

Phylogeny of the leafhopper subfamily Deltocephalinae (Insecta: Auchenorrhyncha: Cicadellidae) and related subfamilies based on morphology

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Abstract Previous phylogenetic analyses of the leafhopper family Cicadellidae based on morphological and molecular data suggested that Deltocephalinae, as traditionally defined, is polyphyletic. These analyses recovered a large clade comprising Deltocephalinae and several other subfamilies. To further elucidate relationships within this large clade of deltocephaline-like leafhoppers, an expanded dataset of 119 morphological characters and 68 taxa was compiled and analysed using cladistic methods. The taxon sample included one or more representatives of nearly all previously recognised tribes of Deltocephalinae, representatives of the non-deltocephaline family-group taxa which grouped with Deltocephalinae in previous analyses, and six putative outgroup taxa drawn from other cicadellid subfamilies. The resulting most parsimonious trees consistently recovered the putative ingroup as monophyletic. However, in agreement with previous analyses, most subfamilies and tribes represented by multiple exemplars were not resolved as monophyletic groups. Based on these results, subfamilies derived from within the deltocephaline lineage include Acostemminae, Arrugadinae, Drakensbergeninae, Eupelicinae, Koebeliinae, Mukariinae, Paraboloponinae, Penthimiinae, Selenocephalinae and Stegelytrinae. The phylogeny indicates that grass specialisation is much more phylogenetically conservative than implied by the current higher classification of leafhoppers. A list of synapomorphies on the strict consensus tree and an illustrated key to all family-group taxa of deltocephaline-like leafhoppers are provided.

Key words Cicadellidae, Deltocephalinae, leafhopper, morphology, parsimony, classification, grassland.

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Introduction

Background

With over 6500 described species placed in nearly 800 genera the leafhopper subfamily Deltocephalinae (sensu Oman *et al.*, 1990) is currently the largest subfamily of Cicadellidae, itself among the largest insect families with over 22 000 described species and with many thousands more awaiting description (Oman *et al.*, 1990; Dietrich *et al.*, 2001; Dietrich & Rakitov, 2002).

Deltocephalines and members of related subfamilies feed preferentially on the phloem sap of a wide variety of vascular plants and show varying degrees of host fidelity. Often, leafhopper genera specialise on a particular plant genus or family. Other genera are less constrained to particular plant taxa, and feed on a variety of herbaceous and woody flowering plants. Perhaps the most conspicuous host use pattern found in the deltocephaline lineage is specialisation on grasses and sedges, occurring almost ubiquitously in at least 11 higher taxa treated here (Cicadulini, Deltocephalini, Paralimnini, Doraturini, Chiasmusini, Hecalini, Macrostelini, Stenometopiini, Eupelicinae, Drakensbergeninae and Mukariinae). In grasslands, deltocephalines are among the most numerically dominant and speciose groups of herbivores (Hamilton, 1995; Whitcomb *et al.*, 1987a, b; Dietrich, 1999). This association has attracted attention in evolutionary studies (see Whitcomb *et al.*, 1987a; b, 1994; Whitcomb & Hicks, 1988; Dietrich *et al.*, 1997; Dietrich, 1999), some of which indicate that some lineages are monophagous to oligophagous within particular genera or higher taxa of grasses (Whitcomb *et al.*, 1987b). Because of their high abundance, degree of host-plant specialisation, and responsiveness to disturbance, conservationists have recognised grassland leafhoppers as excellent indicators of habitat quality and ideal organisms for use in studying grassland biodiversity and conservation (Hamilton, 1999; Biedermann *et al.*, 2005).

By virtue of their ability to transmit plant pathogens, leafhoppers are an economically important group of insects. Deltocephalines account for 117 of 151, or 77%, of cicadellid vector species reported by Nielson (1968), and because of the relative value of the crops they infect, are economically the most important of all groups of leafhoppers (Oman, 1949). For example, species of the Old World genus *Nephotettix* Matsumura transmit tungro and other viruses injurious to rice (Wilson & Claridge, 1985). Another well known deltocephaline vector is *Dalbulus maidis* (DeLong & Wolcott), the corn leafhopper, which, along with some congeners, transmits three different pathogens causing corn stunt, the most important disease affecting maize in Latin America (Nault, 1985).

Deltocephalinae are distributed worldwide, and many tribes are cosmopolitan (Athysanini, Balcluthini, Deltocephalini, Doraturini, Hecalini, Macrostelini, Paralimnini, Platymetopiini, Scaphoideini, Scaphytopiini, Stenometopiini) but other tribes are more locally distributed. For example, Cochlorhinini is endemic to western North America (with one species introduced to Chile), a distribution that is shared with Koebeliina *sensu* Dietrich & Dmitriev (2003). Grypotina *sensu* Dietrich &

Dmitriev (2003) and Fieberiellini are principally Palearctic and Oriental, each with one adventive species in North America. Acinopterini is distributed only in the New World. Eupelicinae exist in most of the world, but are conspicuously absent from the Neotropics, while apparently related groups Drakensbergeninae and Arrugadinae occur in South Africa and South America, respectively. Several tribes placed in Selenocephalinae (Dwightlini, Adamini and Ianeirini) are exclusively Ethiopian. The subfamily Acostemminae is mostly Malagasy. Other selenocephaline tribes (Paraboloponini *sensu* Zhang & Webb 1996, Drabescini, and Selenocephalini) are exclusively Old World, and are most diverse in the tropics. Often, large and distinctive groups typify the fauna of tropical rainforests, including Paraboloponini, Penthimiinae and Scaphoideini of the Asian tropics, the selenocephaline tribes in Africa and Asia, and the *Bahita*-group genera (*sensu* Linnavuori & DeLong, 1978) in the New World tropics.

The ecology of a few deltocephaline species, mainly those of economic importance, has been studied thoroughly. Unfortunately, many species are known only from museum specimens, and virtually nothing is known about their ecology or host associations. Thus, more life history data, in addition to knowledge of phylogenetic relationships, are needed to correctly interpret and frame evolutionary hypotheses and to understand the factors leading to the high diversity of Deltocephalinae.

Classification

The higher classification of Deltocephalinae is unstable and no classifications of the group have been based on explicit phylogenetic hypotheses. Previous attempts to characterise the group are inadequate because different authors emphasised different, sometimes conflicting, suites of morphological characters, and most have focused only on regional faunas which do not provide the broad perspective needed for a comprehensive classification.

Some of the most relevant and inclusive classifications of the group in the past 60 years are those of Evans (1947), Oman (1949), Linnavuori (1959), Metcalf (1967), Hamilton (1975), Linnavuori & Al-Ne'amy (1983), and Oman *et al.* (1990). Evans' (1947) classification was based mostly on the morphology of the head and wings, and Hamilton's (1975) circumscription of Aphrodinae also used some of these characters in combination with those of the legs and chaetotaxy, and to some extent, male genitalia. Oman's (1949) classification of tribes was based mostly on external characters, but generic groupings within his broad circumscription of Deltocephalini were based mostly on the male genitalia. Linnavuori (1959) and Linnavuori & Al-Ne'amy (1983) also utilised external characters of the head and male genitalia, but also emphasised novel chaetotaxic and female genitalic characters. Finally, Metcalf (1967) and Oman *et al.* (1990) provided provisional classifications in their catalogues, but did not support these with morphological characterisations of the recognised groups. Because the classification of Oman *et al.* (1990) is the most recent and thorough classification of all family group taxa of Cicadellidae, and for consistency and ease of communication

in this treatment, we refer to subfamilies and tribes according to this classification except where noted. However, we recognise that recent changes to the classification have been made, and do not intend to discount them by using the classification of Oman *et al.* (1990) here.

Some recent reviews of deltocephaline-like subfamilies have noted the insufficient characterisations of these groups and of Deltocephalinae. Zhang and Webb (1996) reviewed the characters purported to define Selenocephalinae, reporting that some do not occur in all selenocephaline tribes, and that many are also shared with members of Acostemminae, Penthimiinae, and Deltocephalinae. They concluded that Selenocephalinae is not defined by any universally shared apomorphic characters, and that morphological characters purported to separate the group from Deltocephalinae are insufficient.

In describing some unusual Neotropical deltocephalines, Dietrich and Rakitov (2002) provided an expanded classification of Deltocephalinae. Based on molecular (Dietrich *et al.*, 2001) and morphological (Dietrich, 1999) data, they considered Penthimiinae, Eupelicinae, Selenocephalinae and Paraboloponinae to be synonyms of Deltocephalinae. They also provided a morphological characterisation of the subfamily, herein referred to as Deltocephalinae *sensu lato*.

Previous phylogenetic analyses

Few phylogenetic analyses have attempted to resolve relationships within Deltocephalinae, and most of these have focused on relationships within tribes (e.g. Fang *et al.*, 1993; Kamitani, 1999) or genera (e.g. Ross, 1968; Hamilton, 1994; Dietrich *et al.*, 1997). In the most comprehensive cladistic analysis to date, Knight and Webb (1993) analysed the world genera of Balcluthini, Coryphaelini and Macrostelini, and also included the nominate genera of most deltocephaline tribes listed by Oman *et al.* (1990) as outgroup taxa. Their stated goal was not to elucidate the relationships among the deltocephaline tribes, but to resolve relationships among the macrosteline genera and to represent variation in the outgroup. Thus, no conclusions were made regarding the relationships of the other deltocephaline tribes. Nevertheless, they included some characters that were informative only for the outgroup taxa, and in this way contributed to subsequent, more comprehensive analyses. Based on their results, they treated Balcluthini and Coryphaelini as junior synonyms of Macrostelini, and provided a more precise diagnosis of the group. Their results were largely congruent with Triplehorn and Nault's (1985) much more limited analysis of Macrostelini.

Dietrich's (1999) morphology-based phylogenetic analysis of Cicadellidae, which included all recognised subfamilies, grouped leafhoppers into three main lineages. One of these comprised Deltocephalinae and several other subfamilies, including Euacanthellinae, Aphrodinae, Xestocephalinae, Acostemminae, Neobalinae, Stegelytrinae, Mukariinae, Penthimiinae, Paraboloponinae and Selenocephalinae. Four subfamilies were derived from Deltocephalinae: Arrugadinae, Drakensbergeninae, Koebeliinae and Eupelicinae.

Dietrich *et al.* (2001) obtained similar results in a phylogenetic analysis of Membracoidea using 28S rDNA sequence data, recovering a well-supported clade containing Deltoceph-

alinae *s.l.*, and obtaining moderate bootstrap support for a sister-group relationship between this clade and *Placidellus* Evans (Stegelytrinae *sensu* Webb, 1999). The analysis also indicated a possible sister group relationship between *Placidellus* + Deltocephalinae *s.l.* and Neocoelidiinae, but relationships to other Cicadellidae were poorly resolved. Within the deltocephaline clade there was strong support for Acinopterini and Fieberiellini at the base, and strong support for a clade containing the remainder of Deltocephalinae *s.l.* Although the 28S rDNA data appear to resolve more ancient relationships and relatively recent ones (between closely related genera, unpublished data), many intermediate-level relationships remain poorly resolved.

These results agree with comparative morphological studies (e.g. Zhang & Webb, 1996), indicating that Deltocephalinae *sensu* Oman *et al.* (1990) is paraphyletic and that several groups currently treated as separate subfamilies are morphologically derived members of the deltocephaline lineage. Some of these previously recognised subfamilies are poorly defined and their relationships remain obscure. The present study builds on previous analyses by examining relationships within this lineage of 'deltocephaline-like' subfamilies using an expanded taxon sample and a large number of morphological characters. The resulting phylogenetic estimate will begin to form the basis for a revised classification of deltocephaline family-group taxa and will provide a framework for more detailed phylogenetic analyses that test hypotheses concerning the roles of host and habitat use and biogeography in the evolutionary history and diversification of the group.

Materials and methods

Terminal taxa

We used exemplar species as terminal taxa rather than supra-specific terminals, for several reasons. Use of exemplars avoids the assumption of monophyly of previously defined higher taxa, which is highly dubious for many of the larger tribes. For these groups, multiple exemplars were included to span some of the observed morphological diversity. This approach facilitated testing the monophyly of these diverse taxa and tested the ability of the data to resolve some relationships within these groups. Using exemplars also facilitates the addition of data, particularly DNA sequences (see Prendini, 2001 and Yeates, 1995 for further discussion).

When possible, we scored characters for species in the type genus of each tribe. While this approach is not necessarily ideal, as the type may not adequately represent the groundplan of its respective lineage, in most cases, no prior phylogenetic hypotheses were available upon which to base exemplar species selection. Use of type genera will at least help stabilise the nomenclature of higher taxa found not to be monophyletic.

Taxon sampling

The family-group taxa chosen for study reflect current and previous classifications, most notably Oman *et al.* (1990), Hamilton (1975), and Linnavuori & Al-Ne'amy (1983), and

also recent phylogenetic analyses (Dietrich, 1999; Dietrich *et al.*, 2001). About two-thirds of the taxa included here have been traditionally placed in Deltocephalinae (see Table 1 (which is available as “Supplementary data” on Cambridge Journals Online: http://www.journals.cup.org/abstract_S1477200007002617) for a list of taxa included in the analysis). Oman *et al.* (1990) recognised 23 tribes in the subfamily. At least one member of each tribe was included, and multiple members were included for the larger tribes. An effort was also made to include members of the tribes and subtribes recognised by Hamilton (1975) in his alternative classification of Aphrodinae *sensu lato*.

In addition to taxa included by Oman *et al.* (1990) in Deltocephalinae, representatives of other subfamilies were included in cases where recent phylogenetic analyses (Dietrich, 1999; Dietrich *et al.*, 2001) and/or comparative morphological study (Linnavuori, 1979a) indicated a close relationship to Deltocephalinae. Representatives from six of the seven tribes in the subfamily Selenocephalinae (*sensu* Linnavuori & Al-Ne’amy, 1983 and Zhang & Webb, 1996) were examined (representatives of Ianeirini were not available). Others included Acostemminae, Arrugadinae, Drakensbergeninae, Eupelicinae (one of the four tribes, Listrophorini, was not available), Mukariinae and Penthimiinae.

Koebeliinae was included following Dietrich and Dmitriev (2003), who considered this a synonym of the deltocephaline tribe Grypotini. Despite Oman *et al.*’s (1990) placement of *Anoterostemma* in Cicadellinae (Anoterostemmini), the genus was included based on the deltocephaline-like male genitalia and Dmitriev’s (2000, 2002b) placement of the genus in Limotettigini (considered a synonym of Athysanini by Oman *et al.*, 1990). Occinirvanini, transferred from Nirvaninae to Deltocephalinae by Dietrich (2004), was not included.

Stegelytrinae (*sensu* Webb, 1999) was included because previous analysis of 28S rDNA sequences placed *Placidellus* as sister to the remainder of the deltocephaline clade. The type genus, *Stegelytra*, and the Asian genus *Pachymetopius* Matsumura, were included here.

Putative outgroup taxa included *Lystridea* Baker, *Aphrodes* Curtis, *Calliscarta* Stål, *Chinaia* Bruner and Metcalf, *Portanus* Ball, and *Xestocephalus* Van Duzee. *Lystridea* was included because previous analyses placed Errhomenini as the most plesiomorphic member of Cicadellidae. The remaining putative outgroup taxa have at one time or another been suggested to be related to the deltocephaline lineage in previous classifications or in phylogenetic analyses (none with strong support). They were considered putative outgroups, because they were not included in a moderately well-supported clade including Deltocephalinae *s.l.* recovered by analysis of 28S rDNA (Dietrich *et al.*, 2001).

Voucher specimens for all taxa examined, except those on loan from other institutions, are housed at INHS. The data matrix is shown in Table 3.

Morphological characters

In selecting characters for the analysis, we gave preference to those that do not vary extensively within well-defined genera

or tribes. Nevertheless, given the size of this group, the lack of previous phylogenetic hypotheses, the scarcity of constant morphological characters defining higher taxa, and the wealth of highly variable characters, this was a difficult task. Several of the characters included vary within tribes, but were included either because previous authors have cited them as diagnostic for certain higher taxa or because the extent of variation with respect to the phylogeny of the group is not known. However, the most variable characters were excluded in an attempt to reduce the misleading effects of homoplasy.

In defining higher taxa, previous authors have emphasised different body regions in their classifications. Evans (1947) emphasised characters of the head (position of ocelli, position of sutures, etc.) and forewing, but Wagner (1951), Linnavuori (1959), Linnavuori & Al-Ne’amy (1983), Oman (1949) and Hamilton (1975) emphasised the male genitalia and leg chaetotaxy. We drew many of the characters for our analysis from these works.

Some of the most stable external characters, and presumably those most appropriate for higher level phylogenetic studies, include the position of the ocelli, the presence/absence of carinae on the anterior margin of the head, the development of the antennal ledges, the shape of the clypellus (=anteclypeus), the presence/absence of a single fine erect seta on the gena, the development of the lateral carina on the pronotum, the number of antepical cells of the forewing, the development of the appendix, the occurrence of some crossveins in the forewing, development of rows AV and AM and the intercalary row of the profemur, the hind femur macrosetal formula, and the shape, size, and setation of the first hind tarsomere. Although some homoplasy or loss of most or all of these characters occurs, they appear to be relatively stable and helpful in defining some tribes. Less stable external characters include variations in the colour patterns of the body, head, and forewing, reticulate venation of the forewing, and numbers of setae on some setal rows of the legs.

The homology and independence of some chaetotaxic characters is difficult to verify. There appears to be some degree of dependence between fore-, mid-, and hind leg rows of setae, for example. After initial coding, such potentially non-independent characters that showed a perfect correspondence of character states between taxa were combined into a single character (e.g. see character #47, Table 2). Another potential problem is that some leafhoppers appear to display reductions in chaetotaxy and may be coded as ‘absent or reduced’ for several characters. This may potentially give extra weight to what might be an overall reduction in chaetotaxy. However, not all taxa with reduced chaetotaxy have the same suite of reductions.

The male genitalia of this group provide some of the best higher-level characters as well as some of the best species-level characters. Characters that have been used partly to define higher taxa include shape of the style, the orientation of the anterior arms of the connective, the articulation or fusion of the connective with the aedeagus, the presence or absence of the basolateral membranous cleft on the pygofer, the shape of the valve, the articulation or fusion of the valve with the pygofer, the shape and/or fusion of the subgenital plates, the length and degree of sclerotisation of the anal tube, the position

Head

- (1) *Clypellar suture*: (0) straight (Fig. 1a); (1) arcuate (Fig. 1h). (0.062 0.500 0.031)
- (2) *Clypellar suture*: (0) complete; (1) obsolete medially. (0.333 0.333 0.111)
- (3) *Clypellus shape*: (0) tapered or parallel sided (Figs 1a,f,i,j); (1) expanded apically (Figs 1b,c,d,h,k); (2) ovoid. (0.222 0.774 0.172)
- (4) *Clypellus apex*: (0) not or only slightly produced beyond gena (Figs 1a–d,f,h–k); (1) greatly produced beyond gena (Fig. 1e); (2) not attaining normal curve of gena. (0.500 0.000 0.000)
- (5) *Clypellus*: (0) not inflated; (1) inflated. (0.143 0.250 0.036)
- (6) *Apical margin of clypellus*: (0) sinuate (Fig. 1f,i); (1) straight or convex (Figs 1a–d,h,j–k). (0.100 0.100 0.010)
- (7) *Lorum width*: (0) distinctly narrower than clypellus at base (Fig. 1a); (1) subequal to or wider than clypellus at base (Figs 1c,d). (0.111 0.619 0.069)
- Hamilton (1975) cited this character as distinguishing for some groups. It might be argued that it is not independent of character 3, the shape of the clypellus. However, as coded in this analysis, the two characters appear to be independent of each other; all possible character state combinations were observed.
- (8) *Lorum apex*: (0) widely separated from genal margin; (1) not widely separated. (0.333 0.000 0.000)
- (9) *Single fine erect seta on gena near lateral frontal suture*: (0) present (Figs 1a–e,g–k); (1) absent (Fig. 1f). (0.250 0.500 0.125)
- (10) *Proximity of fine seta to lateral frontal suture*: (0) close (Figs 1a–c,e,h–k); (1) distant (Fig. 1d). (0.167 0.706 0.118)
- (11) *One or more long fine setae laterally on frontoclypeus*: (0) present; (1) absent. (0.333 0.333 0.111)
- (12) *Frontoclypeus texture*: (0) shagreen; (1) rugose; (2) punctate; (3) striate; (4) glabrous. (0.667 0.600 0.400)
- (13) *Longitudinal carina on frontoclypeus*: (0) absent; (1) present (Fig. 1f). (0.500 0.000 0.000)
- (14) *Sharply carinate ridge on frontoclypeus below antennal pit*: (0) present; (1) absent. (0.500 0.667 0.333)
- (15) *Frontoclypeus*: (0) not inflated posteroventrally; (1) inflated posteroventrally. (0.333 0.000 0.000)
- (16) *Anterior region of head*: (0) not inflated; (1) inflated (Fig. 1g). (0.500 0.667 0.333)
- (17) *Frontoclypeus length*: (0) longer than wide (Figs 1a–f,h–i,k); (1) shorter than or subequal to width (Fig. 1j). (0.200 0.556 0.111)
- (18) *Lateral frontal suture extent*: (0) reaching ocellus (Figs 1b,d,e,h–k); (1) absent or reaching only part way to ocellus (Figs 1c,f,g). (0.077 0.294 0.023)
- (19) *Lateral frontal suture*: (0) distinctly shorter than clypeogenal suture (Figs 1b,d–e,h,j–k); (1) subequal to or longer than clypeogenal suture (Fig. 1i). (0.125 0.000 0.000)
- (20) *Lateral frontal sutures*: (0) directed mesad of ocelli (Fig. 1b); (1) directed toward middle of ocelli (Figs 1h–i,k); (2) directed laterad of ocelli (Fig. 1d,j); (3) strongly divergent (about 90° angle). (0.150 0.433 0.065)
- (21) *Ratio of length of frontoclypeal-loral suture to clypellar-loral suture*: (0) one third or less (Figs 1a,i); (1) more than one third (Figs 1b–f,h,j–k); (2) more than 1. (0.222 0.588 0.131)
- This is illustrated in Fig. 1a, the ratio of the lengths a:b.
- (22) *Incision of gena*: (0) not incised (Fig. 1b); (1) slightly incised (Figs 1a,c–e,h–k); (2) strongly incised (Fig. 1f). (0.500 0.600 0.300)
- (23) *Position of antennal pits*: (0) near middle or posteroventral (lower) corner of eye (Figs 1a–b,d,h–k); (1) near anterodorsal (upper) corner of eye (Figs 1c,f). (0.167 0.583 0.097)
- (24) *Antenna length*: (0) short; (1) long; (2) very long. (0.200 0.385 0.077)
- (25) *Antennal ledge*: (0) absent (Figs 1a–b,e–f,h–k); (1) weakly developed (carinate or weakly carinate) (Fig. 1d); (2) strongly developed. (0.167 0.750 0.125)

This character was ordered, as there is some degree of continuous variation, where ‘weakly developed’ is intermediate between absent and ‘well-developed.’

- (26) *Mesial margin of eye*: (0) entire (Fig. 1b–h,j–k); (1) notched (Figs 1a,i). (0.091 0.500 0.045)
- (27) *Anterior margin of head*: (0) shagreen; (1) striate or irregularly textured; (2) with numerous carinae (Fig. 1j); (3) with 2 or 3 parallel carinae (Fig. 1d); (4) with a single transverse carina. (0.190 0.614 0.117)

A step matrix was created for this character, where 0→1 = one step, 1→2, 3, or 4 = one step, and 0→2, 3, or 4 = two steps. This orders the character in a way that makes it more costly to go directly from shagreen to any of the carinate states. This reflects the observation that ‘transversally striate’ appears to be intermediate between shagreen and any of the carinate states. Indeed, it is often difficult to determine a distinction between well-developed striations and carinae, as in some of the *Bahita*-group genera. Linnavuori & Al-Ne’amy (1983, p. 18) also observed this in the genus *Jamitettix* Metc. No decision was made on the polarity among the carinate states, as it seems plausible that any of these might arise directly from or become reduced to ‘transversely striate’.

- (28) *Crown*: (0) parallel margined or somewhat produced; (1) strongly produced or elongate. (0.667 0.833 0.556)
- (29) *Crown*: (0) convex; (1) flat or concave. (0.067 0.533 0.036)
- (30) *Crown texture*: (0) shagreen; (1) punctate; (2) irregularly rugose; (3) radially or longitudinally striate. (0.188 0.409 0.077)
- (31) *Crown width*: (0) < or = 2 times width of eye; (1) > 2 times width of eye. (0.100 0.526 0.053)

This is a continuously variable character, and distinctly different states were not obvious. To determine differences between taxa, one specimen of each exemplar species was measured, and the resulting ratios were plotted as categories of ratios (1.01 to 1.25; 1.26 to 1.50, etc.) vs. the occurrence of each category. There was a bimodal distribution, and most fell in a range between 1 and 2 with a mean of about 1.5, but a substantial number of exemplars fell between 2 and 3.

Table 2 Character list. A list of characters and character states used in this analysis. Following the character state descriptions in parentheses are the consistency index, the retention index, and the rescaled consistency index for that character on the tree in Fig. 15.

- (32) *Head width*: (o) as wide as or wider than pronotum; (1) narrower than pronotum. (0.143 0.455 0.065)
 (33) *Position of ocelli*: (o) on crown, just posteriad of anterior margin of head (Fig. 1g); (1) laterally on anterior margin (Figs 1b,d,h-k); (2) posteroventrad of crown margin (Fig. 1e); (3) on crown. (0.333 0.333 0.111)
 (34) *Proximity of ocelli to eyes*: (o) close (Figs 1b,d,i-k); (1) distant (Figs 1e,g,h). (0.091 0.474 0.043)

Thorax

- (35) *Pronotum lateral carina*: (o) absent; (1) present. (0.111 0.529 0.059)
 (36) *Pronotum texture*: (o) without transverse striations; (1) with transverse striations. (0.125 0.462 0.058)

Wings

For some brachypterous taxa, most or all of these characters were coded as not applicable (-). If conspecific or congeneric macropterous specimens were available, the wing characters of the macropterous specimens were combined with other characters of the brachypters.

- (37) *Forewing veins*: (o) not carinate (Figs a-f,h-j); (1) carinate (Fig. 2g). (0.333 0.600 0.200)
 (38) *Appendix*: (o) absent or reduced (Figs 2a,b,g); (1) restricted to anal margin (Figs 2d,f,h-j); (2) extending around wing apex (Figs 2c,e). (0.154 0.450 0.069)

Note: Subsequent to analysis, it was found that *Fieberiella* was mistakenly coded with state (1), instead of state (o). This does not appear to have strongly influenced the results, as the taxa surrounding *Fieberiella* in the tree, *Luheria* and *Acinopterus*, both were scored (o) for this character.

- (39) *R1*: (o) basad of Rs (Figs 1b-c); (1) distad of Rs (Figs 2a,d-e,h). (0.182 0.100 0.018)
 (40) *Crossvein m-cu2*: (o) absent (Figs 2a-b,d-g); (1) present (Figs 2c,h-i). (0.200 0.467 0.093)
 (41) *A1 crossvein (between A1 and claval suture)*: (o) absent (Figs 2e-f); (1) present (Figs 2a-d,h-j). (0.067 0.440 0.029)
 (42) *A veins*: (o) gently curved distally (Figs 2a-c,e-j); (1) strongly curved distally, at right angles with commissural margin (Fig. 2d). (0.250 0.625 0.156)
 (43) *R1*: (o) not confluent with costa (with 3 anteapical cells) (Figs 2a-e,g-j); (1) confluent with costa (with two anteapical cells) (Fig. 2h). (1.000 1.000 1.000)
 (44) *A1-A2 crossvein*: (o) absent (Figs 2a,d-f,h); (1) present (Figs 2b-c,i-j). (0.222 0.417 0.093)
 (45) *Forewing reflexed costal veinlets*: (o) absent (Figs 2a-c,e-j); (1) present (Fig. 2d). (0.500 0.667 0.333)
 (46) *Hind wing submarginal vein*: (o) complete; (1) obscure apically. (0.333 0.000 0.000)

Legs and chaetotaxy

- (47) *Protrochanter*: (o) attaining posterior margin of mesosternum; (1) not attaining posterior margin (mesosternum enlarged). (0.333 0.500 0.167)
 (48) *Protrochanter stout ventroapical seta*: (o) absent (Figs 3b,c); (1) present (Figs 3a,d-e). (0.125 0.562 0.070)
 (49) *Profemur row AM*: (o) with only AM1 present (Figs 3b,e); (1) with 1 or more additional proximal setae (Figs 3a,c); (2) absent (Fig. 3d). (0.333 0.714 0.238)
 (50) *Profemur intercallary row*: (o) not in rows or scattered (Fig. 3b); (1) with more than 5 fine setae in one row (Figs 3a,c,e); (2) greatly reduced or absent (Fig. 3d). (0.286 0.500 0.143)
 (51) *Profemur dorsoapical setae*: (o) with 2 apical setae; (1) with 1 seta or absent. (0.750 0.500 0.375)
 (52) *Profemur row AV*: (o) absent or highly reduced (Fig. 3b); (1) with numerous (more than 4) stout setae (Figs 3a,c,d,e); (2) with a few widely spaced macrosetae. (0.222 0.632 0.140)
 (53) *Profemur row AV setal length*: (o) short (Fig. 3e); (1) long (Figs 3a,c,d). (0.143 0.750 0.107)
 (54) *Profemur row AV*: (o) without setae in apical 1/4; (1) with several thin setae on apical 1/4. (0.333 0.333 0.111)
 (55) *Profemur extra row of setae above intercallary row*: (o) absent; (1) present. (0.500 0.500 0.250)
 (56) *Profemur row PV basal and/or median setae*: (o) absent; (1) present; (2) with one median macroseta. (0.182 0.471 0.086)
 This was initially coded as two separate characters- one character for the basal seta and one for the median setae. However, all taxa that had a basal seta also had median setae, and vice versa. Because of this apparent dependence, they were combined into one character.
 (57) *Profemur row PV apical macroseta*: (o) absent or highly reduced; (1) present. (0.071 0.381 0.027)
 (58) *Protibia dorsal margins*: (o) rounded; (1) bicarinate; (2) at right angles (but not carinate). (0.333 0.333 0.111)
 (59) *Protibia row AD*: (o) without macrosetae; (1) 1 macroseta; (2) 2 or more macrosetae. (0.125 0.533 0.067)
 (60) *Protibia row PV macrosetae*: (o) numerous; (1) 1 to 4; (2) absent. (0.111 0.385 0.043)
 (61) *Mesotrochanter stout apical PV seta*: (o) absent (Fig. 3g); (1) present (Fig. 3h). (0.143 0.250 0.036)
 (62) *Mesotrochanter stout apical AV seta*: (o) absent; (1) present. (0.250 0.400 0.100)
 (63) *Mesotrochanter extra setae*: (o) absent (Fig. 3g); (1) with numerous extra thick or fine setae (Fig. 3f). (0.077 0.625 0.048)
 (64) *Mesofemur row AV setal length*: (o) short (Fig. 3f); (1) long (Fig. 3g). (0.091 0.286 0.026)
 (65) *Mesofemur row AV basal/median setae*: (o) absent or highly reduced (Fig. 3g); (1) with numerous thick setae (Fig. 3f). (0.200 0.500 0.100)

- (66) *Mesofemur row AV apical seta*: (0) absent or highly reduced (Fig. 3g); (1) present (Fig. 3f,h). (0.200 0.429 0.086)
The apical seta of this row is often well-separated from the rest of the setae in this row, and is positioned some distance from the apex of the femur.
- (67) *Metafemur penultimate setae*: (0) 0; (1) 1; (2) 2. (0.500 0.400 0.200)
- (68) *Metafemur penultimate pair of setae*: (0) widely separated; (1) close set. (0.200 0.000 0.000)
- (69) *Metafemur antepenultimate seta*: (0) 0; (1) 1; (2) 2. (0.333 0.500 0.167)
- (70) *Metatibia macrosetae proximally on dorsal surface*: (0) absent; (1) present. (0.500 0.500 0.250)
- (71) *Metatibia cross section: (dorsal surface compared to anterior surface)*: (0) square; (1) rectangular. (0.250 0.625 0.156)
- (72) *Metatibia row PD*: (0) with long and short macrosetae alternating or subequal in length; (1) some macrosetae (especially distally) interspersed with 3–4 much smaller setae. (1.000 1.000 1.000)
- (73) *Metatibia row AD*: (0) with macrosetae only; (1) with macrosetae and smaller intercalary setae. (0.333 0.000 0.000)
- (74) *Metatibia row AV, number of macrosetae*: (0) 6 or fewer; (1) 8 or more. (0.500 0.500 0.250)
- (75) *Metatibia row AV macrosetae*: (0) extending nearly to base; (1) restricted to apical two thirds. (0.143 0.714 0.102)
- (76) *Metatibia row AV*: (0) with macrosetae only; (1) with macrosetae and smaller intercalary setae. (0.250 0.571 0.143)
- (77) *Metatibia shape*: (0) arched throughout its length (Fig. 4b); (1) straight through most of its length and distinctly bent distally, in dorsal view (Fig. 4a). (1.000 1.000 1.000)
- (78) *Platellae at apex of metatibia*: (0) absent; (1) present. (0.250 0.000 0.000)
- (79) *Metatarsomere I length*: (0) shorter than tarsomeres II and III combined (Fig. 4c); (1) equal to or longer than tarsomeres II and III combined (Fig. 4d). (0.333 0.600 0.200)
- (80) *Metatarsomere I dorsoapical pair of setae*: (0) absent or reduced; (1) present. (0.333 0.333 0.111)
- (81) *Metatarsomere I plantar setae*: (0) all simple; (1) one or more platellate. (0.250 0.250 0.062)
- (82) *Metatarsomere I apex*: (0) straight (Fig. 4d); (1) widening apically (Fig. 4c). (0.333 0.600 0.200)
- (83) *Metatarsomere I PV apical seta*: (0) platellate; (1) normal. (0.100 0.625 0.062)
- (84) *Metatarsomere I apical platella*: (0) 3 or fewer; (1) 4 or more. (0.286 0.545 0.156)
- (85) *Metatarsomere I plantar setae*: (0) in two rows; (1) scattered. (1.000 0/0 0/0)
- (86) *Metacoxa macrosetae*: (0) with several macrosetae along midline; (1) absent or reduced along midline. (0.071 0.567 0.040)

Female genitalia

- (87) *Ovipositor*: (0) not protruding far beyond pygofer apex; (1) protruding far beyond pygofer apex. (0.143 0.538 0.077)
- (88) *First valvula*: (0) convex (Figs 5a–c,f–g; 6a,d–e; 7a–b); (1) not strongly convex (Figs 5d–e,h; 6b–c,f–h); (2) strongly concave. (0.222 0.731 0.162)
Interpretation of character states was aided by focusing on the shape of the ramus of the first valvula rather than the overall form including the upper and lower margins.
- (89) *First valvula dorsal sculpturing pattern*: (0) strigate (Figs 5f; 6a,g), concatenate (Fig. 7a), or reticulate (Fig. 6b,c); (1) granulose (Figs 5d–e; 6c), maculose or with definitely delimited scales (Figs 5h; 6h), or imbricate (with overlapping scales) (Fig. 5g); (2) with rectangular shaped scales (Fig. 6e); (3) conchoid, or with semicircular shaped sculpturings (Fig. 6f). (0.429 0.862 0.369)
The several forms appearing as state ‘0’ in this character were combined together because 2 or more of each of these forms were observed in the same taxon, with intermediate forms often occurring at their junction, or because the distinction between these states was sometimes ambiguous. Although some taxa were uniform for one of these sculpturing forms, the co-occurrence with other forms in other taxa makes hypothesising of each form as a homology tenuous (de Pinna, 1991; Wilkinson, 1982). Similarly, several forms were combined in state ‘1’. Terms for sculpturing patterns are from Hill (1970).
- (90) *Position of first valvula sculpturing*: (0) marginal (Figs 5a–c,f–g; 6a,d–e,g; 7a,b); (1) submarginal (Figs 5d,e,h; 6b,c,f,h). (0.200 0.692 0.138)
- (91) *Basal and dorsal elongation of first valvula sculpturing*: (0) absent (Fig. 7a); (1) present (Fig. 7b). (0.143 0.667 0.095)
- (92) *First valvula delimited subtriangular ventroapical sculptured area*: (0) absent (Figs 5a–c,f–h; 6a,b,d–g; 9b,c); (1) present (Figs 5d,e; 6c,h; 9a). (0.250 0.500 0.125)
- (93) *Bases of 1st valvulae*: (0) not extended anteriorly (Figs 9h,i); (1) extended anteriorly (Fig. 9g). (0.250 0.000 0.000)
- (94) *First valvifers*: (0) not fused (Fig. 9i); (1) fused anterodorsally (Fig. 9h). (0.091 0.444 0.040)
Some taxa show intermediate degrees of fusion. For example, there may be lightly sclerotized membranous tissue connecting the valvifers, making distinction of these two states difficult for some taxa.
- (95) *Female pygofer macrosetae*: (0) reduced (= <10) or absent (Fig. 9f); (1) with numerous macrosetae (Figs 9e,g). (0.167 0.615 0.103)
- (96) *Second valvula shape*: (0) broad and gradually tapered apically (Figs 7c,j–l,n; 8a,d); (1) abruptly broadened medially (Figs 7e,m; 8b,c,f,q); (2) slender throughout their length (Figs 7d; 8h,m); (3) gradually expanded medially or subapically (Figs 7g–i; 8g,p,s). (0.182 0.486 0.088)
- (97) *Second valvula dorsal tooth on shaft*: (0) absent; (1) present (Figs 7f,j,l; 8e). (0.111 0.273 0.030)
- (98) *Second valvula teeth*: (0) large and prominent (Figs 7m; 8q); (1) smaller, broader, and more widely-spaced (Figs 7c–f,j–l,n; 8a,d–f,h–o,r); (2) absent (Figs 7g–i; 8g,p,s); (3) obtusely triangular and scalene (Fig. 8b). (0.231 0.412 0.095)
- (99) *Second valvulae teeth*: (0) present on apical 1/3 or more (Figs 7c,f,j–n; 8a–f,i,l–o,q,r); (1) present only on apical 1/4 or less (Figs 7d,e; 8j). (0.167 0.167 0.028)

Male genitalia

- (100) *Valve (sternum IX)*: (0) free (Fig. 14b); (1) fused to pygofer (Fig. 14d); (2) subsumed under plates; (3) partially fused to pygofer. (0.500 0.000 0.000)
- (101) *Valve shape*: (0) not triangular (Figs 10g, 14a); (1) triangular, produced posteromedially (Figs 10b–f). (0.167 0.444 0.074)
- (102) *Articulation of valve with pygofer*: (0) an articulation point (Fig. 14b); (1) longer area of articulation (Fig. 14a). (0.500 0.750 0.375)
- (103) *Pygofer basolateral membranous cleft*: (0) absent (Figs 13b, 14a); (1) present (Figs 13c,d,g). (0.167 0.583 0.097)
- (104) *Pygofer macrosetae*: (0) absent or reduced (< or = 2 rows) (Fig. 13b,f); (1) well differentiated into several rows of macrosetae (Figs 13c–e,g, 14b). (0.077 0.429 0.033)
- (105) *Plate shape*: (0) subrectangular (Fig. 10a); (1) triangular (Figs. 10b–g); (2) expanded medially and tapered apically; (3) plates fused (Figs 12m; 14d); (4) rounded, with a lateral lobe (Fig. 10h); (5) elongate, lobate, rising laterally (Fig. 11n). (0.444 0.500 0.222)
- (106) *Plate macrosetae*: (0) absent (Figs 10a,e); (1) scattered, irregularly arranged (Figs 10b,c,g); (2) uniseriate laterally (Fig. 10f); (3) two lateral rows near margin; (4) uniseriate medially (Fig. 10d); (5) with one or two rows near median margin (Fig. 11n). (0.200 0.412 0.082)
- (107) *Dorsolateral fold on subgenital plate, articulating with style*: (0) absent; (1) present (Figs 10b,e–g). (0.333 0.750 0.250)
- (108) *Style*: (0) linear (median anterior lobe not well developed) (Figs 11a,b,i,k,l,n); (1) broadly bilobed (median anterior lobe well developed) (Figs 11c–h,m; 12a–d). (0.333 0.846 0.282)
- (109) *Style preapical lobe*: (0) absent or undeveloped (Figs 11a,e,i); (1) present (Figs 11b,g,h,k). (0.200 0.333 0.067)
- (110) *Style apophysis*: (0) not elongate (Figs 11a–k,m; 12a–d); (1) elongate (Figs 11 l,n). (0.333 0.600 0.200)
- (111) *Paraphyses of the connective or aedeagus*: (0) absent (Figs 11a,b,d–n; 12a,c,d,k); (1) present (Figs 11c; 12b,j). (0.100 0.182 0.018)
- (112) *Aedeagal shaft basal hinge*: (0) absent (Figs. 12e,g,h,j,l); (1) present (Fig. 12f). (1.000 1.000 1.000)
- (113) *Number of gonopores*: (0) one (Figs. 12e–g,j,l); (1) two (Figs. 11m, 12h,i). (0.333 0.000 0.000)
- (114) *Position of gonopore*: (0) ventral; (1) apical; (2) dorsal; (3) dorsolateral. (0.375 0.375 0.141)
- (115) *Lateral anterior arms of connective*: (0) widely divergent (Figs 11i,k,l,n); (1) somewhat divergent (Y-shaped or U-shaped) (Figs 11b–e,m; 12a–d,k); (2) closely appressed anteriorly (Figs 11f–h). (0.286 0.706 0.202)
- (116) *Connective anteromedial or ventral process*: (0) absent; (1) present. (0.500 0.750 0.375)
- (117) *Connective*: (0) articulated with aedeagus (Figs 11e,g,i; 12g); (1) fused to aedeagus (Figs 11f,j; 12k,l, 13a). (0.143 0.333 0.048)
- (118) *Male 10th segment long lateroventral processes*: (0) absent (Figs 13b,c,f,g); (1) present (Figs 13d,e). (0.500 0.000 0.000)
- (119) *Male 10th segment*: (0) elongate, 2 to 3 times as long as wide at apex, and sclerotised dorsally (Figs 13h,k); (1) short, not sclerotised dorsally (Fig. 13j); (2) very broad and sclerotised dorsally (Fig. 13i). (0.087 0.087 0.008)

Table 2 Continued.

of the gonopore, the number of shafts of the aedeagus, and the presence or absence of paraphyses. Highly variable characters include the specific shapes and sizes of the style, connective, aedeagus and pygofer. Often, the aedeagus has apical or lateral processes that vary widely between species. Similarly, the pygofer often contains spines, hooks, processes or serrations that are unique to individual species and genera. Although these characters are highly variable and useful in species diagnoses, sometimes groups of genera share similar processes, and these characters are therefore useful, in varying degrees, above the species or generic level. One example is the male subgenital plate macrosetal pattern (char. 91). This character is stable in many taxa (e.g., uniseriate laterally, or absent/reduced), but is variable in others, and is sometimes diagnostic for generic groups in large tribes. This character and other similarly variable characters may also be useful, even if somewhat homoplastic, for tribal classification.

Characters of the female genitalia have been cited by some authors as diagnostic for higher taxa (Linnavuori & Al-Ne'amy, 1983; Hill, 1970; Knight & Webb, 1993; Hamilton, 2000), but are often ignored in species and genus descriptions, and therefore little is known of their variability and usefulness in defining higher taxa and of their potential to inform phylogenetic relationships. As in the male genitalia, some characters

have been used for species level distinctions (shape of sternite VII, shape of the bases of the first valvulae, and setation of the pygofer) and others have been cited as diagnostic for higher taxa (the sculpturing pattern of the first valvula, the shape of the second valvula, the presence/absence of a dorsal tooth on the shaft of the second valvula, and the number, size, and shape of the teeth of the second valvula). Because such characters have not been often used in deltocephaline systematics, we gave special attention to defining female genitalic characters.

The 119 characters examined in this study are listed in Table 2, and the state assignments for all taxa are provided in the character state matrix in Table 3. Terminology follows Oman (1949), Kramer (1950), and Hill (1970) except for leg chaetotaxy, which follows the system of Rakitov (1998; also see Dietrich & Rakitov 2002). Many of the characters were taken or modified from Knight and Webb (1993), Kamitani (1999), and Dmitriev (pers. comm.), but several others are used here for the first time.

All taxa were examined and scored independently of previous publications. In most instances, the exemplar species listed in Table 1 were used to score all characters. However, we only had limited specimens for two exemplars, and in order to include as much data as possible, we combined characters from two closely related congeneric species in the

	66666666	666777777777778888888888889999999999	1111111111111111111111111111111111	0123456789012345678901234567890123456789000000000000011111111111111	0123456789
<i>Tetartostylus</i>	10000112	110101110001100110001110000100100	-011121110100120001		
<i>Acostemma</i>	01110112	1101011100011000101000010011201110	-01310010100110100		
<i>Anoterostemma</i>	11000112	1010110000110001010110000000010000104011?	0000110000		
<i>Arrugada</i>	0101111b	10001110001100?101?111010?0302	-01010121110000110000		
<i>Drakensbergena</i>	1??10111	100011011100101010?011100000301001010101110000110000			
<i>Attenuipyga</i>	01010110	-0001111111000010100111101000302	-01011141110000110001		
<i>Eupelix</i>	11010110	-000110111100010100011100000011001010101110000110001			
<i>Paradorydium</i>	10011110	-00011011100001010111101000302	-1--00401?-0000110000		
<i>Koebelia</i>	00001112	0000001110111100101110100000301101011111110000310001			
<i>Mukaria</i>	2100-002	1101011100011001000010000001001001010111110101110101110101			
<i>Parabolopona</i>	11011112	1101011100011001000010010011101001011101110100110001			
<i>Roxasella</i>	11001112	1101011100011001000000010101011001011101110100110002			
<i>Penthimia</i>	01?11112	1101011000011000101000000001100001011111110000110001			
<i>Nielsoniella</i>	21000112	1101011000011001001000000001111001011111010000110001			
<i>Adama</i>	01110112	1101011000011000101100010011101101011101110100010001			
<i>Drabescus</i>	11011111	-00100110001100110000000000111?001010101100000110002			
<i>Dwightla</i>	01011112	1111011000011000100100010011200101010111010100110000			
<i>Hypacostemma</i>	11010112	1101011100011000100000010001111001011121110000110001			
<i>Selenocephalus</i>	01010112	110101100001100010100001001101100101011111000010002			
<i>Stegelytra</i>	01011112	111101110001100010000001000110?010?1011?0?0100?0?0??			
<i>Pachymetopius</i>	0?11011-	-11011000001001100000010001103001011101001000100002			
<i>Aphrodes</i>	11011112	1101011000011101110010000010001000101510011000100001			
<i>Calliscarta</i>	0101-002	0201011010011001001113000001201110-00510011000101000			
<i>Chinaia</i>	1001-012	010101100001100100110010000000110-100500011000101002			
<i>Lystridea</i>	01011112	0200011010011001100100000011201101101510011000111002			
<i>Portanus</i>	11000112	1101011000011001001100010001100031-10540010000111000			
<i>Xestocephalus</i>	2000-001	-101011010011001001023000001401000100550011000101001			

Table 3 Continued.

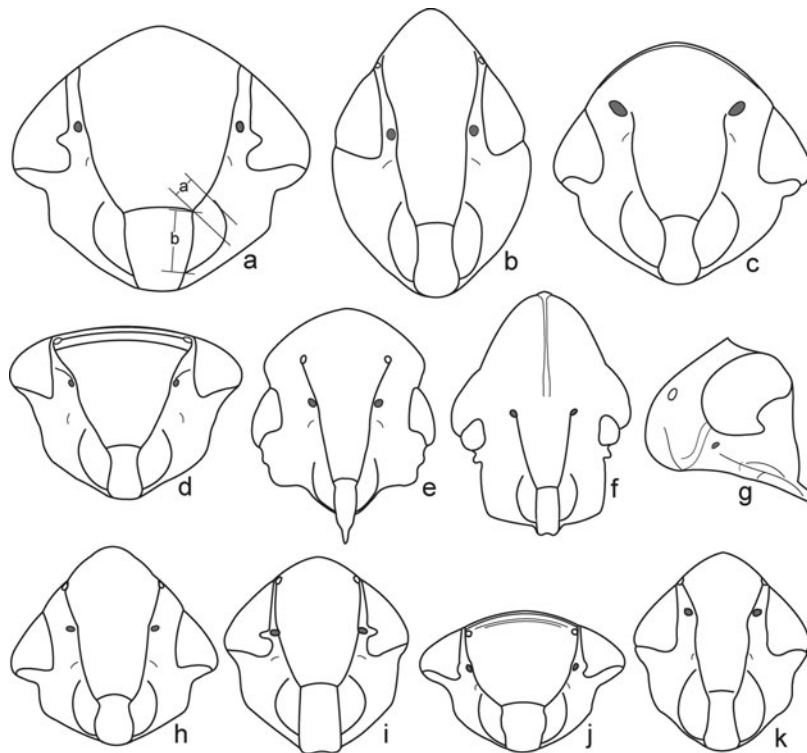


Figure 1 Facial structure. Antennal pits are shaded; ocelli are not. a, *Diplocoenus abdominalis*; b, *Scaphytopius acutus*; c, *Parabolopona* n. sp.; d, *Adama* sp. nov.; e, *Koebelia* sp.; f, *Eupelix cuspidata*; g, *Penthimia americana*, lateral view; h, *Cochlorhinus pluto*; i, *Stirellus bicolor*; j, *Bahita* sp.; k, *Scaphoideus titanus*.

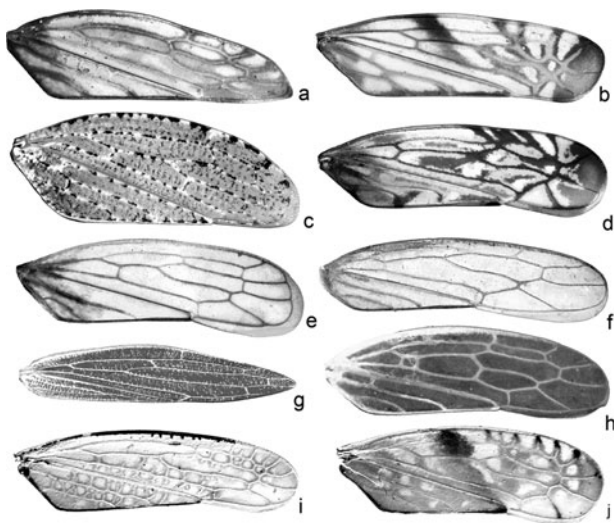


Figure 2 Wings. a, *Acinopterus acuminatus*; b, *Luheria constricta*; c, *Goniagnathus rugulosus*; d, *Scaphoideus titanus*; e, *Exitianus exitiosus*; f, *Balclutha punctata*; g, *Paradorydium lanceolatum*; h, *Deltocephalus balli*; i, *Platymetopius obsoletus*; j, *Fitchana* sp.

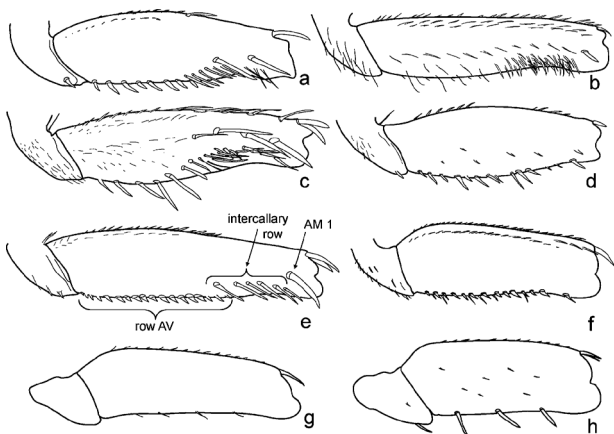


Figure 3 Legs and chaetotaxy. a–e, profemur, anterior view; a, *Acinopterus acuminatus*; b, *Drabescus* sp.; c, *Dwrightla acutipennis*; d, *Attenuipyga platyrhyncus*; e, *Phlepsius intricatus*; f–h, mesofemur, anterior view; f, *Athysanus argentarius*; g, *Balclutha punctata*; h, *Parohinka* sp.

following cases: (1) wing and female characters from one species of *Chiasmus* were combined with the male genitalic characters of another; (2) the male genitalic characters of *Stegelytra erythroneura* were combined with the remaining characters of *S. boliveri*.

Characters which could not be scored from the available specimens were coded as missing (?). Usually, this was necessary when only one sex was available (e.g. *Roxasella*) or when characters could not be determined due to a missing or broken structure or specimen mountings that obscured the character.

Characters that were inapplicable to some taxa were coded as gaps (-), which has the same effect in the analysis

as coding as ‘missing’, but adds clarity to the data matrix. For example, the brachypterous exemplars (*Doratura*, *Drakensbergena* and *Anoterostemma*) were coded with ‘-’ for all of the wing characters. Other instances of inapplicable characters occurred when the structure in question was simply not present. For example, those taxa coded with state ‘0’ for character 57 (mesofemur row AV absent or highly reduced) were coded with ‘-’ for character 56 (length of mesofemur row AV setae).

Cladistic analysis

Maximum parsimony (MP) analyses were performed using PAUP*4b10 (Swofford, 1998) and TNT v1.0 (Goloboff *et al.*, 2003). All characters were given equal weight. All characters were treated as unordered, except for characters 24, 25, 27 and 115. Justification for ordering these characters is given in their character descriptions (Table 2). Taxa in which more than one state was observed in one or more specimens (multistate taxa) were coded as polymorphic for the observed states. Because the exemplar terminal taxon approach was used, these polymorphisms represent true polymorphisms (not supraspecific terminal polymorphisms). Thus, the multistate taxa were treated as ‘polymorphic’ rather than ‘uncertain’. This forced the multiple states to occur in the taxon, rather than just the most parsimonious state assignment (Swofford & Begle, 1993).

Because of the size of the data set and time required to search all possible trees, heuristic searches were necessary. Five hundred random addition sequences using TBR branch swapping were performed. Analyses in TNT were performed with the memory set to hold 30 000 trees (the maximum allowed). The ‘traditional’ tree search was performed using 3000 replicates with TBR branch swapping and saving 10 trees per replicate.

Node support was assessed by calculating decay indices (Bremer, 1988). This was accomplished by using TNT v1.0 (Goloboff *et al.*, 2003) to find the shortest trees not compatible with each node on the strict consensus tree, and computing the differences between the lengths of the resulting trees and the length of the original MP trees.

Lists of apomorphies for each node were produced using PAUP 3.1.1 to avoid a bug in PAUP*4.0b10, which produces inaccurate apomorphy lists. The PAUP 3.1.1 list was verified by examining character state distributions and by comparing to a list of unambiguous apomorphies produced by TNT v1.0. Apomorphies were reconstructed under both ACCTRAN (accelerated transformation) and DELTRAN (delayed transformation) optimisation (Table 4 which is available as ‘Supplementary data’ on Cambridge Journals Online: http://www.journals.cup.org/abstract_S1477200007002617).

Results

Heuristic searches in PAUP*4.0b10 yielded 40 MP trees 862 steps in length. Searches in TNT yielded 20 MP trees of the same length, which produced the same strict consensus tree as the analysis in PAUP*4.0b10 (Fig. 15). The putative ingroup was consistently monophyletic, sister to a clade containing four of the putative outgroup taxa. Some branches received

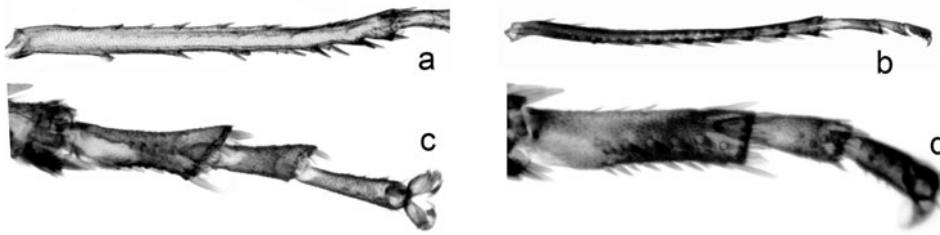


Figure 4 Hind legs. a–b, metatibia, dorsal view; a, *Eupelix cuspidata*; b, *Limotettix (Scleroracus) decumanus*; c–d, metatarsomere, ventral view; c, *Attenuipyga platyrhyncus*; d, *L. (S.) decumanus*.

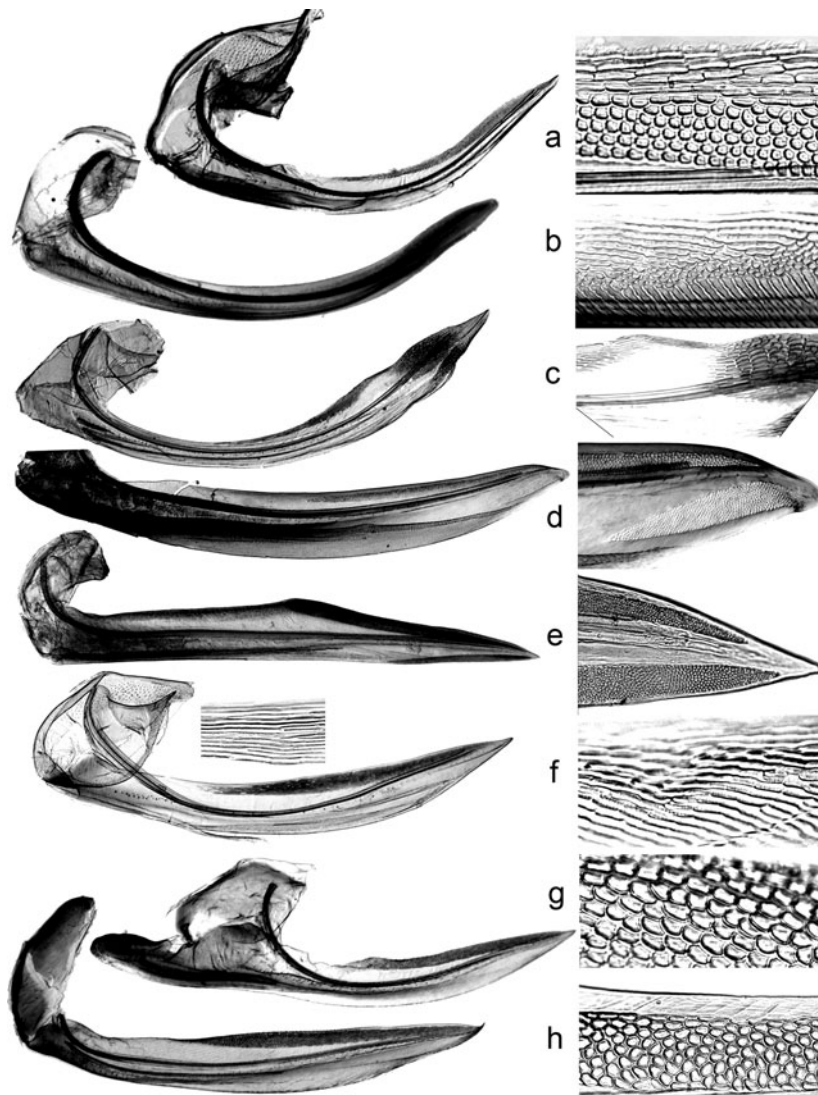


Figure 5 Female first valvula and valvifer. a–h, left = lateral view of valvula; a–c, f–h, right = detail of dorsal sculpturing pattern; d–e, right = detail of apex of valvula; a, *Acinopterus acuminatus*; b, *Acostemma* sp.; c, *Adama* sp. nov.; d, *Arrugada rugosa*; e, *Attenuipyga platyrhyncus*; f, *Bahita* sp., with basal dorsal sculpturing shown above; g, *Diplocolenus abdominalis*; h, *Doratura stylata*.

moderate to high support (Bremer support of 3 or higher), but most branches received support values of 2 or 1.

Of the five subfamilies (*sensu* Oman *et al.*, 1990) for which more than one exemplar was included, Penthimiinae (2 exemplars) and Paraboloponinae (2 exemplars) were recovered as monophyletic. Deltocephalinae (42 exemplars), Selenocephalinae (5 exemplars), and Eupelicinae (3 exem-

plars) were para- or polyphyletic. Of the seven deltocephaline tribes for which more than one exemplar was included, all but one (Cochlorhinini – 2 exemplars) were para- or polyphyletic. Non-monophyletic tribes included Athysanini (12 exemplars), Deltocephalini *sensu* Oman *et al.* (1990) (4 exemplars), Paralimnini (3 exemplars), Hecalini (2 exemplars), Scaphoideini (2 exemplars) and Opsiini (2 exemplars).

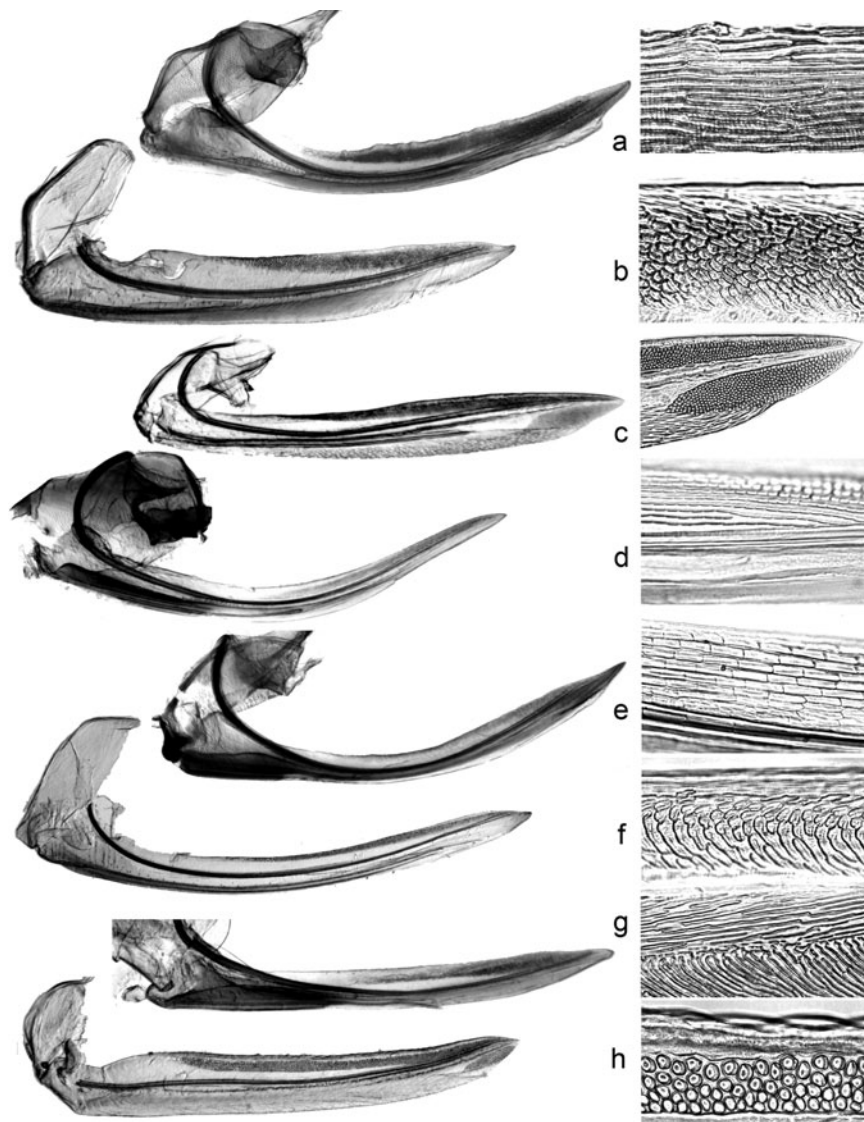


Figure 6 Female first valvula and valvifer. a–h, left = lateral view of valvula; a–b, d–h, right = detail of dorsal sculpturing pattern; c, right = detail of apex of valvula; a, *Drabescus* sp.; b, *Eupelix cuspidata*; c, *Evinus peri.*; d, *Goniagnathus rugulosus*; e, *Grypotes puncticolis*; f, *Koebelia* sp.; g, *Parabolopona* sp. nov.; h, *Paradorydium lanceolatum*.

Discussion

Relationships among tribes and morphological characters

Previous phylogenetic analyses of Cicadellidae as a whole (Dietrich, 1999; Dietrich *et al.*, 2001) indicated that Deltocephalinae as traditionally defined gave rise to several other leafhopper subfamilies (*sensu* Oman *et al.*, 1990), but those analyses did not include a sample of taxa sufficient to test relationships within this lineage of deltocephaline-like leafhoppers. The present analysis is the most comprehensive to date hypothesising relationships among the family-group taxa of this lineage using cladistic methods. Despite low support for much of the resulting tree, some well-supported clades and convincing morphological characters provide additional evidence that several previously delimited subfamilies have their closest relatives in Deltocephalinae *sensu* Oman *et al.*

(1990). The trees resulting from this analysis provided support for some previously proposed relationships, but contradicted others. Below, we discuss some of these relationships and how they compare to previous hypotheses, some aspects of morphological character evolution, and the evolution of grass specialisation in the group based on this phylogenetic hypothesis.

The phylogeny was rooted with *Lystridea*. Placement of the root node in this analysis agrees well with the pattern of relationships of Cicadellidae found by Dietrich *et al.* (2001) based on 28S rDNA data, and the distribution of states in some key characters of the male genitalia also corroborate this rooting scheme. Some of these characters are discussed here.

The putative ingroup was recovered as monophyletic (branch #5). This branch was supported by a decay index of 2, and has 11 unambiguously reconstructed character states and 4 ambiguously reconstructed (ACCTRAN or DELTRAN) character states (see Table 4, available online as above). Of the character transformations reconstructed on this branch,

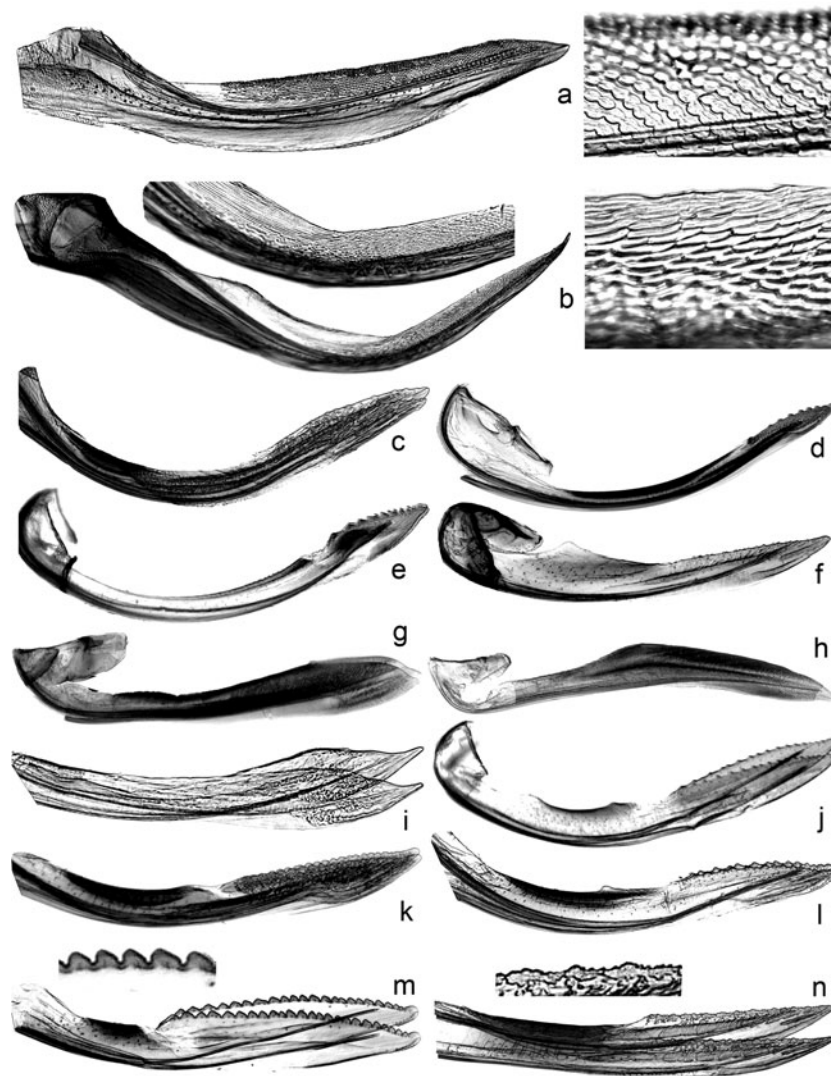


Figure 7 Female first and second valvulae. a–b, first valvula; a, *Penthimia americana*, detail of sculpturing to right; b, *Stegelytra boliveri*, basal sculpturing shown above and apical sculpturing to right; c–n, second valvula; m–n with detail of teeth; c, *Acinopterus acuminatus*; d, *Acostemma* sp.; e, *Adama* sp. nov.; f, *Anoterostemma ivanhoffi*; g, *Arrugada rugosa*; h, *Attenuipyga platyrhyncus*; i, *Balclutha punctata*; j, *Bahita* sp.; k, *Cerrillus* sp.; l, *Cochlorhinus pluto*; m, *Colladonus clitellarius*; n, *Coryphaelus gylenhalii*.

character states 25(1) (antennal ledges weakly developed), 34(0) (ocelli close to eyes), 52(1) (profemur row AV with numerous stout setae), 68(1) (metafemur penultimate pair of setae close-set), 102(0) (articulation of valve with pygofer consisting of a point of articulation; ambiguously reconstructed, and also occurs on branch #6), 105(1) (subgenital plate shape triangular), and 110(0) (style apophysis not elongate) may prove to be useful for defining this group. Indeed, previous authors have cited some of these features as defining Deltocephalinae, and they occur almost ubiquitously within this clade and rarely in other leafhopper groups.

The terminal ingroup taxa subtending branch #11 all possess male genitalia that are not the usual deltocephaline type, and these characters were partly responsible for resolving these taxa near the base of the tree. Despite their atypical male genitalia, three of these taxa, *Luheria*, *Fiebertiella*, and *Acinopterus*, have been traditionally classified in Deltocephalinae.

Several of the male genitalic features distinguishing deltocephalines and related groups are acquired on branch #11: 101(1) (valve triangular, produced posteriorly), 108(1) (style broadly bilobed, with median anterior lobe well developed), and 115(1) (lateral anterior arms of connective somewhat divergent). Others are acquired on branch #6: 103(1) (pygofer with basolateral membranous cleft), and 107(1) (dorsolateral fold on subgenital plate present). Also, character state 116(0) (connective with anteromedial or ventral process) is present in all outgroup taxa except *Aphrodes* and is absent in all ingroup taxa (branch #5).

One other taxon with atypical male genitalia, *Goniagnathus*, was recovered in a clade containing some selenocephaline taxa (branch #12). However, *Goniagnathus* shares several unique characters of the male and female genitalia with *Acostemma*, and these taxa may eventually be shown to be related. Possible synapomorphies uniting these two taxa

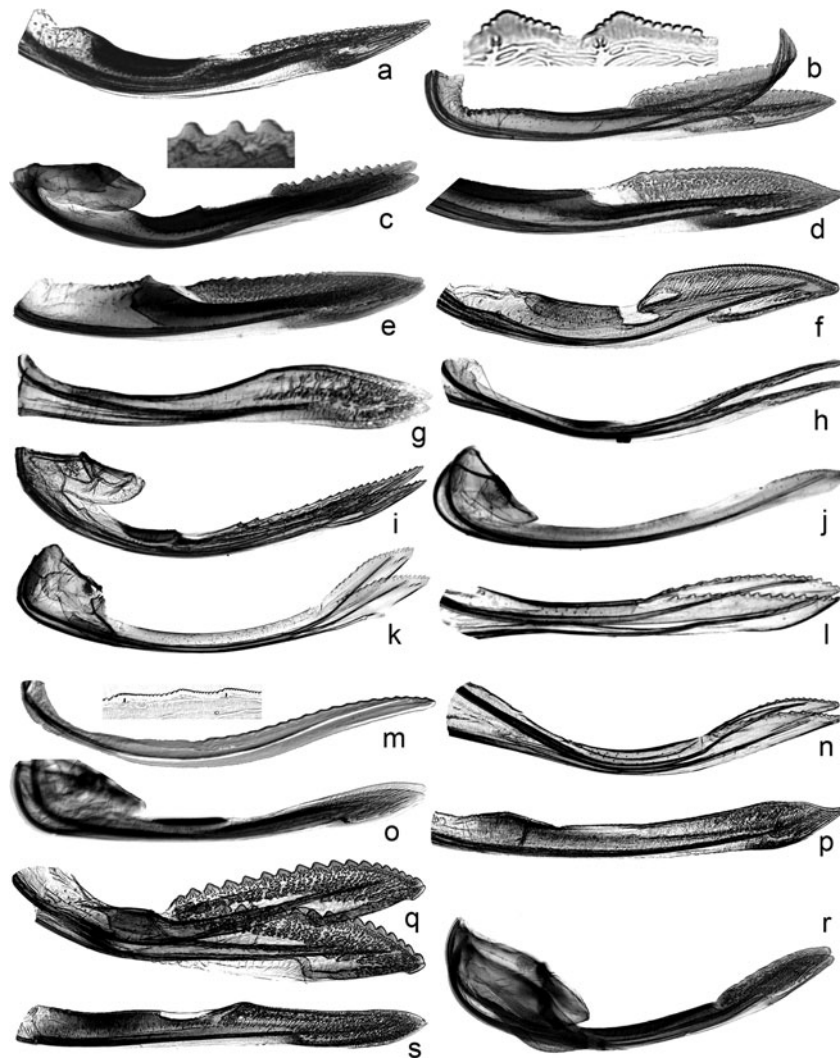


Figure 8 Female second valvula. a–s, left lateral view; b, c, and m with detail of teeth; a, *Diplocolenus abdominalis*; b, *Doratura stylata*; c, *Drabescus* sp.; d, *Drakensbergena fuscovittata*; e, *Eupelix cuspidata*; f, *Eutettix pictus*; g, *Evinus peri*; h, *Goniagnathus rugulosus*; i, *Grypotes puncticolis*; j, *Koebelia* sp.; k, *Luheria constricta*; l, *Mukaria* sp.; m, *Neoaliturus carbonarius*; n, *Opsius stactogalus*; o, *Parabolopona* n. sp.; p, *Paradorydium lanceolatum*; q, *Penthimia americana*; r, *Stegelytra boliveri*; s, *Stirellus bicolor*.

include 96(2) (female second valvula slender throughout length), 105(3) (male subgenital plates fused), and 117(1) (connective fused with the aedeagus).

Several characters of the female genitalia also provided support for large clades. Character state 89(1) (first valvula dorsal sculpturing pattern imbricate, scalelike, maculose, or granulose), a feature used by Linnavuori and Al-Ne'amy (1983) to distinguish Deltoccephalinae from Selenocephalinae, occurs on branch #32 (with reversals at branch #34 and in some terminal taxa). There is a continuous range in the degree of overlap of the scales, or maculae, and this variation may be informative in more detailed studies of the group, but were considered one state in this analysis. *Euscelis* Brulle, *Anoterostemma*, *Limotettix* Sahlberg, and the tribes Deltoccephalini and Paralimnini show a greater degree of scale overlap than *Athysanus* Burmeister and genera on branch #50, most of which have maculae distinctly separate from one another. This broad definition of the character appears to have separated one derived clade from other relatively basal lineages.

Other notable synapomorphies of the female genitalia include: 87(1) (ovipositor protruding far beyond pygofer apex) which occurs on branch #51 (and in the outgroup), with a reversal on branch #59; 88(1) (first valvula not strongly convex) which occurs on branch #35 and is lost and gained within the Paralimnini/Deltoccephalini branch (#45); 92(1) (first valvula with a delimited subtriangular ventroapical sculptured area present) occurs on branch #54 (and is lost in *Koebelia* and branch #59) and on branch #39; and 95(0) (pygofer macrosetae reduced or absent) which occurs on branch #51.

Characters of the leg chaetotaxy, which as a group comprised the largest set of characters, influenced all parts of the tree. One interesting example is found in the grouping of the taxa of branch #56. Unambiguously reconstructed chaetotaxic character states on this branch are 53(1) (profemur row AV setae long), 58(2) (protibia dorsal margin angulate, neither carinate nor rounded), and 71(0) (metatibia cross section square). Chaetotaxic character transformations on the next branch (#57) are 48(1) (protrochanter stout ventroapical seta

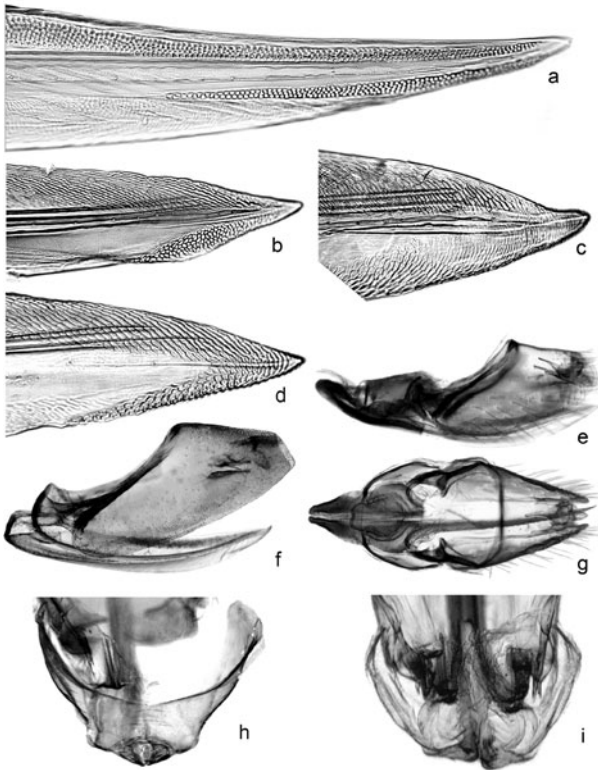


Figure 9 Female valvulae and pygofer. a–d, apex of first valvula; a, *Doratulina viridicans* (Distant); b, *Cerrillus* sp.; c, *Eupelix cuspidata*; d, *Mukaria* sp.; e–g, pygofer; e, *Diplocolenus abdominalis*, lateral view; f, *Attenuipyga platyrhyncus*, lateral view; g, *D. abdominalis*, dorsal view; h–i, first valvifers and bases of first valvulae, dorsal view; h, *Adama* sp. nov.; i, *Grypotes puncticolis*.

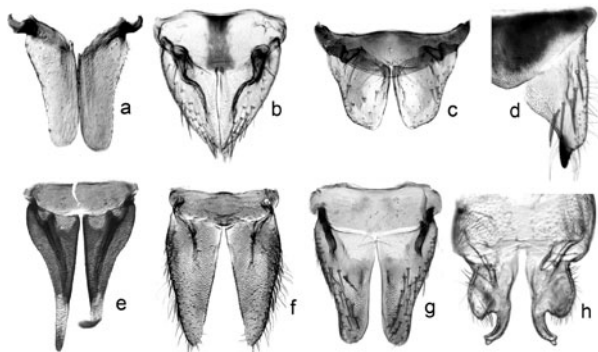


Figure 10 Male subgenital plates and valve. a, *Acinopterus acuminatus*; b, *Athysanus argentarius*; c, *Doratura stylata*; d, *Cicadula melanogaster*; e, *Drabescus* sp.; f, *Eutettix pictus*; g, *Luheria constricta*; h, *Paradoridium lanceolatum*.

present), 50(2) (profemur intercalary row absent or reduced), 69(0) (metafemur with 0 penultimate setae), and 76(1) (metatibia row AV with macrosetae and smaller intercalary setae). Branch #58, consisting of Eupelicinae + Drakensbergeninae, was supported by many chaetotaxic features, several of which are found on the first metatarsomere (Table 4, available online, as above).

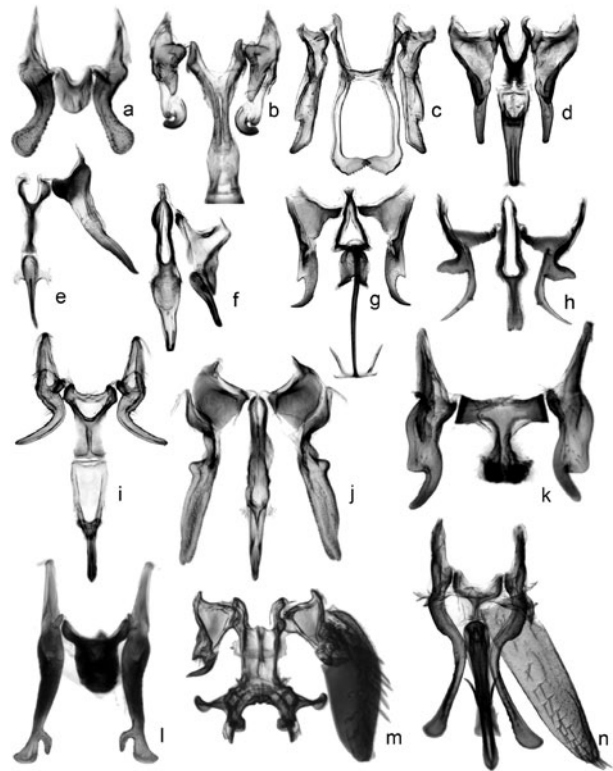


Figure 11 Male genitalia. a–n, connective and styles, ventral view; d–g, i, j, m, n shown with aedeagus; m, n shown with left subgenital plate; a, *Acinopterus acuminatus*; b, *Acostemma* sp.; c, *Adama* sp. nov., with fused paraphyses (=pseudostyli); d, *Athysanus argentarius*; e, *Cicadula melanogaster*; f, *Deltocephalus balli*; g, *Diplocolenus abdominalis*; h, *Doratura stylata*; i, *Fieberiella florii*; j, *Goniagnathus rugulosus*; k, *Luheria constricta*; l, *Pachymetopius decorata*; m, *Mukaria maculata*; n, *Aprhodes bicincta*.

As in the analysis of Dietrich (1999), *Koebelia* was recovered in clade #57 with Eupelicinae and Drakensbergeninae. This contrasts with the conclusions of Dietrich and Dmitriev (2003), who provided morphological and ecological evidence that *Koebelia* is more closely related to *Grypotes* Fieber and allied genera, and with the molecular phylogeny of Dietrich *et al.* (2001). The result presented here may be attributable to convergence in leg chaetotaxy and the structure of the head. *Koebelia*, along with Eupelicinae and Drakensbergeninae, has an elongate and flattened head, which Rakitov (1997) suggested may place functional constraints on the chaetotaxy of the front femur. Lack of brochosome production is also correlated with reduction/despecialisation of leg chaetotaxy (Rakitov, 1997). Because *Koebelia* is often found with a dense coat of brochosomes, while Eupelicinae lack brochosomes, the (possibly convergent) similarities in chaetotaxy of the two groups may be more related to head morphology. Another feature potentially correlated with the absence of brochosomes in Eupelicinae is character 9 (fine erect seta on the gena present/absent), which is present in all deltocephaline groups except for Eupelicinae.

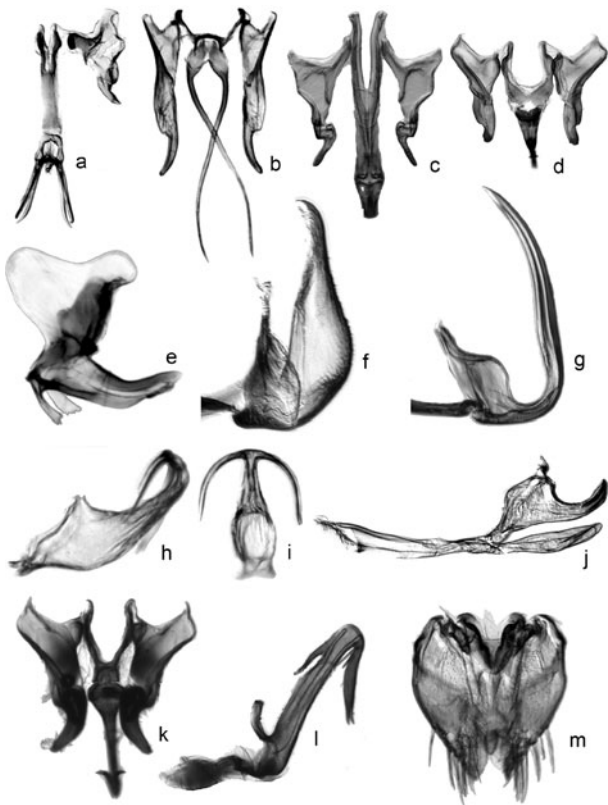


Figure 12 Male genitalia. a–d, k, connective, styles, and aedeagus, ventral view; a, *Opsius stactogalus*; b, *Scaphytopius acutus*, shown with paraphyses and without aedeagus; c, *Stirellus bicolor*; d, *Selenocephalus griseus*; e–h, j, l, aedeagus, lateral view; i, aedeagus, posterior view; e, *Acinopterus acuminatus*; f, *Doratura stylata*; g, *Stirellus bicolor*; h–i, *Neoaliturus carbonarius*; j, *Scaphoideus titanus*, with connective; k–l, *Cochlorhinus pluto*; m, fused subgenital plates and valve, pygofer, ventral view, *Goniagnathus rugulosus*.

Selenocephalinae was not recovered as monophyletic, corroborating Zhang and Webb's (1996) conclusion that the subfamily lacks unique synapomorphies and is not morphologically distinguishable from Deltocephalinae. Parabolponini and Drabescini, which are often placed in Selenocephalinae, were resolved in a clade including Cerillini, Mukariinae, and Penthimiinae (branch #22). These selenocephalines differ from members of the other selenocephaline clade (branch #12) in having the following features, among others: 49(1) (profemur row AM with only AM1), 52(0) (profemur row AV reduced or absent), 64(1) (mesofemur row AV setae long), and 106(0) (male subgenital plate macrosetae reduced or absent).

The two opsiines included in the analysis, *Opsius* Fieber and *Neoaliturus* Distant, did not group together. Both have the aedeagus with two gonopores, the most distinguishing feature of Opsiini, but this feature was outweighed by the substantial differences in other aspects of the morphology, also noted by Emeljanov (1962). *Opsius* and *Neoaliturus* each have distinctive female genitalia, and other aspects of the aedeagus in these two genera are substantially different (Figs 12a,h,i). A more detailed analysis is needed to confirm that the presence of two

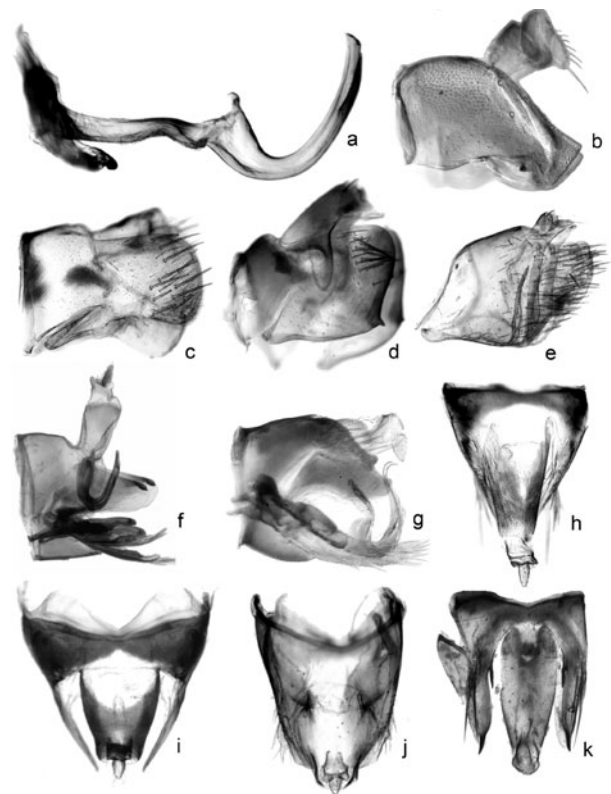


Figure 13 Male genitalia. a, *Acostemma* sp., connective, style, and aedeagus, lateral view; b–g, pygofer, lateral view; b, *Stirellus bicolor*; c, *Athysanus argentarius*; d, *Luheria constricta*; e, *Fieberiella florii*; f, *Dwightia acutipennis*; g, *Limotettix (Scleroracrus) decumanus*; h–k, pygofer and tenth segment, dorsal view; h, *Cicadula melanogaster*; i, *Selenocephalus griseus*; j, *Diplocolenus abdominalis*; k, *Elymana inornata*.

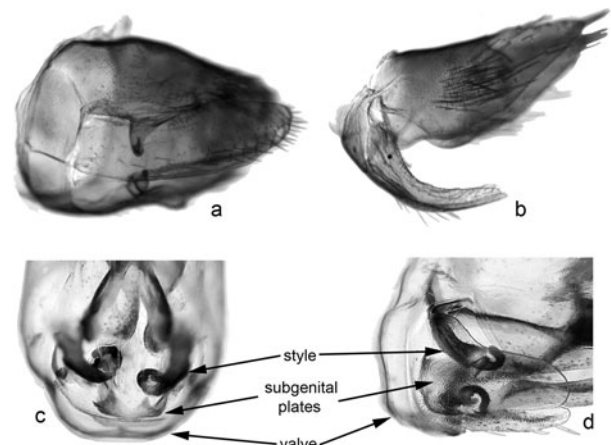


Figure 14 Male genitalia. a–d, valve, subgenital plates, and pygofer; a, *Aphodes bicincta*, ventrolateral view, right subgenital plate removed; b, *Neohecalus lineatus*, lateral view; c–d, *Eryapus* sp. (Acostemminae); c, pygofer and internal genitalia, anterior view; d, lateroventral view.

gonopores in these genera (as well as in Mukariinae) is the result of convergence.

It was not surprising to find Athysanini to be polyphyletic. This is the largest and least well defined tribe (265 genera,

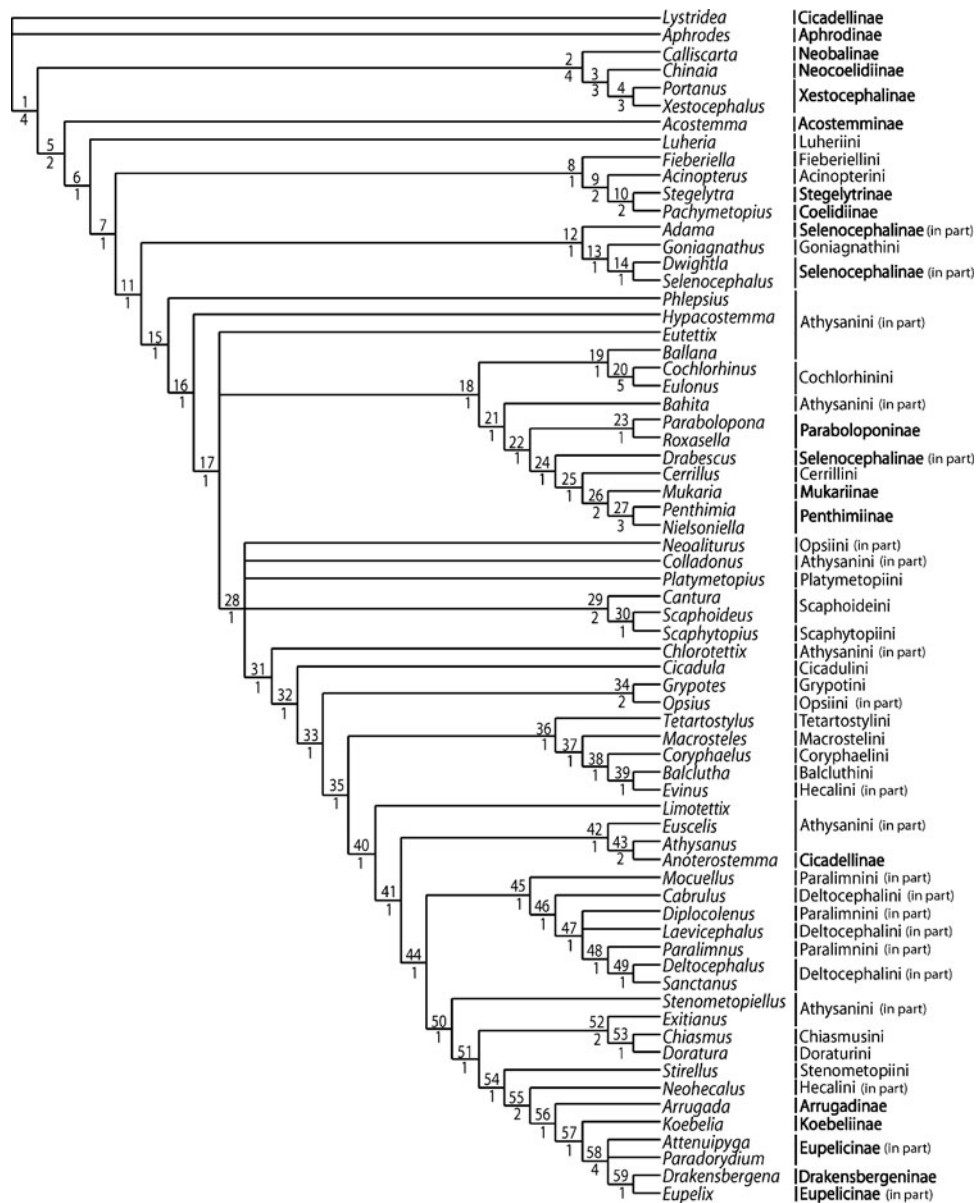


Figure 15 The strict consensus of 40 MP trees 862 steps in length. Length of consensus tree= 870 steps, CI= 0.2023, RI= 0.5174, RCI= 0.1047. Numbers above branches are branch numbers and those below are decay index values.

c. 2200 spp.) of Deltocephalinae. Hecalini was not resolved as monophyletic, as *Evinus* Dlabola was found to be more closely related to *Balclutha* Kirkaldy. These two genera were recovered in a clade (branch #37) with *Macrosteles* Fieber and *Coryphaelus* Puton, thus corroborating Knight and Webb's (1993) definition of Macrostelini.

Evolution of grass specialisation

The present results corroborate the hypothesis (Dietrich, 1999) that grass specialisation is more evolutionarily conservative than suggested by the present classification of leafhoppers. All but one of the grass specialist lineages (Mukariinae – recorded from bamboo) occur in branch #31 and this large clade comprises taxa placed in six different subfamilies by Oman *et al.* (1990). Interestingly, although grass specialisation was presumably acquired along branch #31, reversals to

non-grass feeding appear to have occurred along branch #34 and in *Limotettix*, *Euscelis* and *Koebelia*.

In general, the evolutionary scenario outlined by Whitcomb *et al.* (1987b) is supported, with the two grass-specialist tribes having a linear connective (Paralimnini and Deltocephalini) resolved as a monophyletic group (branch #45), and those taxa with the connective fused to the aedeagus (Deltocephalini *s.s.*) forming a monophyletic group within that clade (branch #49). However, this clade (branch #45) is embedded between several other grass-specialist groups with a Y-shaped connective. The relationship between this group and other grass-specialist groups having a Y-shaped connective, like Cicadulini, Eupelicinae, Hecalini, Doraturini, Macrostelini and the *Faltala* Oman group, should be explored more thoroughly (Zahniser & Webb, 2004). Because most branches on the cladogram received low support, more data will be needed to test the hypotheses presented here.

Classification

Although several previous authors have noted that the classification of Deltocephalinae is unsatisfactory and in need of revision (e.g., Hamilton 1975, 1983; Knight & Webb, 1993; Zhang & Webb, 1996; Dietrich & Rakitov, 2002), the lack of an explicit, comprehensive phylogenetic estimate for the group has hindered efforts to provide a more stable tribal classification. Recent analyses of Cicadellidae as a whole based on morphological (Dietrich, 1999) and molecular data (Dietrich *et al.*, 2001) indicated that Deltocephalinae *sensu* Oman *et al.* (1990) is paraphyletic with respect to several other cicadellid subfamilies. Based on these results, Dietrich and Rakitov (2002), Dietrich and Dmitriev (2003) and Dietrich (2004) treated Eupelicinae, Penthimiinae, Koebeliinae, Paraboloponinae and Selenocephalinae (*sensu* Oman *et al.*, 1990) as synonyms of Deltocephalinae. Although, for simplicity in this article, we referred to groups according to the classification of Oman *et al.* (1990), we continue to recognise these synonymies as valid. Indeed, they are supported by the analysis presented here. Although the entire family group classification of this group should eventually be revised, we refrain from proposing a revised classification here because analyses of DNA sequence data, alone and in combination with morphological data, are ongoing (Zahniser & Dietrich, unpublished). Such combined analyses should provide a more robust basis for a revised tribal classification of Deltocephalinae.

In considering more inclusive definitions of the subfamily, it is important to note that Penthimiinae Kirschbaum 1868 is an older name than Deltocephalinae Dallas 1870 (Dietrich, 2005). According to a strict interpretation of the rule of priority according to the International Code of Zoological Nomenclature (ICZN), if Penthimiinae is considered a synonym of Deltocephalinae, the name of the subfamily should become Penthimiinae. However, Deltocephalinae can be demonstrated to be a long-accepted name, and the fourth edition of the ICZN has provisions for retaining such names (see Article 23.9.1). Moreover, Article 35.5 states that after 1999, names in use at higher rank retain precedence even if it is discovered that a family-group name included at a lower rank is subsequently found to be older. Wagner (1951) and Linnavuori (1959) included Penthimiini as a tribe of Deltocephalinae, and Dietrich and Rakitov (2002) considered the subfamilies to be synonymous. Thus, it appears that Article 35.5 applies, and Deltocephalinae should retain precedence over Penthimiinae.

Conclusion

The present analysis provides the most comprehensive phylogenetic estimate of Deltocephalinae to date. Because taxon sampling was limited and branch support for the resulting trees was low overall, the conclusions reached in this analysis require confirmation through more intensive study. Thus, it is not yet possible to address in detail the various hypotheses concerning the evolution of host associations. The results help to clarify the phylogenetic relationships of some groups with previously contentious taxonomic placement or rank, reveal some interesting hypotheses of relationships among tribes, and add a substantial amount of morphological data in a phylogenetic

context, thus providing a foundation for future, more detailed analyses of this large, ecologically and economically important insect lineage.

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Appendix A. A key to of tribes and subtribes of the deltocephaline group

(An online interactive version of this key is available at <http://ctap.inbus.vivc.edu/zahniser>)

- 1 Subgenital plates fused along their midline (Figs 12m, 14d) and aedeagus fused to connective (Figs 11j, 13a); male valve fused to pygofer (Fig. 14d) or fused to subgenital plates (Fig. 12m); first and second valvulae slender (Figs 5b, 6d, 7d, 8h) 2
- 1' Subgenital plates usually not fused along midline (Figs 10a–h); male valve present, articulated with pygofer (Fig. 14b) and usually with subgenital plates; aedeagus articulated or fused to connective (Figs 11f, 12f,g); first and second valvulae usually relatively broad 3
- 2(1) Anterior margin of head with a distinct carina; forewing appendix reduced (as in Fig. 2a); valve strap-like, fused to pygofer (Fig. 14d); Afrotropical, Oriental **Acostemminae**
- 2' Anterior margin of head not carinate; forewing appendix large, extending around apex of wing (Fig. 2c); valve not apparent externally, fused to subgenital plates (Fig. 12m); Palearctic and Paleotropical **Goniagnathini**
- 3(1) Style linear, point of attachment to connective not developed into pronounced lobe (Figs 11a,i,k,l,n); connective bar-shaped or plate-like (Fig. 11a), T-shaped (Figs 11i,k), or if somewhat Y-shaped, then with anterior arms widely divergent (Figs 11i,l,n) 4
- 3' Style broadly triangular, point of attachment to connective developed into pronounced lobe (Figs 11c–h, 12a–d,k); connective Y-shaped (Figs 11b,d,e, 12a,c,k), U-shaped (Figs 11c, 12b,d), or linear (with the anterior arms closely appressed) (Figs 11f–h) 7
- 4(3) Profemur row AM with numerous preapical macrosetae (as in Fig. 3c); metatibia dorsal surface (between rows AD and PD) with supranumerary macrosetae, especially basally; head much narrower than pronotum; pro- and mesotibia row PD and often row AD with numerous (>6) macrosetae; Palearctic and Paleotropical **Stegelytrinae sensu Webb (1999)**
- 4' Profemur row AM with 0, 1 (Fig. 3a), or rarely 2 preapical macrosetae; metatibia dorsal surface without supranumerary macrosetae; head slightly narrower, as wide as, or wider than pronotum; pro- and mesotibia row PD with fewer than 6 macrosetae 5
- 5(4) Forewing acuminate apically (Fig. 2a) or commissural margin straight; head slightly narrower than pronotum (except *Cariancha* Oman); connective bar-shaped or plate-like (Fig. 11a); aedeagus with dorsal apodeme expanded dorsally (Fig. 12e) (except *Cariancha*); Nearctic, Neotropical **Acinopterini**
- 5' Forewing rounded apically, commissural margin angled at base of appendix (Fig. 2b); head as wide or wider than pronotum; connective T-shaped (Figs 11i,k) or with anterior arms strongly divergent and with a well-defined stem; aedeagus with dorsal apodeme narrow or absent 6
- 6(5) Forewing (Fig. 2b) central anteapical cell constricted medially, outer anteapical cell irregularly shaped and with several strongly pigmented reflexed costal veins; Neotropical **Luhertiini**
- 6' Forewing central anteapical cell parallel-sided, outer anteapical cell parallel-sided and sometimes divided by one or more crossveins; Palearctic, Ethiopian, with one species of *Fieberiella* adventive in North America **Fieberiellini**
- 7(3) Gena acutely emarginate below eye (Fig. 1f); profemur intercalary row absent or with only a few scattered setae (Fig. 3d); metafemur macrosetal formula 2+0 or 2+1; metatarsomere I shorter than metatarsomeres II and III combined and expanded apically (Fig. 4c); metatibia usually straight throughout most of its length and distinctly bent distally (Fig. 4a); head strongly produced; brachypterous (*Drakensbergina*, some *Dorycephalini*) to macropterous with forewing apices at rest not or only slightly overlapping 8
- 7' Gena obtusely emarginate (Figs 1a,c,d,h–k) or not emarginate (Fig. 1b); profemur intercalary row with numerous well differentiated setae (Figs 3a–c,e); metafemur macrosetal formula variable but usually 2+2+1; metatarsomere I longer than metatarsomeres II and III combined and not expanded apically (Fig. 4d); metatibia curved throughout its length (Fig. 4b); head produced or not; wings variously developed, if macropterous, with forewing apices overlapping at rest 12
- 8(7) Ocelli on crown near anterior margin 9
- 8' Ocelli on anterior margin of head 10
- 9(8) Macropterous; crown encroaching on eyes (Fig. 1f); frontoclypeus with median carina (Fig. 1f); Palearctic . . . **Eupelicini**
- 9' Brachypterous; crown not encroaching on eyes; frontoclypeus not carinate; southern Africa **Drakensberginae**
- 10(8) Head produced into large, basally constricted rhomboidal process; Ethiopian **Listrophorini**
- 10' Head, if produced, neither rhomboidal nor basally constricted 11
- 11(9) Forewing clavus with anal veins confluent preapically (except *Dorycephalus* Kouchakewitch); male valve articulated to pygofer; pygofer with oblique basolateral membranous cleft; second valvula humpbacked and concave ventrally (Fig. 7h); Holarctic **Dorycephalini**
- 11' Forewing clavus with anal veins separate throughout their length; male valve fused to pygofer; pygofer without basolateral cleft; second valvula convex ventrally (Fig. 8p); widespread in Old World **Paradorydiini**
- 12(7) Clypellus narrow, more than 3× longer than greatest width, tapered and acute apically, extended well beyond lower margins of genae (Fig. 1e); ocelli usually more than 4× their own width from eyes; metatarsomere I with platellae on plantar surface; (on Pinaceae or *Casuarina*) 13
- 12' Clypellus broad, less than 2.5× longer than greatest width, tapered or expanded apically, apex truncate, extended little if

- at all beyond lower margins of genae (Figs 1a-d,h-k); ocelli usually less than 4× their own width from eyes; metatarsomere I without platellae on plantar surface (except *Cochlorhinini*) 15
- 13(12) Head not or weakly produced, anterior margin rounded or carinate; Palearctic and Oriental, one species introduced to eastern North America **Grypotina (Koebeliini sensu Dietrich & Dmitriev, 2002 in part)**
- 13 Head strongly produced, spatulate 14
- 14(13) Ocelli facial (Fig. 1e); forewing veins pustulate, appendix absent; western North America **Koebeliina (Koebeliini sensu Dietrich & Dmitriev, 2002 in part)**
- 14' Ocelli and antennal bases closer to apex of crown than to eyes; forewing veins not pustulate, appendix present; Australian, Oriental **Occinirvanini**
- 15(12) Genae neither incised nor sinuate (Fig. 1b), visible behind eyes in dorsal view; head produced; frontoclypeus elongate; forewing often with several reflexed costal veinlets; Cosmopolitan **Scaphytopiini**
- 15' Genae incised or sinuate (Figs 1a,c–e,h–k), not visible behind eyes in dorsal view; head produced or not; forewing with or without reflexed costal veinlets 16
- 16(15) Aedeagus bifurcate, with two gonopores 17
- 16' Aedeagus with one shaft and gonopore 21
- 17(16) Stem of connective short; anterior margin of head often with one or more distinct carinae or sharp ridges; face strongly depressed, nearly horizontal, concave in profile; Palearctic **Mukariinae**
- 17' Stem of connective longer, anterior margin of head never with carinae or ridges; face convex, and neither horizontal nor concave; Cosmopolitan 18, **Opsiini**
- 18(17) Subgenital plates with a row of macrosetae; valve not enlarged 19
- 18' Subgenital plates without macrosetae; valve very large 20
- 19(18) Mesial margin of eye notched (as in Figs 1a,i); single T-branched shaft arising from base of aedeagus, with shaft branches forming semicircle (Figs 12h,i) **Circuliferina**
- 19' Mesial margin of eye not notched; aedeagal shafts arising from base separately (Fig. 12a) **Opsiina**
- 20(18) Macropterous; male valve longer than wide, parabolic or lanceolate-paraboloic; lobes of pygofer with ventral pointed processes **Eremophlepsiina**
- 20' Brachypterous; male valve wider than long; lobes of pygofer without ventral processes **Achaeticina**
- 21(16) Connective Y-shaped and fused to or very closely associated with aedeagus (Figs 12k,l); plantar surface of first metatarsomere with platellae; ocelli distant from eyes (Fig. 1h); western North America **Cochlorhinini**
- 21' Connective Y- or U-shaped and articulated with aedeagus or linear and articulated or fused to aedeagus; plantar surface of first metatarsomere without platellae; ocelli close to or distant from eyes 22
- 22(21) Antennal ledges well developed, sometimes seemingly continuous with anterior margin of head; protibiae usually distinctly bicarinate dorsally 23
- 22' Antennal ledges absent or weakly developed (carina may be present, but without distinct ledge); protibiae not bicarinate dorsally 24
- 23(22) Ocelli on anterior margin of head; frontoclypeus longitudinally striate; profemur row AV without macrosetae and with only long, thin setae (Fig. 3b), or with 3 or fewer macrosetae; Palearctic **Drabescini**
- 23' Ocelli usually on crown; frontoclypeus glabrous or finely shagreened; profemur row AV usually with macrosetae; Cosmopolitan, most diverse in Palearctic region **Penthimiinae**
- 24(22) Anterior margin of head with one or more transverse carinae (e.g. Figs 1c,d,j) or strong transverse striations; antennal ledges weakly developed (with an oblique carina as in Fig. 1d); first valvula dorsal sculpturing pattern usually strigate (Figs 5f, 6a,g), with basal sculpturing elongate (Figs 5f, 7b) 25
- 24' Anterior margin of head without carinae or distinct transverse striations (rarely carinate or foliaceous, e.g. in some Hecalini, Arrugadinae, *Chiasmus*, and if so, then first valvula sculpturing maculose or granulose and submarginal); antennal ledges absent or rarely weakly developed; female first valvula dorsal sculpturing pattern variable 32
- 25(24) Frontoclypeus and vertex rugose; head produced, crown much longer medially than next to eyes; postfrontal suture visible on crown in dorsal view; Neotropical **Cerrillini**
- 25' Frontoclypeus shagreen, glabrous, or striate, not rugose; head usually not produced, crown approximately equal in width or slightly longer medially than next to eyes; postfrontal suture not visible on crown in dorsal view 26
- 26(25) Antennal pits near anterodorsal corners of eyes (as in Fig. 1c) 27
- 26' Antennal pits near posteroventral corners of eyes or centrally located (Figs 1d, j) 28
- 27(26) Profemur row AV with very long macrosetae (Fig. 3c), row AM with 2 or 3 macrosetae basad of AM1 (Fig. 3c); antennal pits shallow, not encroaching on frontoclypeus; antennae shorter than half length of body; very large, robust; Ethiopian (Guinean) **Dwightlini**
- 27' Profemur row AV reduced or absent, with at most 3–4 macrosetae, usually with very fine setae (as in Fig. 3b), row AM with only AM1; antennal pits deep, encroaching on frontoclypeus (except *Nirvanguina*); antennae long, at least half as long as body; medium to large-sized; Palearctic **Paraboloponini sensu Zhang & Webb, 1996**
- 28(26) Anterior margin of head with several transverse striations or weak carinae (Fig. 1j) 29
- 28' Anterior margin of head with 2–3 distinct parallel transverse carinae (Fig. 1d) 31
- 29(28) Aedeagus joined to connective by thin membrane, more strongly attached to dorsal part of pygofer; Ethiopian **Adamini**, in part
- 29' Aedeagus closely articulated to connective 30
- 30(29) Slender species; frontoclypeus very narrow, nearly parallel-sided; anterior margin of head sometimes not carinate or transversely striate (*Ianeira*); Ethiopian **Ianeirini**
- 30' Robust species; forewing often with dark brown irroration and false veins or with longitudinal dark shadow in cells, costal margin often with reflexed dark brown veinlets (as in Fig. 2d); frontal region of crown upturned or swollen **Athysanini** in part (some of the *Bahita*-group genera *sensu* Linnavuori & DeLong, 1978 {mostly Neotropical}; also other genera, e.g. *Eutettix* {Nearctic} and *Caffrolix* Lv. {South African}, with anterior margin of head strongly transversely striate, but not necessarily with the wing characters outlined above key here)
- 31(28) Aedeagus joined to connective by thin membrane, more strongly attached to dorsal part of pygofer; first valvula dorsal sculpturing strigate basally and partially reticulate apically (Fig. 5c); long paraphyses (=‘pseudostyles’) present and usually attached to connective (Fig. 11c); Ethiopian **Adamini**, in part
- 31' Aedeagus closely articulated to connective; first valvulae with dorsal sculptured area entirely strigate; long paraphyses

- absent, or if present then not attached to connective; Ethiopian **Selenocephalini**
- 32(24) Connective linear (Figs. 11f,h) or triangular (Fig. 11g), with apices of anterior arms closely appressed 33
- 32' Connective Y-shaped or U-shaped, anterior arms well separated throughout length 36
- 33(32) Subgenital plates fused with valve (suture obsolete) and partially fused medially near bases, apices with sharply pointed process; connective articulated posteriorly with a pair of long paraphyses (=‘pseudostyli’); Palearctic, Ethiopian **Tetartostyliini**
- 33' Subgenital plates separated from valve by distinct suture, not fused basally, apices without sharp processes; paraphyses absent or present (e.g. *Auridius* Oman) 34
- 34(33) Aedeagus with hinge-like joint between base and shaft (Fig. 12f); female first valvula dorsal sculpturing maculose and submarginal (Fig. 5h); second valvula teeth uniformly shaped, obtusely triangular and scalene (Fig. 8b) and regularly spaced; Cosmopolitan **Chiasmmini sensu** Emeljanov (1999), in part (= **Doraturini**)
- 34' Aedeagus without hinge-like joint between base and shaft (Figs 12g,h,j,l); female first valvula dorsal sculpturing imbricate (Fig. 5g) and usually reaching margin; second valvula teeth less uniform in shape (Figs 7n, 8a), not obtusely triangular, and less regularly spaced 35
- 35(34) Connective articulated with aedeagus (Fig. 11g) (fused in a few species of some genera, e.g., *Flexamia* and *Cabrulus* Oman); Cosmopolitan **Paralimnini**
- 35' Connective fused to aedeagus (Fig. 11f); Cosmopolitan **Deltocephalini**
- 36(32) Aedeagus with hinge-like joint between base and shaft (Fig. 12f); female first valvula dorsal sculpturing maculose and submarginal (Fig. 5h); second valvula teeth uniformly shaped (obtusely triangular, Fig. 8b) and regularly spaced; Cosmopolitan **Chiasmmini sensu** Emeljanov (1999), in part (= **Doraturini**)
- 36' Aedeagus without hinge-like joint between base and shaft (Figs 12g,h,j,l); female first and second valvulae variable 37
- 37(36) Macropterous, forewing with 2 antepical cells (Fig. 2f); Cosmopolitan **Macrostelini sensu** Knight & Webb (= **Balcluthini**, **Coryphaelini**)
- 37' Macropterous to brachypterous, forewing with 3 antepical cells (Figs 2a-e,h-j) 38
- 38(37) Crown and face with entire surface strongly rugose; Neotropical **Arrugadinae**
- 38' Crown and face not strongly rugose, at most weakly striate 39
- 39(38) Ocelli closer to eyes than lateral frontal sutures; male pygofer apex often directed posterodorsally (Fig. 14b), with ventral lobes that cross or approach each other, membranous lateral cleft present; subgenital plates more than 2× longer than valve; female first valvula dorsal sculpturing pattern granulose and submarginal (Fig. 5e); second valvula without teeth, humpbacked, and concave ventrally (Fig. 7h); Cosmopolitan **Hecalini sensu** Hamilton, 2000
- 39' Lateral frontal sutures meeting ocelli; metafemur macrosetal formula 2+1, sometimes 2+1+1 or 2+2+1 (some *Stirellus*, *Penestirellus*); clypellus long, extending just beyond normal curve of genae (Fig. 1i); male pygofer with dorsal margin strongly declivous, lateral cleft absent or not membranous basally (Fig. 13b); valve large; subgenital plates short, less than 2× length of valve; female first valvula dorsal sculpturing pattern maculose and submarginal (Fig. 9a); second valvula without teeth and straight ventrally (Fig. 8s); Cosmopolitan **Stenometeopiini** (= **Stirellini**)
- 39'' With neither of the above combinations of characters 40
- 40(39) Male segment X (anal tube) elongate and sclerotised dorsally (Figs. 13h,k) (not elongate in *Knollana* DeLong); small to medium sized, slender, elongate species; usually yellow to ochraceous or pale green, sometimes with black or brown markings on head; Holarctic, Neotropical **Cicadulini**
- 40' Male segment X if sclerotised dorsally, not elongate; size and colour variable 41
- 41(40) Antennae long; paraphyses often present (Fig. 12j), articulated or weakly fused with connective; color brown to ochraceous, tan, or fuscous, head and wings often marked with brown and/or orange; frontoclypeus elongate (Fig. 1k); forewings often with strongly pigmented reflexed costal veinlets (Fig. 2d) (but not in, e.g. *Osbornellus* Ball, *Cantura*); subgenital plates usually long and triangular, often membranous apically, often with fine hairs on margin or dorsally; anterior margin of head rounded to acutely angled, never with numerous transverse striations or carinae; Cosmopolitan **Scaphoideini**
- 41' Antennae relatively short; paraphyses present or absent; color variable; forewing without reflexed costal veins, or if present, then anterior margin of head usually transversely striate or carinate and frontoclypeus broad (*Bahita* group, Fig. 1j); subgenital plates variable, apices not often membranous 42
- 42(41) Frontoclypeus swollen; ocelli on crown; aedeagus with asymmetrical recurved apical process; brachypterous; Palearctic **Anoterostemmina (Limotettigini sensu** Dmitriev 2002 in part)
- 42' Frontoclypeus not swollen; ocelli on anterior margin of head; aedeagal processes, if present, usually symmetrical; macropterous to brachypterous 43
- 43(42) Aedeagus with a single (not paired) sclerotised apophysis, or ‘dorsal connective’, projecting dorsally from atrium (=phallobase) and connected to segment X by membrane (Fig. 13g); male pygofer with dorsal margin thickened, declivous, and often ending in a decurved hook (Fig. 13g); Holarctic **Limotettigina (Limotettigini sensu** Dmitriev 2002 in part)
- 43' Without combination of characters above 44
- 44(43) Large, greenish species; forewing venation reticulate apically; Ethiopian (South Africa) **Hypacostemmini**
- 44' Colour variable; forewing sometimes with reticulate venation, but never green and restricted to apex 45
- 45(44) Crown depressed, excavated, concave in lateral view, sometimes flat; forewing with supranumerary slightly reflexed costal veinlets (Figs. 2i,j); head produced, frontoclypeus relatively elongate; Cosmopolitan **Platmetopiini**
- 45' Crown usually not depressed; forewing without supranumerary costal veinlets (except the *Bahita* group of genera); head usually not produced; frontoclypeus usually broad; Cosmopolitan **Athysanini** in part
- (Note: The last two tribes are difficult to separate, and at this time their circumscriptions are unsatisfactory. Athysanini contains many potentially unrelated genera, and identifying generic groups within this large tribe will be necessary to produce a more satisfactory classification.)

Table 1. Specimens examined.

Subfamily	Tribe	Species	Locality	Institution
Acostemminae		<i>Acostemma</i> sp.	Madagascar: Toliara	CAS
Aphrodinae		<i>Aphrodes bicincta</i> (Schrank)	USA: Illinois	INHS
Arrugadinae		<i>Arrugada rugosa</i> (Osborn)	Bolivia: Yungas	INHS, OSU
Cicadellinae	Anoterostemmini	<i>Anoterostemma ivanhofi</i> (Lethierry)	Kustenl. Monfalc	BMNH, OSU
Cicadellinae	Errhomenini	<i>Lystridea uhleri</i> (Baker)	USA: California	INHS
Deltocephalinae	Acinopterini	<i>Acinopterus acuminatus</i> Van Duzee	USA: Illinois	INHS
Deltocephalinae	Athysanini	<i>Athysanus argentarius</i> Metcalf	USA: Illinois	INHS
Deltocephalinae	Athysanini	<i>Chlorotettix galbanatus</i> Van Duzee	USA: Illinois	INHS
Deltocephalinae	Athysanini	<i>Ballana curvata</i>	USA: California	INHS
Deltocephalinae	Athysanini	<i>Bahita</i> sp.	Peru: Madre de Dios	USNM
Deltocephalinae	Athysanini	<i>Colladonus clitellarius</i> (Say)	USA: Illinois	INHS
Deltocephalinae	Athysanini	<i>Euscelis seriphidii</i> Emeljanov	Kyrgyzstan: Chuy	INHS
Deltocephalinae	Athysanini	<i>Eutettix pictus</i> Van Duzee	USA: Illinois	INHS
Deltocephalinae	Athysanini *	<i>Exitianus exitiosus</i> (Uhler)	USA: Illinois	INHS
Deltocephalinae	Athysanini +	<i>Hypacostemma uniformis</i> (Distant)	South Africa: KZN.	USNM
Deltocephalinae	Athysanini	<i>Phlepsius intricatus</i> (Herrich-Schaffer)	Kyrgyzstan: Dzalal-Abad	INHS
Deltocephalinae	Athysanini	<i>Limotettix (Scleroracus) decumanus</i> (Kontkanen)	Kyrgyzstan: Dzalal-Abad	INHS
Deltocephalinae	Athysanini	<i>Stenometopiellus sigillatus</i> Haupt	Kyrgyzstan: Chuy	INHS
Deltocephalinae	Balcluthini	<i>Balclutha punctata</i> (Thunberg)	USA: Illinois	INHS
Deltocephalinae	Cerrillini	<i>Cerrillus notatus</i> (Osb.) ²	Peru: Madre de Dios	USNM
Deltocephalinae	Chiasmusini	<i>Chiasmus</i> sp., female	Senegal: N'Dierba	USNM
		<i>Chiasmus varicolor</i> , male	Australia: New South Wales	INHS
Deltocephalinae	Cicadulini	<i>Cicadula melanogaster</i> (Provancher)	USA: Illinois	INHS
Deltocephalinae	Cochlorhinini	<i>Cochlorhinus pluto</i> Uhler	USA: California	INHS
Deltocephalinae	Cochlorhinini	<i>Eulonus alnus</i> (Van Duzee)	USA: California	USNM
Deltocephalinae	Coryphaelini	<i>Coryphaelus gylenhalii</i> (Fallen)	Finland (?): Tvarminne	USNM
Deltocephalinae	Deltocephalini	<i>Cabrulus tener</i> (B. T.)	??	INHS
Deltocephalinae	Deltocephalini	<i>Deltocephalus balli</i> Van Duzee	USA: Illinois	INHS
Deltocephalinae	Deltocephalini	<i>Laevicephalus melshemerii</i> (Fitch)	USA: Illinois	INHS
Deltocephalinae	Deltocephalini	<i>Sanctanus sanctus</i> (Say)	USA: Illinois	INHS
Deltocephalinae	Doraturini	<i>Doratura stylata</i> (Boheman)	Kyrgyzstan: Issyk-Kul	INHS
Deltocephalinae	Fieberiellini	<i>Fieberiella florii</i> (Stal)	USA: Illinois	INHS
Deltocephalinae	Goniagnathini	<i>Goniagnathus rugulosus</i> (Hpt.)	Kyrgyzstan: Issyk-Kul	INHS
Deltocephalinae	Grypotini	<i>Grypotes puncticolis</i> (H.-S)	USA: Pennsylvania	INHS
Deltocephalinae	Hecalini	<i>Evinus peri</i> Anufriev	Kyrgyzstan: Dzalal-Abad	INHS
Deltocephalinae	Hecalini	<i>Neohecalus lineatus</i> (Uhler)	USA: Illinois	INHS

Subfamily	Tribe	Species	Locality	Institution
Deltocephalinae	Luheriini	<i>Luheria constricta</i> Osborn	Argentina: Misiones	USNM & OSU
Deltocephalinae	Macrostelini	<i>Macrosteles fascifrons</i> (Stal)	USA: Illinois	INHS
Deltocephalinae	Opsiini	<i>Opsius stactogalus</i> (Fieber)	USA: Illinois	INHS
Deltocephalinae	Opsiini	<i>Neoliturus carbonarius</i> Mit.	Kyrgyzstan: Chuy	INHS
Deltocephalinae	Paralimnini	<i>Paralimnus angusticeps</i> Zachv.	Kyrgyzstan: Issyk-Kul	INHS
Deltocephalinae	Paralimnini	<i>Diplocolenus abdominalis</i> (F.)	Kyrgyzstan: Chuy	INHS
Deltocephalinae	Paralimnini	<i>Mocuellus collinus</i> (Boheman)	Kyrgyzstan: Chuy	INHS
Deltocephalinae	Platymetopiini	<i>Platymetopius obsoletus</i> (Signoret)	Kyrgyzstan: Dzalal-Abad	INHS
Deltocephalinae	Scaphoideini	<i>Cantura jucunda</i> (Uhler)	USA: Illinois	INHS
Deltocephalinae	Scaphoideini	<i>Scaphoideus titanus</i> Ball	USA: Illinois	INHS
Deltocephalinae	Scaphytopiini	<i>Scaphytopius acutus</i> (Say)	USA: Illinois	INHS
Deltocephalinae	Stenometopiini	<i>Stirellus bicolor</i> (Van Duzee)	USA: Illinois	INHS
Deltocephalinae	Tetartostyliini	<i>Tetartostylus</i> sp.	South Africa: WCape Prov.	INHS
Drakensbergeninae		<i>Drakensbergena fuscovittata</i> Linnavuori	South Africa: KZN	NCI
Eupelicinae	Dorycephalini	<i>Attenuipyga platyrhyncus</i> (Osborn)	USA: Illinois	INHS
Eupelicinae	Eupelicini	<i>Eupelix cuspidata</i> (F.)	Kyrgyzstan: Chuy	INHS
Eupelicinae	Paradorydiini	<i>Paradorydium lanceolatum</i> Burm.	Kyrgyzstan: Dzalal-Abad	INHS
Koebeliinae		<i>Koebelia grossa</i> Ball	USA: California	INHS
Mukariinae		<i>Mukaria</i> sp.	India: Assam	USNM
Neobalinae		<i>Calliscarta</i> sp.	Peru	INHS
Neocoelidiinae		<i>Chinaia</i> sp.	Ecuador	INHS
Nirvaninae	Occinirvanini	<i>Occinirvana</i> sp.	Australia: WA	BMNH
Paraboloponinae		<i>Parabolopona</i> n. sp.	Taiwan: Sungkang	TARI
Paraboloponinae		<i>Roxasella</i> sp.	Malaysia: Sabah	USNM
Penthimiinae		<i>Penthimia americana</i> Fitch	USA: Illinois	INHS
Penthimiinae		<i>Nielsoniella vitellina</i> Lv.	Nigeria: New Bussa	USNM
Selenocephalinae	Adamini	<i>Adama (Paracostemma)</i> n. sp.	Central African Republic	MNHN
Selenocephalinae	Drabescini	<i>Drabescus</i> sp.	Nigeria: Ile Ife	USNM, MNHN
Selenocephalinae	Dwightlini \$	<i>Dwightla acutipennis</i> (Linnavuori & Al-Ne'amy)	Central African Republic	USNM, MNHN
Selenocephalinae	Adamini #	<i>Bardera fasciolata</i> (Mel.)	--no locality data--	BMNH
Selenocephalinae	Selenocephalini	<i>Selenocephalus griseus</i> (F.)	Greece: Mt. Parnassos	INHS
Stegelytrinae		<i>Stegelytra boliveri</i> Sign.	Mamosa	USNM
Stegelytrinae		<i>Stegelytra erythroneura</i> Haupt	--no locality data--	BMNH
Stegelytrinae		<i>Pachymetopius decoratus</i> Matsumura	Taiwan: Nantou	INHS
Xestocephalinae	Portanini	<i>Portanus elegans</i> Kramer	Venezuela	INHS
Xestocephalinae	Xestocephalini	<i>Xestocephalus superbus</i> (Prov.)	USA: Illinois	INHS

Table 4.

Branch # or terminal taxon

Lystridea. 3(2), 5(1), 12(4), 15(1), 16(1), 21(2), 23(1), 33(3), 39(0), 55(1), 57(1), 58(2), 69(2), 71(0), 76(1), 87(1), 96(2), 101(1), 115(1), 116(1), 119(2)
Aphrodes. 6(0), 8(0), 12(1), 14(0), 46(1), 49(0), 60(1), 68(1), 81(1), 85(1), 88(1), 95(0), 99(0), 119(1)
1) 1(1), 3(1), 9(0), 18(0), 33(1), 34(0), 37(0), 50(1), 52(0), 54(0), 56(0), 64(0), 86(1)
2) 11(1), 24(1), 29(0), 36(0), 52(0), 56(0), 65(0), 84(0), 86(1), 87(1), 94(0), 104(0), 116(1)
Calliscarta. 34(0), 38(2), 39(0), 54(1), 66(0), 69(2), 76(1), 88(1), 89(3), 96(2), 100(1)
3) 4(2), 14(0), 24(2), 26(1), 27(0), 30(0), 31(0), 32(1), 34(1), 40(1), 49(0), 54(0), 59(1), 60(1), 61(0), 106(0)
Chinaia. 4(2), 8(0), 19(1), 20(1), 23(1), 24(2), 30(0), 31(0), 33(2), 35(0), 47(1), 57(1), 61(0), 90(1), 95(0), 106(0), 119(2)
4) 1(0), 3(0), 9(1), 40(1), 63(0), 68(1), 96(1), 99(0), 106(4)
Portanus. 1(0), 4(2), 6(0), 24(2), 30(3), 31(0), 38(1), 61(1), 65(1), 68(1), 91(1), 96(1), 98(0), 100(3), 101(1), 103(1), 106(4), 110(0), 115(1)
Xestocephalus. 2(1), 4(0), 11(0), 18(1), 24(1), 25(1), 30(0), 31(1), 36(1), 41(1), 46(1), 56(2), 60(2), 61(0), 66(0), 67(1), 76(1), 87(0), 88(2), 89(3), 96(4), 106(5), 119(1)
5) 20(2), 25(1), 34(0), 44(1), 48(1), 52(1), 54(0), 57(0), 62(1), 68(1), 83(0), 91(1), 102(0), 105(1), 110(0)
Acostemma. 6(0), 27(4), 40(1), 56(1), 59(1), 75(1), 86(1), 96(2), 100(1), 105(3), 111(1), 115(1), 117(1)
6) 31(0), 56(0), 86(0), 99(0), 102(0), 103(1), 105(1), 107(1), 119(1)

Luheria. 26(1), 27(2), 31(0), 39(0), 53(0), 56(0), 86(0), 96(0), 99(0), 102(0), 103(1), 105(1), 107(1), 118(1), 119(1)
7) 20(1), 38(1), 41(1), 96(1), 106(2), 119(1)
8) 44(0), 109(0)
Fieberiella. 20(3), 27(2), 38(1), 59(1), 60(1), 106(2), 107(0), 118(1)
9) 20(1), 32(1), 38(0), 64(1), 94(0), 111(1)
Acinopterus. 29(0), 64(1), 105(0), 111(1)
10) 1(0), 6(0), 24(1), 55(1), 56(1), 70(1), 98(3), 119(2)
Stegelytra. 1(0), 10(0), 40(1), 44(1), 48(0), 54(1), 62(0), 64(1), 75(1), 100(1), 104(0), 106(1), 111(1)
Pachymetopius. 2(1), 25(2), 27(2), 36(0), 38(2), 41(0), 59(1), 64(0), 79(0), 83(1), 98(3), 101(1), 110(1), 111(0), 119(2)
11) 38(1), 101(1), 108(1), 115(1)
12) 20(0), 27(3), 39(0), 114(0)
Adama. 27(3), 30(0), 86(1), 87(1), 99(1), 111(1)
13) 17(1), 29(0), 38(2), 64(1), 96(2)
Goniagnathus. 6(0), 27(1), 40(1), 49(0), 60(1), 64(1), 100(2), 105(3), 107(0), 109(0), 117(1)
14) 20(3), 31(1), 56(1), 62(0), 104(0), 106(1), 119(0)
Dwightla. 1(0), 11(1), 18(1), 23(1), 27(3), 42(1), 64(1), 70(1), 87(1), 98(0), 99(1), 108(0), 111(1), 114(1), 119(0)
Selenocephalus. 5(1), 20(3), 27(2), 39(1), 64(0), 86(1), 96(0), 97(1), 119(2)
15) 20(1), 49(0), 53(0), 62(0), 63(0), 91(0), 94(0), 106(2)
Phlepsius. 26(1), 32(1), 63(0), 91(0), 96(0)
16) 29(0), 48(0), 59(1), 60(1), 75(1)
Hypacostemma. 5(1), 17(1), 27(0), 31(1), 63(1), 91(1), 97(1)
17) 10(0), 25(0), 44(0)
Eutettix. 25(1), 63(0), 91(0), 119(0)
18) 20(2), 63(1), 91(1), 96(0), 97(1)
19) 25(0), 94(1), 117(1)
Ballana. 3(0), 57(0), 63(0), 75(0)
20) 34(1), 40(1), 41(0), 59(2), 81(1), 119(0)

Cochlorhinus. 7(0), 20(1), 29(1), 56(1), 78(1)
Eulonus. 1(0)
 21) 1(0), 27(2), 29(1), 42(1), 83(1), 84(0), 106(0), 111(1)
Bahita. 3(0), 5(1), 25(0), 26(1), 29(1), 44(1), 45(1), 60(0), 106(3), 111(1)
 22) 18(1), 23(1), 24(1), 25(1), 52(0), 53(1), 64(1), 106(0), 119(2)
 23) 18(1), 24(1), 27(3), 29(0), 57(0), 111(1)
Parabolopona. 30(0), 88(1), 94(1), 96(1), 97(0), 119(1)
Roxasella. 39(0), 59(2), 63(0), 93(1), 119(2)
 24) 12(3), 20(0), 25(2), 29(1), 31(1), 34(1), 47(1), 91(0), 111(0)
Drabescus. 18(0), 20(1), 24(1), 25(2), 38(2), 44(1), 47(1), 50(0), 58(1), 59(0), 67(1), 69(0), 73(0), 84(1), 91(0), 96(1), 104(0), 109(0), 119(2)
 25) 1(1), 18(1), 24(0), 30(2), 41(0), 60(2), 97(0)
Cerrillus. 12(1), 20(0), 23(0), 25(1), 27(3), 30(2), 32(1), 47(0), 56(1), 91(1), 98(0), 119(2)
 26) 5(1), 16(1), 25(2), 33(0), 42(0), 47(1), 63(0), 91(0), 106(1), 119(1)
Mukaria. 7(0), 30(3), 31(0), 57(0), 63(0), 65(0), 66(0), 88(1), 104(0), 111(1), 113(1), 117(1)
 27) 17(1), 27(1), 29(0), 39(0), 44(1), 58(1), 75(0), 86(1), 96(1)
Penthimia. 30(2), 32(1), 38(2), 39(0), 40(1), 41(1), 48(1), 49(1), 52(1), 56(1), 59(0), 60(0), 63(1), 83(0), 84(1), 98(0)
Nielsoniella. 10(1), 18(0), 30(0), 44(1), 63(0), 64(0), 97(1), 108(0)
 28) 25(0), 27(0), 63(0), 91(0), 98(0)
Neoliturus. 26(1), 57(0), 89(1), 94(1), 96(2), 98(1), 113(1)
Colladonus. 20(2), 41(0), 98(0), 114(2)
Platymetopius. 29(1), 40(1), 59(2), 86(1), 96(0), 98(0), 104(0)
 29) 1(0), 24(1), 42(1), 45(1), 57(0), 94(1), 98(0)
Cantura. 24(1), 26(1), 94(1)

30) 32(1), 111(1)
Scaphoideus. 24(1), 94(0), 96(0), 97(1), 106(4)
Scaphytopius. 20(0), 22(0), 24(0), 27(1), 29(1), 40(1), 44(1), 60(0), 75(0), 83(1), 94(1)
 31) 1(0), 20(2), 30(0), 98(1)
Chlorotettix. 57(0), 83(1), 93(1), 101(0)
 32) 52(0), 89(1)
Cicadula. 24(1), 34(1), 41(0), 53(1), 86(1), 103(0), 106(4), 109(0), 119(0)
 33) 3(0), 96(0)
 34) 65(0), 89(2)
Grypotes. 4(1), 18(1), 34(1), 48(1), 61(0), 71(0), 81(1), 86(1), 106(1), 114(3), 117(1)
Opsiis. 17(1), 30(3), 41(0), 83(1), 94(1), 113(1)
 35) 7(0), 88(1)
 36) 20(1), 35(0), 36(0), 57(0), 61(0), 83(1)
Tetartostylus. 19(1), 36(0), 39(0), 50(2), 57(0), 90(1), 111(1), 115(2)
 37) 43(1), 60(2), 66(0), 86(1), 96(1)
Macrosteles. 18(1), 36(1), 57(0)
 38) 21(0), 36(0), 57(1), 65(0), 104(0)
Coryphaeus. 50(0), 52(1), 60(0), 68(0), 89(0), 104(0)
 39) 7(1), 20(0), 83(0), 90(1), 92(1), 96(3), 98(2)
Balclutha. 1(1), 3(1), 19(1), 20(0), 32(1), 41(0), 51(1), 57(0), 104(1)
Evinus. 6(0), 18(1), 22(2), 26(1), 28(1), 33(0), 34(1), 35(1), 61(1), 95(0), 102(1), 104(0), 105(4), 106(0)
 40) 1(1), 21(0), 26(1), 52(1)
Limotettix. 21(0), 106(3)
 41) 30(3), 59(2)
 42) 17(1), 21(1), 75(0), 119(0)
Euscelis. 25(1), 94(1), 114(2), 119(2)
 43) 10(1), 20(1), 26(0), 31(1), 41(0), 56(1), 106(0), 119(0)
Athysanus. 27(1), 41(0), 53(1), 60(0), 63(1), 82(1), 97(1), 106(1)
Anoterostemma. 15(1), 30(0), 33(0), 34(1), 35(0), 48(1), 50(0), 59(1), 69(0), 86(1), 95(0), 101(0), 104(0), 105(4), 106(0)
 44) 29(1), 86(1)
 45) 1(0), 19(1), 21(0), 35(0), 88(0), 115(2)

Mocuellus. 19(1), **38(0)**, **41(0)**, **63(1)**,
93(1), **114(0)**
46) **40(1)**, **57(0)**
Cabrus. 19(1), **52(0)**, **109(0)**, **117(1)**
47) 19(0), 59(1), **83(1)**
Diplocolenus. 59(2), **93(1)**, **119(2)**
Laevicephalus. **19(1)**, **41(0)**, 59(1), **84(0)**
48) **20(1)**, 59(1), 88(1)
Paralimnus. **8(0)**, **66(0)**, 88(1), **94(1)**,
119(0)
49) **2(1)**, **117(1)**
Deltocephalus. **29(0)**, **84(0)**, 88(1)
Sanctanus. **24(1)**, **41(0)**, 88(0)
50) **96(1)**, **103(0)**, **104(0)**
Stenometopiellus. **3(1)**, **7(1)**, 21(1), **57(0)**,
64(1), **105(4)**, **106(4)**, **119(0)**
51) 21(0), 27(1), **63(1)**, **87(1)**, 90(1), 95(0),
98(2)
52) 10(1), **25(1)**, 27(1), **38(2)**, **53(1)**, 60(0),
98(3), **112(1)**, **114(2)**
Exitianus. **1(0)**, 10(1), **29(0)**, 60(0), 90(0),
95(1)
53) **26(0)**, **35(0)**, 90(1), 95(0), 106(0),
115(2)
Chiasmus. 10(1), **18(1)**, **20(1)**, **21(1)**,
22(2), **30(0)**, **33(0)**, **34(1)**, **36(0)**, **50(2)**,
60(1), **67(1)**, **69(0)**, **71(0)**, **73(0)**, **78(1)**,
79(0), **80(0)**, 106(0)
Doratura. **7(1)**, 10(0), **19(1)**, 60(0), **106(1)**
54) **20(1)**, 30(0), 59(1), 90(1), **92(1)**, 95(0),
96(3)
Stirellus. **6(0)**, **19(1)**, 27(0), **29(0)**, 30(0),
35(0), **39(0)**, 59(1), **105(4)**, **106(4)**

55) **18(1)**, **26(0)**, **28(1)**, **31(1)**, **41(0)**, **56(1)**,
103(1)
Neohecalus. **1(0)**, **27(4)**, 30(3), 59(1),
63(0), **82(1)**, **86(0)**, **104(1)**
56) **7(1)**, 21(1), **36(0)**, 37(1), **53(1)**, **58(2)**,
59(2), 60(0), 64(1), **71(0)**
Arrugada. **3(1)**, **6(0)**, **12(1)**, 21(1), **25(1)**,
27(1), 37(1), **30(2)**, **39(0)**, 60(0), 64(1),
119(0)
57) 27(0), 30(0), 38(0), **48(1)**, **50(2)**, **69(0)**,
76(1), 106(0)
Koebelia. **1(0)**, **4(1)**, **18(0)**, 21(1), **33(2)**,
34(1), **35(0)**, 37(0), 38(0), 60(0), **61(0)**,
63(0), 64(1), **68(0)**, **73(0)**, **78(1)**, **81(1)**,
89(0), **92(0)**, **98(1)**, **99(1)**, **104(1)**, **106(1)**,
114(3)
58) **9(1)**, 20(0), 21(0), **22(2)**, **23(1)**, 37(1),
49(2), **51(1)**, 60(1), 64(0), **67(0)**, **72(1)**,
74(0), **77(1)**, **79(0)**, **80(0)**, **82(1)**, 86(0),
106(0)
Attenuipyga. **5(1)**, **7(0)**, 38(1), **58(0)**, **60(0)**,
74(1), 86(0), **104(1)**, **106(4)**
Paradorydium. **6(0)**, **12(2)**, **13(1)**, **27(1)**,
29(0), **30(1)**, **35(0)**, 38(0), **46(1)**, **52(0)**,
61(0), **64(1)**, 74(0), 86(1), **100(1)**, **103(0)**,
105(4), **119(0)**
59) **33(0)**, **34(1)**, 38(2), 74(0), **87(0)**, **92(0)**,
98(1)
Drakensbergena. **5(1)**, **7(0)**, **9(0)**, **15(1)**,
18(0), 20(0), **25(1)**, **31(0)**, **36(1)**, **48(0)**,
56(0), **58(0)**, **67(1)**, **80(1)**, **119(0)**
Eupelix. **1(0)**, **6(0)**, **13(1)**, **21(1)**, 38(2),
78(1), 86(0), **96(0)**, **97(1)**