scales*: (0) absent; (1) present. Many species of Aedini do not have scales on the postprocoxal membrane, but they are present in *Christophersiomyia*, *Diceromyia* (many species), *Fredwardsius*, *Huaedes* and *Pseudarmigeres* of *Aedes*, *Ar.* (*Leicesteria*), *Hg.* (*Haemagogus*), many species of subgenus *Hs.* (*Heizmannia*), subgenera *Abraedes*, *Gymnometopa*, *Ochlerotatus* (several species) and *Rusticoides* of *Ochlerotatus*, and several species of *Psorophora*. See Zavortink (1972: figs 6, 14, 35) for illustrations of state (0) and Wood *et al.* (1979: figs 18, 23, 32) for state (1).
133. *Base of hindcoxa*: (0) well below dorsal margin of mesomeron; (1) more or less in line with or slightly above dorsal margin of mesomeron. The base of the hindcoxa is well below the dorsal margin of the mesomeron in the majority of Aedini, but it is more or less in line with or slightly above the mesomeron in *Alanstonea*, *Belkinus*, *Leptosomatomyia*, *Pseudarmigeres*, *Scutomyia* and *Ae.* (*Stg.*) *desmotes* of *Aedes*, *Hg.* (*Haemagogus*), *Oc.* (*Chaetocruomyia*), *Armigeres*, *Heizmannia*, *Udaya* and *Zeugomyia*. See illustrations in Harbach & Kitching (1998: fig. 12H, I, respectively) of state (0) and state (1).

134. *Fore-, mid- and hindfemora, subapical white-scaled band*: (0) absent; (1) present. Subapical white-scaled bands on all femora occur in *Fredwardsius* (see Mattingly, 1965: fig. 5A) and *Huaedes* of *Aedes*, subgenera *Finlaya* (the Kochi Group) and *Mucidus* of *Ochlerotatus*, and *Ps.* (*Grabhamia*).
135. *Hindtarsomere 1, pale-scaled area*: (0) absent; (1) present. Pale scales on hindtarsomere 1 often form basal and or apical rings or spots, but may be in the form of a stripe, patch or rings on any surface, or several to numerous single scales intermixed with dark scales.
136. *Foreungues*: (0) both simple; (1) one simple, other toothed; (2) both toothed. Both foreungues bearing a short or long tooth is the usual condition in females of Aedini. However, both foreungues are simple in the following taxa: *Ae.* (*Par.*) *barraudi*, *Ae.* (*Stg.*) *albopictus*, *Ae.* (*Stg.*) *scutellaris* and subgenera *Canraedes*, *Huaedes*, *Leptosomatomyia*, *Lorrainea*, *Scutomomyia* and *Skusea* of *Aedes*, *Hg.* (*Hag.*) *splendens*, *Hs.* (*Heizmannia*), subgenera *Abraedes*, *Chaetocruimyia*, *Geoskusea*, *Howardina*, *Levua*, *Macleaya*, *Pseudoskusea*, *Rhinoskusea* and *Oc.* (*Och.*) *muelleri* of *Ochlerotatus*, *Ps.* (*Grabhamia*), *Ud.* *argyrurus* and *Ze.* *gracilis*. *Udaya lucaris* possesses one unguis with a tooth and the other without.
137. *Foreungues (males)*: (0) both simple; (1) one simple, other toothed; (2) both toothed. Most males of Aedini have one or both foreungues with a tooth. When both unguis are toothed, the larger one of the fore- and midtarsi may possess one or two teeth, e.g. many *Finlaya* and many *Ochlerotatus* (see figures in Wood *et al.*, 1979) of *Ochlerotatus*, these are scored (2). Both unguis are simple (state 0) in subgenera *Alanstonea*, *Belkinus* (see Reinert, 1982: fig. 2), *Canraedes*, *Indusius*, *Leptosomatomyia* and *Lorrainea* of *Aedes*, *Eretmapodites*, *Opifex* and *Ze.* *gracilis*. See Reinert (1972: fig. 3) for state (1) in *Ay.* *griffithi*.
138. *Midungues (males)*: (0) both simple; (1) one simple, other toothed; (2) both toothed. Both midungues simple in males occur in only a few genera and subgenera of Aedini, e.g. *Ae.* (*Stg.*) *aegypti* and subgenera *Alanstonea*, *Belkinus*, *Canraedes*, *Leptosomatomyia*, *Lorrainea*, *Scutomomyia* (some species) of *Aedes*, *Ayurakitia*, *Eretmapodites*, a few *Hs.* (*Heizmannia*), *Oc.* (*Levua*), *Opifex*, some *Udaya* and some *Zeugomyia*. See also the discussion of character 137.
139. *Hindungues (males)*: (0) both simple; (1) both toothed. The hindungues of many aedine males are simple, but they are toothed in others, e.g. subgenera *Christophersiomyia*, *Edwardsaedes* and several *Stegomyia* of *Aedes*, *Oc.* (*Fin.*) *togoi* and subgenera *Halaedes*, *Mucidus*, *Nothoskusea*, *Rusticoidus*, *Zavortinkius*, *Ochlerotatus* (many species) of *Ochlerotatus*, *Ps.* (*Jan.*) *ferox*, *Ps.* (*Psorophora*) and *Ve.* (*Harbachi*).
140. *Hindungues*: (0) both simple; (1) both toothed. Females of many taxa have simple hindungues, but those of other taxa are toothed, e.g. subgenera *Aedes*, *Christophersiomyia*, *Edwardsaedes* and *Stegomyia* (some species) of *Aedes*, *Halaedes*, *Mucidus*, *Nothoskusea*, *Rusticoidus*, *Zavortinkius*, *Ochlerotatus* (many species) and *Finlaya* (a few species) of *Ochlerotatus*, *Janthinosa* and *Psorophora* of *Psorophora*, *Ve.* (*Harbachi*) and *Opifex*. Most groups with toothed hindungues in females also have them toothed in the male (see character 139).
141. *Laterotergite, scales*: (0) absent; (1) present. Most Aedini have numerous, or at least a few, scales on the laterotergite of abdominal segment I. These scales are absent in subgenera *Geoskusea*, *Nothoskusea* and *Ochlerotatus* (several species) of *Ochlerotatus*, *Opifex*, *Ps.* (*Psorophora*) and the outgroup taxa.
142. *Terga, lateral setae (males)*: (0) few, relatively short; (1) numerous, short to moderately long; (2) numerous, long, with apices curved. Numerous, distinctly long, apically curved setae are present in subgenera *Aedes*, *Aedimorphus*, *Albuginosus*, *Edwardsaedes* and *Neomelaniconion* of *Aedes*, *Halaedes*, *Mucidus*, *Protomacleaya*, *Pseudoskusea*, *Rusticoidus*, *Ochlerotatus* (most species) and *Finlaya* (some species) of *Ochlerotatus*, and *Psorophora* (moderately long in *Ps.* (*Pso.*) *howardii*).
143. *Abdominal segment VII, shape*: (0) laterally compressed; (1) dorsoventrally flattened; (2) cylindrical. In dried females, abdominal segment VII (and often also segment VIII) has a distinctive shape when viewed transversely, i.e. laterally compressed, dorsoventrally flattened or cylindrical. The cylindrical shape occurs in *Psorophora* and the outgroup species *Ma. titillans*. See Tanaka *et al.* (1979: fig. 229) for state (0) and his figure 212 for state (1).

Female genitalia

The series of papers on the comparative anatomy of Aedini by Reinert (2000e, f, g, h, i, 2001b, c, d, e, 2002b, c, d, e) should be consulted for illustrations of female genital structures and states for characters 144–157.

144. *Intersegmental membrane between segments VII and VIII*: (0) short; (1) intermediate; (2) long. It is

- evident that the very long intersegmental membrane in *Psorophora* allows almost complete retraction of segment VIII into segment VII.
145. *Tergum VIII*: (0) mostly membranous, without lateral rod-shaped structures; (1) mostly membranous, with heavily pigmented and sclerotized rod-shaped structure laterally on each side; (2) entirely sclerotized (rarely with only small median nonsclerotized area), without lateral rod-shaped structures. Reinert (2000f) discussed and illustrated the development of the lateral rod-shaped structures in *Psorophora*. The reduced sclerotization of tergum VIII of *Oc. (Och.) sollicitans* and related species, and comparison with *Psorophora*, was discussed by Reinert (2002e).
146. *Tergum VIII, setae*: (0) on distal 0.6 or less; (1) on distal 0.7 or more. Some subgenera and species groups have most of the surface (distal 0.7 or more) of tergum VIII covered with numerous setae, e.g. subgenera *Aedes*, *Aedimorphus*, *Alanstonea*, *Canraedes*, *Christophersiomysia*, *Edwardsaedes*, *Fredwardsius*, *Indusius*, *Neomelaniconion* and *Paraedes* of *Aedes*, *Bruceharrisonius*, *Geoskusea*, *Halaedes*, *Kenknightia* (most specimens), *Kompia*, *Levua*, *Mucidus*, *Nothoskusea*, *Ochlerotatus* (most species), *Pseudoskusea*, *Rhinoskusea* and *Rusticoidus* of *Ochlerotatus*, *Ps. (Janthinosoma)*; also *Ae. (Stg.) aegypti*, *Oc. (Fin.) togoi* and *Ve. (Har.) yusafi*. Other groups have few to several setae on the distal 0.6 or less of tergum VIII.
147. *Tergum VIII, scales*: (0) absent; (1) few (1–8 scales); (2) numerous (≥ 9 scales). Some species have tergum VIII without scales, e.g. *Ae. (Adm.) alboscuteclatus*, *Ae. (Can.) masculinus*, *Ae. (Ind.) pulverulentus*, *Oc. (Lev.) geoskusea* and *Ps. (Jan.) ferox*. Some species have only a few (1–8, often only 1–5) scales scattered over the surface, e.g. *Ae. (Blk.) aurotaeniatus*, *Ae. (Lor.) amesii*, *Oc. (Geo.) baisasi* and *Oc. (Geo.) fimbripes* (Edwards). Other species have nearly the entire surface densely covered with numerous scales, e.g. *Ae. (Ala.) brevitibia*, *Ae. (Dic.) furcifer*, *Ae. (Stg.) desmotes*, *Ar. (Arm.) subalbatus*, *Er. quinquevittatus*, *Hg. (Hag.) splendens* and *Ud. argyrurus*.
148. *Sternum VIII, position of seta 2-S*: (0) noticeably posterior to seta 1-S; (1) laterally near same level as seta 1-S. See Reinert (2000e) for a description of seta 2-S in Aedini. Some subgenera and groups have numerous scattered long setae intermixed with shorter setae or have numerous long setae along the median area that do not appear in a distinct pattern. These are coded as ‘?’.
149. *Sternum VIII, scales*: (0) absent; (1) few (1–8 scales); (2) numerous (≥ 10 scales). Scales on sternum VIII may be absent, e.g. *Ae. (Adm.) alboscuteclatus*, *Ae. (Can.) masculinus*, *Ae. (Fre.) vittatus*, *Oc. (Geo.) baisasi* and *Oc. (Lev.) geoskusea*, few (usually 1–4, range 1–8) scattered scales, e.g. *Ae. (Alb.) ngong* and *Oc. (Fin.) macfarlanei*, or numerous and normally in lateral patches or covering most of the surface, e.g. *Ae. (Dic.) furcifer*, *Ae. (Stg.) desmotes*, *Hz. (Hez.) scintillans*, *Oc. (Brh.) greenii* and *Oc. (Rus.) refiki*. A few specimens of some species exhibit a slight overlap between states.
150. *Tergum IX*: (0) wide, width $\geq 2.0 \times$ length; (1) narrower, width $\leq 1.9 \times$ length. Tergum IX is very wide and relatively short in some Aedini, e.g. *Ae. (Ala.) brevitibia* and *Ae. (Blk.) aurotaeniatus*, but in most species it is narrower and longer.
151. *Tergum IX, setae*: (0) absent; (1) present distally; (2) present distally and on much of medial area. Setae are normally present distally on tergum IX in most Aedini; however, they are absent or normally absent in most species of subgenera *Belkinus*, *Canraedes* and *Lorrainea* of *Aedes*, *Eretmapodites*, *Haemagogus*, *Verrallina* and *Zeugnomysia*. Setae are absent in a few other aedine species, e.g. *Ae. (Psa.) michaelikati*, *Hz. (Hez.) complex*, *Oc. (How.) walkeri* and *Oc. (Och.) atropalpus*. They are absent in the outgroup species *Ma. titillans*. In *Psorophora* and *Oc. (Aztecaedes)* (see Reinert, 2002e: fig. 41), setae extend along the apical and much of the median areas.
152. *Postgenital lobe, position of ventral setae*: (0) distal; (1) median; (2) lateral; (3) entire surface. The presence of setae on the distal part of the postgenital lobe is the usual condition in Aedini. *Opifex fuscus* is unique in having numerous (63 or more) setae extending over the entire ventral surface of the postgenital lobe (Reinert, 2001c). Setae that are arranged in a median pattern on the ventral surface of the postgenital lobe in Aedini are unique to *Ae. (Fre.) vittatus* (Reinert, 2000a, i). Setae are present on the lateral areas of the outgroup species *Cs. inornata* and *Or. signifera*.
153. *Upper vaginal sclerite*: (0) absent; (1) present. Most Aedini have a developed upper vaginal sclerite. This structure is absent in *Ae. (Skusea)*, *Oc. (Geo.) longiforceps*, subgenera *Aztecaedes*, *Kompia*, *Ochlerotatus* (most species), *Rhinoskusea*, *Rusticoidus*, *Finlaya* (some species) and *Kenknightia* (some specimens) of *Ochlerotatus*, *Haemagogus* and *Psorophora*.

154. *Lower vaginal sclerite*: (0) absent; (1) present. Absence of the lower vaginal sclerite is the normal condition in Aedini; however, it is well developed in *Verrallina* (Reinert, 1999c, 2001d). Some species of *Oc.* (*Geoskusea*) have a poorly developed lower vaginal sclerite consisting of a small strip connected to the inner surface, along the basal areas, of the lower vaginal lip (Reinert, 2002e). The outgroup species *Cx. quinquefasciatus* has a well-developed, horseshoe-shaped, lower vaginal sclerite on the median area of the membrane of the vaginal wall between the inner margins of the lower vaginal lip. This structure in *Culex* has been frequently misinterpreted in the literature.
155. *Insula*: (0) absent or weakly/poorly developed; (1) liplike; (2) tonguelike. *Aedes* have a tonguelike insula that distinguishes the genus from *Ochlerotatus*, which have a liplike insula (Reinert, 2000d, 2002e). *Armigeres*, *Ayurakitia*, *Eretmapodites*, *Haemagogus*, *Heizmannia*, *Psorophora*, *Udaya* and *Zeugomyia* also have a tonguelike (lingulate) insula, whereas *Opifex* has a liplike insula and *Neomacleaya* and *Verrallina* of *Verrallina* have an ill-defined insula. An insula is absent in *Ve.* (*Harbachius*). See Reinert (1999c) for illustrations and a discussion of the insula in *Verrallina*.
156. *Insular setae*: (0) absent; (1) present in lateral patches; (2) present in median patch. Insular setae are well developed in lateral patches in *Ochlerotatus*, *Opifex*, *Psorophora* and the outgroup taxa *Ma. titillans* and *Or. signifera*. Setae are present in a median patch in *Haemagogus*, *Hs.* (*Heizmannia*) and the outgroup taxa *Cs. inornata* and *Cx. quinquefasciatus*. The setae of subgenus *Heizmannia* are very short whereas they are long and well developed in the other taxa (Reinert, 2002b). In *Hs.* (*Mattinglyia*) and all other genera of Aedini, insular setae are absent but one or more small tuberculi with or without a tiny spicule may be present.
157. *Spermathecal capsule(s)*: (0) one; (1) three. One large and two slightly smaller spermathecal capsules are normally present in Aedini. However, *Ae.* (*Adm.*) *alboscuteallatus* and allied species have one large capsule and two rudimentary ones (Reinert, 1973a; 2000i). A single large capsule is found in *Ae.* (*Adm.*) *argenteopunctatus* (Theobald) and allied species, *Ae.* (*Par.*) *ostentatio* and allied species, *Ae.* (*Canraedes*) (Reinert, 2000i), and subgenera *Finlaya* (Niveus Group except two species) and *Rhinoskusea* of *Ochlerotatus* (Reinert, 2002e).
- Male genitalia*
158. *Tergum IX, setae*: (0) absent; (1) slender; (2) some or all stout and flattened. The development of setae on tergum IX is normally fixed within subgenera of Aedini. See Tanaka *et al.* (1979) for illustrations showing examples of state (0) [their fig. 136, *Ve.* (*Har.*) *nobukonis*], state (1) [their fig. 143, *Ar.* (*Arm.*) *subalbatus*] and state (2) [their fig. 127, *Oc.* (*Geo.*) *baisasi*].
159. *Sternum IX, length*: (0) short; (1) moderately long; (2) long. Sternum IX is moderately long in most Aedini, but it is noticeably longer in *Ae.* (*Canraedes*), *Oc.* (*Rhinoskusea*), *Ve.* (*Harbachius*), *Armigeres*, *Ayurakitia*, *Eretmapodites*, *Heizmannia* [except apparently *Hs.* (*Mat.*) *catesi*], *Udaya* and *Zeugomyia*.
160. *Sternum IX, setae*: (0) absent; (1) present. Setae are present on sternum IX in most Aedini; however, they are absent in subgenera *Fredwardsius*, *Indusius*, *Isoaedes*, *Leptosomatomyia*, *Skusea* and *Stegomyia* of *Aedes*, *Ar.* (*Leicesteria*) and *Opifex*. They are also absent in *Ae.* (*Adm.*) *domesticus* and *Ae.* (*Alb.*) *ngong*. Setae are present in the outgroup species.
161. *Gonocoxite, lateral setae*: (0) mostly short; (1) mostly long. Most of the lateral setae on the gonocoxite are normally long in Aedini, but they are short in subgenera *Indusius* and *Skusea* of *Aedes*, subgenera *Levua* and *Macleaya* of *Ochlerotatus* and *Opifex*. See illustrations in Belkin (1962: figs 207 and 297, respectively) for examples of state (0) and state (1).
162. *Gonocoxite, mesal surface*: (0) entirely membranous; (1) partly or entirely sclerotized. The mesal surface of the gonocoxite is commonly membranous in Aedini; however, this area is partially or completely sclerotized in subgenera *Indusius*, *Neomelaniconion* and *Skusea* of *Aedes*, *Oc.* (*Rhinoskusea*), *Psorophora*, *Udaya*, subgenera *Harbachius* and *Neomacleaya* of *Verrallina*, and *Zeugomyia*, as well as the outgroup species *Cs. inornata*, *Cx. quinquefasciatus* and *Or. signifera*.
163. *Gonocoxite, scales*: (0) absent; (1) present. Species of Aedini normally possess several to numerous scales on the gonocoxite but the monobasic subgenus *Indusius* of *Aedes*, the monobasic genus *Opifex* and members of *Ps.* (*Psorophora*) lack scales on the gonocoxite. Both *Indusius* and *Opifex* (see Belkin, 1962: fig. 207) have numerous short and a few longer setae on a somewhat conical gonocoxite that bears the gonostylus subapically.
164. *Gonostylus, attachment to gonocoxite*: (0) subapical; (1) apical. *Aedes* subgenera *Aedes*, *Canraedes*, *Indusius*, *Neomelaniconion* and *Skusea*

have the gonostylus attached subapically to the gonocoxite, and the gonocoxite has the sternal area developed into an apical projection. Subapical attachment of the gonostylus is also found in *Opifex*, at least some species of subgenera *Diceromyia*, *Lorrainea*, *Paraedes* and *Stegomyia* (Africanus Group) of *Aedes*, and subgenera *Harbachius* (all species) and *Neomacleaya* (nearly all species) of *Verrallina*.

165. *Gonostylus, scales*: (0) absent; (1) present. Scales are normally absent from the gonostylus of Aedini, but they are present in *Ae. (Lorrainea)*, the Mediopunctatus Subgroup (W-Albus Group) of *Ae. (Stegomyia)*, *Ae. (Ala.) brevitibia*, *Ae. (Can.) masculinus*, *Ar. (Lei.) magnus* (Theobald), *Ar. (Lei.) cingulatus* (Leicester), *Ar. (Lei.) omissus* (Edwards) (see Thurman, 1959: figs 41, 46, 47), *Eretmapodites* (see illustrations in Service, 1990) and *Ud. lucaris*.
166. *Gonostylus, development*: (0) moderately long to long, relatively narrow throughout length but distal part narrower and usually somewhat curved mesally; (1) same as state 0 but distal part somewhat expanded; (2) short to moderately long, basal area normally narrow, occasionally broader, median or distal part moderately to greatly expanded, bifurcate or trifurcate. Reinert (2000d) illustrated and pointed out the usefulness of the gonostylar development as a supplemental character for separating genera *Aedes* and *Ochlerotatus*, with a few exceptions. The gonostylus normally exhibits character states (1) and (2) in *Aedes*, whereas it normally exhibits character state (0) in *Ochlerotatus*. Subgenera *Christophersomyia*, *Huaedes* and *Isoaedes* of *Aedes*, *Ae. (Adm.) natronius* Edwards, *Ae. (Dic.) kanarensis* Edwards, *Ae. (Dic.) micropterus* (Giles), *Ae. (Dic.) reginae* Edwards, *Ae. (Neo.) bergerardi* Pajot & Geoffroy and *Ae. (Neo.) monotrichus* Edwards have the gonostylus long, narrow and curved mesally, which is similar to most species of *Ochlerotatus*. In *Ae. (Lorrainea)*, the gonostylus is short and uniform in thickness throughout its length. The distal part of the gonostylus is less expanded and the gonostylar claw is attached more distally in *Ae. (Stg.) africanus* than in the other species of *Stegomyia* examined. *Ochlerotatus (Lev.) geoskusea* differs from other *Ochlerotatus* in having the gonostylus moderately long, moderately broad at the base and gently tapered to a blunt apex. Species of *Oc. (Rhinoskusea)* have the gonostylus moderately long and moderately to greatly expanded distally (see Reinert, 1976b: figs 6–8). *Opifex*

has a relatively short gonostylus with a relatively broad basal area. Some species of *Eretmapodites* have a long gonostylus that is relatively slender throughout its length (other species are moderately thickened near midlength), but it is normally strongly curved mesally near midlength (see illustrations in Service, 1990). *Udaya lucaris* has a relatively long gonostylus with both the median and distal portions somewhat expanded, whereas *Ud. argyrurus* is relatively narrow with the distal part enlarged. Both are scored (2). *Verrallina (Nma.) indica* has a long, slender gonostylus; however, the distal part is bent outward near midlength and the apex is slightly recurved. *Aedes (Albuginosus)* have the gonostylus moderately long with the proximal part moderately broad to about midlength whereas the apical part tapers to a narrow, mesally curved, bluntly pointed apex and the gonostylar claw is long, heavily pigmented, with the apex bluntly rounded and attached on mesal margin of the gonostylus at about midlength (see Reinert, 1987: fig. 2). In *Ae. (Paraedes)* the gonostylus is long, bifid (trifid in *Ae. bonnae* Mattingly), has at least one of the lobes with short, fine spicules forming filelike ridges and the gonostylar claw is absent (see Reinert, 1981: figs 3–9). Among the outgroup species, *Cs. inornata* has a long, slender gonostylus, and *Or. signifera* has a long, relatively slender gonostylus that is somewhat swollen near midlength.

167. *Gonostylar claw*: (0) absent; (1) one; (2) ≥ 2 . *Ochlerotatus (Psk.) postspiraculosus*, *Oc. (Fin.) elsiae* (Barraud) (see Barraud, 1934: fig. 37e) and *Oc. (Fin.) shortti* (Barraud) have two or more setae subapically that are somewhat like the terminal short, stout, blunt-tipped gonostylar claw, but they are thinner, have pointed apices and are not considered to be accessory gonostylar claws. In *Ae. (Stg.) desmotes* (see Huang, 1977a: fig. 14), the gonostylar claw is shorter, thinner, the apex is bluntly pointed and it is noticeably removed from the apex. This species also has a few short and 6–8 long setae on the distal portion of the gonostylus. Three of the long setae are thicker, the others are slender and all have long attenuated apices. In *Ae. (Stegomyia)*, the gonostylar claw is typically moderately long, dark, stout and has a blunt apex (see illustrations in Belkin, 1962). In *Oc. (Fin.) roai* Belkin, it is bifurcate, and in *Oc. (Geo.) kabaenensis* (Brug), *Oc. (Geo.) baisasi* and *Ae. (Lor.) lamelliferus* Bohart & Ingram it is relatively short with a somewhat flared apex (in the last two species it has a few small notches along the apex) (see Bohart

& Ingram, 1946: fig. 28). Other species of *Ae. (Lorrainea)* and the Kochi Group of *Oc. (Finlaya)* normally have a very long and slender gonostylar claw. In *Ae. (Fre.) vittatus* (see Huang, 1977b: fig. 3), the gonostylar claw is long, narrow and strongly curved, whereas in *Oc. (Rus.) rusticus* it is moderately long and sinuous (see Marshall, 1938: fig. 96). In *Oc. (Rhinuskusea)*, the gonostylar claw is short, flared apically, longitudinally striated, heavily pigmented and scooplike (see Mattingly, 1958; Reinert, 1976b: figs 6–8). The gonostylar claw is short, darkly pigmented and beaklike in *Opifex* (see Belkin, 1962: fig. 207). In *Eretmapodites*, it is short and truncate apically. In *Ud. lucaris*, it is long, relatively thick and somewhat bladelike. In *Oc. (Lev.) geoskusea*, the gonostylar claw consists of a pair of short, stout, darkly pigmented spiniforms with curved apices, situated side by side and attached subapically (see Belkin, 1962: fig. 273, as *suvae*). Bohart (1957) reported and illustrated three species, i.e. *Ae. agrihanensis* Bohart, *Ae. rotanus* Bohart and *Ae. saipanensis* Stone, of the Pandani Group of *Ae. (Stegomyia)* that possess short, blunt, double gonostylar claws. Species of *Ae. (Pseudarmigeres)* (see Edwards, 1941: fig. 66a–c, as *Dunnius*) usually have, in addition to the gonostylar claw, several elongate, stout spicules on the inner margin that resemble the gonostylar claw. Species of *Armigeres* have several to numerous short and stout gonostylar claws positioned in a short or long row on the inner margin (see illustrations in Macdonald, 1960; Steffan, 1968). Several species of *Ae. (Aedimorphus)* (see Reinert, 1973a: figs 34, 37, 42) have multiple gonostylar claws. The gonostylar claw is absent in subgenera *Aedes*, *Belkinius*, *Canraedes*, *Edwardsaedes*, *Indusius* and *Paraedes* of *Aedes*, *Verrallina* (all subgenera) and *Ze. gracilis*. Of the outgroup species, *Cs. inornata* has a short claw with a small apical notch, *Ma. titillans* has a short, dark, blunt-tipped spiniform, and *Or. signifera* has a short, longitudinally striated claw with a flared apex. *Culex quinquefasciatus* has a short and narrow claw.

168. *Claspette*: (0) absent; (1) with basal, setose plaque variously developed (setae simple, specialized or both) or with relatively short, thin or thick stem with slender or stout seta(e) or spiniform(s); (2) moderately long to long, columnar stem with single, more-or-less flattened or cylindrical filament; (3) with two basal branches, one branch more or less columnar, the other variously developed. The claspettes and the basal mesal lobes are homologous structures in *Aedini*

that can be identified as such by their connection basomesally to a spiculate, more-or-less narrow, somewhat troughlike aedeagal guide (see Reinert, 1999b, 2000d). Reinert (2000d) stated that this structure is apparently nearly lost in species of subgenera *Geoskusea* and *Pseudoskusea* of *Ochlerotatus* because it appears to be reduced to a spiculate aedeagal guide and a short thin strip extending laterally onto the basosternal portion of the mesal surface of the gonocoxite, and bears one or a few short, thin, inconspicuous setae. He also reported that in *Oc. (Rhinuskusea)* the claspette is without a filament, and is bifurcate in two species. In *Oc. (Brh.) greenii* the claspette comprises a median, ventral, columnar stem with a terminal, large, flattened filament, and a narrow lateral arm extending from the base of the stem and bears several setae some of which are flattened (see Reinert, 2003: fig. 2A). Reinert (1981: figs 3–9) described and illustrated the uniquely developed claspette of *Ae. (Paraedes)*, which consists of two basally connected arms. One arm is long, narrow and curved with three setae apically, whereas the other is broader, variously developed and bears 3–5 flattened setae apically or subapically, except in *Ae. chrysoscuta* (Theobald) and *Ae. ostentatio* in which numerous short to moderately long setalike spicules are on the distal part in place of the flattened setae. The filament is absent in *Oc. (Not.) chathamicus* and the stem is developed as a bluntly rounded, lobe-like process that is densely covered with short, thin setae (see Belkin, 1968: fig. 20). In *Oc. (Halaedes)*, the claspette appears to be developed as an oblong plaque bearing a number of curved, lanceolate setae, and the dorsal lateral part is fused with the basomesal portion of the tergal surface of the gonocoxite (see Belkin, 1962: fig. 210). In *Oc. (Rusticoidus)* and some species of *Oc. (Ochlerotatus)*, the claspette stem is moderately to greatly swollen subapically or near midlength, e.g. *Oc. aenigmaticus* (Cerqueira & Costa) and *Oc. atlanticus* (see Carpenter & LaCasse, 1955: fig. 117). The following species of subgenus *Ochlerotatus*, e.g. *Oc. clelandi* (Taylor), *Oc. diantaeus* (Howard, Dyar & Knab), *Oc. imperfectus* (Dobrotworsky), *Oc. intrudens* (Dyar) (see Carpenter & LaCasse, 1955: fig. 165), *Oc. nigrithorax* (Marquart), *Oc. pullatus* (Coquillett), *Oc. sagax* (Skuse), *Oc. sapiens* (Marks), *Oc. thibaulti* (Dyar & Knab), *Oc. vittiger* (Skuse), and species of *Oc. (Mucidus)*, e.g. *Oc. aurantius* (Theobald) and *Oc. quadripunctis* (Ludlow), possess a short, thumblike process on the stem subapically or near midlength. Other species of these subgen-

- era appear to have an additional basolateral, caudally directed, long process bearing setae in addition to the columnar stem and filament, e.g. *Oc. aenigmaticus*, *Oc. atlanticus*, *Oc. pertinax* (Grabham) (see Belkin *et al.*, 1970: fig. 71), *Oc. serratus* (Theobald) and *Oc. tormentor* (Dyar & Knab). In *Oc. (Rusticoidus)*, the claspette filament is relatively short and transversely annulate (see Gutsevich *et al.*, 1974: figs 133, 135). Arnell (1973) pointed out that in *Hg. (Conopostegus)* and two species of subgenus *Haemagogus*, i.e. *Hg. anastasionis* Dyar and *Hg. chrysochlorus* Arnell, the claspette filament is inserted in a distinct alveolus on the apex of the claspette stem. However, in the other species of *Haemagogus* the alveolus is either incomplete or entirely absent at the base of the filament. *Psorophora* have the claspette variously developed from a short plaque, e.g. *Ps. (Gra.) columbiana* and *Ps. (Gra.) jamaicensis*, to a long, flattened stem, e.g. *Ps. (Pso.) ciliata* and *Ps. (Jan.) ferox*, that projects dorsocaudally and bears a few to several specialized setae with flattened, fringed or simple apices, or several slender, simple setae, and none or one or more flattened, broadened and strongly contorted filaments (see Belkin *et al.*, 1970: figs 57, 59, 66). These species of *Haemagogus* and *Psorophora* are scored as (1).
169. *Opisthophallus*: (0) absent; (1) narrow with median area somewhat expanded, projecting nearly straight between basal pieces; (2) moderately broad to broad, projecting caudally between basal pieces. The two taxa examined that possess an opisthophallus, *Verrallina* and *Cx. quinquefasciatus*, also have a prosophallus. See Reinert (1974, 1999c) for a discussion and illustrations of these structures in *Verrallina*. 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. It is narrow in *Cx. quinquefasciatus*, the median area is somewhat expanded and it extends nearly straight between the basal pieces.
170. *Aedeagus*: (0) single tubelike, scooplike or troughlike structure; (1) comprises two lateral plates (aedeagal sclerites). Reinert (2000d) illustrated and reported that in *Aedes* the aedeagus is divided into two lateral plates that normally bear several stout lateral or apical teeth, or both, and the plates are usually not, or are only weakly, fused apically. Species of subgenus *Christophersiomyia* appear to have two lateral plates with the distal portions strongly curved mesally and fused at the apex, and without teeth (except *Ae. gombokensis*, which has two or three short, stout teeth laterally). Species of subgenus *Bothaella* have the distal portion 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 *Ae. helenae*). Some species of subgenus *Lorrainea* appear to have the aedeagus divided into two lateral plates, with the apices lightly fused and slightly extended posteriorly. In some subgenera, 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. The aedeagus is unknown for the monobasic subgenus *Indusius* of *Aedes* (see Reinert, 1976a). The aedeagus of *Ayurakitia*, *Eretmapodites*, *Heizmannia*, *Udaya*, *Verrallina* and *Zeugnomyia* consists of two lateral plates. Species of *Ochlerotatus* have the aedeagus simple and tubelike, scooplike or troughlike. Mohrig (1969) provided illustrations and a discussion of the simple form of a number of European species of subgenera *Ochlerotatus* and *Rusticoidus*.
171. *Proctiger, sternal arm*: (0) absent; (1) present. A sternal arm on the proctiger is present in subgenus *Isoaedes* (see Reinert, 1979: fig. 3) and some species groups of subgenera *Aedimorphus*, *Neomelaniconion* and *Stegomyia* of *Aedes*, *Eretmapodites*, *Hs. (Heizmannia)*, subgenera *Harbachi* and *Neomacleaya* of *Verrallina*, and *Ar. (Arm.) breinli*.
172. *Proctiger, cercal setae*: (0) absent; (1) present. Cercal setae are absent in *Aedes* (except see below), *Ayurakitia*, *Eretmapodites*, *Heizmannia*, *Udaya*, *Verrallina* and *Zeugnomyia*. They are present, minute and uniform in length in the other genera of Aedini. However, *Op. fuscus* is an exception and has minute and some larger cercal setae. Two species of *Aedes*, *Ae. (Dic.) kanarensis* (see Tewari *et al.*, 1990) and *Ae. (Stg.) calceatus* Edwards (see Huang, 1981), have a few long to very long, stout cercal setae, but because of their unusual development and location these are considered to be a departure from normal. Also, a few species of Edwards' (1932) Group C of *Ae. (Aedimorphus)*, e.g. *Ae. argenteopunctatus* (Theobald), *Ae. minutus* (Theobald) and *Ae. punctothoracis* (Theobald), have a few minute cercal setae (see Reinert, 2000d).

PHYLOGENETIC ANALYSES

Phylogenetic analyses with characters assigned equal weights (EW) were performed using WinClada version 1.0000 (Nixon, 1999–2002). Preliminary analyses

using repeated heuristic searches with identical parameters, carried out with NONA v. 2 (Goloboff, 1993), often failed to find the same number of most parsimonious cladograms (MPCs) each time and some runs even failed to find an MPC. This suggests that there are a number of quite different islands of MPCs for the present data, of which NONA sometimes failed to find any or all, even using 100 000 replicates and ten trees held at each step. Therefore, we analysed the data using the Parsimony Ratchet (Nixon, 1999), which was developed as a means of helping circumvent the islands of trees problem. Each Ratchet analysis undertook 20 000 iterations per replicate, with one tree held per replicate and 17 characters sampled each time.

The results of the EW analyses showed that the data were highly homoplastic (see below). In view of this, we considered it appropriate to differentially weight the characters and down-weight those that were most homoplastic. We therefore analysed the data using implied weights (IW) as implemented by PIWE v. 3.0 (Goloboff, 1997). We used the default value of the concavity constant $K = 3$ because more extreme weighting functions caused outgroup taxa to be placed well within the ingroup. We performed all analyses by heuristic search, using 1000 replications (mult*1000) and ten starting cladograms per replicate (hold/10).

We checked that the Ratchet had found the MPCs, and all of them, by inputting its output file (*.rat) into NONA and then using the command 'best' to select only the MPCs. This was necessary because the *.rat files contained 20 001 cladograms (from the 20 000 iterations), not all of which were most parsimonious. We then searched for successively longer cladograms than minimum using the commands 'sub n ' (where n is the number of steps greater than minimum) and 'find*' (to search for all cladograms of minimum length + n), up to a maximum of 100 000 cladograms. We then applied the 'best' command again to this set of 100 000 cladograms to confirm that the included set of MPCs was the same as that with which we started. This was not always the case. Although this procedure never found shorter cladograms than the Ratchet, it often did find (many) more MPCs. For example, 20 000 Ratchet iterations applied to the immature stages data alone (see below) found 19 MPCs, but the checking procedure increased this number to 4590. This successive use of higher values of n in an iterative sequence of suboptimal cladogram searches is the basis of calculating Bremer supports using NONA (see below) and it was during such calculations conducted as part of preliminary analyses that we noticed the number of MPCs from which the Bremer support calculations were based was greater than that which the Ratchet had found initially. A similar procedure was applied to the out-

put from PIWE, except that it was unnecessary to apply the initial 'best' command because the tree file of fittest cladograms does not include any suboptimal topologies that need to be removed. Following the recommendations of Nixon & Carpenter (1996), agreement in grouping within sets of MPCs was summarized using strict consensus trees.

We assessed clade support using Bremer support (Bremer, 1994) and its derivative, relative Bremer support (Goloboff & Farris, 2001). For characters with equal weights, the Bremer support of a clade is the number of extra steps required to lose that clade from a strict consensus tree of MPCs and near-minimum length cladograms. Relative Bremer support is a more fine-grained assessment of support that takes account of the amount of favourable and contradictory evidence. It is useful for differentiating among clades that have the same Bremer support but for which the quality of that support differs. The interpretation of Bremer support and relative Bremer support for differentially weighted data is more difficult because it is measured in terms of fit rather than length. Nevertheless, these statistics are still useful for comparing the support of different clades within a cladogram. Kitching (2002) provided a brief explanation of Bremer support and relative Bremer support, together with the commands used to calculate them using NONA and PIWE.

All illustrated cladograms were initially prepared using WinClada and imported into Microsoft Word 97 documents as *.emf picture files. The images were then cropped, resized and positioned on pages using the image editing tools. Bremer support values and special features such as arrows were produced using the Autosshapes of the Drawing Toolbar function and pasted where required.

RESULTS AND DISCUSSION

In the following sections, in which we describe the results of the various analyses, we refer only to unambiguously optimized characters (Nixon & Carpenter, 1996), unless otherwise stated. In those figures in which characters are mapped onto branches, solid circles indicate 'unique' characters. These are characters that are placed onto the cladogram only once, although they may be interpreted as undergoing subsequent transformation or secondary reversal. Characters mapped as open circles are placed on more than one branch of the cladogram.

ANALYSIS OF ADULT DATA

The existing classification of *Aedini* is based mainly on characters of the adult stage. Therefore, we first tested

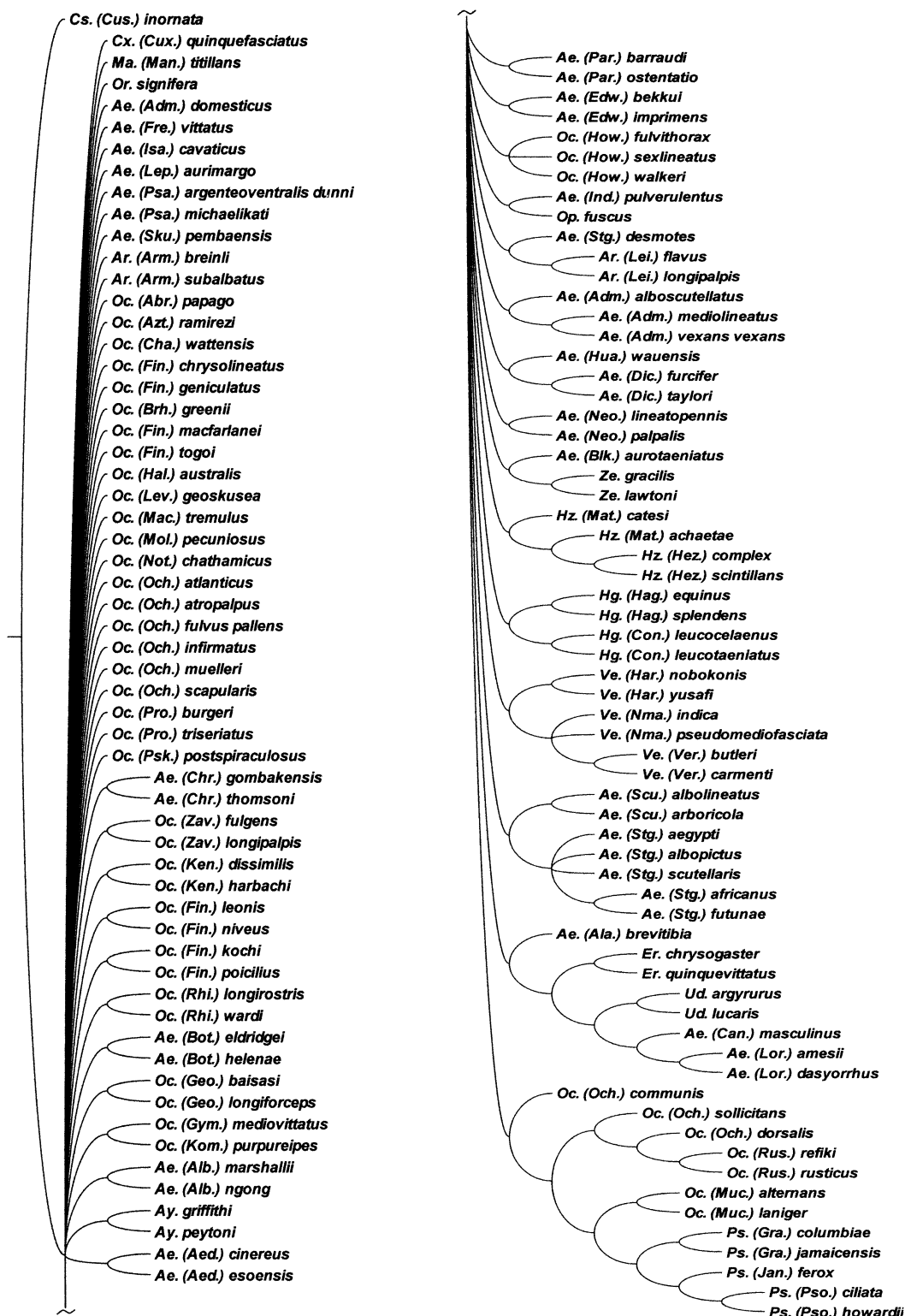


Figure 1. Strict consensus of 4537 MPCs of 871 steps (CI = 0.14, RI = 0.69) obtained from analysis of adult data under equal weights. Groups in polytomies in this and subsequent consensus trees (Figs 2, 3, 4, 7) are arranged in order of increasing size, such that single taxa are listed at the top of the tree and the largest groups at the bottom. No significance should be read into this aspect of the sequence.

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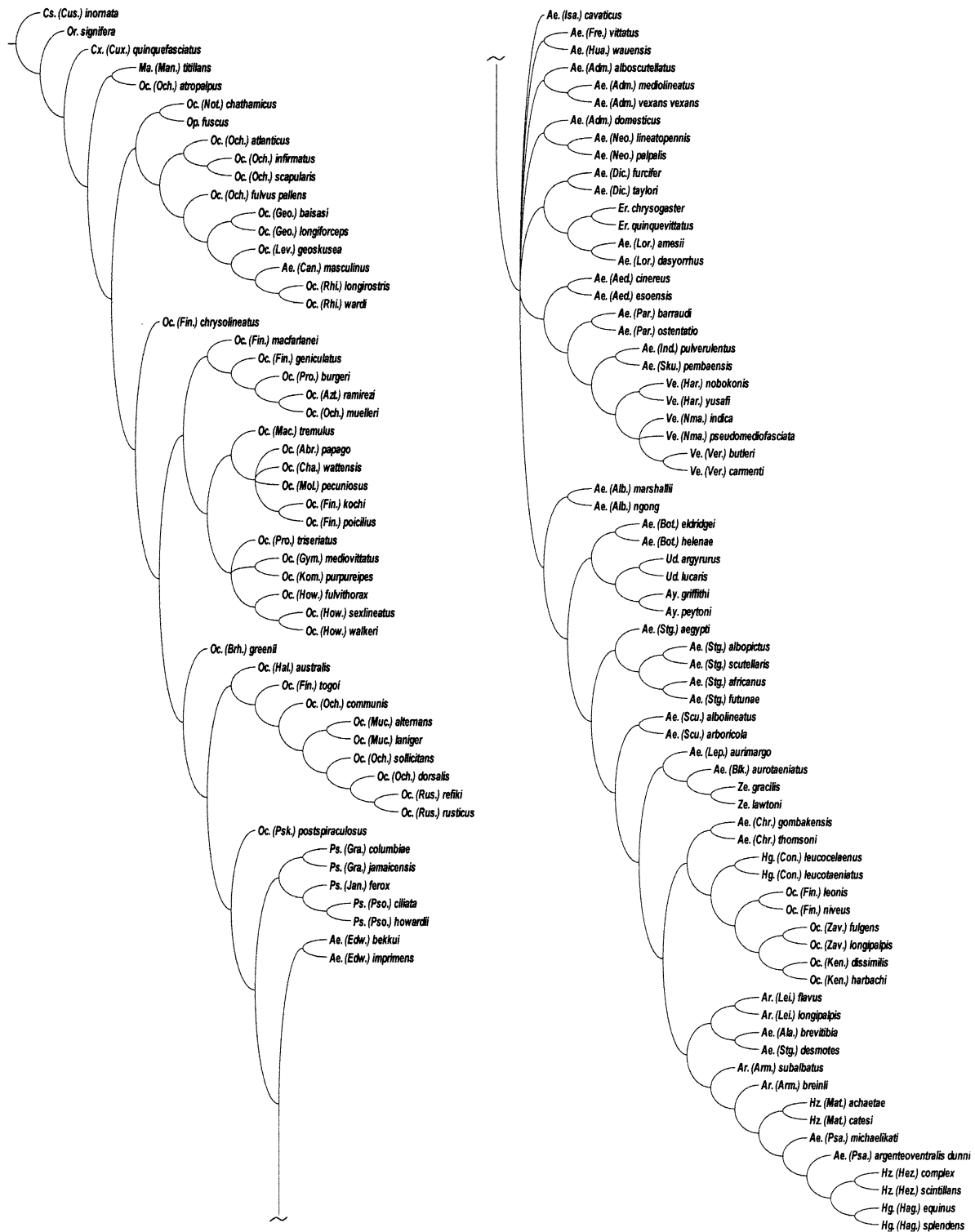


Figure 2. Strict consensus of eight MPCs (Fit = 596.4) obtained from analysis of adult data under implied weights.

whether the adult data included in the present analysis (characters 84–172) would indeed support the existing classification. Analysis using EW produced 4537 MPCs of 871 steps (CI = 0.14, RI = 0.69). The

strict consensus tree (SCT) of these MPCs is shown in Figure 1. Overall, the results do not reflect the existing classification of Aedini. Three of the outgroup taxa, *Cx. quinquefasciatus*, *Ma. titillans* and *Or. signifera*,

are included as members of the tribe in some of the MPCs. Only eight of the 12 existing aedine genera appear as monophyletic lineages (*Ayurakitia*, *Eretmapodites*, *Haemagogus*, *Heizmannia*, *Psorophora*, *Udaya*, *Verrallina* and *Zeugomyia*) and their relationships with the various subgeneric groups of *Aedes* and *Ochlerotatus* are generally unresolved. Except for *Ae. (Pseudarmigeres)* and *Oc. (Protomacleaya)*, the other subgenera of *Aedes* and *Ochlerotatus* represented by two species (ten of the 22 *Aedes* subgenera and five of the 22 *Ochlerotatus* subgenera) are recovered as monophyletic groups. The cladogram indicates that the four largest subgenera (i.e. *Aedimorphus* and *Stegomyia* of *Aedes* and *Finlaya* and *Ochlerotatus* of *Ochlerotatus*, each represented by more than two species in the analysis), are not monophyletic.

The analysis of adult data using IW produced eight MPCs (Fit = 596.4), the SCT of which is shown in Figure 2. The topology of this cladogram is much more fully resolved, as expected when greater weight is accorded those characters that display greater cladistic consistency. Although more fully resolved, the results of this analysis also do not reflect existing classification. *Mansonia titillans* is included as a member of Aedini in a sister relationship with *Oc. (Och.) atropalpus* at the base of the clade. The remainder of the tribe is portrayed as a largely paraphyletic assemblage of *Aedes* and *Ochlerotatus* with the other existing genera interspersed. Only six existing genera, i.e. *Ayurakitia*, *Eretmapodites*, *Psorophora*, *Udaya*, *Verrallina* and *Zeugomyia*, are recovered as monophyletic groups. As in the EW analysis, with the exception of *Ae. (Pseudarmigeres)* and *Oc. (Protomacleaya)*, the subgenera of *Aedes* and *Ochlerotatus* represented by two species are here also recovered as monophyletic taxa. Likewise, none of the four large subgenera, each represented in the analysis by more than two species, is found to be monophyletic. In the case of subgenus *Stegomyia*, *Ae. (Stg.) desmotes* shares a closer relationship with species of *Armigeres* than it does with the other species of *Stegomyia* included in the analysis.

ANALYSIS OF IMMATURE STAGES DATA

Data derived from immature stages have, until recently, rarely been used explicitly in Aedini systematics, either to reconstruct the phylogeny or in classification. We were therefore curious to see how this new subset of data (characters 1–83) would perform and whether, by itself, it would produce a phylogenetic hypothesis congruent with that from the analysis of the adult data.

Analysis using EW produced 4590 MPCs of 831 steps (CI = 0.11, RI = 0.66). The SCT of these MPCs (not shown) was almost completely unresolved. The

only clades recovered were *Ae. (Neo.) palpalis* + *Ve. (Nma.) indica*, and *Ae. (Edw.) imprimens* + (*Ae. (Edw.) bekkui* + *Ae. (Neo.) lineatopennis*). Under IW, 1158 MPCs (Fit = 295.9) were found, the SCT of which (not shown) was also highly unresolved. The only clades present were *Oc. (Och.) communis* + *Oc. (Och.) dorsalis*, and *Ae. (Edw.) bekkui* + (*Ae. (Edw.) imprimens* + *Ae. (Adm.) vexans vexans*).

The lack of resolution in both SCTs was disappointing and gives the impression that the immature stages data contain very little phylogenetic signal. However, if these data were truly mostly noise, then given the size of the data set, we might expect many millions of MPCs. That we found only 4590/1158 is indicative of quite strong signal. However, rather than a single signal, the immature stages data set seems to contain several equally strong but contradictory signals. These signals support conflicting topologies that are sufficiently different in the placements of certain taxa to cause considerable collapse of the SCT structure. We chose not to undertake a rigorous analysis of this phenomenon, for example, by conducting a jackknife analysis with each of the taxa removed in turn, due to the extremely long computational time such a study would require. However, a rapid survey of the MPCs provided examples of taxa that were placed in markedly different positions. For example, in one subset of topologies, *Ae. (Ind.) pulverulentus* is the sister-group of all taxa except *Cs. (Cus.) inornata*. In an alternative subset of topologies, *Ae. (Ind.) pulverulentus* is placed towards the apex of a large clade of 50 taxa. Constructing the SCT of these two MPCs alone results in the collapse of at least 19 branches. It would not take many such widely divergently placed taxa to collapse the SCT completely. However, one of these conflicting patterns of relationship may be what is termed a 'secondary signal'. Secondary signals are those that are too weak to determine a MPC in each of two or more separate data sets (in the present case, adults and immature stages), but which emerge to dominate in a combined analysis. This occurs because when data sets are combined in a simultaneous analysis, signal is additive, whereas noise is averaged (Wenzel & Siddall, 1999). By measuring the strength of evidence supporting disparate results, simultaneous analysis allows a secondary signal to emerge (Nixon & Carpenter, 1996) and maximizes the power of the resulting phylogenetic hypothesis (Kluge & Wolf, 1993).

ANALYSIS OF TOTAL DATA SET

Analysis of the combined data set under EW produced 97 MPCs of 1836 steps (CI = 0.12, RI = 0.65), the SCT of which is shown in Figure 3. Combining

the adult and immature stages data results in fewer MPCs and a more resolved SCT than was found when either of the two data subsets was analysed separately. However, the recovered relationships are still unsatisfactory. *Mansonia titillans* is once again included in Aedini, this time as the unambiguous sister-group of *Psorophora* (although it is worth noting that this clade is present in the preferred hypothesis of generic relationships recovered by Harbach & Kitching, 1998). *Aedes* and *Ochlerotatus* are again paraphyletic, and *Op. fuscus* is now paired with *Oc. (Not.) chathamicus*, rather than with *Ae. (Ind.) pulverulentus* (Fig. 1). Improvements include the recovery of *Armigeres* as a monophyletic genus and *Ae. (Pseudarmigeres)* as a monophyletic subgenus. Otherwise the EW analysis of the combined data recovered most of the monophyletic groups found in the EW analysis of adult data.

However, equal weighting implies that all characters provide equally strong evidence of relationship, an assumption that would seem unwarranted in the current data, where the observed character consistency indices range from the remarkably low (CI = 0.03) to perfect fit (CI = 1.00). Some characters would appear to offer much better support than others. We considered that down-weighting the more homoplastic characters by the application of implied weighting (IW) was preferable, particularly as this method also always resulted in less ambiguous results (in terms of the number of MPCs found; see above). We therefore chose the results of the IW analysis of the combined data as the preferred hypotheses of relationships among the Aedini taxa.

Under IW, eight MPCs (Fit = 596.4) were found, the SCT of which (including Bremer (above) and relative Bremer supports (below) for each clade) is shown in Figure 4A, B. The conflict among the eight IW MPCs consists of three sets of two mutually exclusive topologies. These occur in all possible combinations, hence $2 \times 2 \times 2$ or eight MPCs. One of the patterns of relationship from each of the three sets is shown in Figure 5A–C, and the alternative topologies in Figure 6A–C, with the supporting, unambiguously optimized characters mapped on them.

The first pair of alternative topologies involves the relationships of *Oc. (Och.) communis*. It is placed either as the sister-group of a clade comprising *Oc. (Och.) infirmatus*, *Oc. (Och.) scapularis*, *Oc. (Och.) atlanticus* and *Oc. (Och.) fulvus pallens* (Fig. 5A), or a clade comprising *Oc. (Och.) sollicitans*, *Oc. (Och.) dorsalis*, *Oc. (Rus.) refiki* and *Oc. (Rus.) rusticus* (Fig. 6A). Character 149: 1 supports the former placement and character 99: 1 supports the latter. However, both characters are highly homoplastic: character 99 has 19 steps (CI = 0.05, RI = 0.57) in Figure 6A, and character 149 has 16 steps (CI = 0.12, RI = 0.63) in Figure 5A.

The second pair of alternative topologies disagree in the placement of the clade comprising the ten taxa *Oc. (Zavortinkius)*, *Oc. (Kenknightia)*, *Oc. (Bruceharrisonius)* and *Psorophora*. In one subset of topologies (Fig. 6A), this clade is the sister-group of another large clade comprising *Oc. (Geoskusea)* to *Oc. (Rusticoidus)*. In the other subset, these two clades form a paraphyletic group, with the *Oc. (Zavortinkius)* + *Oc. (Kenknightia)* + *Oc. (Bruceharrisonius)* + *Psorophora* clade placed as the sister-group of the remaining Aedini (Fig. 5A). Characters 85: 0 and 87: 2 support the former topology, and character 10: 1 supports the latter topology. Again, all three characters are highly homoplastic. Character 10 has 21 steps (CI = 0.04, RI = 0.63) in Figure 5A, whereas characters 85 and 87 have 32 steps (CI = 0.06, RI = 0.51) and 24 steps (CI = 0.12, RI = 0.66), respectively, in Figure 6A.

In addition, each of these basal alternative topologies has an associated alternative distal topology with *Aedes*. When *Oc. (Zavortinkius)*, *Oc. (Kenknightia)*, *Oc. (Bruceharrisonius)* and *Psorophora* is the sister-group of the clade comprising *Oc. (Geoskusea)* to *Oc. (Rusticoidus)* (Fig. 6A), the small *Aedes* clade of *Ae. (Adm.) mediolineatus*, *Ae. (Ind.) pulverulentus* and *Ae. (Sku.) pempaensis* is placed as the sister-group of a clade comprising *Ae. (Paraedes)*, *Ae. (Aedes)* and *Verrallina*. When the two basal clades have a paraphyletic relationship (Fig. 5C), the clade of *Ae. (Paraedes)*, *Ae. (Aedes)* and *Verrallina* is the sister-group of a different *Aedes* clade, one comprising *Ae. (Adm.) domesticus*, *Ae. (Adm.) alboscutellatus*, *Ae. (Adm.) vexans vexans*, *Ae. (Neomelaniconion)* and *Ae. (Edwardsaedes)*.

Character 10: 1 supports the former relationship within *Aedes* and characters 85: 2 and 135: 0 support the latter. The reason why each of the distal topologies is intimately linked with a specific basal topology is due largely to how the changes within two characters, 10 and 85, are optimized across the cladograms. The basal pattern of relationships in Figure 5A is supported by character 10: 1 and the distal pattern by character 85: 2. In contrast, the basal pattern of relationships in Figure 6A is supported by character 85: 0 and the distal pattern by character 10: 1. It is this 'opposite' optimization, in which the character that supports the basal pattern of relationships in one subset of topologies supports the distal pattern in the other, that is responsible for both the ambiguity in the recovered patterns of relationship and the linkage between the basal and distal resolutions.

The third pair of alternative topologies concerns the ambiguous placements in the centre of the cladogram of *Oc. (Mac.) tremulus* and *Oc. (Cha.) watten-sis* with respect to a clade comprising *Oc. (Mol.)*

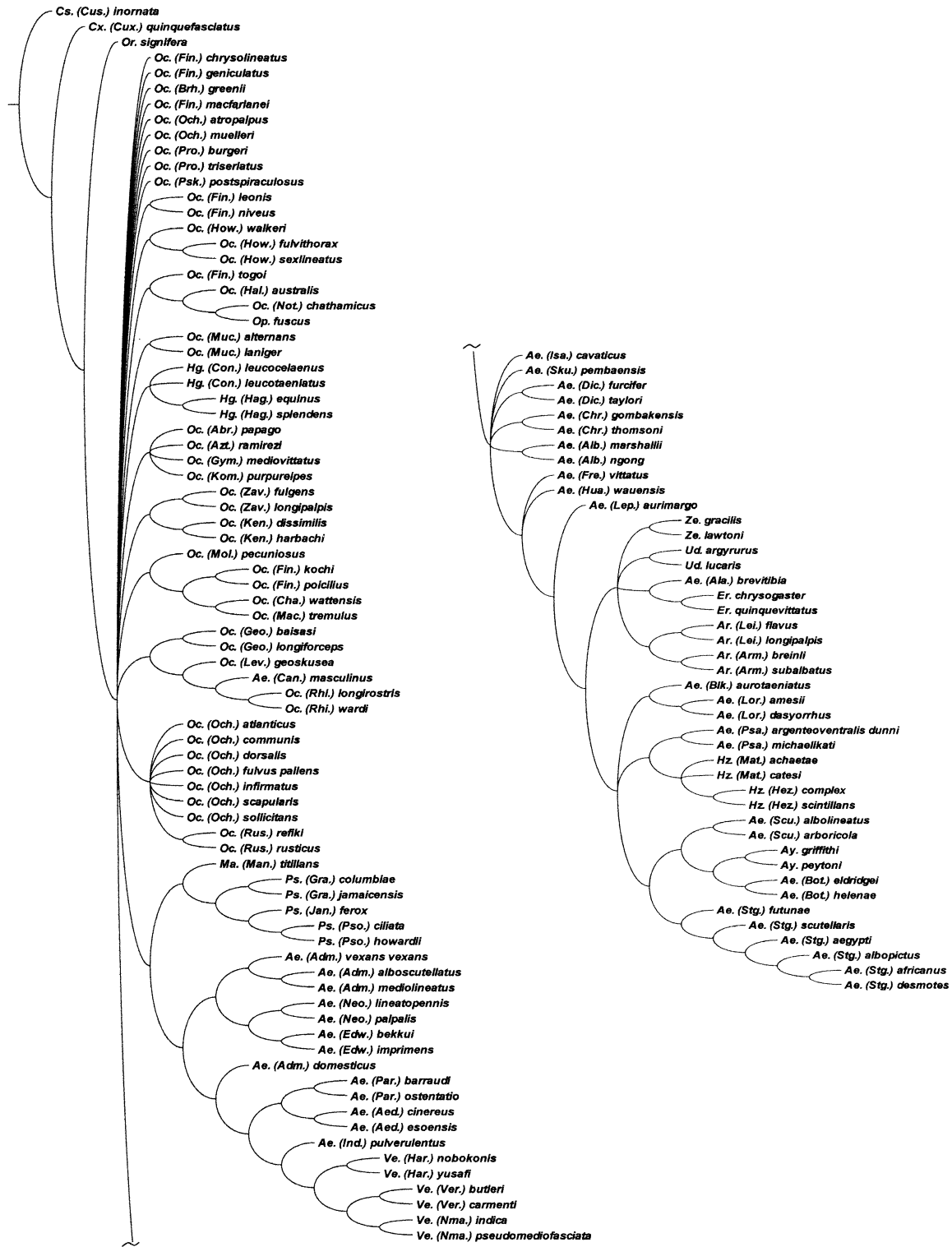


Figure 3. Strict consensus of 97 MPCs of 1836 steps (CI = 0.12, RI = 0.65) obtained from analysis of combined adult and immature stages data under equal weights.

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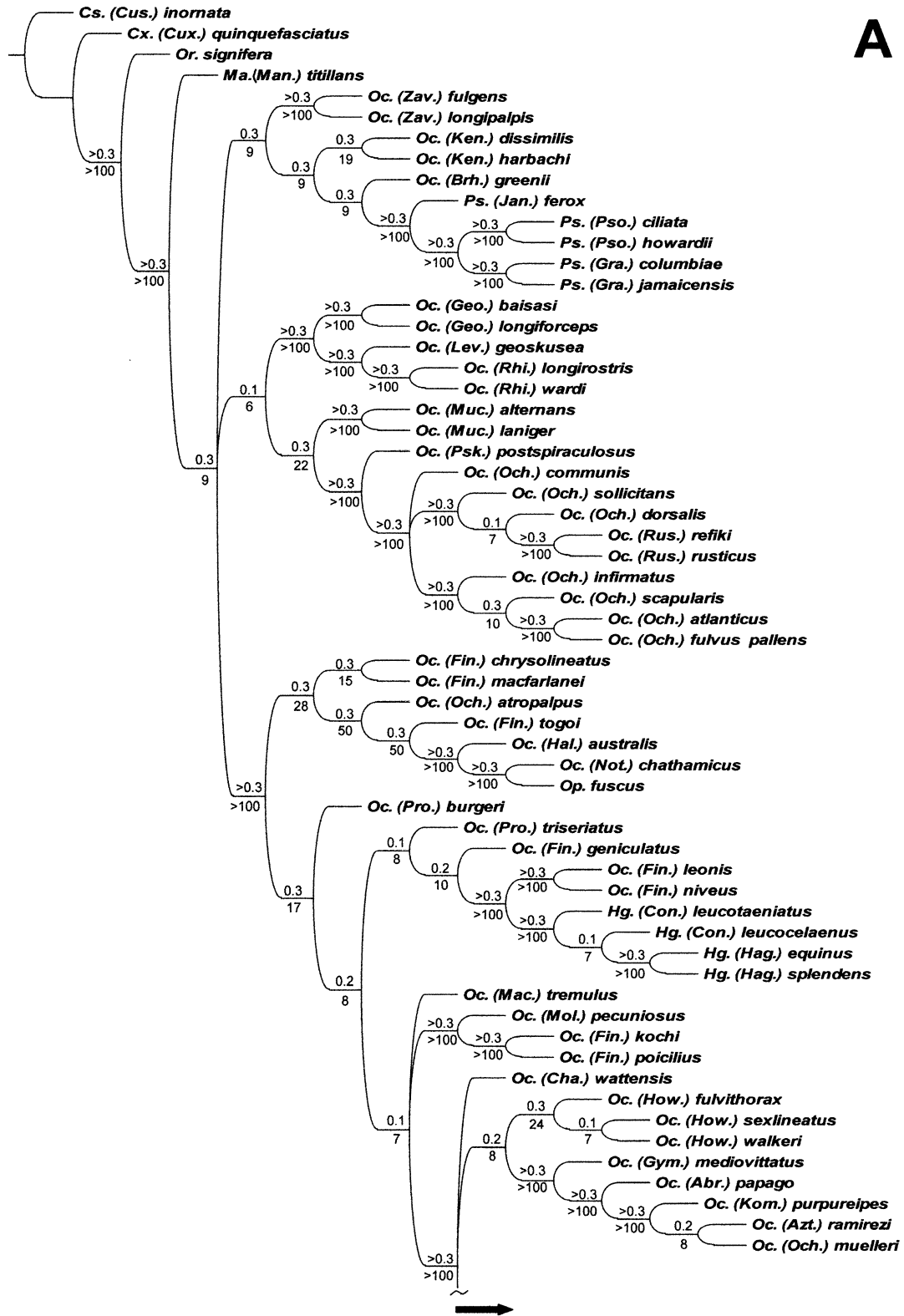


Figure 4. Strict consensus of eight MPCs (Fit = 596.4) obtained from the analysis of combined adult and immature stages data under implied weights. Bremer support and relative Bremer support values of each clade are indicated above and below the branches, respectively. The clade comprising *Ve. indica* and *Ve. pseudomediofaciata* has zero Bremer support and should have been shown as collapsed.

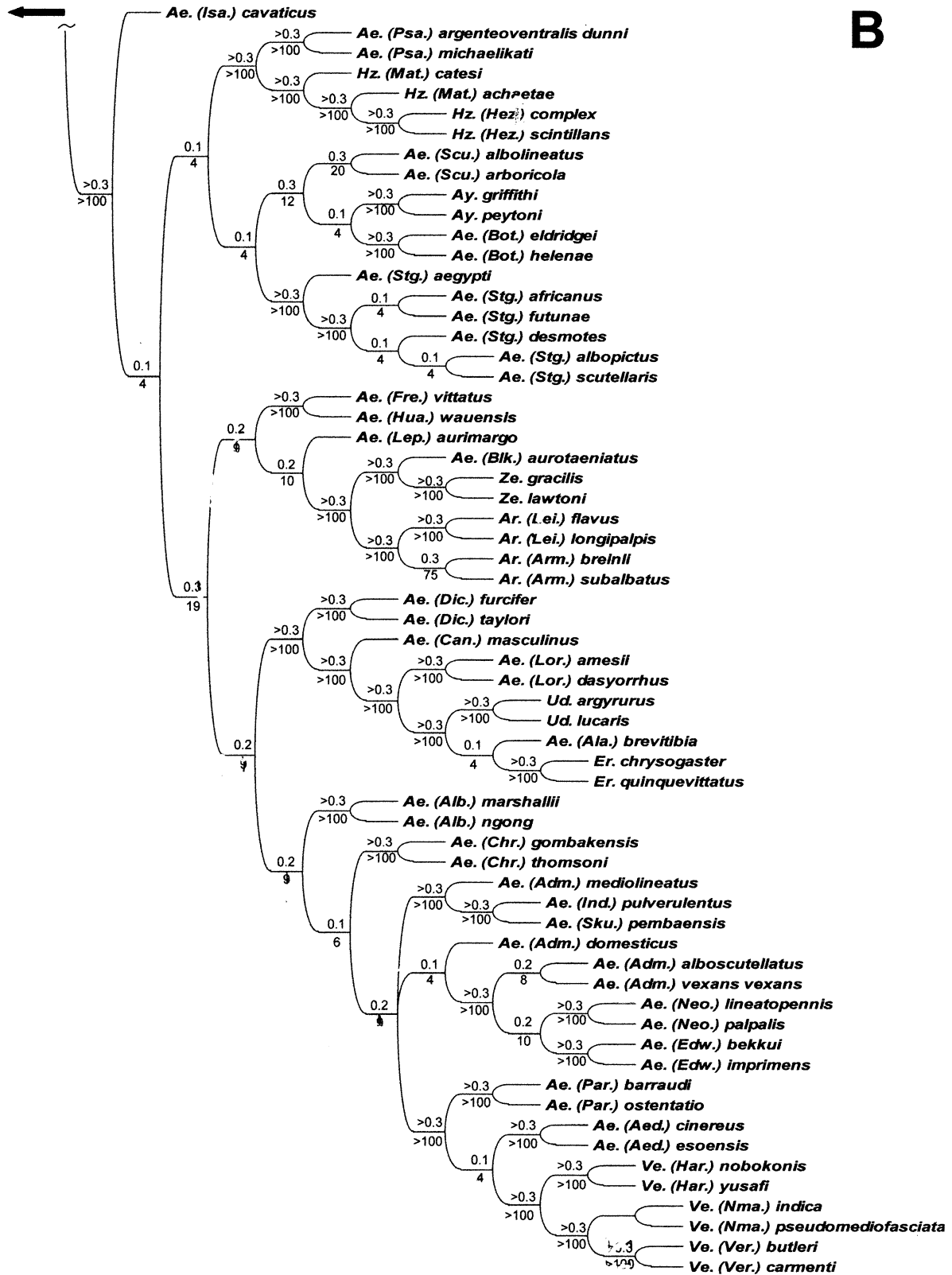


Figure 4. Continued

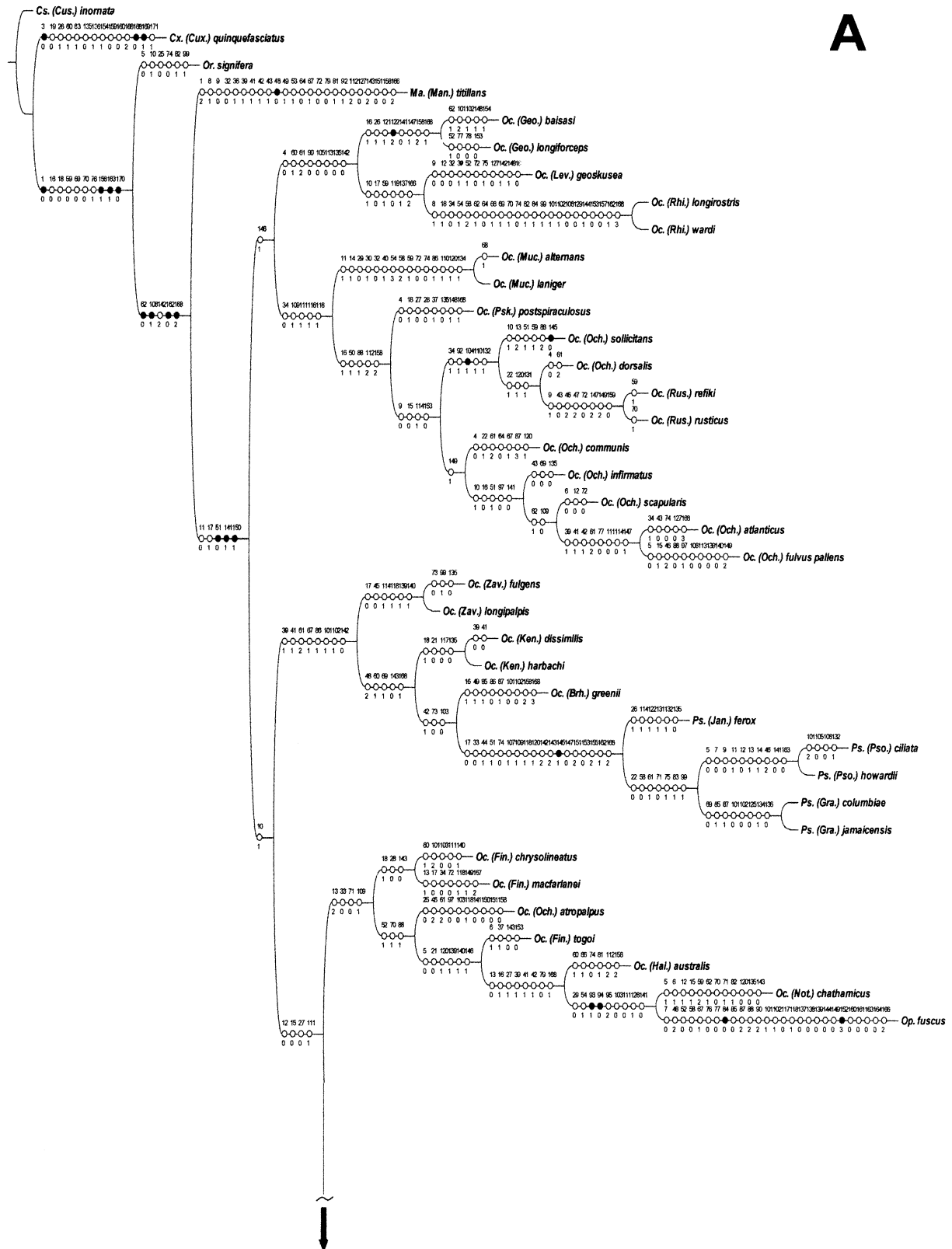


Figure 5. One of the eight MPCs obtained from analysis of the total data under implied weights. This cladogram includes one of each of the three sets of two conflicting topologies. The other three sets of conflicting topologies obtained in the analysis are shown in Figure 6. See text for details.

B

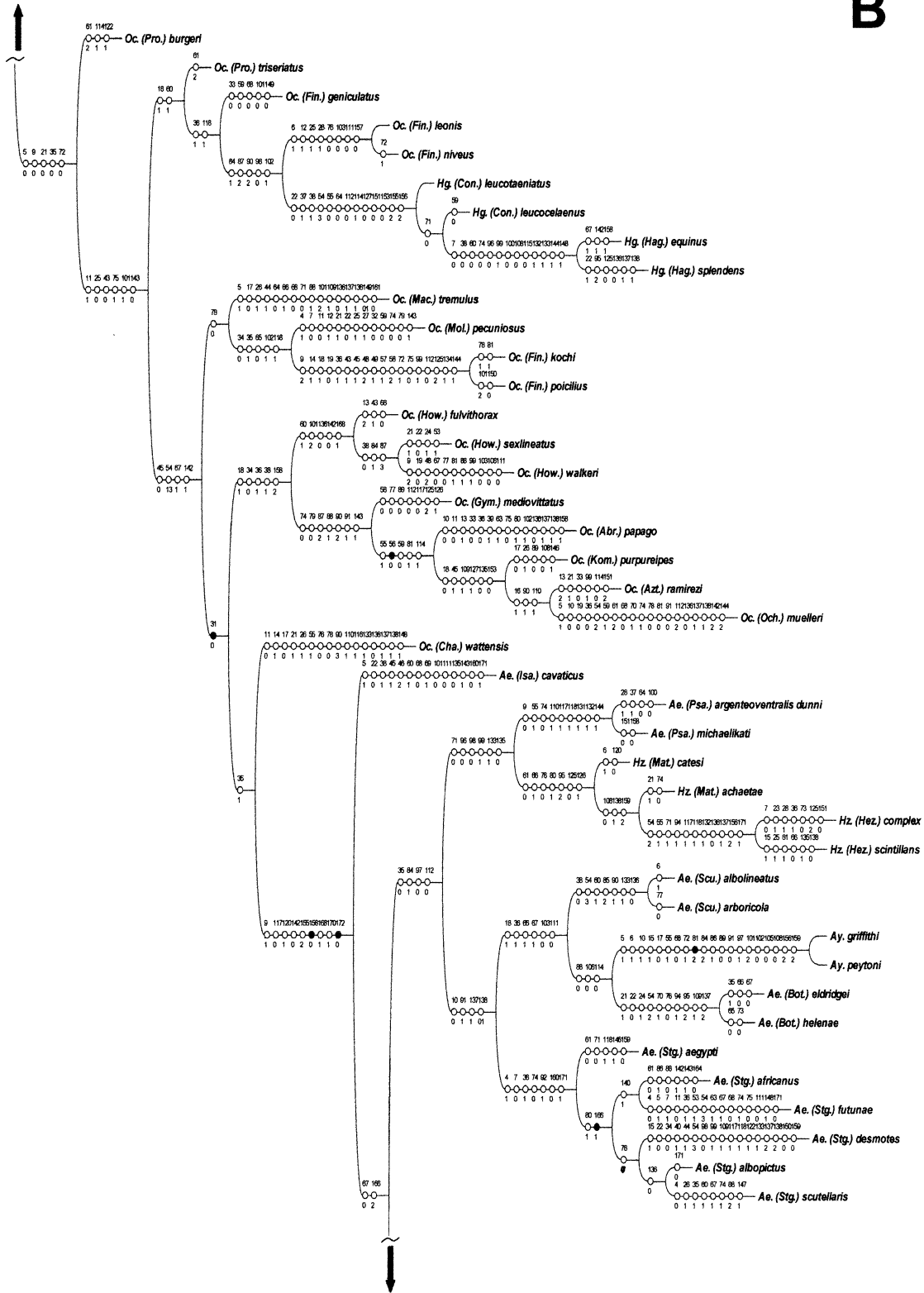


Figure 5. Continued

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C

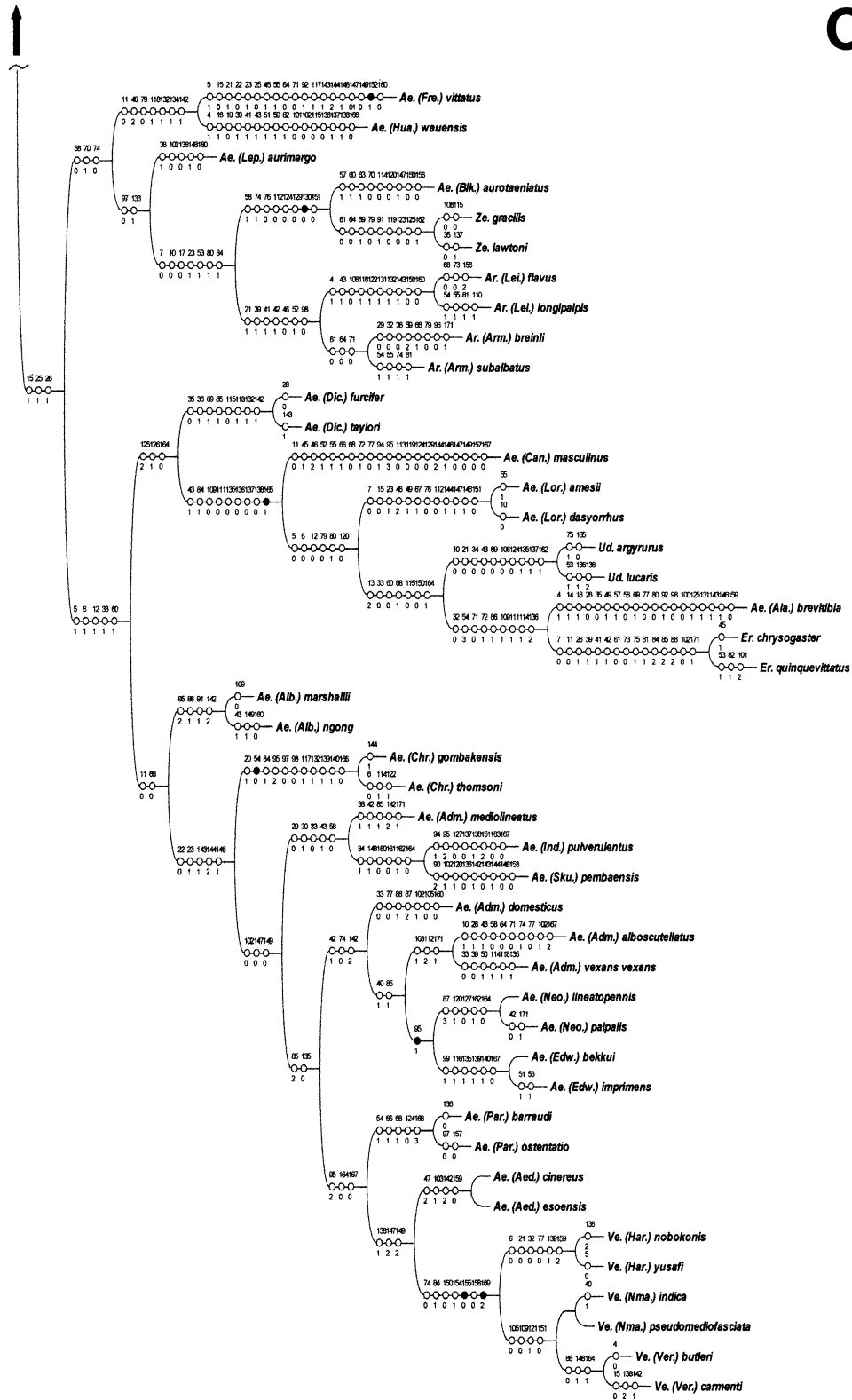


Figure 5. Continued

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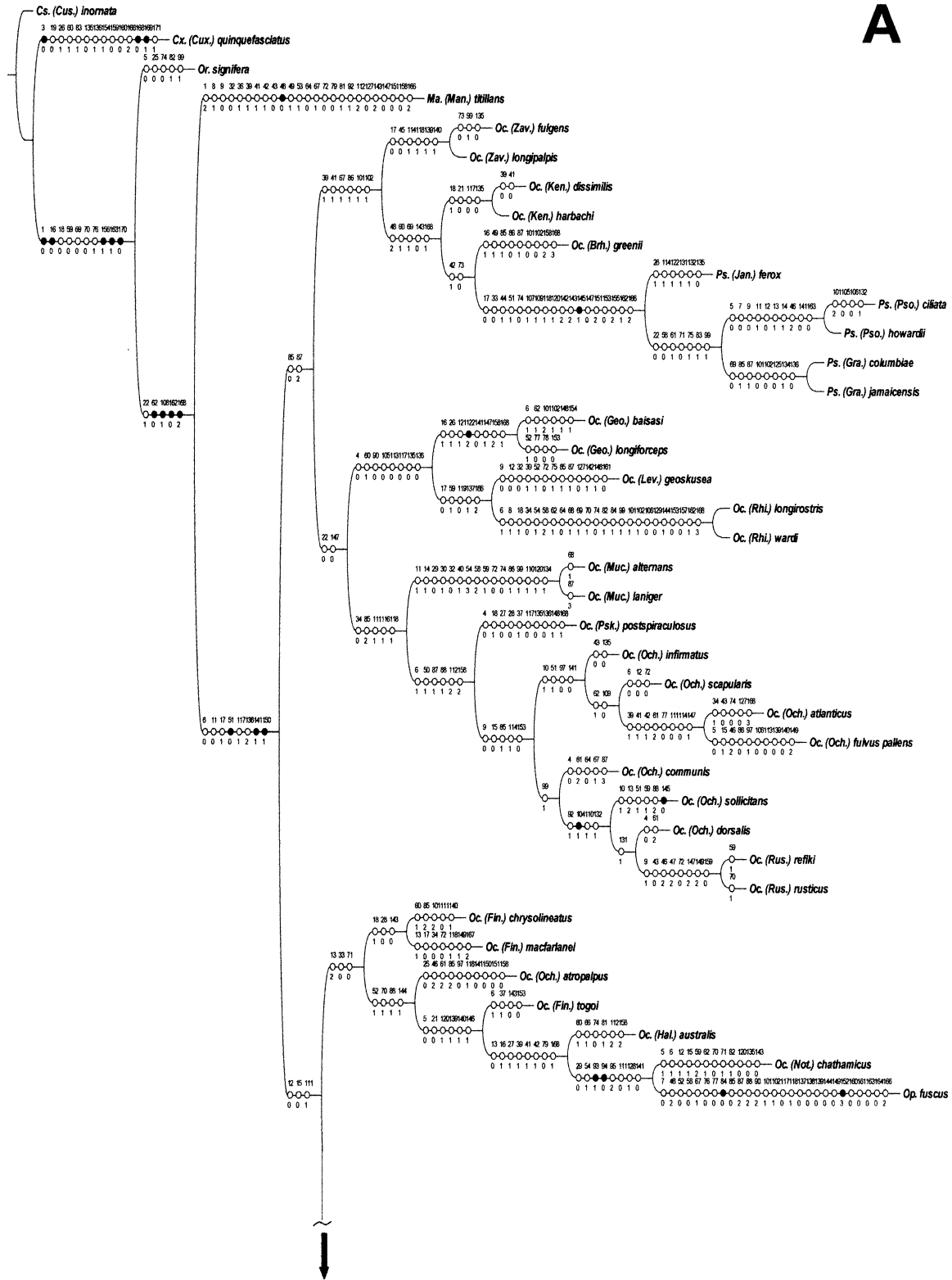


Figure 6. One of the eight MPCs obtained from analysis of the total data under implied weights. This cladogram includes the alternate topologies from each of three sets of two conflicting topologies. See Figure 5 for the other three sets of conflicting topologies and text for details.

B

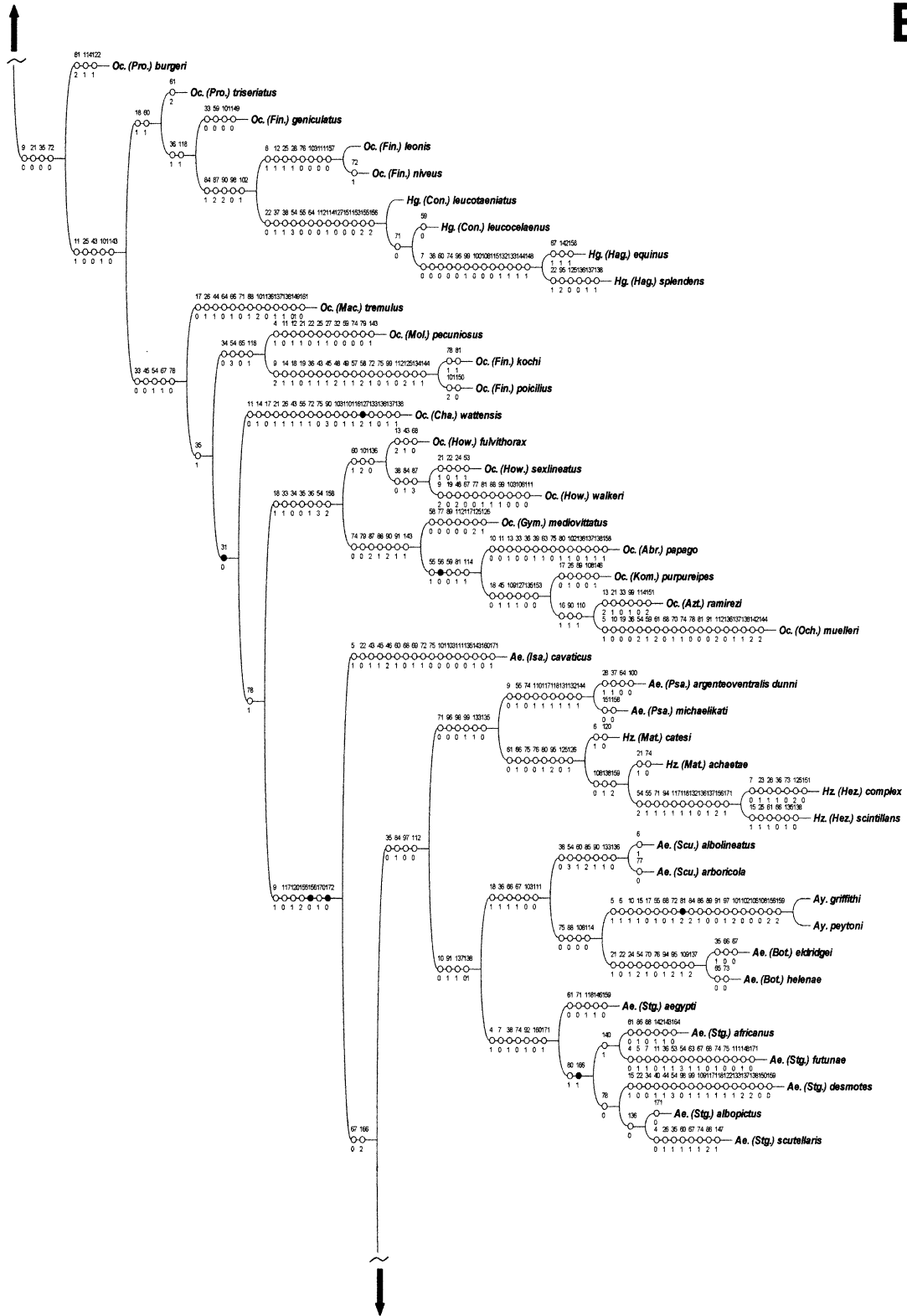


Figure 6. Continued

C

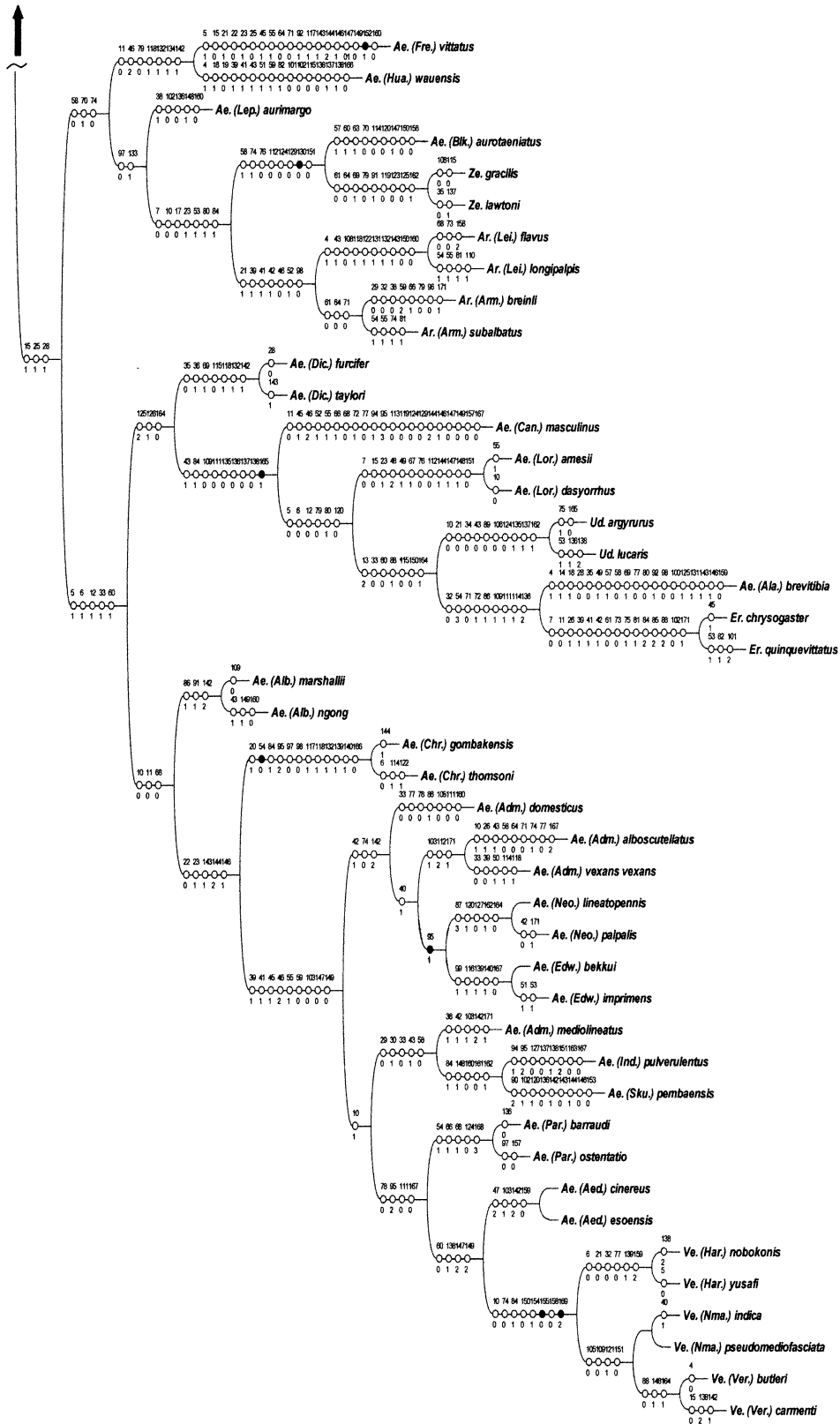


Figure 6. Continued

pecuniosus, *Oc. (Fin.) kochi* and *Oc. (Fin.) poicilius*, and another consisting of *Oc. (How.) fulvithorax* to *Oc. (Och.) muelleri*. In one subset of topologies (Fig. 5B), *Oc. (Mac.) tremulus* is the sister-group of the *Oc. (Mol.) pecuniosus* + *Oc. (Fin.) kochi* + *Oc. (Fin.) poicilius* clade, and *Oc. (Cha.) wattensis* is the most distal of the four groups. In the alternative subset of topologies (Fig. 6B), the four groups are paraphyletic, with *Oc. (Mac.) tremulus* most basal and the *Oc. (How.) fulvithorax* to *Oc. (Och.) muelleri* clade most distal. The conflict is due to different interpretations of transformation in characters 31, 35 and 78.

We carefully studied the different hypotheses of character transformation responsible for each of the alternative patterns of relationship in Figures 5 and 6, but we were unable to select, even subjectively, one of the eight MPCs as a preferred cladogram. All eight must therefore be treated as equally valid hypotheses of relationship at the present time.

Overall, the relationships within the SCT derived from the IW analysis of all data (Fig. 4) are an improvement over those found by equal weighting (Fig. 3). *Mansonia* is placed basal to a monophyletic Aedini and all existing genera except *Ochlerotatus* and *Aedes* are recovered as monophyletic. *Ochlerotatus* forms a polyphyletic assemblage basal to *Aedes*. This group (Fig. 4A) includes *Haemagogus* and *Psorophora*, and *Opifex* in a sister-group relationship with *Oc. (Not.) chathamicus*. *Aedes* (Fig. 4B) is polyphyletic relative to seven existing genera, *Armigeres*, *Ayurakitia*, *Eretmapodites*, *Heizmannia*, *Udaya*, *Verrallina* and *Zeugomyia*. It is worth noting that *Aedes* would be monophyletic if these seven genera were to be subsumed within it. With the exception of *Ae. (Aedimorphus)*, *Oc. (Finlaya)*, *Oc. (Ochlerotatus)* and *Oc. (Protomacleaya)*, all subgenera with two or more species included in the analysis were recovered as monophyletic.

CLASSIFICATION OF AEDINI

The existing classification of Aedini generally follows Edwards' (1932) concept of fewer genera but with numerous subgenera. Belkin (1962) stated 'I am in full agreement with the practice, following Edwards, of recognizing few genera and many subgenera, since this appears to reflect the evolution of the family'. However, Belkin stated (p. 318) that the internal classification of Aedini was in need of thorough revision. He further noted (p. 326) that many of the subgenera might have to be subdivided into smaller natural groups because they appeared to be

heterogeneous assemblages of superficially similar forms.

Despite 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). As Zavortink (1990) pointed out: 'At the beta level of taxonomy, ... the species are studied in greater detail and are 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 should be 225. Only 39 are currently recognized (Reinert, 2001a). Likewise, the number of aedine genera falls far short of the number expected for a tribe the size of Aedini. In proportion to the family (about 3200 species), the tribe (about 1200 species) should theoretically include 87 genera.

It is clear that the classification of Aedini is in need of revision and we consider that the results of the IW analysis of the combined adult and immature stages data would form the best present basis for doing so. However, we recognize that many of the included relationships are poorly supported (Fig. 4), with Bremer support values of only 0.1 or 0.2. The inclusion of new data or reinterpretations of our character coding could also markedly alter these groupings. A comparison with the results under EW (Fig. 3) shows also that many of the more inclusive groupings are dependent upon the weighting regime we employed and workers who reject differential weighting could feel justified in rejecting any resultant reclassification simply on that basis alone. We are therefore reluctant to make sweeping changes based on the patterns of relationship summarized in Figure 4.

However, we are equally reluctant to leave the generic classification of Aedini in its current parlous state, especially the two large and highly polyphyletic genera, *Aedes* and *Ochlerotatus*. Thus, we propose that a reasonable and conservative compromise would be to recognize as genera those groups that are 'weighting independent', i.e. those that are common to the results of both the EW (Fig. 3) and IW (Fig. 4) analyses. These groups are shown in Figure 7, which is the SCT formed from the 97 EW MPCs and eight IW MPCs.

There are 29 clades, each comprising between two and nine taxa. Another 30 taxa (including *Mansonia*) fall into a basal unresolved polytomy. Nine of these are monobasic subgenera of *Aedes* and *Ochlerotatus*: *Ae. (Belkinius)*, *Ae. (Fredwardsius)*,

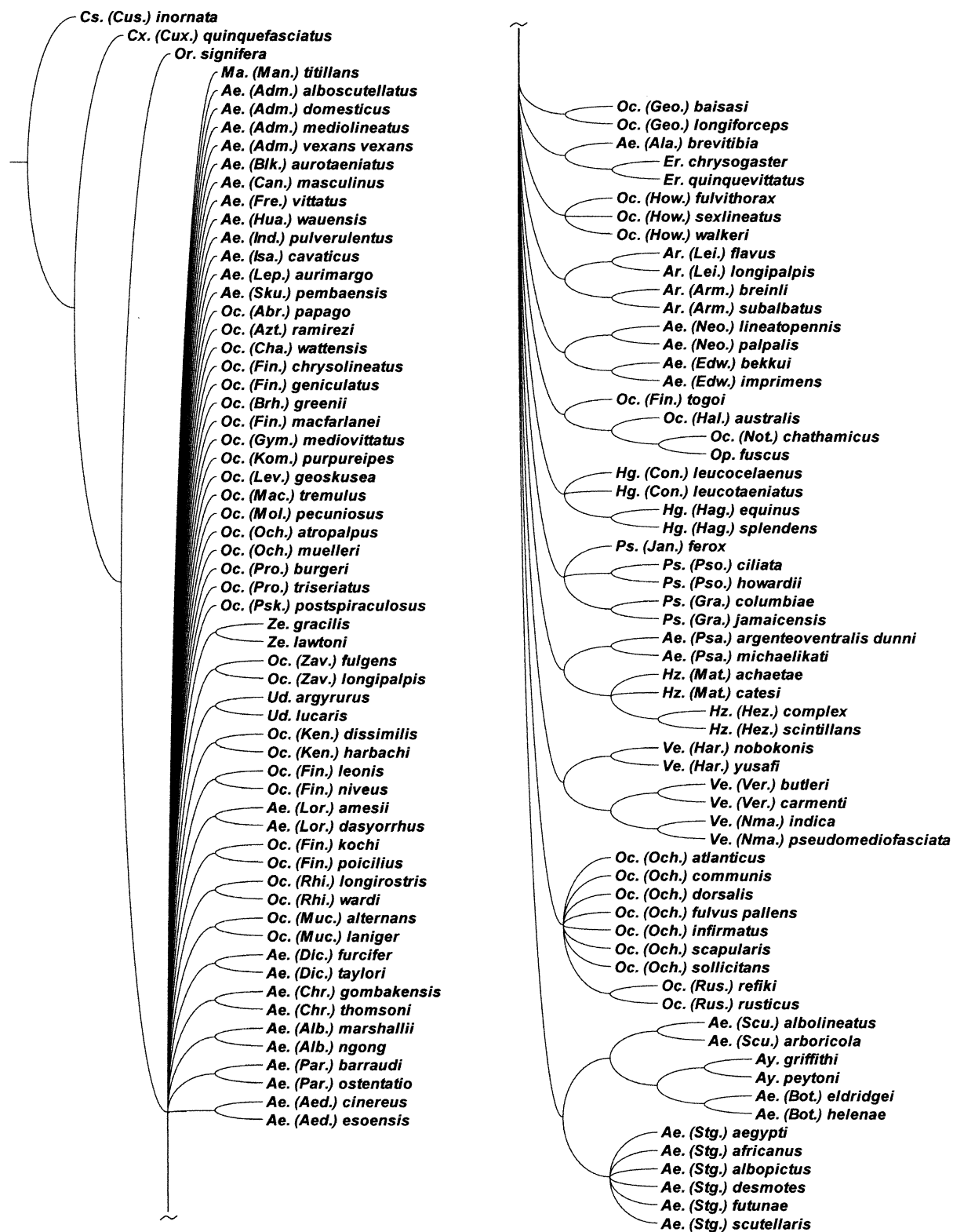


Figure 7. Strict consensus of the 97 MPCs obtained under equal weights and the eight MPCs obtained under implied weights based on analysis of the combined data. The monophyletic groups that survive this process are those that are weighting independent.

Ae. (Indusius), *Ae. (Isoaedes)*, *Ae. (Leptosomatomyia)*, *Oc. (Abraedes)*, *Oc. (Aztecaedes)*, *Oc. (Gymnometopa)* and *Oc. (Kompia)*. We propose to elevate all of these to genus level. In addition, we propose generic status for three small subgenera within the basal polytomy, i.e. *Ae. (Huaedes)* (three species), *Ae. (Skusea)* (four species) and *Oc. (Levua)* (three species), that we regard as monophyletic groups. *Gymnometopa*, *Kompia*, *Leptosomatomyia* and *Skusea* were originally recognized as genera and are thus restored to their original status. We treat the other 17 unresolved basal aedine taxa as *incertae sedis* (see Appendix 4). Further work is required to clarify their relationships and generic assignments. As two or more species of *Ae. (Aedimorphus)*, *Oc. (Finlaya)*, *Oc. (Ochlerotatus)* and *Oc. (Protomacleaya)* are arrayed as singleton taxa within this group, it is most unlikely that these subgenera will be shown to be monophyletic.

Most of the clades with two or more included taxa have IW Bremer support values of at least 0.3. The exceptions are *Eretmapodites* + *Ae. (Alanstonea)* (0.1), *Ae. (Neomelaniconion)* + *Ae. (Edwardsaedes)* (0.2) and *Ayurakitia* + *Ae. (Bothaella)* (0.1). Seven clades are existing genera (*Ayurakitia*, *Armigeres*, *Haemagogus*, *Psorophora*, *Udaya*, *Verrallina* and *Zeugomyia*) and retain that status. Fifteen are presently treated as subgenera of *Aedes* and *Ochlerotatus*: *Ae. (Aedes)*, *Ae. (Albuginosus)*, *Ae. (Bothaella)*, *Ae. (Christophersiomyia)*, *Ae. (Diceromyia)*, *Ae. (Lorrainea)*, *Ae. (Paraedes)*, *Ae. (Scutomyia)*, *Ae. (Stegomyia)*, *Oc. (Geoskusea)*, *Oc. (Howardina)*, *Oc. (Kenknightia)*, *Oc. (Mucidus)*, *Oc. (Rhinoskusea)* and *Oc. (Zavortinkius)*. We propose to raise all of these to genus level. Thus seven of these taxa, *Christophersiomyia*, *Diceromyia*, *Howardina*, *Mucidus*, *Paraedes*, *Scutomyia* and *Stegomyia*, are reinstated to their original status.

The remaining seven clades require additional consideration. *Ochlerotatus (Finlaya)* is divided into six lineages. We raise the clade consisting of *Oc. (Fin.) kochi*, *Oc. (Fin.) poicilius* and relatives (see Appendix 4) to generic rank as *Finlaya* (type species = *Culex kochi* Dönitz) and elevate *Downsiomyia* Vargas (type species = *Stegomyia nivea* Ludlow) from synonymy with *Finlaya* as the generic name for the clade comprising *Oc. (Fin.) leonis*, *Oc. (Fin.) niveus* and their relatives (see Appendix 4). Three of the remaining four species, *Oc. (Fin.) chrysolineatus*, *Oc. (Fin.) geniculatus* and *Oc. (Fin.) macfarlanei*, fall within the basal polytomy of 30 taxa and are treated as '*Ochlerotatus*' subgenus '*Finlaya*' *incertae sedis* (see Appendix 4). The status of the fourth species, *Oc. (Fin.) togoi*, is considered below.

The third clade comprises *Ae. (Alanstonea)* and *Eretmapodites*. There are two options available,

either raising *Ae. (Alanstonea)* to genus rank or treating it as a subgenus of *Eretmapodites*. We choose the first, because support for the *Ae. (Alanstonea)* + *Eretmapodites* clade is very weak (Bremer support = 0.1) and the supporting characters are all homoplastic. Further study may not corroborate a close relationship between these two taxa and so generic status for *Ae. (Alanstonea)* is the more conservative course.

Fourth is a clade consisting of two *Aedes* subgenera, *Ae. (Neomelaniconion)* + *Ae. (Edwardsaedes)*, the Bremer support for which, although not minimal, is still quite weak (0.2). We note that a unique character, 95: 1, does support this sister-group relationship (see Fig. 5C). However, it is part of a larger multi-state character, the other states of which are optimized another 14 times on the cladogram, giving character 95 a total length of 15 steps (CI = 0.20, RI = 0.63). Thus, support for the *Ae. (Neomelaniconion)* + *Ae. (Edwardsaedes)* clade is not as strong as it might first appear and we again opt for the conservative line, i.e. we propose generic status for these two taxa.

The pairing of *Heizmannia* and *Ae. (Pseudarmigeres)* (fifth clade) has slightly higher Bremer support (0.3) but the six supporting characters (Fig. 5) are all homoplastic. Therefore, we choose to treat *Ae. (Pseudarmigeres)* as a distinct genus rather than reducing it to subgeneric rank within *Heizmannia*.

Ochlerotatus (Ochlerotatus) (sixth clade) is divided into three lineages, two of which, *Oc. (Och.) atropalpus* and *Oc. (Och.) muelleri*, are part of the basal polytomy. The remaining seven taxa of *Oc. (Ochlerotatus)* analysed here, including the type species of *Ochlerotatus*, *Oc. confirmatus* Lynch Arribalzaga (currently treated as a synonym of *Oc. scapularis*) form a reasonably well-supported group (Bremer support = > 0.3), which can be regarded as *Ochlerotatus* s.s. However, nested within this group are the two species of *Oc. (Rusticoidus)*. The support for this subgenus as the sister-group of *Oc. (Och.) dorsalis* is minimal (Bremer support = 0.1) but that of the other branches within *Oc. (Ochlerotatus)* is much stronger (all 0.3 or higher) and the inclusion of *Oc. (Rusticoidus)* within this taxon appears reasonable. We therefore treat *Rusticoidus* as a subgenus within the restricted *Ochlerotatus*. The other species of *Ochlerotatus* s.s. are not assigned to subgenera as this is beyond the scope of the present study. Considerable work will be needed to resolve the relationships of these species in conjunction with those now treated as '*Ochlerotatus*' subgenus '*Ochlerotatus*' *incertae sedis* (see Appendix 4).

The final clade comprises *Oc. (Fin.) togoi*, *Oc. (Hal-aedes)*, *Oc. (Nothoskusea)* and *Opifex*. The support

for all three branches within this clade is quite good (Bremer support = 0.3 or higher) but most supporting characters are homoplastic. The notable exceptions are two features relating to the male antennae, 93:1 and 94:0. These characters are part of the support for the sister-group relationship between *Oc. (Nothoskusea)* and *Opifex*, and are unique to these two taxa. We consider this close relationship between *Oc. (Nothoskusea)* and *Opifex* to be sufficiently strong to justify the transfer of *Nothoskusea* to *Opifex* as a subgenus. In contrast, the characters supporting the relationships of *Opifex* with *Oc. (Halaedes)* and *Oc. (Fin.) togoi* are weaker and these taxa are better treated as separate genera. A new genus, *Tanakaius* gen. nov., is described in Appendix 3 to accommodate *Oc. (Fin.) togoi*, the monotypic member of the Togo Subgroup (subgroup VI) of *Finlaya* Group D (Knight & Marks, 1952), and *Oc. (Fin.) savoryi*. *Halaedes* (three species), *Nothoskusea* and *Opifex* (both monobasic) have distributions in the New Zealand Subregion of the Australasian Region. *Halaedes* also occur on the Australian continent. The distributional links between these three taxa, and especially between *Nothoskusea* and *Opifex*, provide additional evidence supporting a close relationship. The distribution of *Tanakaius* gen. nov. in the eastern Palaearctic is congruous with a more distant relationship.

A revised classification of Aedini based on the above proposals, which results in the formal recognition of 46 genera, is presented in Appendix 4. Those species not included in the analysis but whose classification is affected by the changes proposed here are also included. Proposed two-letter abbreviations for the genera recognized here, including applicable abbreviations recommended by Reinert (2001a), are listed in Appendix 5.

FINAL COMMENTS

This study is the first phylogenetic analysis of Aedini as a whole, and the results are the first to demonstrate, based on explicit methodology, which parts of the generic-group classification of the tribe are problematic. The lack of basal resolution and branch support in the cladograms makes it impossible to fully resolve the relationships among the genera, but it is obvious that the traditional generic classification was only partially based on natural relationships. Additional morphological data may provide a clearer view of the relationships between closely related genera, but are unlikely to resolve deeper relationships within the tribe. Nevertheless, the hypotheses of relationships emanating from the present analyses provide a framework for further investigation of basal divergence. Some potential phylogenetically informa-

tive characters may be derived from the morphology of larval mouthparts, the ontogeny of larval and pupal chaetotaxy, behavioural characteristics and DNA sequences. Evidence for resolving basal relationships will most likely come from molecular studies.

The classification of the tribe proposed above is significantly different from the traditional system within Culicidae of recognizing a few genera and numerous subgenera that was initiated by Edwards (1932). The formal recognition of 46 genera within Aedini will come as a shock to many nontaxonomists and taxonomists who are disturbed by changes to customary usage. However, these individuals should be aware that cladistics, unlike the intuitive methods of classification used in the past (i.e. methods based on overall phenetic similarity or difference with all characters equally weighted and without regard to phylogenetic history), is an explicit method of classification that employs hypotheses of character homology to group taxa hierarchically into nested sets. In the present study, as in all cladistic studies, the characters are explicitly defined, a data matrix included, analytical methods specified and the analyses repeatable. Finally, we stress that our study removes the evidently paraphyletic 'large' genera, with a necessary fragmentation of traditional taxa and a subjective decision that the fragments be treated as genera rather than subgenera under a different arrangement of larger units, and emphasize that this is merely the first step toward achieving a natural classification of Aedini.

We believe that a stable classification based on natural relationships will lead to a more effective means of identification and provide an evolutionary framework for biological studies. The next step will be to resolve the relationships and placement of taxa of uncertain taxonomic position to achieve a more robust classification, and provide up-to-date diagnoses and keys for the identification of generic-level taxa and the species they encompass.

ACKNOWLEDGEMENTS

We thank Bruce A. Harrison (Public Health Pest Management, North Carolina Department of Environment and Natural Resources, Winston-Salem, NC), Christopher J. Humphries (Department of Botany, The Natural History Museum, London), and Richard C. Wilkerson (Walter Reed Biosystematics Unit (WRBU), Smithsonian Institution, Washington, DC), for critically reviewing the manuscript and providing valuable comments. This paper was also improved as a result of comments by Thomas J. Zavortink (Bohart Museum (BM), Department of Entomology, University of California, Davis (CA)). Thanks also to Desmond H.

Foley and Greg Daniels (University of Queensland Insect Collection, Department of Zoology and Entomology, University of Queensland, Brisbane, Australia), Thomas V. Gaffigan and Richard C. Wilkerson (WRBU), Theresa M. Howard (The Natural History Museum, London), Francis Schaffner (Laboratoire/Cellule Entomologie, EID Mediterranee, Montpellier, France), Gary J. Steck (Florida State Collection of Arthropods, Division of Plant Industry, Gainesville, Florida) and Thomas J. Zavortink (BM) for the loan of specimens. Appreciation is expressed to Donald R. Barnard and Robert Vander Meer (CMAVE) for providing research facilities to JFR and to Richard C. Wilkerson for funding a trip for JFR to examine specimens at the U.S. National Museum of Natural History. Special thanks to Theresa M. Howard for providing numerous dissections of male heads and preparing the cladograms.

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APPENDIX 1

List of species examined in detail during the comparative morphological analysis. An asterisk following a species-author combination denotes a type species of a generic-level taxon. Distribution of species is indicated by region: 1, Nearctic; 2, Palearctic; 3, Afrotropical; 4, Oriental; 5, Australasian; 6, Neotropical. An asterisk following a geographic region indicates a relatively recent introduction.

Genus	Subgenus	Species	Distribution
<i>Aedes</i>	<i>Aedes</i> Meigen	<i>cinereus</i> Meigen*	1,2
		<i>esoensis</i> Yamada	2
	<i>Aedimorphus</i> Theobald	<i>alboscuteallatus</i> (Theobald)	2,4,5
		<i>domesticus</i> (Theobald)*	3
		<i>mediolineatus</i> (Theobald)	4
		<i>vexans vexans</i> (Meigen)	1,2,3,4,5
		<i>brevitibia</i> (Edwards)	4
	<i>Alanstonea</i> Mattingly	<i>marshallii</i> (Theobald)*	3
	<i>Albuginosus</i> Reinert	<i>ngong</i> (van Someren)	3
	<i>Belkinius</i> Reinert	<i>aurotaeniatus</i> Edwards*	4
	<i>Bothaella</i> Reinert	<i>eldridgei</i> Reinert	4
		<i>helenae</i> Reinert*	4
	<i>Canraedes</i> Edwards	<i>masculus</i> Mattingly	4
	<i>Christophersiomyia</i> Barraud	<i>gombakensis</i> Mattingly	4
		<i>thomsoni</i> (Theobald)*	4
	<i>Diceromyia</i> Theobald	<i>furcifer</i> (Edwards)*	3
		<i>taylori</i> Edwards	3
	<i>Edwardsaedes</i> Belkin	<i>bekkui</i> Magi	2
		<i>imprimens</i> (Walker)*	2,4,5
	<i>Fredwardsius</i> Reinert	<i>vittatus</i> (Bigot)*	2,3,4
	<i>Huaedes</i> Huang	<i>wauensis</i> Huang*	5
	<i>Indusius</i> Edwards	<i>pulverulentus</i> Edwards*	4
	<i>Isoaedes</i> Reinert	<i>cavaticus</i> Reinert*	4
	<i>Leptosomatomyia</i> Theobald	<i>aurimargo</i> Edwards*	5
	<i>Lorrainea</i> Belkin	<i>amesii</i> (Ludlow)	4
		<i>dasyorrhhus</i> King & Hoogstraal*	5
	<i>Neomelaniconion</i> Newstead	<i>lineatopennis</i> (Ludlow)	4,5
	<i>palpalis</i> (Newstead)*	3	
<i>Paraedes</i> Edwards	<i>barraudi</i> (Edwards)*	4	
	<i>ostentatio</i> (Leicester)	4	

APPENDIX 1 *Continued*

Genus	Subgenus	Species	Distribution
	<i>Pseudarmigeres</i> Stone & Knight	<i>argenteoventralis dunnii</i> (Evans)*	3
		<i>michaelikati</i> van Someren	3
	<i>Scutomyia</i> Theobald	<i>albolineatus</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*,5*,6*
		<i>africanus</i> (Theobald)	3
		<i>albopictus</i> (Skuse)	1*,2,3*,4,5,6*
		<i>desmotes</i> (Giles)	4
		<i>futunae</i> Belkin	5
		<i>scutellaris</i> (Walker)	5
<i>Armigeres</i>	<i>Armigeres</i> Theobald	<i>breinli</i> (Taylor)	5
		<i>subalbatus</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>Eretmapodites</i> Theobald		<i>chrysogaster</i> Graham	3
		<i>quinquevittatus</i> Theobald*	3
<i>Haemagogus</i>	<i>Conopostegus</i> Dyar	<i>leucocelaenus</i> (Dyar & Shannon)*	6
		<i>leucotaeniatus</i> (Komp)	6
	<i>Haemagogus</i> Williston	<i>equinus</i> Theobald	6
		<i>splendens</i> Williston*	6
<i>Heizmannia</i>	<i>Heizmannia</i> Ludlow	<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>Ochlerotatus</i>	<i>Abraedes</i> Zavortink	<i>papago</i> (Zavortink)*	1
	<i>Aztecaedes</i> Zavortink	<i>ramirezi</i> (Vargas & Downs)*	1
	<i>Bruceharrisonius</i> Reinert	<i>greenii</i> (Theobald)*	4
	<i>Chaetocruiomia</i> Theobald	<i>wattensis</i> (Taylor)	5
	<i>Finlaya</i> Theobald	<i>chrysolineatus</i> (Theobald)	4
		<i>geniculatus</i> (Olivier)	2
		<i>kochi</i> (Dönitz)*	5
		<i>leonis</i> (Colless)	4
		<i>macfarlanei</i> Edwards	4
		<i>niveus</i> (Ludlow)	4
		<i>poicilius</i> (Theobald)	4,5
		<i>togoi</i> (Theobald)	1*,2,4
	<i>Geoskusea</i> Edwards	<i>baisasi</i> (Knight & Hull)	4
		<i>longiforceps</i> (Edwards)	5
	<i>Gymnometopa</i> Coquillett	<i>mediovittatus</i> (Coquillett)*	6
	<i>Halaedes</i> Belkin	<i>australis</i> (Erichson)*	5
	<i>Howardina</i> Theobald	<i>fulvithorax</i> (Lutz)	6
		<i>sexlineatus</i> (Theobald)	6
		<i>walkeri</i> (Theobald)*	6
	<i>Kenknightia</i> Reinert	<i>dissimilis</i> (Leicester)*	4
		<i>harbachi</i> (Reinert)	4
	<i>Kompia</i> Aitken	<i>purpureipes</i> (Aitken)*	1
	<i>Levua</i> Stone & Bohart	<i>geoskusea</i> (Amos)*	5
	<i>Macleaya</i> Theobald	<i>tremulus</i> (Theobald)*	5
	<i>Molpemyia</i> Theobald	<i>pecuniosus</i> (Edwards)	5
	<i>Mucidus</i> Theobald	<i>alternans</i> (Westwood)*	5
		<i>laniger</i> (Wiedemann)	4

APPENDIX 1 *Continued*

Genus	Subgenus	Species	Distribution
	<i>Nothoskusea</i> Dumbleton	<i>chathamicus</i> (Dumbleton)*	5
	<i>Ochlerotatus</i> Lynch Arribalzaga	<i>atlanticus</i> (Dyar & Knab)	1
		<i>atropalpus</i> (Coquillett)	1,2*
		<i>communis</i> (de Geer)	1,2
		<i>dorsalis</i> (Meigen)	1,2,4
		<i>fulvus pallens</i> Ross	1,6
		<i>infirmatus</i> Dyar & Knab	1
		<i>muelleri</i> (Dyar)	1
		<i>scapularis</i> (Rondani)*	1,6
		<i>sollicitans</i> (Walker)	1,6
	<i>Protomacleaya</i> Theobald	<i>burgeri</i> (Zavortink)	1
		<i>triseriatus</i> (Say)*	1
	<i>Pseudoskusea</i> Theobald	<i>postspiraculosus</i> (Dobrotworsky)	5
	<i>Rhinoskusea</i> Edwards	<i>longirostris</i> (Leicester)*	4,5
		<i>wardi</i> (Reinert)	4
	<i>Rusticoidus</i> Shevchenko & Prudkina	<i>refiki</i> (Medschid)*	2
		<i>rusticus</i> (Rossi)	2
	<i>Zavortinkius</i> Reinert	<i>fulgens</i> Edwards	3
		<i>longipalpis</i> (Grünberg)*	3
<i>Opifex</i> Hutton		<i>fuscus</i> Hutton*	5
<i>Psorophora</i>	<i>Grabhamia</i> Theobald	<i>columbiae</i> (Dyar & Knab)	1,6
		<i>jamaicensis</i> (Theobald)*	6
	<i>Janthinosoma</i> Lynch Arribalzaga	<i>ferox</i> (von Humboldt)	1,6
	<i>Psorophora</i> Robineau-Desvoidy	<i>ciliata</i> (Fabricius)*	1,6
		<i>howardii</i> Coquillett	1,6
<i>Udaya</i> Thurman		<i>argyrurus</i> (Edwards)*	4
		<i>lucaris</i> Macdonald & Mattingly	4
<i>Verrallina</i>	<i>Harbachius</i> Reinert	<i>nobokonis</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> Theobald	<i>butleri</i> (Theobald)*	4,5
		<i>carmeni</i> (Edwards)	5
<i>Zeugomyia</i> Leicester		<i>gracilis</i> Leicester*	4
		<i>lawtoni</i> Baisas	4
OUTGROUP TAXA			
<i>Culex</i>	<i>Culex</i> Linnaeus	<i>quinquefasciatus</i> Say	1*,2*,3,4*,5*,6*
<i>Culiseta</i>	<i>Culiseta</i> Felt	<i>inornata</i> (Williston)	1
<i>Mansonia</i>	<i>Mansonia</i> Blanchard	<i>titillans</i> (Walker)*	1,6
<i>Orthopodomyia</i> Theobald		<i>signifera</i> (Coquillett)	1,6

	1	1	1	1	1	1	1	1	1	1	1	1
	6	6	6	6	6	6	6	6	6	7	7	7
	1	2	3	4	5	6	7	8	9	0	1	2
<i>Oc. (Zav.) fulgens</i>	1	0	1	1	0	0	1	2	0	0	0	1
<i>Oc. (Zav.) longipalpis</i>	1	0	1	1	0	0	1	2	0	0	0	1
<i>Op. fuscus</i>	0	0	0	0	0	2	1	1	0	0	0	1
<i>Ps. (Gra.) columbiae</i>	1	1	1	1	0	2	1	1	0	0	0	1
<i>Ps. (Gra.) jamaicensis</i>	1	1	1	1	0	2	1	1	0	0	0	1
<i>Ps. (Jan.) ferox</i>	1	1	1	1	0	2	1	1	0	0	0	1
<i>Ps. (Pso.) ciliata</i>	1	1	0	1	0	2	1	1	0	0	0	1
<i>Ps. (Pso.) howardii</i>	1	1	0	1	0	2	1	1	0	0	0	1
<i>Ud. argyrurus</i>	1	1	1	1	0	2	1	1	0	1	0	0
<i>Ud. lucaris</i>	1	1	1	1	1	2	1	1	0	1	0	0
<i>Ve. (Har.) nobokonis</i>	1	1	1	0	0	2	0	1	2	1	1	0
<i>Ve. (Har.) yusafi</i>	1	1	1	0	0	2	0	1	2	1	1	0
<i>Ve. (Nma.) indica</i>	1	1	1	0	0	2	0	1	2	1	1	0
<i>Ve. (Nma.) pseudomediofasciata</i>	1	1	1	0	0	2	0	1	2	1	1	0
<i>Ve. (Ver.) butleri</i>	1	0	1	1	0	2	0	1	2	1	0	0
<i>Ve. (Ver.) carmenti</i>	1	0	1	1	0	2	0	1	2	1	0	0
<i>Ze. gracilis</i>	1	1	1	1	0	2	0	1	0	1	0	0
<i>Ze. lawtoni</i>	1	1	1	1	0	2	1	1	0	1	0	0

APPENDIX 3: DESCRIPTION OF TANAKAIUS GEN. NOV.

TANAKAIUS REINERT, HARBACH & KITCHING, GEN. NOV.

Type species: *Culicelsa togoi* Theobald, 1907

Females

Head. Antenna 0.57–0.67 × length of proboscis, pedicel with numerous moderate-sized partially overlapping scales and few short setae on mesal surface; maxillary palpus 0.20–0.27 × length of proboscis, with four palpomeres; proboscis 1.05–1.28 × length of forefemur, dark-scaled; vertex with narrow decumbent scales, dark ones posterior to eyes, pale ones on median and posterior areas; occiput with numerous long erect forked scales extending cephalad over most of vertex; eyes narrowly separated above antennal pedicels; ocular line narrow, with narrow pale scales; ocular setae numerous; interocular space small, with narrow pale scales and 2–4 setae; clypeus bare.

Thorax. Scutum covered with narrow curved scales except bare median prescutellar space and narrow area between lateral prescutellar area and posterior supraalar area, scales brown except for pale ones forming stripe on acrostichal area to prescutellar area, where it splits and extends along mesal margins of prescutellar setae, stripe on dorsocen-

tral area to near prescutellar area, line on anterior margin of scutal fossal area, line on posterior margin of scutal fossal area and extending caudad on mesal part of supraalar area, and stripe laterally on antealar and supraalar areas, patches of pale scales on anterior promontory and antedorsocentral areas. Setae on following areas: anterior promontory, acrostichal (anterior and posterior), antedorsocentral, dorsocentral (anterior and posterior), scutal fossal, antealar, supraalar, prescutellar and parascutellar; scutellum with narrow curved pale scales on all lobes, several dark brown setae on each lobe; mesopostnotum bare; antepnота widely separated, with numerous broad pale scales and numerous setae; postpronotum covered with broad pale and dark scales, with posterior setae; prespiracular area bare; postspiracular area with broad pale scales, setae present; subspiracular area with elongate patch of broad pale scales; paratergite with broad pale scales; upper proepisternum with patch of broad pale scales, 5–12 setae, lower area bare; mesokatepisternum with upper and lower patches of broad pale scales, few upper and numerous posterior setae; prealar knob with numerous setae, lower area with patch of broad pale scales; mesepimeron with large patch of broad pale scales on upper and median areas, numerous upper posterior setae, lower anterior setae present or absent; mesomeron bare, with dorsal margin well above hindcoxa; metameron bare.

Legs. Ante- and postprocoxal membranes bare; coxae with broad scales, with several setae; femora dark-scaled with apex pale-scaled, also with incomplete, variously developed, pale-scaled stripe on anterior and posterior surfaces; tibiae dark-scaled, with few pale scales or band apically; tarsi dark-scaled or with narrow to moderate-sized pale-scaled bands basally on some tarsomeres and narrow pale-scaled bands apically on some tarsomeres; tarsi each with two ungues, equal in size, toothed.

Wing. Veins dark-scaled on dorsal and ventral surfaces except costa with narrow pale-scaled antero-basal area; remigial setae absent; vein R₂ longer than R₂₊₃; alula with row of narrow dark scales on posterior margin; upper calypter with row of numerous setae on posterior margin; halter with pedicel pale, capitellum with pale and few dark scales.

Abdomen. Terga dark-scaled, tergum I with laterotergite pale-scaled, terga II–VII with pale-scaled, basolateral patches, numerous short setae along posterior and lateral margins; sterna dark-scaled with basolateral white-scaled patches often connected basomesally; segments VII and VIII laterally compressed.

Genitalia. Tergum VIII moderately pigmented, covered with minute spicules, numerous short and few moderately long setae on distal 0.69–0.75, numerous spatulate scales on distal 0.44–0.65 (in *Ta. togoi*) or small patch on each side of midline, total of approximately 14–16 scales (in *Ta. savoryi*), apex gently convex with several short curved and five or six moderately long and long stout straight setae, basal margin wider and gently concave, basolateral seta minute, VIII-Te index 0.57–0.74, VIII-Te/IX-Te index 2.47–2.91, length 0.30–0.34 mm, width 0.43–0.53 mm; sternum VIII moderately pigmented, covered with minute spicules, with numerous curved short setae on distal 0.87–0.94. Several moderately long to long setae primarily on mesal area, patch of spatulate scales on each side (very large in *Ta. togoi* and small in *Ta. savoryi*) on distal 0.65–0.79; apical margin with very shallow median emargination, with numerous short curved setae and three short straight setae on each side of midline, basal margin gently concave, basolateral seta absent, VIII-S index 0.70–0.75, length 0.40–0.43 mm, width 0.54–0.61 mm; tergum IX moderately pigmented, covered with minute spicules, those on basolateral area longer, comprising single moderately long and moderately wide plate with apical margin V-shaped, 9–17 short setae distally on each side of midline, 19–30 total setae, basal margin gently concave, IX-Te index 0.68–0.91, length 0.11–0.13 mm, width 0.14–0.18 mm; insula moderately pigmented, covered with minute spicules, liplike, four or five moderately long setae laterally on each side, eight or nine total setae; lower vaginal lip moderately pigmented, narrow, covered with minute spicules, lower vaginal sclerite absent; upper vaginal lip heavily pigmented, covered with minute spicules, narrow with posterior margin broadly rounded, upper vaginal sclerite absent, spermathecal eminence membranous, ill-defined, somewhat broadly ovoid; postgenital lobe moderately pigmented, covered with short spicules, those on distal half of lateral margins longer, moderately long, moderately wide, apex sharply rounded (*Ta. togoi*) or flat (*Ta. savoryi*), basal area broad, 15–18 short and one (rarely two) moderately long setae distally on each side of midline, 33–37 total setae, ventral PGL/Ce index 0.59–0.71, dorsal PGL index 0.89–1.17, ventral PGL index 1.53–2.00, ventral length 0.14–0.17 mm; proctiger with scattered minute spicules, membranous; cercus moderately pigmented, covered with short spicules, moderately long, moderately wide, apex broadly rounded with two moderately long (most lateral) and five to six long (most distal) setae, basal margin notched, dorsal surface with scales absent, several short and two to three long setae on distal 0.56–0.60, ventral surface with 2–4 short setae on apicolateral margin, cercus index 2.20–2.35, Ce/dorsal PGL index 2.38–2.94, length 0.23–0.25 mm, width

0.10–0.11 mm; three spermathecal capsules with several small pores near orifices, spherical, one capsule slightly larger than other two; accessory gland duct lightly pigmented, moderately long.

Males

Similar to females in general habitus.

Head. Antenna 0.56–0.61 × length of proboscis, whorls with numerous long setae directed dorsally and ventrally, distal two flagellomeres elongate; maxillary palpus approximately 0.65–0.81 × length of proboscis, with five narrow palpomeres, palpomeres 2 and 3 moderately long, palpomeres 4 and 5 shorter, with few short setae lateroventrally and apically; proboscis 1.20–1.34 × length of forefemur.

Legs. Fore-, mid- and hindtarsi each with two ungues, each toothed, fore- and midungues unequal in size, hindungues equal in size.

Genitalia. Tergum IX narrowly connected laterally to sternum IX, moderately pigmented, short, pair of small approximated lobes on posterior margin, each with 4–16 short to moderately long slender curved setae, folded area on each side laterad of lobes; gonocoxite triangular in outline, moderately pigmented, moderately long spiculate dorsal surface with short slender setae on basomesal area and moderately long to long ones on distal area, dorsolateral, lateral and ventral surfaces with numerous spatulate scales from near base to apex, long stout setae on lateral and distal parts of ventral surfaces, ventral surface with basal area very wide, mesal margin bearing irregular row or two rows of numerous moderately long and long slender slightly curved fusiform scales on most of length; gonostylus attached apically to gonocoxite, moderately long, 0.50–0.60 × length of gonocoxite, spiculate, narrow but proximal half broader and tapering to narrower distal half, 1–3 short thin setae subapically, gonostylar claw attached apically, short, narrow, apex truncate; claspette comprising moderately long spiculate slender stem with 0–2 minute setae subapically, connected with its mate by spiculate aedeagal guide, claspette filament pigmented, long, strongly curved, with apex narrowly pointed; proctiger with paraproct narrow, proximal part moderately pigmented, distal part darkly pigmented with apex strongly curved into short beaklike point, 2–5 minute cercal setae; tergum X moderately pigmented, relatively narrow, curved; phallosome with aedeagus simple, scooplike with apex narrowed, more or less ovoid, relatively short, paramere narrow, 0.70–0.95 × length of aedeagus, basal piece moderately wide, moderately long; sternum IX with lateral, basal and median areas

moderately pigmented, remainder lightly pigmented, moderately long, spiculate, with 4–8 short to moderately long setae on median posterior area.

Pupae

Cephalothorax. Seta 1-CT longer than 3-CT, 1–3-CT single to 4-branched; 4-CT single to 7-branched, shorter than 5-CT; 5-CT with 2–8 branches; 7-CT with 2–7 branches, $3.6\text{--}3.7 \times$ length of 6-CT; 10-CT $<$ 12-CT $<$ 11-CT length; 10-CT with 2–7 branches; 11-CT single to 3-branched; 12-CT single to 6-branched.

Trumpet. Index 2.05–3.13; pinna $0.42\text{--}0.61 \times$ length of trumpet; tracheoid area basal, weakly developed.

Abdomen. Seta 6-I single to 5-branched, noticeably thinner and shorter than 7-I; 1-II with 2–36 slender branches, moderately long; 2-II short, single or 2-branched, laterad of 1-II; 4-II with 2–9 branches; 5-II single to 4-branched, moderately long, slender, mesad of 4-II; 6-II single to 5-branched, shorter than 7-II; 1-III single to 8-branched; 3-III moderately long, single or 2-branched; 6-III moderately long, slender, single to 4-branched; 5-V stout, single to 3-branched, longer than tergum VI dorsal length; 2-VI single or 2-branched; 3-VI single to 4-branched, laterad of 1,2-VI; 6-VII short, single to 7-branched, posteromesad of 9-VII; 9-VII long, stout, with 2–9 branches; 9-VIII long, stout, with 6–19 aciculate branches.

Paddle. Broad; index 0.89–1.07; without fringe of long, hairlike spicules; midrib well developed, extending to near apex; seta 1-Pa single.

Fourth-instar larva

Head. Seta 1-C single, attenuate; 4-C short, with 4–8 branches, at same level or very slightly posterior to 5-C; 5-C inserted far anteriorly, moderately long, with 6–16 branches, laterad of 4-C; 6-C laterad of, and at same level as, 5-C, slightly longer than 5,7-C, with 6–13 branches; 7-C posterolaterad of 4–6-C, with 6–10 branches; 11-C with 3–13 branches; 13-C single, laterad of 12-C; 19-C absent; dorsomentum with 20–36 teeth; labiogula short, length less than width; ventro-median cervical sclerite present.

Antenna. Short, spiculate, length $0.26\text{--}0.36$ mm, seta 1-A with 3–6 branches (rarely 2-branched), not reaching apex of antennal shaft; 2,3-A inserted apically on shaft.

Thorax. Seta 1-P $>$ 2-P $>$ 3-P length; 4-P relatively long, aciculate, single; 8-P short, single or 2-branched; 5,7-M approximately equal in length; 2,6-T single.

Abdomen. Setae 6-I-IV long, stout, aciculate, 6-I–III with three or more branches, 6-II longer than 6-III; 7-I,II long, stout, aciculate, with 2–3 branches; 12-I short, single or 2-branched; 8-II short, with two or three branches; 3-V much longer than 5-V; 1-VII very short to short, slender, with 2–6 branches; 2-VII very short, single; 3-VII single or 2-branched; 12-VII single, posteromesad of 13-VII; 2,4-VIII single, 2-VIII rarely 2-branched; comb in patch of 42–167 scales; saddle small, length $0.25\text{--}0.53$ mm, incomplete ventrally, with small spicules on posterodorsal area; 1-X short, single to 3-branched, inserted ventrad of saddle; 2-X relatively short, with 5–11 branches; 3-X long, single; 4-X comprised of 12–14 moderately long, multiple-branched setae attached to grid with both lateral and transverse bars (occasionally one precratal seta); 4 anal papillae, very short, with apices broadly rounded.

Siphon. Index 1.70–2.30, short, basal and apical widths approximately equal, with attached acus, pecten of 16–27 evenly spaced spines; 1-S long, aciculate, with 6–10 branches, inserted on distal $0.16\text{--}0.28$ of siphon distad of pecten.

TYPE SPECIES DESCRIPTION: *TANAKAIUS TOGOI* (THEOBALD, 1907)

Female

Head. Antenna $0.60\text{--}0.67 \times$ length of proboscis, pedicel with numerous white and occasionally few pale brown, moderate-sized, partially overlapping scales and few short pale setae on mesal surface, flagellomere 1 with small, broad, brown scales and occasionally few white ones on lateral area; maxillary palpus $0.25\text{--}0.27 \times$ length of proboscis, dark brown-scaled with few white scales dorsoapically on palpomere 3 and apical area of palpomere 4; proboscis $1.05\text{--}1.14 \times$ length of forefemur; vertex with narrow decumbent scales, patch of dark brown ones posterior to eyes and white to yellowish white on median and posterior areas and extending over occiput, postgena with broad scales, white except for small patch of dark brown ones at about level of antepnotum; occiput with numerous long dark brown, erect, forked scales extending cephalad over most of vertex except several pale ones on area of vertex with pale decumbent scales; ocular line with narrow white or yellowish white scales; ocular setae dark brown; interocular space with narrow, white scales and 2–4 pale or brown setae; clypeus brown.

Thorax. Scutum dark brown, covered with narrow, curved, brown scales except for yellowish white ones forming moderately narrow stripe on acrostichal area from anterior margin to prescutellar area

where it splits and extends as narrow line along mesal margins of prescutellar setae, narrow stripe on dorsocentral area extending from anterior margin to near prescutellar area, narrow line along much of outer anterior margin of scutal fossal area, narrow line along posterior margin of scutal fossal area and extending caudad on mesal part of supraalar area to posterior of scutum, and broad stripe on lateral part of antealar and supraalar areas, patches of snowy white scales on anterior promontory and antedorsocentral areas; supraalar area also with few pale setae at wing base; scutellum with narrow, yellowish-white, curved scales on all lobes; pleural integument brown; antepnotum with numerous broad white scales on anterior, lateral and posterior surfaces; postpronotum covered with broad scales, white ones on dorsal and ventral areas and brown ones in middle, 3–7 posterior setae; postspiracular area with patch of broad white scales, 3–7 setae; subspiracular area with elongate patch of broad white scales; paratergite with broad white scales; upper proepisternum with patch of broad white scales, 7–12 setae; mesokatepisternum with upper and lower patches of broad white scales; lower prealar area with patch of broad white scales; mesepimeron with large patch of broad white scales on upper and median areas, numerous upper posterior and 1–3 lower anterior setae.

Legs. Forecoxa with patch of broad scales, white ones above and below separated by brown ones, midcoxa with dorsal and lower anterior patches of broad white scales, hindcoxa with patch of broad white scales on dorsal and anterior areas; fore-, mid- and hindfemur brown-scaled with apex white-scaled, forefemur also with anterior surface with white-scaled stripe ventrally from base but not reaching apex, posterior surface with broad median white-scaled stripe from base to near apex, midfemur also with anterior surface with white-scaled stripe from base but not reaching apex, proximal part of stripe moderately broad and distal part narrow, posterior surface with proximal approximately 0.70 white-scaled except distal part narrower, hindfemur also with broad white-scaled stripe on proximal 0.60–0.70 of anterior surface, stripe becoming narrower distally, posterior surface with proximal approximately 0.60 white-scaled except distal part narrower; fore-, mid- and hindtibiae brown-scaled, with few white scales dorsobasally and small white-scaled, apical band, foretibia also with an indistinct very narrow white-scaled line on posteroventral surface; tarsi brown-scaled but foretarsus also with narrow white-scaled bands basally on tarsomeres 1–4, midtarsus also with somewhat wider white-scaled bands basally on tarsomeres 1–4 and narrow white-scaled

bands apically on tarsomeres 1–3, hindtarsus also with medium-sized white-scaled bands basally on tarsomeres 1–5 and narrow white-scaled bands apically on tarsomeres 1–4.

Abdomen. Terga brown-scaled, tergum I with laterotergite white-scaled, terga II–VII with white-scaled basolateral patches extending onto lateral margins of dorsal surface and usually forming narrow basal bands dorsally, bands occasionally incomplete.

Genitalia. Tergum VIII with numerous short and few moderately long setae on distal 0.70–0.75, numerous spatulate scales on distal 0.44–0.65, VIII-Te index 0.64–0.74, VIII-Te/IX-Te index 2.47–2.91, length 0.31–0.34 mm, width 0.43–0.49 mm; sternum VIII with distal 0.87–0.88 covered with numerous short curved setae, several moderately long to long setae primarily on mesal area, very large patch of spatulate scales on each side on distal 0.73–0.79, VIII-S index 0.70–0.71, length 0.40–0.43 mm, width 0.56–0.61 mm; tergum IX with 9–17 short setae distally on each side of midline, 19–30 total setae, IX-Te index 0.70–0.91, length 0.12–0.13 mm, width 0.14–0.18 mm; postgenital lobe with apex sharply rounded, 15–18 short and one (rarely two) moderately long seta(e) distally on each side of midline, 35–37 total setae, ventral PGL/Ce index 0.64–0.71, dorsal PGL index 1.14–1.17, ventral PGL index 1.74–2.00, ventral length 0.16–0.17 mm; cercus with several short and two or three long setae on distal 0.56–0.60, cercus index 2.20–2.27, Ce/dorsal PGL index 2.38–2.90, length 0.23–0.25 mm, width 0.11 mm.

Male

Head. Antenna 0.57–0.62 × length of proboscis; maxillary palpus 0.72–0.81 × length of proboscis, brown-scaled with narrow white-scaled band apically on palpomere 3 and narrow white-scaled band basally on palpomeres 4 and 5; proboscis 1.20–1.34 × length of forefemur.

Thorax. Scutum with pale-scaled stripes and areas less distinct; pleural areas with fewer setae; mesepimeron with setae on lower anterior area absent in some populations (see Tanaka *et al.*, 1979).

Legs. Foretarsus with tarsomere 4 brown-scaled.

Genitalia. Tergum IX with lobes on posterior margin each with 10–16 setae; gonocoxite with dorsal surface bearing patch of short slender setae on basomesal area, few short to moderately long thin setae scattered over remainder of surface from about midlength to apex, several spatulate

scales along lateral margin; gonostylus approximately $0.50 \times$ length of gonocoxite, one or occasionally two short thin setae subapically; proctiger with two or three minute cercal setae; paramere approximately $0.95 \times$ length of aedeagus; sternum IX with 5–9 setae.

Pupa

Cephalothorax. Seta 1–3-CT with 2–4 branches; 4-CT with 2–7 branches; 5-CT with 3–8 branches.

Trumpet. Index 3.03–3.13; pinna $0.42\text{--}0.58 \times$ length of trumpet.

Abdomen. Seta 6-I single to 4-branched; 1-II with 10–36 slender branches; 4-II with 4–9 branches; 6-II single to 4-branched; 1-III with 3–8 branches; 3-III moderately long, single, occasionally 2-branched; 2-VI slightly mesad of 1-VI; 6-VII short, with 2–7 branches; 9-VII with 4–9 branches, tips aciculate; 9-VIII with 8–19 aciculate branches.

Paddle. Index 0.89–1.07.

Fourth-instar larva

Head. Seta 5-C with 6–14 branches; 6-C with 7–13 branches; 11-C with 6–13 branches; dorsomentum with 30–36 teeth.

Antenna. Shaft dark, gently tapering from base to apex.

Abdomen. Setae 6-I,II with 3–5 branches; 6-III with 3–6 branches; 7-I,II with two or three branches; comb in patch of 64–167 scales; 1-X short, single to 3-branched; 2-X with 8–11 branches.

Siphon. Index 1.75–2.30; with pecten of 18–27 spines; seta 1-S with 6–9 branches, inserted on distal $0.19\text{--}0.28$ of siphon.

Illustrations

Illustrations of females, males and genitalia and fourth-instar larvae as well as tables of larval setal branching for *Ta. togoi* and *Ta. savoryi* are provided in Tanaka *et al.* (1979) and of pupae and tables of pupal setal branching in Tanaka (2002). Matsuo *et al.* (1972a, b) and Linley & Chan (1991) published photographs of the egg of *Ta. togoi*. Female genitalia of *Ta. togoi* are illustrated in

LaCasse & Yamaguti (1950), Hara (1957) and Mohrig (1967).

Bionomics

Immatures of *Ta. togoi* and *Ta. savoryi* normally occur in brackish water in rock pools of coastal areas, but *Ta. togoi* has sometimes been collected in fresh water in containers. Females of both species have been collected biting humans throughout the day.

Distribution

Tanakaius togoi: Canada (British Columbia, introduced from Asia, see Belton, 1980; Belton & Belton, 1990), China (including Hainan Island, Hong Kong, Macau and Manchuria), Japan (including Bonin Islands, Marcus Island, Ogasawara Islands and Ryukyu Archipelago), Malaysia (peninsula, east and west coasts), Russian Federation (Sakhalin Island, Siberia), South Korea, South Prymorye, Southern Kurile Islands, Taiwan, Thailand, United States (Washington state) and Vietnam. *Tanakaius savoryi*: Japan (Ogasawara Islands).

Discussion

Species of *Tanakaius* have been previously classified as follows: *Culicelsa* Felt, in part of Theobald (1907); *Aedes* (*Finlaya*), in part of Edwards (1921), Hara (1957), Kurihara (1963), Gutsevich *et al.* (1974), Bohart & Ingram (1946) and LaCasse & Yamaguti (1950); *Aedes* (*Ochlerotatus*) *Globus Finlaya*, in part of Martini (1929–1931); *Aedes* (*Finlaya*) Group G, in part of Edwards (1932); *Aedes* (*Finlaya*) Group D (Aureostriatus-group: *Hulecoeteomyia*), Subgroup VI (Togoi) of Knight & Marks (1952); *Aedes* (*Finlaya*) Group D of Bohart (1957); *Aedes* (*Finlaya*) Togoi Group of Tanaka *et al.* (1979); *Aedes* (*Finlaya*) *Chrysolineatus* Section, Crassipalpus Series, Sublineatofemor Branch, Lophocoxa Subbranch, *Togoi* and *Yunnanensis* Groups, in part of Meng (1981); and *Aedes* (*Finlaya*) *Ae. chrysolineatus* group, *Ae. togoi* subgroup of Lu & Ji (1997).

Etymology

Tanakaius is masculine and named in honour of Dr Kazuo Tanaka in recognition of his outstanding contributions to the taxonomy of the mosquitoes of Japan and adjacent areas.

KEYS TO INCLUDED SPECIES

Adults

- Maxillary palpus dark-scaled; tarsi dark-scaled..... *Ta. savoryi*
 Maxillary palpus with white-scaled areas; tarsi with white-scaled basal bands..... *Ta. togoi*

Female genitalia

- Sternum VIII with patch of about 10–14 scales on each side of midline;
 postgenital lobe with apex flat..... *Ta. savoryi*
 Sternum VIII with large patch of numerous scales on each side of midline;
 postgenital lobe with apex sharply rounded..... *Ta. togoi*

Male genitalia

- Tergum IX with 4–8 setae on each posterior lobe..... *Ta. savoryi*
 Tergum IX with 10–16 setae on each posterior lobe..... *Ta. togoi*

Pupae

- Seta 1-II with 2–8 branches..... *Ta. savoryi*
 Seta 1-II with 10–36 branches..... *Ta. togoi*

Fourth-instar larvae

- Dorsomentum with 20–23 teeth; seta 3-VII slender, shorter than seta 4-VII..... *Ta. savoryi*
 Dorsomentum with 30–36 teeth; seta 3-VII stout, noticeably longer than seta 4-VII..... *Ta. togoi*

APPENDIX 4

CHECKLIST AND CONSPECTUS OF
RECLASSIFICATION OF AEDINI

Where it is not possible to assign species confidently to any of the proposed genera, they are retained for the time being in the old broad concept of the genus-level taxon in which they were previously placed. For example, those unassigned species previously placed in *Ochlerotatus* (*Finlaya*) are listed under '*Ochlerotatus* *sensu auctorum*', subgenus '*Finlaya*' Theobald, 1903 *sensu auctorum*. The checklist includes all species recognized as valid at the end of October 2003. Where necessary, the terminations of species names have been changed to agree in gender with generic names in accordance with Articles 31.2 and 34.2 of the *International Code of Zoological Nomenclature* (ICZN, 1999). Footnotes pertaining to a few taxa are listed below (before the checklist).

Notes

¹Edwards (1924) synonymized *nocturnus* Theobald, 1903 with *vexans* Meigen, 1830. Belkin (1962) provisionally elevated *nocturnus* to species rank, but recognized its status as uncertain. Reinert (1973a) formally synonymized *nocturnus* with *vexans* and indicated that morphological characters of specimens from islands of the Pacific and Southeast Asian populations fell within the range of characters for this taxon elsewhere within its distribution. Lee *et al.* (1982) chose to 'retain *nocturnus* as a species partly because the synonymizing of *nocturnus*

under *vexans* gives *vexans* an extraordinary wide distribution far greater than that achieved by any other non-domestic species.' The latter action is unjustified because it was not supported with diagnostic or differential data of any type; therefore, *nocturnus* should remain a synonym of *vexans*.

²The status of several species treated by Edwards (1917) is confusing. On pages 202 and 203, he indicated that genus *Aedes* included subgenera *Armigeres*, *Stegomyia*, *Ochlerotatus*, *Aedes* and *Skusea*. It is obvious that this was Edwards' intended usage of these names. However, on pages 206 and 208 he described *durhami* and *maiae* as new species of genus *Armigeres*. We regard this usage by Edwards as a *lapsis calmi*. Similar *lapsis calmi* also occur on pages 209–224 for the other subgenera of *Aedes* treated by Edwards.

³Reinert (1990) synonymized *leucopleurus* Rozeboom, 1946 with *Aedes aureostriatus* Doleschall, 1857. This formal act has been overlooked since it was published.

⁴Leicester (1908) provided a brief description of *Aioretomyia perdita* from his memory of a single specimen that was previously lost. Because no type specimen exists and the species has not been reported in literature during the past 95 years, its identity is doubtful and it is herein considered a *nomen dubium*.

- Aedini Belkin, 1962
- Abraedes* Zavortink, 1970, **stat. nov.**, raised to genus rank
papago (Zavortink, 1970), **comb. nov.**
- Aedes* Meigen, 1818
cinereus Meigen, 1818
dahuricus Danilov, 1987
esoensis Yamada, 1921
geminus Peus, 1970
mubiensis Luh & Shih, 1958
rossicus Dolbeskin, Gorickaja & Mitrofanova, 1930
sasai Tanaka, Mizusawa & Saugstad, 1975
yamadai Sasa, Kano & Takahasi, 1950
- '*Aedes*' *sensu auctorum*
 Subgenus '*Aedimorphus*' Theobald, 1903 *sensu auctorum*
abnormalis (Theobald, 1909)
 ssp. *kabwachensis* Edwards, 1941
adami Geoffroy, 1971
aerarius McIntosh, 1975
albocephalus (Theobald, 1903)
albodorsalis Fontenille & Brunhes, 1985
alboscuteclatus (Theobald, 1905)
alboventralis (Theobald, 1910)
apicoannulatus (Edwards, 1912)
argenteopunctatus (Theobald, 1901)
argenteoscutellatus Carter & Wijesundara, 1948
bambiotai Geoffroy, 1987
bancoi Geoffroy, 1987
bedfordi Edwards, 1936
bevisi (Edwards, 1915)
boneti Gil Collado, 1936
 ssp. *kumbae* Chwatt, 1948
caecus (Theobald, 1901)
caliginosus (Graham, 1910)
centropunctatus (Theobald, 1913)
chamboni Cornet, 1968
culicinus Edwards, 1922
cumminsii (Theobald, 1903)
 ssp. *mediopunctata* (Theobald, 1909)
dalzieli (Theobald, 1910)
dauidi Basio, 1971
dentatus (Theobald, 1904)
dialloi Hamon & Brengues, 1965
domesticus (Theobald, 1901)
durbanensis (Theobald, 1903)
 ssp. *angolae* Ribeiro & Ramos, 1974
eboensis Rickenbach & Ferrara, 1965
eritreae Lewis, 1942
falabreguesi Hamon, 1957
filicis Ingram & de Meillon, 1927
fowleri (Charmoy, 1908)
gandarai da Cunha Ramos, Capela & Ribeiro, 1995
gibbinsi Edwards, 1935
gouldi Reinert, 1972
grenieri Hamon, Service, Adam & Taufflieb, 1961
grjebinei Hamon, Taufflieb & Maillot, 1957
hirsutus (Theobald, 1901)
 ssp. *adenensis* Edwards, 1941
holocinctus Edwards, 1941
hopkinsi Edwards, 1936
insolens Edwards, 1936
irritans (Theobald, 1901)
jamesi (Edwards, 1914)
karooensis Muspratt, 1961
lamborni Edwards, 1923
leesoni Edwards, 1932
 ssp. *vernus* Lewis, 1944
leptolabis Edwards, 1936
leucarthrius (Speiser, 1909)
lokojoensis Service, 1959
longiseta Edwards, 1936
lottei Hamon & Brengues, 1965
lowisii (Theobald, 1910)
mansouri Qutubuddin, 1959
masoalensis Fontenille & Brunhes, 1985
mathioti Fontenille & Brunhes, 1985
mattinglyi Hamon & Rickenbach, 1954
mediolineatus (Theobald, 1901)
microstictus Edwards, 1936
minutus (Theobald, 1901)
mixtus Edwards, 1936
mutilus Edwards, 1936
natronius Edwards, 1932
nigricephalus (Theobald, 1901)
nigrostriatus (Barraud, 1927)
nyounae Hamon & Adam, 1959
oakleyi Stone, 1939
ochraceus (Theobald, 1901)
orbitae Edwards, 1922
ovazzai Hamon & Adam, 1959
pachyurus Edwards, 1936
pallidostriatus (Theobald, 1907)
pampangensis (Ludlow, 1905)
phyllolabis Edwards, 1929
pipersalatus (Giles, 1902)
pseudotarsalis van Someren, 1946
pubescens Edwards, 1925
punctifemoris (Ludlow, 1921)
punctothoracis (Theobald, 1909)
quasiunivittatus (Theobald, 1901)
reali Hamon & Adam, 1959
rickenbachi Hamon & Adam, 1959
semlikiensis van Someren, 1950
senyavinesis Knight & Hurlbut, 1949
seychellensis (Theobald, 1912)
simulans (Newstead & Carter, 1911)
smithburni van Someren, 1950
stenoetrus (Theobald, 1907)

- stenoscutus* Edwards, 1912
subdentatus Edwards, 1936
syntheticus Barraud, 1928
taeniorhynchoides (Christophers, 1911)
tarsalis (Newstead, 1907)
tauffliebi Rickenbach & Ferrara, 1965
tricholabis Edwards, 1941
 ssp. *bwamba* van Someren, 1950
trimaculatus (Theobald, 1905)
trukensis Bohart, 1957
veeniae McIntosh, 1975
vexans (Meigen, 1830)¹
 ssp. *arabiensis* (Patton, 1905)
 ssp. *nipponii* (Theobald, 1907)
wendyae Service, 1959
wigglesworthi Edwards, 1941
yangambiensis de Meillon & Lavoipierre, 1944
yvonneae Edwards, 1941
- Subgenus 'Cancraedes' Edwards, 1929 *sensu auctorum*
cancricomes Edwards, 1922
curtipes Edwards, 1915
indonesiae Mattingly, 1958
kohkutensis Mattingly, 1958
mamoedjoensis Mattingly, 1958
masculinus Mattingly, 1958
palawanicus Mattingly, 1958
penghuensis Lien, 1968
simplex (Theobald, 1903)
thurmanae Mattingly, 1958
- Alanstonea* Mattingly, 1960, **stat. nov.**, raised to genus rank
brevitibia (Edwards, 1914), **comb. nov.**
treubi (de Meijere, 1910), **comb. nov.**
- Albuginosus* Reinert, 1987, **stat. nov.**, raised to genus rank
capensis (Edwards, 1924), **comb. nov.**
gilliesi (van Someren, 1962), **comb. nov.**
haworthi (Edwards, 1923), **comb. nov.**
kapretwae (Edwards, 1941), **comb. nov.**
kennethi (Muspratt, 1956), **comb. nov.**
marshallii (Theobald, 1901), **comb. nov.**
ngong (van Someren, 1950), **comb. nov.**
stokesi (Evans, 1929), **comb. nov.**
teesdalei (van Someren, 1954), **comb. nov.**
- Armigeres* Theobald, 1901
 Subgenus *Armigeres*
alkatirii Toma, Miyagi & Syafruddin, 1995
apoensis Bohart & Farner, 1944
aureolineatus (Leicester, 1908)
azurini Basio, 1971
baisasi Stone & Thurman, 1958
bhayungi Thurman & Thurman, 1958
breinli (Taylor, 1914)
- candelabrifera* Brug, 1939
confusus Edwards, 1915
conjungens Edwards, 1914
denbesteni Brug, 1925
durhami (Edwards, 1917)²
ejercitoi Baisas, 1935
fimbriatus Edwards, 1930
foliatus Brug, 1931
giveni Edwards, 1926
hybridus Edwards, 1914
joloensis (Ludlow, 1904)
jugraensis (Leicester, 1908)
kesseli Ramalingam, 1987
kinabaluensis Ramalingam, 1972
kuchingensis Edwards, 1915
lacuum Edwards, 1922
maiae (Edwards, 1917)²
malayi (Theobald, 1901)
manalangi Baisas, 1935
maximus Edwards, 1922
milnensis Lee, 1944
moultoni Edwards, 1914
obturbans (Walker, 1859)
papuensis Peters, 1963
setifer Delfinado, 1966
seticoxitus Luh & Li, 1981
subalbatus (Coquillett, 1898)
 var. *chrysocorporis* Hsieh & Liao, 1956
theobaldi Barraud, 1934
yunnanensis Dong, Zhou & Dong, 1995
- Subgenus *Leicesteria* Theobald, 1904
annulipalpis (Theobald, 1910)
annulitarsis (Leicester, 1908)
balteatus Macdonald, 1960
cingulatus (Leicester, 1908)
dentatus Barraud, 1927
digitatus (Edwards, 1914)
dolichocephalus (Leicester, 1908)
flavus (Leicester, 1908)
inchoatus Barraud, 1927
lepidocoxitus Dong, Zhou & Dong, 1995
longipalpis (Leicester, 1904)
magnus (Theobald, 1908)
menglaensis Dong, Zhou & Dong, 2002
omissus (Edwards, 1914)
pectinatus (Edwards, 1914)
pendulus (Edwards, 1914)
traubi Macdonald, 1960
vimoli Thurman & Thurman, 1958
- Nomina dubia*
striocrura (Giles, 1904)
ventralis (Walker, 1860)
- Ayurakitia* Thurman, 1954
griffithi Thurman, 1954
peytoni (Reinert, 1972)

- Aztecaedes* Zavortink, 1972, **stat. nov.**, raised to genus rank
ramirezi (Vargas & Downs, 1950), **comb. nov.**
- Belkinus* Reinert, 1982, **stat. nov.**, raised to genus rank
aurotaeniatus (Edwards, 1922), **comb. nov.**
- Bothaella* Reinert, 1973, **stat. nov.**, raised to genus rank
brownscutuma (Dong, Zhu & Dong, 1999), **comb. nov.**
eldridgei (Reinert, 1973), **comb. nov.**
helenae (Reinert, 1973), **comb. nov.**
kleini (Reinert, 1973), **comb. nov.**
- Christophersiomyia* Barraud, 1923, **stat. nov.**, restored to genus rank
annulirostris (Theobald, 1905), **comb. nov.**
chionodes (Belkin, 1962), **comb. nov.**
gombakensis (Mattingly, 1959), **comb. nov.**
ibis (Barraud, 1931), **comb. nov.**
thomsoni (Theobald, 1905), **comb. nov.**
- Diceromyia* Theobald, 1911, **stat. nov.**, restored to genus rank
adersi (Edwards, 1917), **comb. nov.**
agastyai (Tewari & Hiriyan, 1992), **comb. nov.**
bananea (Wolfs, 1958), **comb. nov.**
cordellieri (Huang, 1986), **comb. nov.**
coulangesi (Rodhain & Boutonnier, 1983), **comb. nov.**
fascipalpis (Edwards, 1912), **comb. nov.**
flavicollis (Edwards, 1928), **comb. nov.**
franciscoi (Mattingly, 1959), **comb. nov.**
furcifera (Edwards, 1913), **comb. nov.**
grassei (Doucet, 1951), **comb. nov.**
iyengari (Edwards, 1923), **comb. nov.**
madagascarensis (van Someren, 1949), **comb. nov.**
mefouensis (Ferrara, 1974), **comb. nov.**
meronephada (Dyar & Shannon, 1925), **comb. nov.**
microptera (Giles, 1901), **comb. nov.**
nummata (Edwards, 1923), **comb. nov.**
periskelata (Giles, 1902), **comb. nov.**
pseudonummata (Reinert, 1973), **comb. nov.**
punctipes (Edwards, 1921), **comb. nov.**
ramachandrai (Reuben, 1967), **comb. nov.**
reginae (Edwards, 1922), **comb. nov.**
reubenae (Tewari & Hiriyan, 1992), **comb. nov.**
scanloni (Reinert, 1970), **comb. nov.**
sylvatica (Brunhes, 1983), **comb. nov.**
taylori (Edwards, 1936), **comb. nov.**
tiptoni (Grjebine, 1953), **comb. nov.**
whartoni (Mattingly, 1965), **comb. nov.**
zethus (de Meillon & Lavoipierre, 1944), **comb. nov.**
- Downsiomyia* Vargas, 1950, **stat. nov.**, from synonymy with *Finlaya*, raised to genus rank
albolateralis (Theobald, 1908), **comb. nov.**
albonivea (Barraud, 1934), **comb. nov.**
axitiosa (Kulasekera, Knight & Harbach, 1990), **comb. nov.**
dorseyi (Knight, 1946), **comb. nov.**
ganapathi (Colless, 1958), **comb. nov.**
harinasutai (Knight, 1978), **comb. nov.**
idjenensis (Brug, 1934), **comb. nov.**
inermis (Colless, 1958), **comb. nov.**
lactea (Knight, 1946), **comb. nov.**
laoagensis (Knight, 1946), **comb. nov.**
leonis (Colless, 1958), **comb. nov.**
litorea (Colless, 1958), **comb. nov.**
mikrokopion (Knight & Harrison, 1988), **comb. nov.**
mohani (Knight, 1969), **comb. nov.**
nipponica (LaCasse & Yamaguti, 1948), **comb. nov.**
nishikawai (Tanaka, Mizusawa & Saugstad, 1979), **comb. nov.**
nivea (Ludlow, 1903), **comb. nov.**
niveoides (Barraud, 1934), **comb. nov.**
novonivea (Barraud, 1934), **comb. nov.**
omorii (Lien, 1968), **comb. nov.**
pexa (Colless, 1958), **comb. nov.**
pseudonivea (Theobald, 1905), **comb. nov.**
saperoi (Knight, 1946), **comb. nov.**
sinensis (Chow, 1950), **comb. nov.**
subnivea (Edwards, 1922), **comb. nov.**
vana (Colless, 1958), **comb. nov.**
watteni (Lien, 1968), **comb. nov.**
- Edwardsaedes* Belkin, 1962, **stat. nov.**, raised to genus rank
bekkui (Mogi, 1977), **comb. nov.**
imprimens (Walker, 1860), **comb. nov.**
pingpaensis (Chang, 1965), **comb. nov.**
- Eretmapodites* Theobald, 1901
adami Ferrara & Eouzan, 1974
argyrurus Edwards, 1936
brenguesi Rickenbach & Lombrici, 1975
brottesi Rickenbach, 1967
caillardi Rickenbach, Ferrara & Eouzan, 1968
chrysogaster Graham, 1909
corbeti Hamon, 1962
dracaenae Edwards, 1916
eouzani Rickenbach & Lombrici, 1974
ferrarai Rickenbach & Eouzan, 1970
forcipulatus Edwards, 1936
germaini Rickenbach & Eouzan, 1970
gilletti van Someren, 1949
grahami Edwards, 1911
grenieri Hamon & van Someren, 1961
haddowi van Someren, 1949

- hamoni* Grjebine, 1972
harperi van Someren, 1949
hightoni van Someren, 1947
inornatus Newstead, 1907
intermedius Edwards, 1936
jani Rickenbach & Lombrici, 1976
lacani Rickenbach & Eouzan, 1970
leucopous Graham, 1909
mahaffyi van Someren, 1949
marcellei Adam & Hamon, 1959
mattinglyi Hamon & van Someren, 1961
melanopous Graham, 1909
mortiauxi da Cunha Ramos & Ribeiro, 1990
oedipodeios Graham, 1909
parvipluma Edwards, 1941
pauliani Grjebine, 1950
penicillatus Edwards, 1941
plioleucus Edwards, 1941
 ssp. *brevis* Edwards, 1941
productus Edwards, 1941
quinquevittatus Theobald, 1901
ravissei Rickenbach & Eouzan, 1970
rickenbachi Ferrara & Eouzan, 1974
salauni Rickenbach, Ferrara & Eouzan, 1968
semisimplicipes Edwards, 1914
silvestris Ingram & de Meillon, 1927
 ssp. *conchobius* Edwards, 1941
subsimplicipes Edwards, 1914
tendeiroi da Cunha Romos, Ribeiro & Machado, 1992
tonsus Edwards, 1941
vansomereni Hamon, 1962
wasoni Edwards, 1941
 ssp. *douceti* Adam & Hamon, 1959
- Finlaya* Theobald, 1903, **stat. nov.**, restored to genus rank, restricted to Kochi Group
alocasicola (Marks, 1947), **comb. nov.**
ananae (Knight & Laffoon, 1946), **comb. nov.**
avistylus (Brug, 1939), **comb. nov.**
bougainvillensis (Marks, 1947), **comb. nov.**
burnetti (Belkin, 1962), **comb. nov.**
crocea (Knight & Laffoon, 1946), **comb. nov.**
dobrotworskyi (Marks, 1958), **comb. nov.**
fijiensis (Marks, 1947), **comb. nov.**
flavipennis Giles, 1904, **comb. nov.**
franclemonti (Belkin, 1962), **comb. nov.**
freycinetiae (Laird, 1957), **comb. nov.**
fuscipalpis (Belkin, 1962), **comb. nov.**
fuscitarsis (Belkin, 1962), **comb. nov.**
gahnicola (Marks, 1947), **comb. nov.**
gani (Bonne-Wepster, 1940), **comb. nov.**
gressitti (Bohart, 1947), **comb. nov.**
hollingsheadi (Belkin, 1962), **comb. nov.**
horotoi (Taylor, 1972), **comb. nov.**
hui (Bohart, 1957), **comb. nov.**
josephinae (Marks, 1958), **comb. nov.**
- knighti* (Stone & Bohart, 1944), **comb. nov.**
kochi (Dönitz, 1901), **comb. nov.**
lewelleni (Starkey & Webb, 1946), **comb. nov.**
lutea (Ludlow, 1905), **comb. nov.**
maffii (Taylor & Tenorio, 1974), **comb. nov.**
medleri (Knight & Laffoon, 1946), **comb. nov.**
neogeorgiana (Belkin, 1962), **comb. nov.**
oceanica (Belkin, 1962), **comb. nov.**
poicilia Theobald, 1903, **comb. nov.**
samoana Grünberg, 1913, **comb. nov.**
schlosseri (Belkin, 1962), **comb. nov.**
solomonis (Stone & Bohart, 1944), **comb. nov.**
sorsogonensis (Banez & Jueco, 1966), **comb. nov.**
stonei (Knight & Laffoon, 1946), **comb. nov.**
tutuillae (Ramalingam & Belkin, 1965), **comb. nov.**
wallacei (Edwards, 1926), **comb. nov.**
- Fredwardsius* Reinert, 2000, **stat. nov.**, raised to genus rank
 vittatus (Bigot, 1861), **comb. nov.**
- Geoskusea* Edwards, 1929, **stat. nov.**, raised to genus rank
 baisasi (Knight & Hull, 1951), **comb. nov.**
 becki (Belkin, 1962), **comb. nov.**
 daggyi (Stone & Bohart, 1944), **comb. nov.**
 fimbripes (Edwards, 1924), **comb. nov.**
 kabaenensis (Brug, 1939), **comb. nov.**
 longiforceps (Edwards, 1929), **comb. nov.**
 lunulata (King & Hoogstraal, 1946), **comb. nov.**
 perryi (Belkin, 1962), **comb. nov.**
 tonsus (Edwards, 1924), **comb. nov.**
- Gymnometopa* Coquillett, 1905, **stat. nov.**, restored to genus rank
 mediovittata (Coquillett, 1906), **comb. nov.**
- Haemagogus* Williston, 1896
Subgenus *Conopostegus* Dyar, 1925
 clarki (Galindo, Carpenter & Trapido, 1953)
 leucocelaenus (Dyar & Shannon, 1924)
 leucophoebus (Galindo, Carpenter & Trapido, 1953)
 leucotaeniatus (Komp, 1938)
Subgenus *Haemagogus*
 acutisentis Arnell, 1973
 aeritinctus Galindo & Trapido, 1967
 albomaculatus Theobald, 1903
 anastasionis Dyar, 1921
 andinus Osorno-Mesa, 1944
 argyromeris Dyar & Ludlow, 1921
 baresi Cerqueira, 1960
 boshelli Osorno-Mesa, 1944
 capricornii Lutz, 1904
 celeste Dyar & Nunez Tovar, 1927
 chalcospilans Dyar, 1921
 chrysochlorus Arnell, 1973

equinus Theobald, 1903
iridicolor Dyar, 1921
janthinomys Dyar, 1921
lucifer (Howard, Dyar & Knab, 1913)
mesodentatus Komp & Kumm, 1938
nebulosus Arnell, 1973
panarchys Dyar, 1921
regalis Dyar & Knab, 1906
soperi Levi-Castillo, 1955
spgazzinii Brethes, 1912
splendens Williston, 1896
tropicalis Cerqueira & Antunes, 1938

Halaedes Belkin, 1962, **stat. nov.**, raised to genus rank

ashworthi (Edwards, 1921), **comb. nov.**
australis (Erichson, 1842), **comb. nov.**
wardangensis (Brust, Ballard, Driver, Hartley, Galway & Curran, 1998), **comb. nov.**

Heizmannia Ludlow, 1905

Subgenus *Heizmannia*

aurea Brug, 1932
aureochaeta (Leicester, 1908)
carteri Amerasinghe, 1993
chandi Edwards, 1922
chengi Lien, 1968
communis (Leicester, 1908)
complex (Theobald, 1910)
covelli Barraud, 1929
demeilloni Mattingly, 1970
funerea (Leicester, 1908)
greenii (Theobald, 1905)
heterospina Gong & Lu, 1986
himalayensis Edwards, 1922
indica (Theobald, 1905)
kana Tanaka, Mizusawa & Saugstad, 1979
kanhsienensis Tung, 1955
lii Wu, 1936
macdonaldi Mattingly, 1957
mattinglyi Thurman, 1959
menglianensis Lu & Gong, 1986
menglianeroides Dong, Dong & Zhou, 2003
persimilis Mattingly, 1970
propinqua Mattingly, 1970
proxima Mattingly, 1970
reidi Mattingly, 1957
ruiliensis Dong, Zhou & Wang, 1997
scanloni Mattingly, 1970
scintillans Ludlow, 1905
taiwanensis Lien, 1968
tengchongensis Dong, Wang & Zhou, 2002
thelmae Mattingly, 1970
viridis Barraud, 1929

Subgenus *Mattinglyia* Lien, 1968

achaetae (Leicester, 1908)

catesi (Lien, 1968)
discrepans (Edwards, 1922)
occidentayunnana (Gong & Lu, 1991)
tripunctata (Theobald, 1908)

Howardina Theobald, 1903, **stat. nov.**, restored to genus rank

albonotata (Coquillett, 1906), **comb. nov.**
allotecnon (Kumm, Komp & Ruiz, 1940), **comb. nov.**
arboREALIS (Bonne-Wepster & Bonne, 1920), **comb. nov.**
argyritis (Dyar & Nunez Tovar, 1927), **comb. nov.**
aureolineata (Berlin, 1969), **comb. nov.**
auritis Theobald, 1907, **comb. nov.**
aurivittata (Cerqueira, 1943), **comb. nov.**
bahamensis (Berlin, 1969), **comb. nov.**
brevis (Berlin, 1969), **comb. nov.**
brevivittata (Berlin, 1969), **comb. nov.**
busckii (Coquillett, 1906), **comb. nov.**
cozumelensis (Diaz Najera, 1966), **comb. nov.**
ecuadoriensis (Berlin, 1969), **comb. nov.**
eleanorae (Berlin, 1969), **comb. nov.**
fulvithorax (Lutz, 1904), **comb. nov.**
grabhami (Berlin, 1969), **comb. nov.**
guatemala (Berlin, 1969), **comb. nov.**
guerrero (Berlin, 1969), **comb. nov.**
inaequalis Grabham, 1907, **comb. nov.**
ioliota (Dyar & Knab, 1913), **comb. nov.**
leei (Berlin, 1969), **comb. nov.**
lorraineae (Berlin, 1969), **comb. nov.**
marinkellei (Berlin, 1969), **comb. nov.**
martinezi (Berlin, 1969), **comb. nov.**
osornoi (Berlin, 1969), **comb. nov.**
pseudodminiciei (Komp, 1936), **comb. nov.**
quadrivittata (Coquillett, 1902), **comb. nov.**
septemstriata (Dyar & Knab, 1907), **comb. nov.**
sexlineata (Theobald, 1901), **comb. nov.**
spinosa (Berlin, 1969), **comb. nov.**
stenei (Thompson, 1956), **comb. nov.**
vanemdeni (Martini, 1931), **comb. nov.**
walkeri (Theobald, 1901), **comb. nov.**
whitmorei (Dunn, 1918), **comb. nov.**

Huaedes Huang, 1968, **stat. nov.**, raised to genus rank

medialis (Brug, 1932), **comb. nov.**
variepietus (King & Hoogstraal, 1946), **comb. nov.**
wauensis (Huang, 1968), **comb. nov.**

Indusius Edwards, 1934, **stat. nov.**, raised to genus rank

pulverulentus (Edwards, 1922), **comb. nov.**

- Isoaedes* Reinert, 1979, **stat. nov.**, raised to genus rank
cavaticus (Reinert, 1979), **comb. nov.**
- Kenknighthia* Reinert, 1990, **stat. nov.**, raised to genus rank
dissimilierodes (Dong, Zhou & Dong, 2002), **comb. nov.**
dissimilis (Leicester, 1908), **comb. nov.**
gaffigani (Reinert, 1990), **comb. nov.**
harbachi (Reinert, 1990), **comb. nov.**
karwari (Barraud, 1924), **comb. nov.**
lerozeboomi (Reinert, 1990), **comb. nov.**
leucomeres (Giles, 1904), **comb. nov.**
litwakae (Reinert, 1990), **comb. nov.**
luzonensis (Rozeboom, 1946), **comb. nov.**
paradissimilis (Rozeboom, 1946), **comb. nov.**
pecori (Reinert, 1990), **comb. nov.**
wilkersoni (Reinert, 1990), **comb. nov.**
- Kompia* Aitken, 1941, **stat. nov.**, restored to genus rank
purpureipes (Aitken, 1941), **comb. nov.**
- Leptosomatomyia* Theobald, 1905, **stat. nov.**, restored to genus rank
aurimargo (Edwards, 1922), **comb. nov.**
- Levua* Stone & Bohart, 1944, **stat. nov.**, raised to generic rank
dufouri (Hamon, 1953), **comb. nov.**
fryeri (Theobald, 1912), **comb. nov.**
geoskusea (Amos, 1944), **comb. nov.**
- Lorrainea* Belkin, 1962, **stat. nov.**, raised to generic rank
amesii (Ludlow, 1903), **comb. nov.**
celebica (Mattingly, 1959), **comb. nov.**
dasyorrhus (King & Hoogstraal, 1946), **comb. nov.**
fumida (Edwards, 1928), **comb. nov.**
lamellifera (Bohart & Ingram, 1946), **comb. nov.**
- Mucidus* Theobald, 1901, **stat. nov.**, restored to genus rank
alternans (Westwood, 1835), **comb. nov.**
aurantius (Theobald, 1907), **comb. nov.**
 ssp. *chrysogaster* Taylor, 1927, **comb. nov.**
ferinus (Knight, 1947), **comb. nov.**
grahamii Theobald, 1909, **comb. nov.**
laniger (Wiedemann, 1820), **comb. nov.**
lucianus (Muspratt, 1959), **comb. nov.**
mucidus (Karsch, 1887), **comb. nov.**
nigerrimus Theobald, 1913, **comb. nov.**
painei (Knight, 1948), **comb. nov.**
quadripunctis (Ludlow, 1910), **comb. nov.**
quasiferinus (Mattingly, 1961), **comb. nov.**
- scatophagoides* Theobald, 1901, **comb. nov.**
sudanensis Theobald, 1908, **comb. nov.**
tonkingi (Gebert, 1948), **comb. nov.**
- Neomelaniconion* Newstead, 1907, **stat. nov.**, raised to genus rank
albicosta (Edwards, 1913), **comb. nov.**
albothorax (Theobald, 1907), **comb. nov.**
aurovenatum (Worth, 1960), **comb. nov.**
bequaerti (Wolfs, 1947), **comb. nov.**
bergerardi (Pajot & Geoffroy, 1971), **comb. nov.**
bolense (Edwards, 1936), **comb. nov.**
carteri (Edwards, 1936), **comb. nov.**
circumluteolus (Theobald, 1908), **comb. nov.**
crassiforceps (Edwards, 1927), **comb. nov.**
ellinorae (Edwards, 1941), **comb. nov.**
flavimargo (Edwards, 1941), **comb. nov.**
fuscinerve (Edwards, 1914), **comb. nov.**
jamoti (Hamon & Rickenbach, 1954), **comb. nov.**
lineatopenne (Ludlow, 1905), **comb. nov.**
 ssp. *aureum* (Gutzevich, 1955), **comb. nov.**
luridum (McIntosh, 1971), **comb. nov.**
luteolaterale (Theobald, 1901), **comb. nov.**
mcintoshii (Huang, 1987), **comb. nov.**
monotrichus (Edwards, 1936), **comb. nov.**
palpale Newstead, 1907, **comb. nov.**
pogonurus (Edwards, 1936), **comb. nov.**
punctocostale (Theobald, 1909), **comb. nov.**
taeniarostre (Theobald, 1909), **comb. nov.**
unidentatum (McIntosh, 1971), **comb. nov.**
- Ochlerotatus* Lynch Arribalzaga, 1891
 Subgenus *Rusticoidus* Shevchenko & Prudkina, 1973
albescens (Edwards, 1921)
bicristatus (Thurman & Winkler, 1950)
krymmontanus (Aleksiev, 1989)
lepidonotus (Edwards, 1920)
provocans (Walker, 1848)
quasirusticus (Torres Canamares, 1951)
refiki (Medschid, 1928)
rusticus (Rossi, 1790)
 var. *subtrichurus* (Martini, 1927)
subdiversus (Martini, 1926)
- Unassigned to subgenus
atlanticus (Dyar & Knab, 1906)
communis (de Geer, 1776)
dorsalis (Meigen, 1830)
fulvus (Wiedemann, 1828)
 ssp. *pallens* (Ross, 1943)
infirmatus (Dyar & Knab, 1906)
scapularis (Rondani, 1848)
sollicitans (Walker, 1856)
- '*Ochlerotatus*' *sensu auctorum*
 Subgenus '*Bruceharrisonius*' Reinert, 2003 *sensu auctorum*

- alektorovi* (Stackelberg, 1943)
aureostriatus (Doleschall, 1857)³
doonii (Wattal, Bhatia & Kalra, 1958)
christophersi (Edwards, 1922)
greenii (Theobald, 1903)
hurlbuti (Lien, 1967)
okinawanus (Bohart, 1946)
taiwanus (Lien, 1968)
- Subgenus 'Chaetocruuiomyia' Theobald, 1910 *sensu auctorum*
- calabyi* (Marks, 1963)
elchoensis (Taylor, 1929)
humeralis (Edwards, 1922)
macmillani (Marks, 1964)
moloiensis (Taylor, 1929)
spinosipes Edwards, 1922
tulliae (Taylor, 1929)
wattensis (Taylor, 1929)
- Subgenus 'Finlaya' Theobald, 1903 *sensu auctorum*
- albilabris* (Edwards, 1925)
alboannulatus (Macquart, 1850)
albocinctus (Barraud, 1924)
albotaeniatis (Leicester, 1904)
alius (Lien, 1968)
alongi (Galliard & Ngu, 1947)
alticola (Bonne-Wepster, 1948)
anggiensis (Bonne-Wepster, 1937)
argenteitarsis (Brug, 1932)
argyronotum (Belkin, 1962)
assamensis (Theobald, 1908)
auronitens (Edwards, 1922)
australiensis (Theobald, 1910)
banksi (Edwards, 1922)
barnardi (Edwards, 1924)
biocellatus (Taylor, 1915)
britteni (Marks & Hodgkin, 1958)
buxtoni (Belkin, 1962)
cacharanus (Barraud, 1923)
candidoscutellum (Marks, 1947)
chrysolineatus (Theobald, 1907)
chungi (Lien, 1968)
clintoni (Taylor, 1946)
cogilli (Edwards, 1922)
crossi (Lien, 1967)
deccanus (Barraud, 1923)
derooki (Brug, 1932)
dobodurus (King & Hoogstraal, 1946)
eatoni Edwards, 1916
echinus Edwards, 1920
elsiae (Barraud, 1923)
 ssp. vicarius (Lien, 1968)
embuensis (Edwards, 1930)
feegradei (Barraud, 1934)
fengi (Edwards, 1935)
formosensis (Yamada, 1921)
geniculatus (Olivier, 1791)
- gilcolladoi* (Sanchez-Covisa Villa, Rodriguez Rodriguez & Guillen Llera, 1985)
gilli (Barraud, 1924)
gonguoensis (Gong & Lu, 1986)
gracilelineatus (Bonne-Wepster, 1937)
gubernatoris (Giles, 1901)
 var. kотиensis (Barraud, 1934)
hancocki (van Someren, 1962)
harperi (Knight, 1948)
harveyi (Barraud, 1923)
hatorii (Yamada, 1921)
hollandius (King & Hoogstraal, 1946)
ingrami (Edwards, 1930)
inquinatus (Edwards, 1922)
iwi (Marks, 1955)
japonicus (Theobald, 1901)
 ssp. shintienensis (Tsai & Lien, 1950)
 ssp. amamiensis (Tanaka, Mizusawa & Saugstad, 1979)
 ssp. yaeyamensis (Tanaka, Mizusawa & Saugstad, 1979)
jugraensis (Leicester, 1908)
keefei (King & Hoogstraal, 1946)
khazani (Edwards, 1922)
kiangsiensis (Tung, 1955)
koreicoides (Sasa, Kano & Hayashi, 1950)
koreicus (Edwards, 1917)²
lauriei Carter, 1920
lepchanus (Barraud, 1923)
loi (Lien, 1968)
lophoventralis (Theobald, 1910)
luteostriatus (Robinson, 1950)
macdougalli (Edwards, 1922)
macfarlanei Edwards, 1914
mackerrasi (Taylor, 1927)
mallochi (Taylor, 1944)
melanopterus (Giles, 1904)
milsoni (Taylor, 1915)
mjobergi (Edwards, 1926)
monocellatus (Marks, 1948)
nigrorhynchus (Brug, 1931)
ningheensis (Lei, 1989)
notoscriptus (Skuse, 1889)
 ssp. montanus (Brug, 1939)
novalbitarsis (King & Hoogstraal, 1946)
nyasae (Edwards, 1930)
occidentalis (Skuse, 1889)
oreophilus Edwards, 1916
pallirostris (Edwards, 1922)
palmarum (Edwards, 1924)
papuensis (Taylor, 1914)
peipingensis (Feng, 1938)
plagosus (Marks, 1959)
plumiferus (King & Hoogstraal, 1946)
prominens (Barraud, 1923)
pseudotaeniatus (Giles, 1901)

- pulchrithorax* (Edwards, 1939)
pulchriventer (Giles, 1901)
quasirubithorax (Theobald, 1910)
queenslandis (Strickland, 1911)
quinquelineatus (Edwards, 1922)
reinerti (Rattanarithikul & Harrison, 1988)
rizali (Banks, 1906)
roai (Belkin, 1962)
rubiginosus (Belkin, 1962)
rubrithorax (Macquart, 1850)
rupestris (Dobrotworsky, 1959)
saxicola Edwards, 1922
seoulensis (Yamada, 1921)
shehzadae (Qutubuddin, 1972)
sherki (Knight, 1948)
shortti (Barraud, 1923)
simlensis (Edwards, 1922)
sintoni (Barraud, 1924)
stanleyi (Peters, 1963)
stevensoni (Barraud, 1923)
subalbitarsis (King & Hoogstraal, 1946)
subauridorsum (Marks, 1948)
subbasalis (Dobrotworsky, 1962)
suffusus (Edwards, 1922)
tonkinensis (Galliard & Ngu, 1947)
toxopeusi (Bonne-Wepster, 1948)
tsiliensis (King & Hoogstraal, 1946)
tubbutiensis (Dobrotworsky, 1959)
unicinctus (Edwards, 1922)
versicolor (Barraud, 1924)
wasselli (Marks, 1947)
watasei (Yamada, 1921)
wellmanii (Theobald, 1905)
yunnanensis (Gaschen, 1934)
- Subgenus '*Macleaya*' Theobald, 1903 *sensu auctorum*
littlechildi (Taylor, 1933)
stoneorum (Marks, 1977)
tremulus (Theobald, 1903)
- Subgenus '*Molpemyia*' Theobald, 1910 *sensu auctorum*
auridorsum (Edwards, 1922)
pecuniosus (Edwards, 1922)
purpureus (Theobald, 1910)
- Subgenus '*Ochlerotatus*' Lynch Arribalzaga, 1891
sensu auctorum
aboriginis (Dyar, 1917)
abserratus (Felt & Young, 1904)
aculeatus (Theobald, 1903)
aenigmaticus (Cerqueira & Costa, 1946)
akkeshiensis (Tanaka, 1998)
albineus (Seguy, 1923)
albifasciatus (Macquart, 1838)
aloponotum (Dyar, 1917)
ambreensis (Rodhain & Boutonnier, 1983)
andersoni (Edwards, 1926)
angustivittatus (Dyar & Knab, 1907)
annulipes (Meigen, 1830)
- antipodeus* Edwards, 1920
atactavittatus (Arnell, 1976)
atropalpus (Coquillett, 1902)
auratus (Grabham, 1906)
aurifer (Coquillett, 1903)
behningi (Martini, 1926)
bejaranoi (Martinez, Carcavallo & Prosen, 1960)
berlandi (Seguy, 1921)
bimaculatus (Coquillett, 1902)
biskraensis (Brunes, 1999)
bogotanus (Arnell, 1976)
breedensis (Muspratt, 1953)
burjaticus (Kuchartshuk, 1973)
burpengaryensis (Theobald, 1905)
caballus (Theobald, 1912)
cacozelus (Marks, 1963)
calcariae (Marks, 1957)
calumnior (Belkin, Heinemann & Page, 1970)
campestris (Dyar & Knab, 1907)
camptorhynchus (Thomson, 1869)
canadensis (Theobald, 1901)
 ssp. mathesoni (Middlekauff, 1944)
cantans (Meigen, 1818)
 var. subvexans (Martini, 1922)
cantator (Coquillett, 1903)
caspius (Pallas, 1771)
 ssp. meirai (Ribeiro, Ramos, Capela & Pires, 1980)
 var. hargreavesi Edwards, 1920
cataphylla (Dyar, 1916)
chelli Edwards, 1915
churchillensis (Ellis & Brust, 1973)
clelandi (Taylor, 1914)
clivis (Lanzaro & Eldridge, 1992)
coluzzii (Rioux, Guilvard & Pasteur, 1998)
comitatus (Arnell, 1976)
condolecens (Dyar & Knab, 1907)
continentalis (Dobrotworsky, 1960)
crinifer (Theobald, 1903)
cunabulanus (Edwards, 1924)
cyprius (Ludlow, 1920)
cyprioides (Danilov & Stupin, 1982)
decticus (Howard, Dyar & Knab, 1917)
deficiens (Arnell, 1976)
deserticola (Zavortink, 1969)
detritus (Haliday, 1833)
diantaeus (Howard, Dyar & Knab, 1913)
duplex (Martini, 1926)
dupreei (Coquillett, 1904)
dzeta (Seguy, 1924)
edgari (Stone & Rosen, 1952)
eidsvoldensis (Mackerras, 1927)
epactius (Dyar & Knab, 1908)
eucephalaeus (Dyar, 1918)
euedes (Howard, Dyar & Knab, 1913)
euiris (Dyar, 1922)
euplocamus (Dyar & Knab, 1906)

- excrucians* (Walker, 1856)
explorator (Marks, 1964)
fitchii (Felt & Young, 1904)
flavescens (Müller, 1764)
flavidorsalis (Luh & Lee, 1975)
flavifrons (Skuse, 1889)
fluviatilis (Lutz, 1904)
grossbecki (Dyar & Knab, 1906)
gutzevichi (Dubitsky & Deshevykh, 1978)
hakusanensis (Yamaguti & Tamaboko, 1954)
harrisoni (Muspratt, 1953)
hastatus (Dyar, 1922)
hesperonotius (Marks, 1959)
hexodontus (Dyar, 1916)
hodgkini (Marks, 1959)
hokkaidensis (Tanaka, Mizusawa & Saugstad, 1979)
hortator (Dyar & Knab, 1907)
hungaricus (Mihalyi, 1955)
imperfectus (Dobrotworsky, 1962)
impiger (Walker, 1848)
 ssp. *daisetsuzanus* (Tanaka, Mizusawa & Saugstad, 1979)
implicatus (Vockeroth, 1954)
incomptus (Arnell, 1976)
increpitus (Dyar, 1916)
inexpectatus (Bonne-Wepster, 1948)
intermedius (Danilov & Gornostaeva, 1987)
intrudens (Dyar, 1919)
jacobinae (Serafim & Davis, 1933)
jorgi (Carpintero & Leguizamon, 2000)
juppi (McIntosh, 1973)
kasachstanicus (Gutsevich, 1962)
laguna (Arnell & Nielsen, 1972)
lasaensis (Meng, 1962)
 ssp. *gyirongensis* (Ma, 1982)
lepidus (Cerqueira & Paraense, 1945)
leucomelas (Meigen, 1804)
linesi (Marks, 1964)
longifilamentus (Su & Zhang, 1988)
luteifemur (Edwards, 1926)
macintoshi (Marks, 1959)
mariae (Sergent & Sergent, 1903)
martineti (Senevet, 1937)
mcdonaldi (Belkin, 1962)
melanimon (Dyar, 1924)
meprai (Martinez & Prosen, 1953)
mercurator (Dyar, 1920)
milleri (Dyar, 1922)
mittchellae (Dyar, 1905)
montchadskyi (Dubitsky, 1968)
monticola (Belkin & McDonald, 1957)
muelleri (Dyar, 1920)
nevadensis (Chapman & Barr, 1964)
nigrinus (Eckstein, 1918)
nigripes (Zetterstedt, 1838)
nigrithorax (Macquart, 1847)
nigrocanus (Martini, 1927)
nigromaculis (Ludlow, 1906)
niphadopsis (Dyar & Knab, 1918)
nivalis (Edwards, 1926)
normanensis (Taylor, 1915)
nubilis (Theobald, 1903)
obturbator (Dyar & Knab, 1907)
oligopistus (Dyar, 1918)
patersoni (Shannon & del Ponte, 1928)
pectinatus (Arnell, 1976)
pennai (Antunes & Lane, 1938)
perkinsi (Marks, 1949)
pertinax (Grabham, 1906)
perventor (Cerqueira & Costa, 1946)
phaecasiatus (Marks, 1964)
phaeonotus (Arnell, 1976)
phoeniciae (Coluzzi & Sabatini, 1968)
pionips (Dyar, 1919)
procax Skuse, 1889
pseudonormanensis (Marks, 1949)
pulcritarsis (Rondani, 1872)
 ssp. *asiaticus* (Edwards, 1926)
pullatus (Coquillett, 1904)
punctodes (Dyar, 1922)
punctor (Kirby, 1837)
purpuraceus (Brug, 1932)
purpureifemur (Marks, 1959)
purpuriventris (Edwards, 1926)
ratcliffi (Marks, 1959)
raymondi (del Ponte, Castro & Garcia, 1951)
rempeli (Vockeroth, 1954)
rhyacophilus (da Costa Lima, 1933)
riparius (Dyar & Knab, 1907)
riparioides (Su & Zhang, 1987)
sagax (Skuse, 1889)
sapiens (Marks, 1964)
schizopinax (Dyar, 1929)
schtakelbergi (Shingarev, 1928)
scutellalbum (Boshell-Manrique, 1939)
sedaensis (Lei, 1989)
sergievi (Danilov, Markovich & Proskuryakova, 1978)
serratus (Theobald, 1901)
shannoni (Vargas & Downs, 1950)
sierrensis (Ludlow, 1905)
silvestris (Dobrotworsky, 1961)
simanini (Gutsevich, 1966)
sinkiangensis (Hsiao, 1977)
spencerii (Theobald, 1901)
 ssp. *idahoensis* (Theobald, 1903)
spilotus (Marks, 1963)
squamiger (Coquillett, 1902)
sticticus (Meigen, 1838)
stigmaticus (Edwards, 1922)
stimulans (Walker, 1848)
stramineus (Dubitzky, 1970)

- stricklandi* Edwards, 1912
subalbirostris (Klein & Marks, 1960)
surcoufi (Theobald, 1912)
synchytus (Arnell, 1976)
taeniorhynchus (Wiedemann, 1821)
tahoensis (Dyar, 1916)
thelcter (Dyar, 1918)
theobaldi (Taylor, 1914)
thibaulti (Dyar & Knab, 1910)
tormentor (Dyar & Knab, 1906)
tortilis (Theobald, 1903)
trivittatus (Coquillett, 1902)
turneri (Marks, 1963)
upatensis (Anduze & Hecht, 1943)
varipalpus (Coquillett, 1902)
ventrovittis (Dyar, 1916)
vigilax (Skuse, 1889)
 ssp. *ludlowae* (R. Blanchard, 1905)
 ssp. *vansomeranae* (Mattingly, 1955)
vittiger (Skuse, 1889)
washinoi (Lanzaro & Eldridge, 1992)
zammitii (Theobald, 1903)
- Subgenus 'Protomacleaya' Theobald, 1907 *sensu auctorum*
- aitkeni* (Schick, 1970)
alboapicus (Schick, 1970)
amabilis (Schick, 1970)
argyrothorax (Bonne-Wepster & Bonne, 1920)
berlini (Schick, 1970)
bertrami (Schick, 1970)
braziliensis (Gordon & Evans, 1922)
brelandi (Zavortink, 1972)
buenaventura (Schick, 1970)
burgeri (Zavortink, 1972)
campana (Schick, 1970)
casali (Schick, 1970)
chionotum (Zavortink, 1972)
daryi (Schick, 1970)
diazi (Schick, 1970)
gabriel (Schick, 1970)
galindoi (Schick, 1970)
hendersoni (Cockerell, 1918)
heteropus (Dyar, 1921)
homoeopus (Dyar, 1922)
idanus (Schick, 1970)
impostor (Schick, 1970)
insolitus (Coquillett, 1906)
knabi (Coquillett, 1906)
kompi (Vargas & Downs, 1950)
metoecopus (Dyar, 1925)
niveoscutum (Zavortink, 1972)
podographicus (Dyar & Knab, 1906)
sandrae (Zavortink, 1972)
schicki (Zavortink, 1972)
schroederi (Schick, 1970)
sumidero (Schick, 1970)
- tehuantepec* (Schick, 1970)
terrens (Walker, 1856)
thorntoni (Dyar & Knab, 1907)
triseriatus (Say, 1823)
vargasi (Schick, 1970)
zavortinki (Schick, 1970)
zoosophus (Dyar & Knab, 1918)
- Subgenus 'Pseudoskusea' Theobald, 1907 *sensu auctorum*
- bancroftianus* (Edwards, 1921)
culiciformis (Theobald, 1905)
multiplex (Theobald, 1903)
postspiraculosus (Dobrotworsky, 1961)
- Subgenus uncertain
- daliensis* (Taylor, 1916)
- Opifex* Hutton, 1902
- Subgenus *Nothoskusea* Dumbleton, 1962, transferred from *Ochlerotatus*
- chathamicus* (Dumbleton, 1962), **comb. nov.**
- Subgenus *Opifex*
- fuscus* Hutton, 1902
- Paraedes* Edwards, 1934, **stat. nov.**, restored to genus rank
- barraudi* Edwards, 1934, **comb. nov.**
bonneae (Mattingly, 1958), **comb. nov.**
chrysoseuta (Theobald, 1910), **comb. nov.**
collessi (Mattingly, 1958), **comb. nov.**
menoni (Mattingly, 1958), **comb. nov.**
ostentatio (Leicester, 1908), **comb. nov.**
pagei (Ludlow, 1911), **comb. nov.**
thailandensis (Reinert, 1976), **comb. nov.**
- Pseudarmigeres* Stone & Knight, 1956, **stat. nov.**, raised to genus rank
- albomarginatus* (Newstead, 1907), **comb. nov.**
argenteoventralis (Theobald, 1909), **comb. nov.**
 ssp. *dunni* (Evans, 1928), **comb. nov.**
kummi (Edwards, 1930), **comb. nov.**
michaelikati (van Someren, 1946), **comb. nov.**
 ssp. *gurneri* (van Someren, 1946), **comb. nov.**
natalensis (Edwards, 1930), **comb. nov.**
- Psorophora* Robineau-Desvoidy, 1827
- Subgenus *Grabhamia* Theobald, 1903
- cingulata* (Fabricius, 1805)
columbiae (Dyar & Knab, 1906)
confinnis (Lynch Arribalzaga, 1891)
dimidiata Cerqueira, 1943
discolor (Coquillett, 1903)
infinis (Dyar & Knab, 1906)
insularia (Dyar & Knab, 1906)
jamaicensis Theobald, 1901
leucocnemis Martini, 1931

- paulli* Paterson & Shannon, 1927
pruinosa Martini, 1935
pygmaea (Theobald, 1903)
santamarinae Broche, 2000
signipennis (Coquillett, 1904)
varinervis Edwards, 1922
- Subgenus *Janthinosoma* Lynch Arribalzaga, 1891
albigena (Peryassu, 1908)
albipes (Theobald, 1907)
amazonica Cerqueira, 1960
champerico (Dyar & Knab, 1906)
circumflava Cerqueira, 1943
cyanescens (Coquillett, 1902)
discrucians (Walker, 1856)
ferox (von Humboldt, 1819)
febrigi Edwards, 1922
forceps Cerqueira, 1939
horrida (Dyar & Knab, 1908)
johnstonii (Grabham, 1905)
lanei Shannon & Cerqueira, 1943
longipalpus Randolph & O'Neill, 1944
lutzii (Theobald, 1901)
mathesoni Belkin & Heinemann, 1975
melanota Cerqueira, 1943
mexicana (Bellardi, 1859)
pilosa Duret, 1971
pseudoalbipes Duret, 1971
pseudomelanota Barata & Cotrim, 1971
totonaci Lassmann, 1951
varipes (Coquillett, 1904)
- Subgenus *Psorophora*
ciliata (Fabricius, 1794)
cilipes (Fabricius, 1805)
holmbergii Lynch Arribalzaga, 1891
howardii Coquillett, 1901
lineata (von Humboldt, 1819)
ochripes (Macquart, 1850)
pallescens Edwards, 1922
pilipes (Macquart, 1834)
saeva Dyar & Knab, 1906
stonei Vargas, 1956
- Nomina dubia*
goeldii (Giles, 1904)
marmorata (Philippi, 1865)
perterrens (Walker, 1856)
- Rhinoskusea* Edwards, 1929, **stat. nov.**, raised to genus rank
longirostris (Leicester, 1908), **comb. nov.**
pillaii (Mattingly, 1958), **comb. nov.**
portonovoensis (Tewari & Hiriyan, 1992), **comb. nov.**
wardi (Reinert, 1976), **comb. nov.**
- Scutomyia* Theobald, 1904, **stat. nov.**, restored to genus rank
- albolineata* (Theobald, 1904), **comb. nov.**
arboricola (Knight & Rozeboom, 1946), **comb. nov.**
bambusicola (Knight & Rozeboom, 1946), **comb. nov.**
boharti (Knight & Rozeboom, 1946), **comb. nov.**
hoogstraali (Knight & Rozeboom, 1946), **comb. nov.**
impatibilis (Walker, 1859), **comb. nov.**
laffooni (Knight & Rozeboom, 1946), **comb. nov.**
platylepida (Knight & Hull, 1951), **comb. nov.**
pseudalbolineata (Brug, 1939), **comb. nov.**
- Skusea* Theobald, 1903, **stat. nov.**, raised to genus rank
cartroni (Ventrillon, 1906), **comb. nov.**
lambrechti (van Someren, 1971), **comb. nov.**
moucheti (Ravaonjanahary & Brunhes, 1977), **comb. nov.**
pembaensis (Theobald, 1901), **comb. nov.**
- Stegomyia* Theobald, 1901, **stat. nov.**, restored to genus rank
aegypti (Linnaeus, 1762), **comb. nov.**
 ssp. *formosa* (Walker, 1848), **comb. nov.**
africana Theobald, 1901, **comb. nov.**
agrihanensis (Bohart, 1957), **comb. nov.**
albopicta (Skuse, 1895), **comb. nov.**
alcasidi (Huang, 1972), **comb. nov.**
alorensis (Bonne-Wepster & Brug, 1932), **comb. nov.**
amalthea (de Meillon & Lavoipierre, 1944), **comb. nov.**
andrewsi (Edwards, 1926), **comb. nov.**
angusta (Edwards, 1935), **comb. nov.**
annandalei Theobald, 1910, **comb. nov.**
 ssp. *horishensis* (Yamada, 1921), **comb. nov.**
 var. *quadricincta* (Barraud, 1923), **comb. nov.**
aobae (Belkin, 1962), **comb. nov.**
apicoargentea Theobald, 1909, **comb. nov.**
 ssp. *denderensis* (Wolfs, 1949), **comb. nov.**
bambusae (Edwards, 1935), **comb. nov.**
burnsi (Basio & Reisen, 1971), **comb. nov.**
bromeliae Theobald, 1911, **comb. nov.**
calceata (Edwards, 1924), **comb. nov.**
chaussieri (Edwards, 1923), **comb. nov.**
chemulpoensis (Yamada, 1921), **comb. nov.**
contigua (Edwards, 1936), **comb. nov.**
cooki (Belkin, 1962), **comb. nov.**
corneti (Huang, 1986), **comb. nov.**
cozi (Cornet, 1973), **comb. nov.**
craggi Barraud, 1923, **comb. nov.**
cretina (Edwards, 1921), **comb. nov.**
daitensis (Miyagi & Toma, 1981), **comb. nov.**
deboeri (Edwards, 1926), **comb. nov.**
demeilloni (Edwards, 1936), **comb. nov.**
dendrophila (Edwards, 1921), **comb. nov.**
desmotes Giles, 1904, **comb. nov.**
dybasi (Bohart, 1957), **comb. nov.**

- edwardsi* Barraud, 1923, **comb. nov.**
flavopicta (Yamada, 1921), **comb. nov.**
 ssp. *downsi* (Bohart & Ingram, 1946), **comb. nov.**
 ssp. *miyarai* (Tanaka, Mizusawa & Saugstad, 1979), **comb. nov.**
fraseri Edwards, 1912, **comb. nov.**
futunae (Belkin, 1962), **comb. nov.**
galloisi (Yamada, 1921), **comb. nov.**
galloisiodes (Liu & Lu, 1984), **comb. nov.**
gardnerii Ludlow, 1905, **comb. nov.**
 ssp. *imitator* Leicester, 1908, **comb. nov.**
grantii Theobald, 1901, **comb. nov.**
guamensis (Farner & Bohart, 1944), **comb. nov.**
gurneyi (Stone & Bohart, 1944), **comb. nov.**
hakanssoni (Knight & Hurlbut, 1949), **comb. nov.**
hansfordi (Huang, 1997), **comb. nov.**
hebridea (Edwards, 1926), **comb. nov.**
heischi (van Someren, 1951), **comb. nov.**
hensilli (Farner, 1945), **comb. nov.**
hoguei (Belkin, 1962), **comb. nov.**
horrescens (Edwards, 1935), **comb. nov.**
josiahae (Huang, 1988), **comb. nov.**
katherinensis (Woodhill, 1949), **comb. nov.**
keniensis (van Someren, 1946), **comb. nov.**
kenyae (van Someren, 1946), **comb. nov.**
kesseli (Huang & Hitchcock, 1980), **comb. nov.**
kivuensis (Edwards, 1941), **comb. nov.**
krombeini (Huang, 1975), **comb. nov.**
lamberti (Ventrillon, 1904), **comb. nov.**
langata (van Someren, 1946), **comb. nov.**
ledgeri (Huang, 1981), **comb. nov.**
lilii Theobald, 1910, **comb. nov.**
luteocephala Newstead, 1907, **comb. nov.**
maehleri (Bohart, 1957), **comb. nov.**
malayensis (Colless, 1962), **comb. nov.**
malikuli (Huang, 1973), **comb. nov.**
marshallensis (Stone & Bohart, 1944), **comb. nov.**
mascarensis (MacGregor, 1924), **comb. nov.**
masseyi (Edwards, 1923), **comb. nov.**
mattinglyorum (Huang, 1994), **comb. nov.**
maxgermaini (Huang, 1990), **comb. nov.**
mediopunctata Theobald, 1905, **comb. nov.**
 var. *sureilensis* (Barraud, 1934), **comb. nov.**
metallica (Edwards, 1912), **comb. nov.**
mickevichae (Huang, 1988), **comb. nov.**
muroafcete (Huang, 1997), **comb. nov.**
neoafricana (Cornet, Valade & Dieng, 1978), **comb. nov.**
neogalloisi (Chen & Chen, 2000), **comb. nov.**
neopandani (Bohart, 1957), **comb. nov.**
njombiensis (Huang, 1997), **comb. nov.**
noalbopicta (Barraud, 1931), **comb. nov.**
opok (Corbet & van Someren, 1962), **comb. nov.**
palauensis (Bohart, 1957), **comb. nov.**
pandani (Stone, 1939), **comb. nov.**
patriciae (Mattingly, 1954), **comb. nov.**
paullusi (Stone & Farner, 1945), **comb. nov.**
pernotata (Farner & Bohart, 1944), **comb. nov.**
perplexa Leicester, 1908, **comb. nov.**
polynesiensis (Marks, 1951), **comb. nov.**
poweri Theobald, 1905, **comb. nov.**
pseudalbopicta Borel, 1928, **comb. nov.**
pseudoafricana (Chwatt, 1949), **comb. nov.**
pseudonigeria Theobald, 1910, **comb. nov.**
pseudoscutellaris Theobald, 1910, **comb. nov.**
quasiscutellaris (Farner & Bohart, 1944), **comb. nov.**
rhungkiangensis (Chang & Chang, 1974), **comb. nov.**
riversi (Bohart & Ingram, 1946), **comb. nov.**
robinsoni (Belkin, 1962), **comb. nov.**
rotana (Bohart & Ingram, 1946), **comb. nov.**
rotumae (Belkin, 1962), **comb. nov.**
ruwenzori (Haddow & van Someren, 1950), **comb. nov.**
saimedres (Huang, 1988), **comb. nov.**
saipanensis (Stone, 1945), **comb. nov.**
schwetzi (Edwards, 1926), **comb. nov.**
scutellaris (Walker, 1859), **comb. nov.**
 ssp. *malayensis* (Colless, 1962), **comb. nov.**
scutoscripta (Bohart & Ingram, 1946), **comb. nov.**
seampi (Huang, 1974), **comb. nov.**
seatoi (Huang, 1969), **comb. nov.**
segermanae (Huang, 1997), **comb. nov.**
sibirica (Danilov & Filippova, 1978), **comb. nov.**
simpsoni Theobald, 1905, **comb. nov.**
soleata (Edwards, 1924), **comb. nov.**
strelitziae (Muspratt, 1950), **comb. nov.**
subalbopicta (Barraud, 1931), **comb. nov.**
subargentea (Edwards, 1925), **comb. nov.**
tabu (Ramalingam & Belkin, 1965), **comb. nov.**
tongae (Edwards, 1926), **comb. nov.**
tulagiensis (Edwards, 1926), **comb. nov.**
unilineata (Theobald, 1906), **comb. nov.**
upolensis (Marks, 1957), **comb. nov.**
usambara (Mattingly, 1953), **comb. nov.**
varuae (Belkin, 1962), **comb. nov.**
vinsoni (Mattingly, 1953), **comb. nov.**
wadai (Tanaka, Mizusawa & Saugstad, 1979), **comb. nov.**
w-albus Theobald, 1905, **comb. nov.**
woodi (Edwards, 1922), **comb. nov.**
Nomina dubia
ciliaris (Linnaeus, 1767), **comb. nov.**
nivea (von Eichwald, 1837), **comb. nov.**
rimandoi (Basio, 1971), **comb. nov.**
Tanakaius Reinert, Harbach & Kitching, **gen. nov.**
savoryi (Bohart, 1957), **comb. nov.**
togoi (Theobald, 1907), **comb. nov.**
Udaya Thurman, 1954
argyrurus (Edwards, 1934)

- lucaris* Macdonald & Mattingly, 1960
subs similis (Barraud, 1927)
- Verrallina* Theobald, 1903
 Subgenus *Harbachius* Reinert, 1999
abdita (Barraud, 1931)
consonensis (Reinert, 1973)
fragilis Leicester, 1908
hamistylus (Laffoon, 1946)
indecorabilis Leicester, 1908
nobukonis (Yamada, 1932)
pahangi (Delfinado, 1968)
ramalingami (Reinert, 1974)
robertsi (Laffoon, 1946)
srilankensis (Reinert, 1977)
stunga (Klein, 1973)
uniformis (Theobald, 1910)
yusafi (Barraud, 1931)
- Subgenus *Neomacleaya* Theobald, 1907
adusta (Laffoon, 1946)
agrestis (Barraud, 1931)
andamanensis (Edwards, 1922)
assamensis Bhattacharyya, Tewari, Prakesh, Mohapatra & Mahanta, 2004
atriisimilis (Tanaka & Mizusawa, 1973)
atria (Barraud, 1928)
campylostylus (Laffoon, 1946)
cauta (Barraud, 1928)
clavata (Barraud, 1931)
comata (Barraud, 1931)
comosa (Reinert, 1974)
cretata (Delfinado, 1967)
cyrtolabis (Edwards, 1928)
gibbosa (Delfinado, 1967)
harrisonica (Reinert, 1974)
hispidata (Delfinado, 1967)
incerta (Edwards, 1922)
indica (Theobald, 1907)
johnsoni (Laffoon, 1946)
johorensis (Reinert, 1974)
komponga (Klein, 1973)
lankaensis (Stone & Knight, 1958)
latipennis (Delfinado, 1967)
leicesteri (Edwards, 1917)
macrodixoa (Dyar & Shannon, 1925)
margarsen (Dyar & Shannon, 1925)
neomacrodixoa (King & Hoogstraal, 1947)
nigrotarsis (Ludlow, 1908)
notabilis (Delfinado, 1967)
nubicola (Laffoon, 1946)
panayensis (Ludlow, 1914)
petrolephantus (Wijesundara, 1951)
philippinensis (Delfinado, 1968)
phnoma (Klein, 1973)
prioekanensis (Brug, 1931)
protuberans (Delfinado, 1967)
- pseudodiurna* (Theobald, 1910)
pseudomediofasciata (Theobald, 1910)
pseudovarietas (Reinert, 1974)
rami (Barraud, 1928)
rara (Delfinado, 1968)
sabahensis (Reinert, 1974)
seculata (Menon, 1950)
singularis (Leicester, 1908)
sohni (Reinert, 1974)
spermathecus (Wijesundara, 1951)
torosa (Delfinado, 1967)
uncus (Theobald, 1901)
vallistris (Barraud, 1928)
varietas (Leicester, 1908)
virilis Leicester, 1908
yerburyi (Edwards, 1917)
- Subgenus *Verrallina*
azureosquamata (Bonne-Wepster, 1948)
bifoliata (King & Hoogstraal, 1947)
butleri (Theobald, 1901)
carmenti (Edwards, 1924)
cuccioi (Belkin, 1962)
cunninghami (Taylor, 1944)
dux (Dyar & Shannon, 1925)
embiensis (Huang, 1968)
foliformis (King & Hoogstraal, 1947)
funerea (Theobald, 1903)
iriomotensis (Tanaka & Mizusawa, 1973)
killertonis (Huang, 1968)
leilae (King & Hoogstraal, 1947)
lineata (Taylor, 1914)
lugubris (Barraud, 1928)
mccormicki (Belkin, 1962)
milnensis (King & Hoogstraal, 1947)
multifolium (King & Hoogstraal, 1947)
obsoleta (Huang, 1968)
parasimilis (King & Hoogstraal, 1947)
pipkini (Bohart, 1957)
quadrifolium (Brug, 1934)
quadrispinata (King & Hoogstraal, 1947)
reesi (King & Hoogstraal, 1947)
sentania (King & Hoogstraal, 1947)
similis (Theobald, 1910)
simpla (King & Hoogstraal, 1947)
trispinata (King & Hoogstraal, 1947)
vanapa (Huang, 1968)
variabilis (Huang, 1968)
- Nomen dubium*
perdita Leicester 1908, **stat. nov.**⁴
- Zavortinkius* Reinert, 1999, **stat. nov.**, raised to genus rank
brunhesi (Reinert, 1999), **comb. nov.**
brygooi (Brunhes, 1971), **comb. nov.**
fulgens (Edwards, 1917), **comb. nov.**
geoffroyi (Reinert, 1999), **comb. nov.**

huangae (Reinert, 1999), **comb. nov.**
interruptus (Reinert, 1999), **comb. nov.**
longipalpis (Grünberg, 1905), **comb. nov.**
monetus (Edwards, 1935), **comb. nov.**
mzooi (van Someren, 1962), **comb. nov.**
phillipi (van Someren, 1949), **comb. nov.**
pollinator (Graham, 1910), **comb. nov.**

Zeugomyia Leicester, 1908
aguilari Baisas & Feliciano, 1953
fajardoi Baisas & Feliciano, 1953
gracilis Leicester, 1908
lawtoni Baisas, 1946

APPENDIX 5

Recommended two-letter abbreviations for aedine genera.

Abraedes Zavortink = *Ab.*
Aedes Meigen = *Ae.*
Alanstonea Mattingly = *As.*
Albuginosus Reinert = *Al.*
Armigeres Theobald = *Ar.*
Ayurakitia Thurman = *Ay.*
Aztecaedes Zavortink = *Az.*
Belkinus Reinert = *Be.*
Bothaella Reinert = *Bo.*
Christophersomyia Barraud = *Cr.*
Diceromyia Theobald = *Di.*
Downsiomyia Vargas = *Do.*
Edwardsaedes Belkin = *Ed.*
Eretmapodites Theobald = *Er.*

Finlaya Theobald = *Fl.*
Fredwardsius Reinert = *Fr.*
Geoskusea Edwards = *Ge.*
Gymnometopa Coquillett = *Gy.*
Haemagogus Williston = *Hg.*
Halaedes Belkin = *Ha.*
Heizmannia Ludlow = *Hh.*
Howardina Theobald = *Hw.*
Huaedes Huang = *Hu.*
Indusius Edwards = *In.*
Isoaedes Reinert = *Ia.*
Kenknightia Reinert = *Ke.*
Kompia Aitken = *Ko.*
Leptosomatomyia Theobald = *Lp.*
Levua Stone & Bohart = *Le.*
Lorrainea Belkin = *Lo.*
Mucidus Theobald = *Mu.*
Neomelaniconion Newstead = *Ne.*
Ochlerotatus Lynch Arribalzaga = *Oc.*
Opifex Hutton = *Op.*
Paraedes Edwards = *Pr.*
Pseudarmigeres Stone & Knight = *Pa.*
Psorophora Robineau-Desvoidy = *Ps.*
Rhinoskusea Edwards = *Rh.*
Scutomyia Theobald = *Sc.*
Skusea Theobald = *Sk.*
Stegomyia Theobald = *St.*
Tanakaius Reinert, Harbach & Kitching = *Ta.*
Udaya Thurman = *Ud.*
Verrallina Theobald = *Ve.*
Zavortinkius Reinert = *Za.*
Zeugomyia Leicester = *Ze.*