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New tribal placements, reinstatements and synonymies in the leafhopper subfamily Deltocephalinae (Hemiptera: Cicadellidae)

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Abstract. The higher classification of Deltocephalinae Fieber, 1869 (992 genera, 7243 species) is revised to reflect the results of recent phylogenomic analyses of 730 terminal taxa and > 160 000 nucleotide positions, which provided well-resolved and supported estimates of relationships among major deltocephaline lineages. The revised classification recognizes 30 monophyletic tribes and 24 subtribes. Diagnostic morphological characters of the newly redefined tribes are discussed and a revised key to tribes is provided. Proposed changes include the following: Athysanini Van Duzee, 1892 is redefined to include the nominotypical subtribe (corresponding to the previously recognized Holarctic *Athysanus*-group of genera), subtribe Cochlorhinina Oman, 1943 stat. nov., and Koebeliina Baker, 1897 stat. nov. (= Grypotinae Haupt, 1929 syn. nov.). Eupelicini Sahlberg, 1871 is redefined to include the nominotypical subtribe, Drakensbergenina Linnavuori, 1979 stat. nov., Paradorydiina Evans, 1936, and Stenometopiina Baker, 1923 stat. nov. Penthimiini Kirschbaum, 1868 includes junior synonym Magnentiini Linnavuori, 1978 syn. nov. Platymetopiini Haupt, 1928 is reinstated from synonymy under Athysanini to include the Palearctic type genus and most of the endemic Neotropical genera previously included in Athysanini; it also includes Cerrillini Linnavuori, 1975 syn. nov. Scaphoideini Oman, 1943 is redefined to include the nominotypical subtribe, Drabescina Ishihara, 1953 stat. nov. (= Paraboloponidae Ishihara, 1953, syn. reinstated), and Phlepsiina Zahniser & Dietrich, 2013 stat. nov. Selenocephalini Fieber, 1872, is redefined to include the nominotypical subtribe Selenocephalina (= Ianeirini Linnavuori, 1978 syn. nov., Adamini Linnavuori & Al-Ne'amy, 1983 syn. nov., and Dwightlini McKamey, 2003 syn. nov.) and subtribes Bonaspeiina Zahniser & Dietrich, 2013 stat. nov., and Hypacostemmina Linnavuori & Al-Ne'amy, 1983 stat. nov. Vartini Zahniser & Dietrich, 2013 is redefined to include the nominotypical subtribe, Punctulina Dai *et al*., 2017 stat. nov., and Bambusanina subtribe nov., which is erected to include seven bamboo-feeding genera formerly placed in Athysanini. Several genera are also transferred among tribes based on the recent phylogenomic results. A complete list of tribes, subtribes, and their included genera is provided. *Paramesanus* Dlabola, 1979 syn. nov. is considered a junior synonym of *Awasha* Heller & Linnavuori, 1968 resulting in the new combination *Awasha wittmeri* (Dlabola, 1979) comb. nov. *Mascoitanus* Linnavuori & Heller, 1961 stat. nov., formerly a subgenus of *Brasilanus* Linnavuori, 1959, is raised to generic status resulting in the new combination *Mascoitanus lateralis* (Linnavuori & Heller, 1961) comb. nov. *Omanellinus* Zhang 1999 syn. nov. is considered a junior synonym of *Omanella* Merino, 1936, resulting in the new combination, *Omanella populus* (Zhang, 1999) comb. nov. *Xugyrosus* nom. nov., is proposed as a replacement name for *Gyrosus* Xu & Zhang, 2023, resulting in the new combination, *Xugyrosus deltodontus* (Xu & Zhang, 2023) comb. nov.

Keywords. Auchenorrhyncha, Membracoidea, phylogenomics, phylogeny, morphology.

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Introduction

Deltocephalinae Fieber, 1869 currently includes more genera and species (992 genera, 7243 species) than any other subfamily of leafhoppers (Dmitriev *et al*. 2022 onward) and is also the most economically important leafhopper group due to the role of numerous species as vectors of plant pathogens (Nielson 1968; Dietrich 2013; Trivellone 2018; Cao *et al*. 2022).

The classification of Deltocephalinae has fluctuated substantially over the past 35 years. The classifications of Evans (1947), Oman (1949) and the Metcalf catalogue (e.g., Metcalf 1967) formed the basis for relatively modern classifications. Some attempts to revise the classification of Deltocephalinae (e.g., Hamilton 1975; Anufriev & Emeljanov 1988) were not followed by subsequent authors, including Oman *et al*. (1990), who proposed a family-group classification of Cicadellidae including Deltocephalinae comprised of 23 tribes. The first explicit phylogenetic analyses of Cicadellidae based on morphological (Hamilton 1983; Dietrich 1999) and molecular data (Dietrich *et al*. 2001) indicated that Deltocephalinae sensu Oman *et al*. (1990) is paraphyletic. Based on these results, several subfamilies recognized by Oman *et al*. (1990) were considered synonyms of Deltocephalinae (Emeljanov 1999; Dietrich & Rakitov 2002). Subsequent, more detailed analyses of Deltocephalinae and related groups based on morphological characters and molecular data (Zahniser & Dietrich 2008, 2010) supported synonymizing several additional groups with Deltocephalinae.

Zahniser & Dietrich (2013) revised the tribal classification based on phylogenetic analyses of a dataset comprising 152 exemplar taxa, morphological characters, and nucleotide sequences from two genes (~2800 bp of 28S and ~350 bp of histone H3) obtained through Sanger sequencing. Although their analysis included representatives of all previously recognized deltocephaline tribes, Zahniser & Dietrich (2013) were only able to include a small fraction of known deltocephaline genera in their analysis, basing their tribal placements on examination of representatives of most genera and the presence or absence of characters defining the tribes. Because the phylogenetic relationships of most genera were unknown during the last revision and because of homoplasy and the instability of some morphological characters used to define deltocephaline tribes, the current tribal classification is unsettled in some respects.

The recent comprehensive phylogenomic analysis of Cao *et al*. (2022), comprising 479 genera and 730 terminal taxa representing all recognized deltocephaline tribes and > 160 000 nucleotide positions (Fig. 1; Supp. file 2), provided a well-resolved phylogenetic backbone for this subfamily and a much more detailed understanding of the relationships among deltocephaline genera. It supported the monophyly of most of the smaller tribes recognized by Zahniser & Dietrich (2013) but also corroborated the previous phylogenetic results that showed some of the larger tribes, including Athysanini Van Duzee, 1892 and Scaphoideini Oman, 1943, are para- or polyphyletic. More detailed analyses of individual lineages including tribes and other well-supported groups that are restricted to particular regions, habitats or host plants (some currently underway), will be needed to support a comprehensive reclassification of the genera. Nevertheless, some changes to the classification are well-supported by the results of Cao *et al*. (2022) and are proposed below. These include reinstating some tribes previously treated as junior synonyms of Athysanini, reducing some previously recognized tribes to subtribal status to better reflect their phylogenetic relationships, synonymizing some tribes and subtribes, and changing the tribal placements of certain genera sampled in recent analyses and some apparently related genera not yet included in phylogenetic datasets.

Material and methods

Morphological data were compiled by examining specimens deposited in the Illinois Natural History Survey insect collection (INHS), primarily the DNA vouchers listed in Cao *et al*. (2022: table s1), the US National Museum of Natural History (USNM), and borrowed from other collections (see Acknowledgments below), or, when specimens were not available for study, the primary taxonomic literature. Habitus images were taken with a Nikon DS-Fi2 digital camera mounted on a Nikon SMZ18 stereo microscope. Images of the female ovipositor structures were taken with a Nikon DS-Fi2 digital camera mounted on a Nikon Eclipse Ni compound microscope or a Jenoptik Arktur digital camera attached to an Olympus BH 40 compound microscope. Images taken at separate focal planes were stacked with Helicon Focus 6 or automatic stacking and edited in Adobe Photoshop. Valvulae of the ovipositor and the gonoplac were separated from the pygofer and from each other and placed on a microscope slide with a drop of glycerine and covered with a cover slip which flattened these structures. SEM images of uncoated specimens were taken with a Hitachi TM3030+ desktop scanning electron microscope. Some figures are composites of two or more images and may show slight distortion at the edges of individual images. Male and female genitalia preparations were made by removing the abdomen, soaking overnight in cold 10% KOH solution or on a warming plate for 10 minutes, rinsing with water and storing in glycerine. Morphological character data and images were compiled using TaxonWorks (TaxonWorks Community 2022). Morphological terminology follows Dietrich *et al*. (2022). Nomenclature for rows of leg setae follows Rakitov (1998) wherein AD = anterodorsal, AM = anteromedial, AV = anteroventral, PD = posterodorsal, and PV = posteroventral.

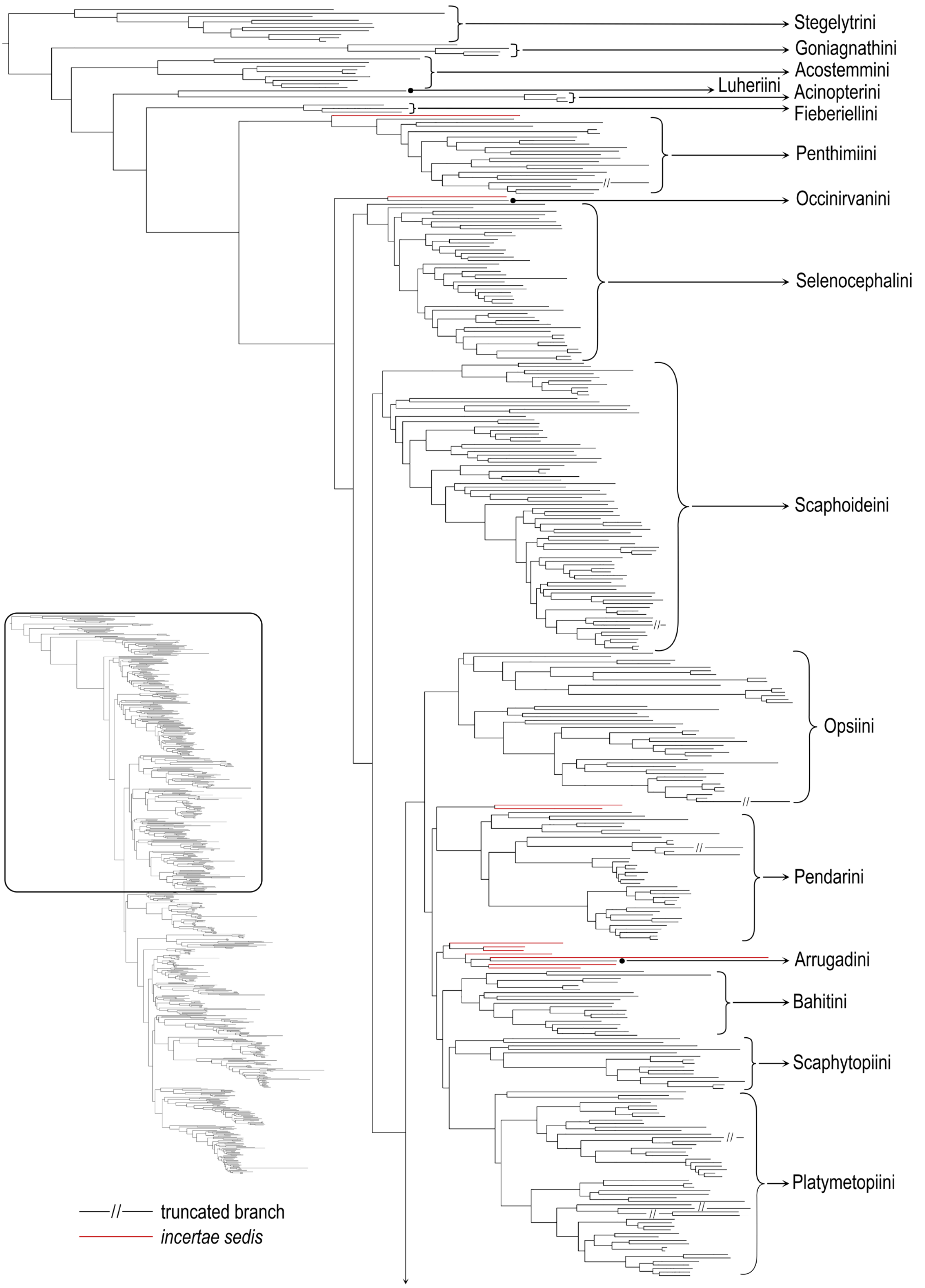

Fig. 1 (continued on next page). Consensus maximum likelihood tree of Deltocephalinae Fieber, 1869 based on a concatenated nucleotide dataset comprising 163 365 positions, showing revised classification. This tree corresponds to Cao *et al*. (2022: fig. s1).

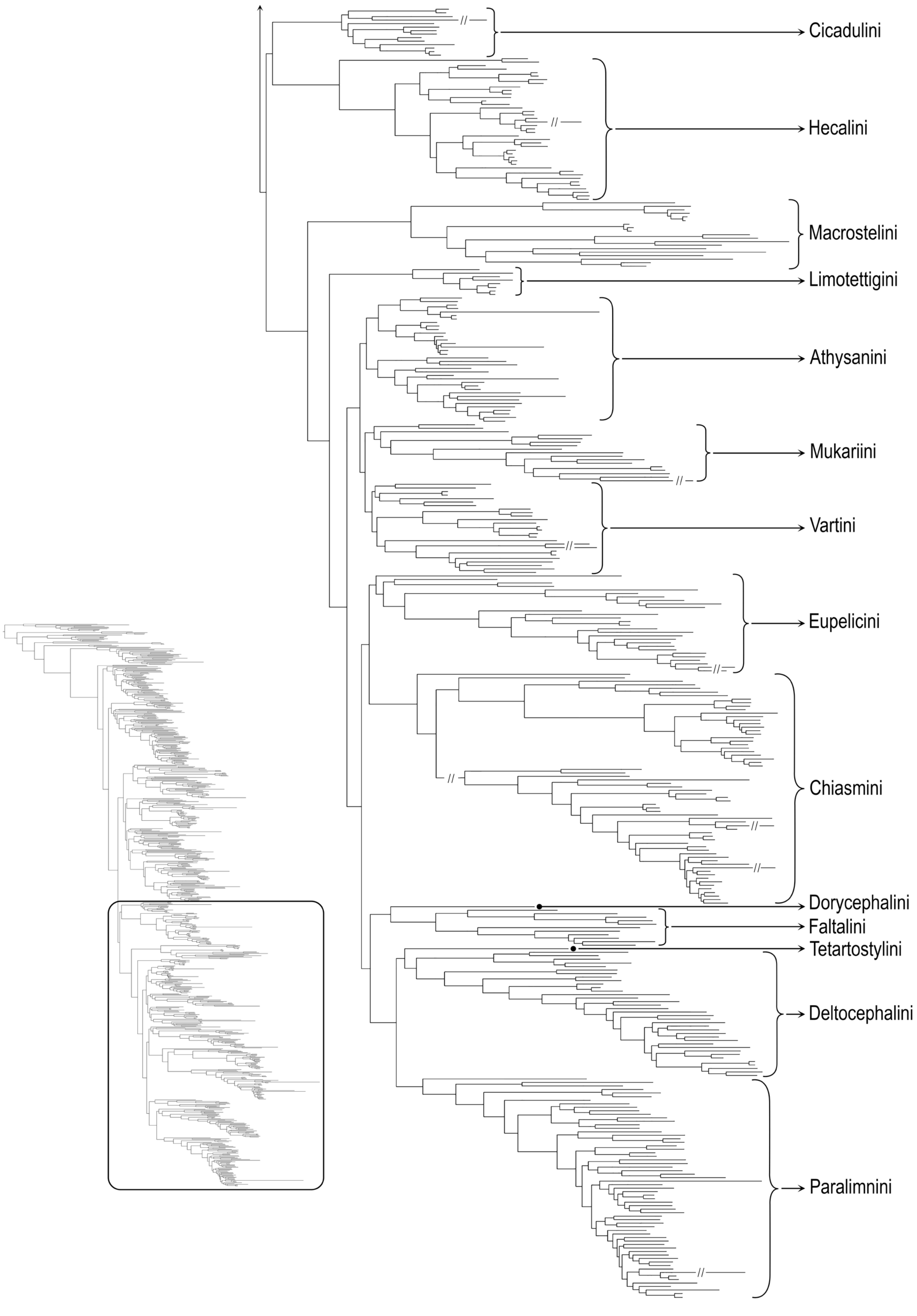

Fig. 1 (continued).

Results

The revised higher classification is given below, followed by diagnoses and notes for tribes and subtribes which received significant taxonomic changes or otherwise deserve commentary. A full list of the tribes, subtribes, and their included genera is provided (Supp. file 1).

Class Insecta Linnaeus, 1758
Order Hemiptera Linnaeus, 1758
Suborder Auchenorrhyncha Duméril, 1805
Superfamily Membracoidea Rafinesque, 1815
Family Cicadellidae Latreille, 1825
Subfamily Deltocephalinae Fieber, 1869

- Tribe Acinopterini Oman, 1943
- Tribe Acostemmini Evans, 1972
- Tribe Arrugadini Linnavuori, 1965
- Tribe Athysanini Van Duzee, 1892
  - Subtribe Athysanina Van Duzee, 1892 stat. nov.
  - Subtribe Cochlorhinina Oman, 1943 stat. nov.
  - Subtribe Koebeliina Baker, 1897 stat. nov.
- Tribe Bahitini Zahniser & Dietrich, 2013
- Tribe Chiasmini Distant, 1908
- Tribe Cicadulini Van Duzee, 1892
- Tribe Deltocephalini Fieber, 1869
- Tribe Dorycephalini Oman, 1943
- Tribe Eupelicini Sahlberg, 1871
  - Subtribe Drakensbergenina Linnavuori, 1979 stat. nov.
  - Subtribe Eupelicina Sahlberg, 1871
  - Subtribe Paradorydiina Evans, 1936
  - Subtribe Stenometopiina Baker, 1923 stat. nov.
- Tribe Faltalini Zahniser & Dietrich, 2010
- Tribe Fieberiellini Wagner, 1951
- Tribe Goniagnathini Wagner, 1951
- Tribe Hecalini Distant, 1908
  - Subtribe Glossocratina Dmitriev, 2002
  - Subtribe Hecalina Distant, 1908
- Tribe Limotettigini Baker, 1915
- Tribe Luheriini Linnavuori, 1959
- Tribe Macrostelini Kirkaldy, 1906
- Tribe Mukariini Distant, 1908
- Tribe Occinirvanini Evans, 1966
- Tribe Opsiini Emeljanov, 1962
  - Subtribe Achaeticina Emeljanov, 1962
  - Subtribe Circuliferina Emeljanov, 1962
  - Subtribe Eremophlepsiina Dmitriev, 2006
  - Subtribe Opsiina Emeljanov, 1962
- Tribe Paralimnini Distant, 1908
  - Subtribe Aglenina Dmitriev, 2004
  - Subtribe Paralimnina Distant, 1908
- Tribe Pendarini Dmitriev, 2009
- Tribe Penthimiini Kirschbaum, 1868

Tribe Platymetopiini Haupt 1929 reinstated
Tribe Scaphoideini Oman, 1943
    Subtribe Drabescina Ishihara, 1953 stat. nov.
    Subtribe Phlepsiina Zahniser & Dietrich, 2013 stat. nov.
    Subtribe Scaphoideina Oman, 1943 stat. nov.
Tribe Scaphytopiini Oman, 1943
Tribe Selenocephalini Fieber, 1872
    Subtribe Bonaspeiina Zahniser & Dietrich, 2013 stat. nov.
    Subtribe Hypacostemmina Linnavuori & Al-Ne'amy, 1983 stat. nov.
    Subtribe Selenocephalina Fieber, 1872
Tribe Stegelytrini Baker, 1915
Tribe Tetartostylini Wagner, 1951
Tribe Vartini Zahniser & Dietrich, 2013
    Subtribe Bambusanina subtribe nov.
    Subtribe Punctulina Dai, Zahniser, Viraktamath & Webb, 2017 stat. nov.
    Subtribe Vartina Zahniser & Dietrich, 2013 stat. nov.

Tribe **Arrugadini** Linnavuori, 1965

Diagnosis

Large brown and yellow leafhoppers, texture of head and face strongly rugose, lateral margins of pronotum longer than the basal width of eye, first valvula dorsal sculpturing pattern granulose and submarginal, first valvula with distinctly delimited ventroapical sculpturing, and second valvula gradually expanded apically and without teeth.

Remarks

Our current concept of this tribe encompasses only the type genus, *Arrugada* Oman, 1939. Its relationships to other Neotropical deltocephaline tribes and genera were somewhat unstable in the phylogenomic analyses of Cao *et al*. (2022) (Fig. 1; Supp. file 2). *Arrugada* was consistently placed as sister to the morphologically disparate genus *Chimaerotettix* Dietrich & Rakitov, 2002 (here considered incertae sedis) in concatenated maximum likelihood analyses but was sister to a clade comprising *Baroma* Oman, 1938 and *Yungasia* Linnavuori, 1959 (also incertae sedis) in the coalescent gene tree analysis. In addition to those genera, *Carelmapu* Linnavuori, 1959, *Concepciona* Linnavuori & DeLong, 1977, *Consepusa* Linnavuori & DeLong, 1977, and *Huancabamba* Linnavuori, 1959 were resolved in the clade with *Arrugada*. Branches separating these genera and clades in the phylogenies of Cao *et al*. (2022) are very short but the individual terminal taxa are on relatively long branches, indicating that they are genetically divergent in addition to their considerable morphological differences. Additional phylogenetic analyses with denser taxon sampling and comparative morphological analyses within this group of Neotropical genera will be needed to further resolve the relationships of these genera and determine whether they share any distinctive morphological characters. Pending further study, we consider these genera as incertae sedis in Deltocephalinae, within the large clade of almost entirely New World genera comprising tribes Bahitini, Pendarini, Scaphytopiini and Platymetopiini (as redefined below).

Distribution

Neotropical.

Tribe **Athysanini** Van Duzee, 1892

Remarks

This tribe has long been treated as a taxonomic dumping ground for genera of Deltocephalinae that do not fit the definitions of the smaller, morphologically better-defined tribes included in the subfamily. Previous phylogenetic analyses based on both morphology (Zahniser & Dietrich 2008) and molecular data (Zahniser & Dietrich 2010, 2013; Cao *et al*. 2022) have shown that the tribe, as defined by previous authors, e.g., Oman *et al*. (1990) and Zahniser & Dietrich (2013), is polyphyletic. The phylogenomic results of Cao *et al*. (2022) (Fig. 1; Supp. file 2) recovered several independent lineages of genera previously included in Athysanini. Among the larger of such groups is a clade that includes the endemic New World tribes Bahitini, Pendarini and Scaphytopiini as well as most of the endemic Neotropical genera previously placed in Athysanini. The latter genera are here included in the revalidated tribe Platymetopiini (see below). Another large clade includes the mostly Indomalayan bamboo-specialist tribes Mukariini and Vartini. These two clades and their included tribes and subtribes are treated separately below.

A third large clade recovered by Cao *et al*. (2022) comprises Athysanina as recognized here (= the *Athysanus* group sensu Zahniser & Dietrich 2013) as well as two groups which are newly considered subtribes of Athysanini here, the western Nearctic subtribe Cochlorhinina and the Holarctic subtribe Koebeliina. Cochlorhinina shares with some Athysanina one or two dorsal teeth on the fused portion of the second valvulae, and some (e.g., *Gloridonus* Ball, 1936) share a relatively broad frontoclypeus and parallel-sided anteclypeus with Athysanina. Some members of Koebeliina are relatively derived morphologically, possessing an elongated and flattened head which is perhaps related to their unusual habit of specialization on pines; they do not share obvious characters with Athysanina other than the presumably symplesiomorphic Y-shaped connective articulated to the aedeagus. Koebeliina and some Cochlorhinina share the presence of platellae on the plantar surface of metatarsomere I and some Koebeliina, e.g., *Grypotes puncticollis* (Herrich-Schäffer, 1834), share with Cochlorhinina a Y-shaped connective fused to the aedeagus. The characterizations of Cochlorhinina and Koebeliina remain unchanged from their tribal diagnoses and descriptions (Dietrich & Dmitriev 2003; Zahniser & Dietrich 2013). Grypotinae Haupt, 1929 syn. nov., a small group of five genera, was previously included as a subtribe of Koebeliini. It is here considered a synonym of Koebeliina, previously containing only the type genus, with which it shares several morphological synapomorphies (Dietrich & Dmitriev 2003) and host plant specialization on *Pinus* spp. All recent phylogenetic analyses of Deltocephalinae strongly support a close relationship between *Koebelia* Baker, 1897 and sampled genera of Grypotinae. Cao *et al*. (2022) recovered one clade of Athysanina (including *Athysanus* Burmeister, 1838) as sister to Cochlorhinina and another (including *Anoterostemma* Löw, 1885, *Thamnotettix* Zetterstedt, 1837 and *Euscelis* Brullé, 1832) as sister to Koebeliina. Although it may eventually be possible to recognize both clades of Athysanina as separate subtribes, consistent morphological characters that distinguish members of these two clades have not been found; thus, they are here considered to belong to a single subtribe, Athysanina.

Tribe Athysanini, as here recognized, although well-supported as a monophyletic group, remains somewhat morphologically heterogeneous and difficult to diagnose based on a few morphological characters. Thus, we have not attempted a formal re-diagnosis of the tribe, although most included genera may be recognized by the characters provided for the nominotypical subtribe below. As mentioned above, subtribes Cochlorhinina and Koebeliina are smaller groups that share the Y-shaped connective found in Athysanina but each have distinctive characters that easily separate them from other Athysanini.

Distribution

Nearctic, Palearctic, Oriental.

Included subtribes

Athysanina, Cochlorhinina stat. nov., Koebeliina stat. nov. (= Grypotinae Haupt syn. nov.).

Fig. 2. Athysanini Van Duzee, 1892: Athysanina Van Duzee, 1892. **A–E**. *Streptanus aemulans* (Kirschbaum, 1868) (A–B, E: ♀, USNM, USNMENT01513526; C–D: ♀, USNM, USNMENT01513518). **F–J**. *Athysanus argentarius* Metcalf, 1955 (♀, INHS). **A**. Dorsal habitus. **B**. Lateral habitus. **C**. Head and pronotum, dorsal view, SEM. **D**. Detail of crown, dorsal view, SEM. **E**. Face. **F**. First valvula, lateral view. **G**. Detail of first valvula apex. **H**. Second valvula, lateral view. **I**. Detail of second valvula apex. **J**. Gonoplac, lateral view. Scale bar: A = 1 mm.

Subtribe **Athysanina** Van Duzee, 1892 stat. nov.

Fig. 2

Athysanina Van Duzee, 1892: 299.
Phrynomorphini Kirkaldy, 1907: 39.
Thamnotettixaria Distant, 1908: 351.
Euscelidae Haupt, 1926: 308.
Anoterostemminae Haupt, 1929: 243.
Bobacellini Kusnezov, 1929: 270.
Allygidiina Dmitriev, 2006: 96.

Diagnosis

Moderately large, relatively robust deltocephalines, ground color usually tan, head with crown rounded to face, frontoclypeus relatively broad, anteclypeus usually parallel-margined or tapered distally, male pygofer often with an upturned ventral lobe, connective Y-shaped and articulated to aedeagus, first valvula with dorsal sculpturing areolate or granulose with elements of sculpture not organized into distinct rows, second valvulae usually with one or two dorsal teeth on basal fused section.

Remarks

In his description of *Aindrahamia* Linnavuori, 1965, Linnavuori (1965) stated that it is very similar to *Allygus* Fieber, 1872. In addition to shared external characters, they share the pygofer apex with a short, upturned lobe. Based on these similarities and its similarity to *Allygidius* Ribaut, 1948 and *Zercanus* Dlabola, 1965, *Aindrahamia* is included in Athysanina. *Morinda* Emeljanov, 1972 was placed in Cicadulini by Hamilton (1975) and this was followed by Oman *et al*. (1990) and Zahniser & Dietrich (2013). Emeljanov (1999) included it in his broad circumscription of Athysanini, and Hamilton (1997) considered it a subgenus of *Euscelis* Brullé, 1832 (Athysanina). *Morinda* conforms to the definition of Athysanina given here, and more closely resembles this group than Cicadulini which are smaller and slender. *Morinda* is therefore moved to Athysanina here.

Distribution

Nearctic, Palearctic.

Newly included genera

Aindrahamia Linnavuori, 1965; *Morinda* Emeljanov, 1972.

Tribe **Bahitini** Zahniser & Dietrich, 2013

Diagnosis

Medium-sized robust brown deltocephalines with symmetrical markings consisting of spots, stripes, bands or large unicolorous areas, head usually wider than pronotum, rarely strongly produced, crown usually with transverse preapical groove, crown-face transition often with one or more transverse carinae, gena angulately incised below eye, forewing usually with reflexed costal veins, appendix well developed but not extended around wing apex.

Remarks

The phylogeny of Cao *et al*. (2022) (Fig. 1; Supp. file 2) recovered a well-supported clade that corresponds to Bahitini sensu Zahniser & Dietrich (2013) with a few exceptions. *Brincadorus* Oman, 1938 was included in Bahitini by Zahniser & Dietrich (2013) based on the possession of transverse carinae on the anterior margin of the head and a tumid and tapering anteclypeus, but in the analyses of Cao *et al*. (2022) it grouped instead with a large clade of mostly endemic Neotropical genera previously included in Athysanini but here included in the revalidated tribe Platymetopiini (restored from synonymy under Athysanini; see below). Camisão *et al*. (2024), citing the Cao *et al*. (2022) analyses, removed *Brincadorus* from Bahitini and considered it incertae sedis in Deltocephalinae (see below, Platymetopiini). *Concepciona* Linnavuori & DeLong, 1977 was placed in Bahitini by Zahniser & Dietrich (2013) but was not resolved with other members of the tribe by Cao *et al*. (2022) and is therefore removed from the tribe and considered incertae sedis in Deltocephalinae.

Conversely, two Neotropical genera previously placed in Athysanini, *Bergolix* Linnavuori, 1959 and *Hegira* Oman, 1938, grouped with Bahitini in the recent phylogenomic analyses and are here transferred to that tribe. *Bergolix* possesses a transverse preapical groove on the crown as in other Bahitini, but *Hegira* does not. The Neotropical genus *Eovulturnops* Evans, 1947 was placed in Penthimiini by Evans (1947) based on its depressed body and spatulate head with concave face, but this genus consistently grouped with Bahitini in the analyses of Cao *et al*. (2022); it resembles other Bahitini in having transverse carinae on the anterior margin of the head, a broad and robust body form, several supernumerary costal crossveins in the forewing and the male subgenital plate with a single row of lateral macrosetae.

Distribution

Nearctic, Neotropical.

Newly included genera

Bergolix Linnavuori, 1959 (from Athysanini); *Eovulturnops* Evans, 1947 (from Penthimiini); *Hegira* Oman, 1938 (from Athysanini).

Excluded genera

Concepciona Linnavuori & DeLong, 1977 (to Deltocephalinae, incertae sedis).

Tribe **Cicadulini** Van Duzee, 1892

Cicadulini Van Duzee, 1892: 300.
Procepitina Dmitriev, 2002: 641.

Diagnosis

Medium sized, slender, usually stramineous deltocephalines, anterior margin of head often with paired black spots, frontoclypeus longer than maximum width, anteclypeus widened distally, forewing with three anteapical cells, male pygofer often with differentiated dorsal and ventral lobes each of which may be produced into conical, triangular, or spine-like process, male segment X long and strongly sclerotized, subgenital plates sometimes with a row of macrosetae near the middle and with long fine setae laterally and macrosetae reduced in number, first valvulae with dorsal sculpture scale-like (imbricate), second valvulae with small teeth interspersed between larger teeth on distal blade.

Remarks

According to descriptions and illustrations of the male genitalia provided by Vilbaste (1967), *Albicostella* Ishihara, 1953 fits the tribal diagnosis of Cicadulini provided above. Zhang *et al*. (2021) noted the similarity of *Neomacednus* Xing & Li, 2011 and *Protensus* Zhang & Dai, 2001 to *Albicostella*, so these genera are therefore placed in Cicadulini. Lindberg (1954) noted that *Amblytelinus* Lindberg, 1954 is similar to *Mocydiopsis* Ribaut, 1939 and illustrates a long segment X, relatively short pygofer, and aedeagus similar to that of other Cicadulini, justifying its placement here. *Knullana* DeLong, 1941 was included in Cicadulini by Oman *et al*. (1990) and followed by Zahniser & Dietrich (2013) based on its well-sclerotized and somewhat elongated male anal tube. The analyses of Cao *et al*. (2022)

(Fig. 1; Supp. file 2) consistently placed *Knullana* in a clade comprising the endemic Nearctic genera *Omanana* DeLong, 1942 and *Spathanus* DeLong, 1945 and the cosmopolitan genus *Osbornellus* Ball, 1932 indicating that it is more properly placed in Scaphoideini. Species of *Knullana* have the following characters which support placement in Scaphoideini: head narrower than the pronotum, subgenital plate apex long and membranous, and lateral margin of the subgenital plate with numerous long fine setae. Some species also have a paraphysis articulated between the connective and aedeagus, a structure that occurs in some Scaphoideini but is rare in other deltocephaline tribes. Based on its similarity to *Hardya* Edwards, 1922, *Sardius* Ribaut, 1946 is moved to Cicadulini. Dlabola (1980) stated that *Biluscelis* Dlabola, 1980 is closely related to *Bilusius* Ribaut, 1942 (Athysanina) and/or *Dudanus* Dlabola, 1956 (Cicadulini). *Biluscelis* has the subgenital plates with a row of four macrosetae distant from the lateral margin and a relatively long and sclerotized male segment X. Based on these characters, it is included in Cicadulini. More study is needed to determine the placement of *Bilusius* and other genera of Athysanini that were not sampled in the recent molecular analyses.

Niranjana *et al*. (2019) recently placed *Pseudosubhimalus* Ghauri, 1974 in Cicadulini based on the results of molecular phylogenetic analyses.

Distribution

Nearctic, Neotropical, Palearctic.

Newly included genera

Albicostella Ishihara, 1953 (from Athysanini); *Amblytelinus* Lindberg, 1954 (from Athysanini); *Biluscelis* Dlabola, 1980 (from Athysanini); *Hardya* Edwards, 1922 (from Athysanini); *Neomacednus* Xing & Li, 2011 (from Athysanini); *Protensus* Zhang & Dai, 2001 (from Athysanini); *Sardius* Ribaut, 1946 (from Athysanini); *Watanabella* Vilbaste, 1969 (from Athysanini).

Excluded genus

Knullana DeLong, 1941 (to Scaphoideini, unplaced to subtribe).

Tribe **Deltocephalini** Fieber, 1869

Diagnosis

Small to medium sized deltocephalines, crown usually angulately produced in dorsal view, anteclypeus tapered or parallel-sided, lorum narrower than anteclypeus, connective linear with anterior arms closely appressed and fused to aedeagus, style often with medial anterior arm produced, first valvula dorsal sculpturing imbricate.

Remarks

Heller & Linnavuori (1968) suggested that *Awasha* Heller & Linnavuori, 1968 is related to *Paramesus* Fieber, 1866 (Paralimnini) but their drawings of the male genitalia of the type species show that the aedeagus is linear and fused to the connective, indicating that it is more properly placed in Deltocephalini. Dlabola's (1979) drawings of *Paramesanus wittmeri* Dlabola, 1979 (the type species of *Paramesanus* Dlabola, 1979) indicate that it is very closely related to *Awasha basicornis* Heller & Linnavuori, 1968 and should, therefore, be included in the older genus with *Paramesanus* treated as a junior synonym of *Awasha*, creating the new combination *Awasha wittmeri* (Dlabola, 1979) comb. nov. The former species differs from the latter in having the median pair of aedeagal processes extended beyond the shaft apex.

The analysis of Cao *et al*. (2022) (Fig. 1; Supp. file 2) consistently grouped the Oriental genus *Loeia* Duan, 2017, previously placed in Deltocephalini based on its linear connective fused to the aedeagus, with Vartini, but its position with respect to the three recognized subtribes was unstable. *Loeia* differs from Deltocephalini by its large size, parallel-margined crown (not produced), larger lorum, and anteclypeus expanding toward apex. The subtribe Punctulina of Vartini includes some other genera that have the male connective linear but articulated to the aedeagus (e.g., *Bambuphaga* Ramaiah *et al*., 2023). The ovipositor of *Loeia* is nearly identical to that of *Hecalusina* He *et al*., 2008, a genus previously placed in Hecalini but shown to be unrelated to other Hecalini by Catanach & Dietrich (2017) and grouped with Punctulina in the analysis of Cao *et al*. (2022). Dietrich (2025) revised the genus and placed it in Punctulini based on its phylogenetic analyses of Cao *et al*. (2022) and the characters shared with other members of that group. This placement is followed here except as subtribe Punctulina of Vartini. Another Oriental genus, *Yuanamia* Duan & Zhang, 2006 also grouped with Punctulina in the analysis of Cao *et al*. (2022). However, the included sample of *Yuanamia* showed high similarity to a sample representing an undescribed genus of Punctulina that is quite dissimilar from *Yuanamia* and we found no morphological characters supporting the relationship; therefore, the DNA sample of *Yuanamia* may have been contaminated and we retain *Yuanamia* in Deltocephalini pending further study.

Cabrellus Emeljanov, 1964 has the connective articulated with the aedeagus. Its placement is corrected here to Paralimnini. *Zilkaria* de Menezes, 1974 was previously placed in Athysanini. Its small size, tapered anteclypeus, style with medial anterior arm produced, and linear connective in addition to the author's comparison to related genera *Planicephalus* Linnavuori, 1954 and *Loreta* Linnavuori, 1959 suggest it belongs in Deltocephalini (de Menezes 1974).

Cabrulus Oman, 1949 possesses a linear connective fused with the aedeagus and has therefore traditionally been placed in Deltocephalini (Oman *et al*. 1990; Zahniser & Dietrich 2013). However, Ross & Hamilton (1972) cited characters that support a close relationship between *Cabrulus* and *Orocastus* Oman, 1949 (Paralimnina) which has a linear connective articulated with the aedeagus. The relationship to Paralimnina was supported by the molecular phylogenetic analyses of Fang *et al*. (1993), and *Cabrulus* is therefore transferred to that subtribe. Other instances of the fusion of the aedeagus and connective in Paralimnina are known, e.g., in the *Flexamia prairiana* group of species (Whitcomb & Hicks 1988).

Distribution

Cosmopolitan.

Newly included genera

Awasha Heller & Linnavuori, 1968 (from Athysanini) [= *Paramesanus* Dlabola, 1979 syn. nov. (formerly treated as a valid genus of Paralimnini)]; *Zilkaria* Menezes, 1974.

Excluded genera

Alodeltocephalus Evans, 1966 (to Limotettigini); *Cabrellus* Emeljanov, 1964 (to Paralimnini: Paralimnina); *Cabrulus* Oman, 1949 (to Paralimnini: Paralimnina).

Tribe **Eupelicini** Sahlberg, 1871

Diagnosis

Small to medium-sized, usually stramineous or brown deltocephalines, sometimes with bold symmetrical markings, head often strongly produced, body surfaces often conspicuously granulose, forewing veins sometimes slightly to strongly elevated, male pygofer usually with posterodorsal margin well sclerotized and strongly sloping posteroventrad, connective elongate with stem well developed and arms only slightly divergent, aedeagus simple and without processes but apex often bifid, first valvula with dorsal sculpture usually granulose and submarginal, second valvula usually without teeth on dorsal margin.

Remarks

The analysis of Cao *et al*. (2022) (Fig. 1; Supp. file 2) grouped Eupelicini (sensu Zahniser & Dietrich 2013, including Eupelicina and Paradorydiina) in a clade with Drakensbergenini, Stenometopiini and *Evinus* Dlabola, 1977, a genus most recently included in Macrostelini (Lu *et al*. 2011). *Eupelix* Germar, 1821 was either sister to the remaining members of the clade or was sister to *Drakensbergena* Linnavuori, 1961 or to *Drakensbergena* + *Evinus*. The phylogenetic results of Cao *et al*. (2022) and the unique combination of morphological synapomorphies listed above suggest that these three tribes should be combined into a single tribe with Drakensbergenina, Paradorydiina, and Stenometopiina treated as subtribes of Eupelicini. *Evinus* is currently considered unplaced to subtribe within Eupelicini.

The generic concepts in Stenometopiina have been unstable over the past 60 years. Vilbaste (1965; followed by, e.g., Oman *et al*. 1990 and Zahniser & Nielson 2012) recognized *Doratulina* Melichar, 1903 and numerous generic synonyms for most Old World species and *Stirellus* Osborn & Ball, 1902 for most New World species, while Emeljanov (1962; followed by Day & Fletcher 1994; Xing & Li 2010; Duan *et al*. 2016, 2019) considered *Stirellus* in a much broader sense, including *Doratulina* and synonyms and most of the known species. Throughout the history of this group, *Hodoedocus* Jacobi, 1910 has consistently been considered a separate valid genus. However, the results of Cao *et al*. (2022) clearly show that it is nested well within an Old World clade of species. Therefore, *Hodoedocus* should be considered a synonym of either *Stirellus* or *Doratulina*, depending on the concept of the genera that is adopted. Alternatively, a more detailed analysis of this lineage, including representatives of the many genus-level taxa presently considered junior synonyms of *Stirellus* or *Doratulina*, may eventually justify revalidating some of these taxa based on external morphological characters (e.g., head structure, wing venation). The male genitalia of this group are unusual in being less variable among species than is the case in most other deltocephaline tribes. This was the main justification for synonymizing several genera previously recognized based on external morphology but with highly similar male genitalia. The taxon sampling of Cao *et al.* (2022) supports a monophyletic clade of New World species (4 spp. sampled) that includes the type species of *Stirellus*, and this clade is sister to a monophyletic clade of Old World species (13 spp. sampled). Further studies are needed to clarify the generic concepts.

Distribution

Cosmopolitan.

Included subtribes

Drakensbergenina stat. nov., Eupelicina, Paradorydiina, Stenometopiina stat. nov.

Newly included genus

Evinus Dlabola, 1977 (from Macrostelini), unplaced to subtribe.

Tribe **Hecalini** Distant, 1908

Diagnosis

Medium sized to large, depressed, stramineous, green, or brown leafhoppers, sometimes with symmetrical orange or reddish markings, crown parabolically produced, pronotum with lateral margin as long as or longer than the basal width of the eye, ocelli closer to eyes than to laterofrontal sutures, apodemes of male sternite I long and relatively narrow, apodemes of male sternite II broad and well-developed, male pygofer often produced or pointed posterodorsally, segment X withdrawn into pygofer, aedeagus usually with one or two pairs of apical processes, first valvula dorsal sculpturing granulose to maculose and submarginal, often with distinctly delimited ventroapical sculpturing, second valvula usually arcuate and without teeth.

Remarks

The analysis of Cao *et al.* (2022) (Fig. 1; Supp. file 2) recovered this group as previously defined (Hamilton 2000; Zahniser & Dietrich 2013) as monophyletic with strong support, with the exception of the morphologically aberrant Oriental genus *Hecalusina* which grouped with Punctulina. Morphological characters not present in Hecalini but shared by *Hecalusina* and Punctulina include the elongate, divergent and capitate male 2S abdominal apodemes and the linear connective.

Similar to the study by Catanach & Dietrich (2017), the results of the Cao *et al.* (2022) analysis show that the type genus, *Hecalus* Stål, 1864 is polyphyletic, with groups of species inhabiting different continents forming unrelated clades; thus, a revised species-level classification is needed.

Distribution

Cosmopolitan.

Included subtribes

Glossocratina, Hecalina.

Excluded genus

Hecalusina He, Zhang & Webb, 2008 (to Vartini: Punctulina).

Tribe **Limotettigini** Baker, 1915

Diagnosis

Small to medium sized deltocephalines, usually with symmetrical dark markings, head wider than pronotum, crown not strongly produced, anteclypeus parallel-sided or tapered, male pygofer with spine-like process arising from the dorsal margin, dorsal connective well sclerotized and articulated between aedeagus and base of segment X.

Remarks

The analyses of Cao *et al.* (2022) (Fig. 1; Supp. file 2) consistently supported the monophyly of this tribe as delimited by Zahniser & Dietrich (2013) but indicated that *Arawa* Knight, 1975, a genus previously included in Athysanini and known from New Zealand and Australia, is sister to the remaining Limotettigini. This genus has a relatively broad head, tapered anteclypeus, spinelike process arising from the dorsal margin of the male pygofer and sclerotized dorsal connective, as in other Limotettigini. Hence, *Arawa* is here transferred to this tribe.

Arahura Knight, 1975 is a New Zealand-endemic genus with three described species. Knight (1975) suggested that it is closely related to *Arawa*. It shares a sclerotized dorsal connective with other Limotettigini along with other similarities in the genitalia and external morphology and is transferred here to Limotettigini.

Alodeltocephalus Evans, 1966 is an Australian-endemic genus and was originally included in Deltocephalini (Evans 1966). Knight (1975) redescribed the genus and placed it in Euscelini Van Duzee, 1917, providing re-descriptions and illustrations of two of the included species. Oman *et al*. (1990) listed the genus in tribe Deltocephalini, which was followed by Zahniser & Dietrich (2013). Knight's (1975) illustration shows the connective is Y-shaped with a short or long stem, articulated with the aedeagus, indicating that it does not belong in Deltocephalini. Although *Alodeltocephalus* lacks a dorsal spine on the male pygofer, its external morphology including head structure and shortened forewings, and the overall structure of the male genital capsule and genitalia resemble those of *Arahura* and some *Arawa*. The genus is, therefore, assigned to Limotettigini.

Distribution

Australian, Nearctic, Oriental, Palearctic.

Newly included genera

Alodeltocephalus Evans, 1966 (from Deltocephalini); *Arahura* Knight, 1975 (from Athysanini); *Arawa* Knight, 1975 (from Athysanini).

Tribe **Macrostelini** Kirkaldy, 1906

Macrostelini Kirkaldy, 1906: 342.
Balcluthini Baker, 1915: 50.
Gnathodini Baker, 1915: 50.
Coryphaeini Emeljanov, 1962: 395, unavailable due to homonymy of the type genus.
Coryphaelini Nast, 1972: 490.

Diagnosis

Small to medium sized, slender, often stramineous, yellow, or greenish deltocephalines, usually with symmetrical dark markings, forewing with 2 anteapical cells, subgenital plate usually with membranous digitate apical lobe, male pygofer macrosetae sometimes plumose.

Remarks

The analyses of Cao *et al.* (2022) (Fig. 1; Supp. file 2) consistently supported the monophyly of this tribe, as delimited by Knight & Webb (1993) and Zahniser & Dietrich (2013) with three exceptions. *Cortona* Oman, 1938 grouped with Deltocephalini, corroborating the transfer of this genus to that tribe by Duan *et al*. (2017). *Teyasteles* Linnavuori, 1969 grouped with Paralimnini, which is consistent with its linear connective articulated to the aedeagus. *Evinus* grouped as sister to *Drakensbergena* in a larger clade comprising Drakensbergenini, Eupelicini and Stenometopiini. Thus, although these three genera resemble Macrostelini in having only two anteapical cells in the forewing, they share morphological synapomorphies with other tribes and are here excluded from Macrostelini.

Distribution

Cosmopolitan.

Excluded genera

Evinus Dlabola, 1977 (to Eupelicini, unplaced to subtribe); *Teyasteles* Linnavuori, 1969 (to Paralimnini: Paralimnina).

Tribe **Opsiini** Emeljanov, 1962

Diagnosis

Stramineous, yellow, green, or brown deltocephalines, color pattern often including irregular brown spots or lines and larger round white spots bordered with brown, connective Y-shaped and articulated with aedeagus, aedeagus with two shafts or pair of distal branches, each bearing a separate gonopore.

Remarks

Except for the diagnostic character of the divided aedeagus with two gonopores (also occurring in a few other genera of Deltocephalinae), Opsiini is heterogeneous morphologically. The analyses of Cao *et al*. (2022) (Fig. 1; Supp. file 2) support the monophyly of Opsiini including the subtribes Opsiina, Circuliferina and Eremophlepsiina (subtribe Achaeticina, endemic to Central Asia, was not included in the analysis but its inclusion in the tribe is not considered controversial), with the following exceptions. The Afrotropical genus *Pseudobalbillus* Jacobi, 1912, previously placed in Mukariini based on the depressed body and produced head with horizontal face, grouped with Opsiini; this genus has the aedeagus divided into two shafts, each bearing its own gonopore, as in Opsiini and in some species of *Mukaria* Distant, 1908 (which differ in having the aedeagus fused to the connective). Other aspects of the male genitalia of *Pseudobalbillus* are more similar to those of Opsiini including the distally attenuate and membranous subgenital plates and the lack of processes on the pygofer. Based on these similarities and its placement as sister to Opsiini in the analyses of Cao *et al.* (2022), *Pseudobalbillus* is here transferred from Mukariini to Opsiini.

Lampridius Distant, 1918, was previously placed in Opsiini based on its bifurcate aedeagus, and *Paralampridius* Dai *et al*., 2011 was included in Opsiini due to its close resemblance to *Lampridius*, despite the aedeagus having a single shaft and gonopore. The analysis of Cao *et al*. (2022) consistently placed *Paralampridius* as sister to Vartina within a larger clade comprising bamboo-specialist leafhoppers of the tribes Mukariini and Vartini. *Lampridius* and *Paralampridius* share with some Vartina a similar color pattern consisting of symmetrical orange spots or lines, male abdominal apodemes of segment II long, strongly divergent and flared apically (also shared with Punctulina), and the subgenital plates and valve fused. *Lampridius* and *Paralampridius* have the dorsal ground color white or pale bluish green in live specimens (bright green in both live and pinned specimens in other Vartina) and the head rounded (angulately produced in other Vartina). *Lampridius* and *Paralampridius* are here transferred to Vartina based on their shared characters with Vartina and their close relationship to this subtribe revealed in the recent molecular analyses.

Also placed in the bamboo-specialist clade by the analysis of Cao *et al*. (2022) was the Oriental genus *Alishania* Vilbaste, 1969, which has the aedeagal shaft divided distally and superficially resembling Circuliferina. This genus grouped with *Neurotettix* Matsumura, 1914, *Abrus* Dai & Zhang, 2002, *Branchana* Li. 2024, *Bambusana* Anufriev, 1969 and *Bambusananus* Li & Xing, 2024, all of which were previously included in Athysanini and are placed here in the newly described subtribe Bambusanina of Vartini (see below).

Vilbaste's (1961) drawings of the aedeagus of *Scenergates viridis* (Vilbaste, 1961) clearly indicate that this genus has two aedeagal shafts, each with its own gonopore, thus justifying its transfer to Opsiini. The unusual body form is related to its behavior, unique among Cicadellidae, of forming galls on camelthorn, *Alhagi maurorum* Medik. (Fabaceae) (Rakitov & Appel 2012).

Nesophrosyne Kirkaldy, 1907 and *Orosius* Distant, 1918 were previously placed in subtribe Opsiina but were resolved well within a clade including the genera of Circuliferina *Dixianus* Ball, 1918, *Lycioides* Oman, 1949, and *Neoaliturus* Distant, 1918. Circuliferina has been previously defined by having the mesal margin of the eye notched and a T-shaped aedeagus, with a single shaft arising from the base and paired gonopore-bearing branches diverging more apically (Emeljanov 1999; Zahniser & Dietrich 2008; Dai *et al*. 2010; El-Sonbati *et al*. 2016; Du *et al*. 2019). It has apparently been overlooked that most, but not all, species of *Orosius* have the mesal margin of the eye notched like other Circuliferina, and two of four species of *Nesophrosyne* examined here have the mesal margin notched. Thus, this character partially supports placement of *Orosius* and *Nesophrosyne* in Circuliferina, and the molecular data strongly support this placement for both genera and they are therefore here transferred to Circuliferina. *Paraorosius* El-Sonbati & Wilson, 2016, which is closely related to *Orosius*, is also transferred to Circuliferina.

Despite possessing paired aedeagal shafts, *Nesophryne* Kirkaldy, 1907 was placed in Athysanini by Oman *et al*. (1990), and this was followed by Zahniser & Dietrich (2013). *Nesophryne* and *Kirkaldiella*

Osborn, 1935, both Hawaiian endemics, were stated to be related to *Nesophrosyne*, another Hawaiian endemic genus, and *Orosius* by Knight & Webb (1988). On this basis and their shared biogeographic pattern, *Nesophryne* and *Kirkaldiella* are moved to Circuliferina along with *Nesophrosyne* and *Orosius* (see above).

The condition of the shafts of the aedeagus, whether separated at their base or forming a common shaft at the base, is apparently more variable than previously appreciated. Similarly, one of the key characters for defining Opsiini, that of the bifurcate aedeagus bearing two gonopores, displays homoplasy, occurring rarely in other distantly related tribes of Deltocephalinae including Acostemmini (*Alocoelidia* Evans, 1954), Mukariini (*Mukaria*), and Vartini (*Alishania* and *Lampridius*).

Distribution

Cosmopolitan.

Included subtribes

Achaeticina, Circuliferina, Eremophlepsiina, Opsiina.

Newly included or transferred genera

Kirkaldiella Osborn, 1935 (to Circuliferina, from Opsiina) *Nesophrosyne* Kirkaldy, 1907 (to Circuliferina, from Opsiina); *Nesophryne* Kirkaldy, 1907 (to Circuliferina, from Athysanini); *Orosius* Distant, 1918 (to Circuliferina, from Opsiina); *Paraorosius* El-Sonbati & Wilson, 2016 (to Circuliferina, from Opsiina); *Pseudobalbillus* Jacobi, 1912 (to Opsiini, unplaced to subtribe; from Mukariini); *Scenergates* Emeljanov, 1972 (to Opsiini, unplaced to subtribe; from Athysanini).

Excluded genera

Alishania Vilbaste, 1969 (to Vartini: Bambusanina); *Lampridius* Distant, 1918 (to Vartini: Vartina); *Paralampridius* Dai, Dietrich & Zhang, 2011 (to Vartini: Vartina).

Tribe **Paralimnini** Distant, 1908

Diagnosis

Small to medium sized usually stramineous or brown leafhoppers with symmetrical markings; head with anteclypeus tapered or parallel-sided, lorum narrower than anteclypeus, connective with anterior arms closely appressed and articulated with aedeagus, female first valvula sculpturing imbricate, maculose or granulose.

Remarks

Afrosus Linnavuori, 1959 was originally erected as a subgenus of *Palus* DeLong & Sleesman, 1929 (Linnavuori 1959) (= *Cosmotettix* Ribaut, 1942) and included in tribe Deltocephalini, which then included taxa presently placed in Paralimnini. This taxon was elevated to status as a separate genus by Emeljanov (1966) who stated that it is closely related to *Sorhoanus* Ribaut, 1946 but Oman *et al.* (1990), followed by Zahniser & Dietrich (2013), incorrectly included it in Deltocephalini. The original description and illustrations clearly indicate that the connective of *Afrosus* is loop-shaped, with convergent anterior arms, and is articulated to the aedeagus, features that clearly justify placing it in Paralimnini.

Teyasteles was originally placed in Macrostelini by Linnavuori (1969) based on the presence of only two anteapical cells in the forewing, but Webb & Heller (1990) correctly pointed out that the form of the connective matches that found in Paralimnini and transferred it to that tribe. Zahniser & Dietrich (2013), following Oman *et al*. (1990), incorrectly listed the genus in Macrostelini but the correct placement is Paralimnini, as confirmed by the phylogenetic results of Cao *et al*. (2022) (Fig. 1; Supp. file 2).

Emeljanov (1964) originally described *Cabrellus* Emeljanov, 1964 as a subgenus of *Sorhoanus* but more recently Emeljanov (1999) elevated it to status as a separate genus. Both Oman *et al*. (1990) and Zahniser & Dietrich (2013) listed *Cabrellus* in Deltocephalini, but the characters and illustrations provided by Emeljanov (1964, 1999) clearly place the genus in Paralimnini as indicated by Emeljanov (1999).

Linnavuori (1960) placed *Wakaya* Linnavuori, 1960 in Deltocephalini but his original description and illustrations indicate that the connective is articulated to the aedeagus. Oman *et al*. (1990) listed the genus in Deltocephalini and this placement was followed by Zahniser & Dietrich (2013). Webb & Viraktamath (2009) listed two new combinations in this genus under Paralimnini, implicitly including the genus in this tribe. Based on the articulated connective with anterior arms appressed, this appears to be the correct tribal placement for the genus.

Distribution

Cosmopolitan.

Included subtribes

Aglenina, Paralimnina.

Newly or confirmed included genera in Paralimnina

Afrosus Linnavuori, 1959 (from Deltocephalini); *Cabrellus* Emeljanov, 1964 (from Deltocephalini); *Cabrulus* Oman, 1949 (from Deltocephalini); *Teyasteles* Linnavuori, 1969 (from Macrostelini); *Wakaya* Linnavuori, 1960 (from Deltocephalini).

Tribe **Pendarini** Dmitriev, 2009
Fig. 3

Diagnosis

Medium sized to large ochraceous, yellowish, greenish, or brownish deltocephalines, sometimes with brown irrorate markings or ramose pigment lines, crown usually relatively short and broad, wider than pronotum, crown between eyes distinctly wider than eye, crown convex to nearly flat (not concave), crown texture sometimes completely or partly shagreen to base, anteclypeus parallel-sided or broadened distally. Nymph with crown-face transition carinate, face with medial longitudinal carina in upper part, acrometope with anterior margin tracing anterior carina of head, abdomen with 4–6 longitudinal rows of very short macrosetae, and pygofer lobes attenuate and parallel to each other.

Remarks

This tribe was originally recognized based on the unique morphology of the nymphs, which have a carinate crown-face transition, a median longitudinal carina on the upper part of the face and elongate, tapered pygofer lobes, none of which are retained in the adult. The nymphs of most genera included in the tribe have not yet been studied, but several genera are here added to the tribe based on the phylogenomic results of Cao *et al*. (2022) (Fig. 1; Supp. file 2). A well-resolved and supported clade was resolved that includes the genera previously placed in Pendarini and the genera *Neophlepsius* Linnavuori, 1955, *Scaphoidula* Osborn, 1923, *Caphodus* Oman, 1938, *Andanus* Linnavuori, 1959, *Mesadorus* Linnavuori, 1955, *Doleranus* Ball, 1936, *Neomesus* Linnavuori, 1959, and *Egenus* Oman, 1938. These genera are moved to Pendarini here. Linnavuori (1959) correctly asserted that *Scaphoidula* and *Caphodus* are closely related. *Doleranus* shares the completely shagreen texture of the crown with the related genera *Chlorotettix* Van Duzee, 1892, *Copididonus* Linnavuori, 1954, and *Ileopeltus* Cwikla, 1988. *Chlorotettix* was polyphyletic in the Cao *et al*. (2022) analyses, but all sampled species were resolved within this group of genera plus *Neomesus* and *Egenus*.

Based on the shape of the head, brown reticulated and irrorate color pattern of the forewings, and similar male genitalia, *Krameraxus* Maldonado-Capriles, 1968 appears to be related to *Paraphlepsius* Baker,

Fig. 3. Pendarini Dmitriev, 2009. **A–E**. *Tropicanus pulchripennis* (Baker, 1898) (♀, USNM, USNMENT01513120). **F–J**. *Paraphlepsius occidentalis* (Baker, 1898) (♀, USNM, USNMENT01513107). **A**. Dorsal habitus. **B**. Lateral habitus. **C**. Head and pronotum, dorsal view, SEM. **D**. Detail of crown, dorsal view, SEM. **E**. Face. **F**. First valvula, lateral view. **G**. Detail of first valvula apex. **H**. Second valvula, lateral view. **I**. Detail of second valvula apex. **J**. Gonoplac, lateral view. Scale bar: A = 1 mm.

1897, and it is here moved to Pendarini. *Garapita* Oman, 1938 shares with *Caphodus* reflexed veins originating from the outer anteapical cell of the forewing, the ovipositor relatively straight ventrally, the first valvula with strigate sculpturing, and second valvula with obliquely triangular and serrated teeth extending for ⅔ the length of the valvula; *Garapita* is therefore included in Pendarini here. Linnavuori (1959) and Linnavuori & DeLong (1978) suggested that *Serratus* Linnavuori, 1959 and *Mocolinna* McKamey, 2003 (= *Mocoa* Linnavuori & DeLong, 1978) are related to *Copididonus*, and on this basis they are included in Pendarini here. Cheng (1980) stated that his new genus *Aplanatus* Cheng, 1980 is related to *Chlorotettix* and it shares a color pattern similar to some *Copididonus*; it is therefore included in Pendarini here. Based on its high similarity to *Mesadorus* Linnavuori, 1955, *Mimodorus* Linnavuori, 1959 is included in Pendarini. *Mimodorus* and *Mesadorus* both have the crown distinctly convex and elevated above the pronotum and crown texture completely shagreen, which is also shared with *Chlorotettix* and related genera. They also possess a brown irrorate color pattern that is similar to *Paraphlepsius* and related genera. Linnavuori (1959) stated that *Lojanus* Linnavuori, 1959 is similar to *Chlorotettix*, and the genera share the completely shagreen texture of the crown. *Mexicananus* DeLong, 1944 is known only from the female and is placed in Pendarini here based on its color pattern which is very similar to that of *Tropicanus* DeLong, 1944.

Bolotheta Kramer, 1963 and *Neohegira* Linnavuori & DeLong, 1978 were consistently resolved as sister to each other in the analyses of Cao *et al*. (2022), and one analysis placed these genera as sister to the clade including Pendarini, but the subtending branch was short, did not receive maximum branch support, and was not consistently resolved among different analyses. These genera are currently considered incertae sedis in Deltocephalinae.

Distribution

Cosmopolitan.

Newly included genera (all from Athysanini except where noted)

Andanus Linnavuori, 1959; *Aplanatus* Cheng, 1980; *Caphodus* Oman, 1938 (from Scaphoideini); *Doleranus* Ball, 1936; *Egenus* Oman, 1938; *Garapita* Oman, 1938; *Krameraxus* Maldonado-Capriles, 1968; *Lojanus* Linnavuori, 1959; *Mesadorus* Linnavuori, 1955; *Mexicananus* DeLong, 1944; *Mimodorus* Linnavuori, 1959; *Mocolinna* McKamey, 2003; *Neomesus* Linnavuori, 1959; *Neophlepsius* Linnavuori, 1955 (from Scaphoideini); *Scaphoidula* Osborn, 1923 (from Scaphoideini); *Serratus* Linnavuori, 1959.

Tribe **Penthimiini** Kirschbaum, 1868

Penthimiini Kirschbaum, 1868: 14.
Thaumastoscopidae Baker, 1923: 349.
Magnentiini Linnavuori, 1978: 34, syn. nov.

Diagnosis

Medium sized to large, squat, robust, often black or brown leafhoppers, often with ventral part of face and/or entire ventral side flattened and dorsal side convex, ocelli on crown and distant from eyes, antennal ledge strong, protibia dorsally flattened and bicarinate, forewing with appendix large and extending around the wing apex.

Remarks

The analyses of Zahniser & Dietrich (2013) were inconsistent in the phylogenetic relationships of genera in this tribe but the increased taxon sampling and dataset of Cao *et al*. (2022) (Fig. 1; Supp. file 2) yielded a strongly supported clade that includes most of the sampled genera of Penthimiini. *Magnentius*

Sing-Pruthi, 1930, the type genus of Magnentiini (also including *Ndua* Linnavuori, 1978) was found nested within that clade. Therefore, Magnentiini is considered a new synonym of Penthimiini here.

Many of the morphological characters that help to define Penthimiini appear to be associated with the dorsally dome-like and ventrally flattened shape of most included genera, which are prone to homoplasy and has resulted in some genera being placed to this tribe which are not closely related to true Penthimiini. This is the case for *Perugrampta* Kramer, 1965 and related Neotropical genera (Dietrich & Rakitov 2002) and *Citorus* Stål, 1866 which were previously included in Penthimiini but have since been moved to other tribes. This is also the case for *Eovulturnops*, which grouped with Bahitini, and *Jafar* Kirkaldy, 1903 and *Musosa* Linnavuori, 1977, which grouped with Selenocephalini in the analyses of Cao *et al.* (2022).

The enigmatic Australian genus *Euleimonios* Kirkaldy, 1906 was resolved as sister to the Penthimiini clade in the analyses of Cao *et al*. (2022). It shares no obvious diagnostic morphological characters with Penthimiini and possesses inflated lora which partly or nearly entirely cover and obscure the anteclypeus, a unique character in Deltocephalinae. It also has the subgenital plates fused to each other and to the valve, which is unusual in the subfamily, and the anterior arms of the connective appressed to each other, as in Paralimnini. Its sister-group relationship to Penthimiini with strong branch support is remarkable, but it is connected by a relatively long branch, suggesting that it represents an evolutionary divergent lineage distinct from other Deltocephalinae. It is considered incertae sedis in Deltocephalinae here.

Distribution

Cosmopolitan.

Newly included genera

Magnentius Singh-Pruthi, 1930 (formerly Magnentiini); *Ndua* Linnavuori, 1978 (formerly Magnentiini).

Excluded genera

Eovulturnops Evans, 1947 (to Bahitini); *Jafar* Kirkaldy, 1903 (to Selenocephalini); *Musosa* Linnavuori, 1977 (to Selenocephalini).

Tribe **Platymetopiini** Haupt, 1929 reinstated

Fig. 4

Platymetopiini Haupt, 1929: 245.
Mesamiini Oman, 1943: 16.
Colladonini Bliven, 1955: 1.
Cerrillini Linnavuori, 1975: 49, syn. nov.

Diagnosis

Head with crown usually depressed, depressed either side of midline, or sometimes flat or not depressed, anterior margin of head usually at least slightly produced and angulate and usually with two pairs of black spots on margin and margin usually well-defined and crimped, anteclypeus constricted near base, forewing color pattern usually including numerous round white translucent spots, costal margin usually with extra crossveins basad of Rs fork, first hind tarsomere with four or fewer platellae in ventroapical row, male pygofer usually with ventral process, subgenital plates with macrosetae uniseriate, first valvulae with dorsal sculptured area consisting of well-delimited horizontal rows of concatenate sculpture basally and becoming more oblique toward apex, second valvulae with median dorsal cleft well delimited, distal blades usually with numerous close-set conical teeth.

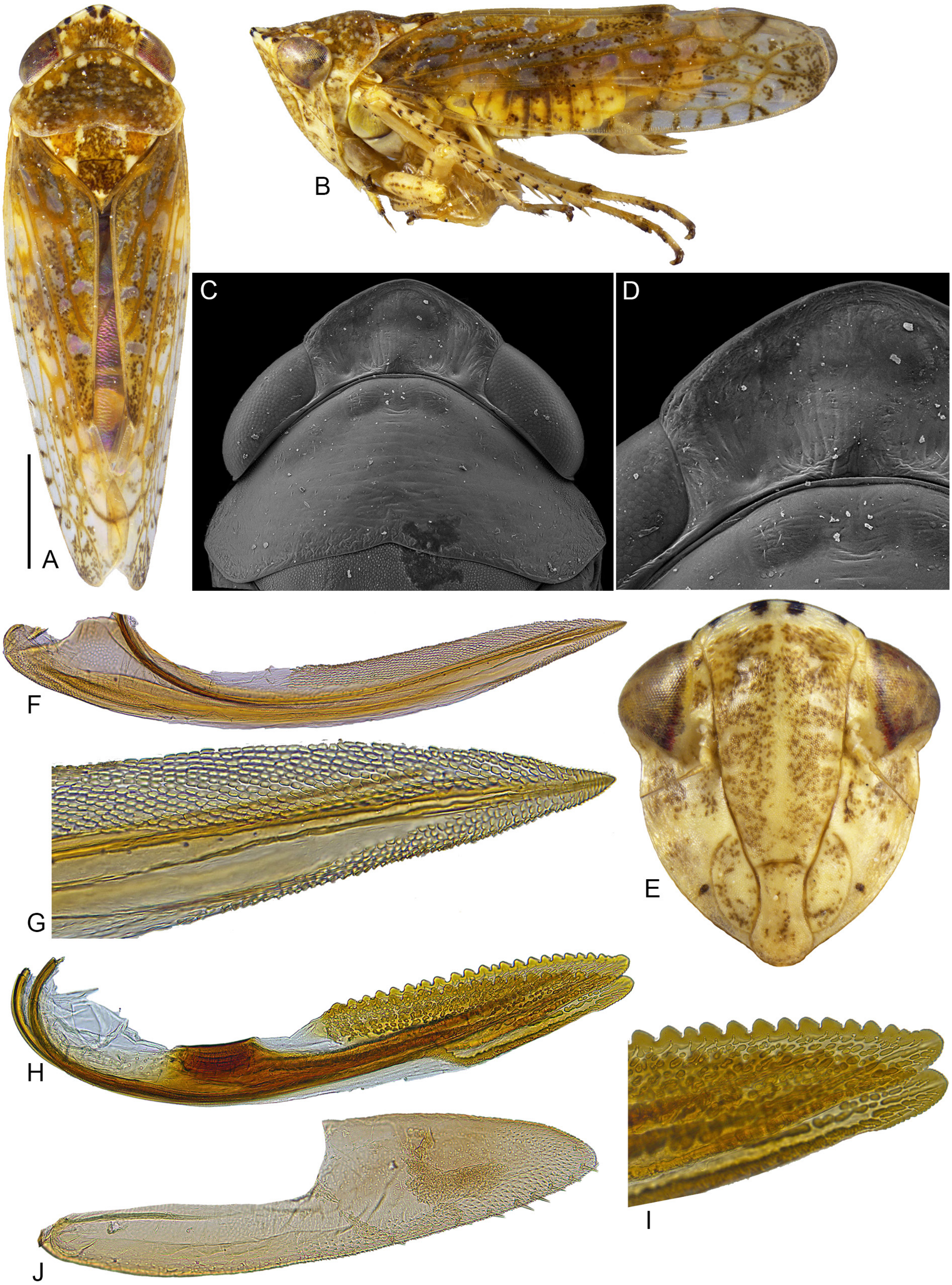

Fig. 4. Platymetopiini Haupt, 1929 reinstated. **A**–**E**. *Acunasus luteus* DeLong, 1945 (♂, USNM, USNMENT01513092). **F**–**J**. *Platymetopius pardalis* Emeljanov, 1964 (♀, INHS). **A**. Dorsal habitus. **B**. Lateral habitus. **C**. Head and pronotum, dorsal view, SEM. **D**. Detail of crown, dorsal view, SEM. **E**. Face. **F**. First valvula, lateral view. **G**. Detail of first valvula apex. **H**. Second valvula, lateral view. **I**. Detail of second valvula apex. **J**. Gonoplac, lateral view. Scale bar: A = 1 mm.

Remarks

Platymetopiini was treated as a valid tribe by Oman *et al*. (1990), as a subtribe of Athysanini by Dmitriev (2006), and as a synonym of Athysanini by Zahniser & Dietrich (2013). It is here reinstated as a valid tribe. As here defined, this tribe corresponds to a large lineage of mostly endemic New World genera (except the Palearctic type genus) that was resolved by the analyses of Cao *et al*. (2022) (Fig. 1; Supp. file 2). These genera were formerly included in Athysanini due to the Y-shaped connective articulated to the aedeagus and the absence of other distinctive morphological traits used to diagnose other deltocephaline tribes. Due to the substantial morphological diversity within this lineage, the above diagnosis does not entirely apply to all genera here included in the tribe.

Cerrillus Oman, 1938, the type genus of the monotypic Cerrillini Linnavuori, 1975, was derived within the clade of Platymetopiini, as defined here; Cerrillini is therefore considered a synonym of Platymetopiini. Zahniser & Dietrich (2013) considered Cerrillini a synonym of the broadly circumscribed Athysanini.

Brincadorus was removed from Bahitini, and along with *Saltadorus* Camisão *et al*., 2024, was considered incertae sedis by Camisão *et al.* (2024). They are included here in Platymetopiini based on the results of the analyses of Cao *et al.* (2022). Camisão *et al*. (2024) corrected the identifications of the taxa included in those analyses, i.e., "*Brincadorus laticeps* Oman, 1938" of Cao *et al*. (2022) was corrected to *B. cruceno* Camisão *et al*., 2024 and "*Brincadorus* n.sp." was corrected to *Saltadorus dietrichi* Camisão *et al*., 2024. Linnavuori & Heller (1961) described *Mascoitanus* Linnavuori & Heller, 1961 as a subgenus of *Brasilanus* Linnavuori, 1959, but it differs from the type subgenus significantly in the more robust shape and numerous characters of the male genitalia. *Mascoitanus* stat. nov. is raised to generic status here. It is related to *Brincadorus* with which it shares a similar robust shape and yellowish color, metatarsomere I apex with three platellae, pygofer with a falcate process arising posterodorsally and directed inwardly, and a linear connective with anterior arms appressed, and to *Saltadorus* with which it shares a sclerotized gonoduct recurved and extending out of the atrium of the aedeagus. It differs from those genera in lacking numerous transverse carinae on the anterior margin of the head and crown (head is shagreen anteriorly in *Mascoitanus* but with granules transversely elongate, appearing to be a transitional state to the transversely carinate condition in *Brincadorus*) and has the subgenital plates fused to each other and to the valve. *Brincadorus* and *Saltadorus* also have an unusual but different modification of the subgenital plates. The only known species is *M. lateralis* (Linnavuori & Heller, 1961) comb. nov., from Peru. One male specimen from Peru, Madre de Dios, Manu, Pakitza (USNM) was observed. The relationship of *Brasilanus* s. str. to other genera of Deltocephalinae is unclear, and it is considered here to be incertae sedis in Deltocephalinae.

Colladonus Ball, 1936 was included in Platymetopiina by Dmitriev (2006), and this and related genera were resolved within the Platymetopiini clade by the analyses of Cao *et al*. (2022). In addition to the genera of this group sampled in the analyses, *Caladonus* Oman, 1949, *Floridonus* Oman, 1949, *Fridonus* Oman, 1949, *Nigridonus* Oman, 1949, *Nurenus* Oman, 1949, *Paracolladonus* Nielson, 1988, and *Paranurenus* Nielson, 1988 have been suggested by previous authors to be closely related to *Colladonus* (Oman 1949; Nielson 1988) and are placed in Platymetopiini here. *Ancudana* DeLong & Martinson, 1974, known from Chile, possesses an upturned pygofer spine originating from the posteroventral corner and the style apophysis apex short, sharp, and directed abruptly outward, characters shared with the *Colladonus* group, and it is therefore included in Platymetopiini here.

Brazosa Oman, 1938 and *Zabrosa* Oman, 1949 also grouped within the Platymetopiini clade recovered by Cao *et al*. (2022) and were resolved as sister to each other. Pinedo-Escatel & Dietrich (2020) suggested that *Goiattus* Pinedo-Escatel, 2020, *Napo* Linnavuori & DeLong, 1976, *Pseudalaca* Linnavuori, 1959, *Pseudonapo* Pinedo-Escatel & Dietrich, 2020, and *Spaltumtettix* Pinedo-Escatel & Dietrich, 2020 are related to *Brazosa* and *Zabrosa*. Of the former genera, only *Napo* was sampled by Cao *et al*. (2022) and was placed within the Platymetopiini clade, but in a position relatively distant from *Brazosa* and *Zabrosa*. The type species, *N. brazosellus* Linnavuori & DeLong, 1976 did not group with "*Napo* n.sp." suggesting that the latter specimen represents a separate genus. The genera discussed by Pinedo-Escatel & Dietrich (2020) are included in Platymetopiini here, but further analysis is needed to clarify their relationships to each other and to other Platymetopiini. *Dolyobius* Linnavuori, 1959 and *Paratanus* Young, 1957 were resolved as sister to each other, and this clade was sister to the *Brazosa*/*Zabrosa* clade.

Oman's (1949) placement of *Norvellina* Ball, 1931 and *Aplanus* Oman, 1949 near each other was supported by a close relationship between the two resolved by Cao *et al*. (2022). Nielson & Haws (1992) noted characters shared between *Aplanus* and their newly described *Aplanusiella* Nielson & Haws, 1992.

A clade including the type genus of the tribe, *Platymetopius* Burmeister, 1838, was resolved by Cao *et al*. (2022) that also included *Neocrassana* Linnavuori, 1959, *Eusora* Oman, 1949, *Norvellina*, *Aplanus*, *Mesamia* Ball, 1907, *Fitchana* Oman, 1949, *Bandara* Ball, 1931, *Comayagua* Linnavuori & DeLong, 1978, *Bardana* DeLong, 1980, *Angulanus* DeLong, 1946, *Conversana* DeLong, 1967, and *Eusama* Oman, 1949. Ball (1931) asserted that *Bandara* and *Twiningia* Ball, 1931 are closely related to *Mesamia*. Oman (1949) placed *Omansobara* Xing, 2017 (= *Sobara* Oman, 1949) and *Twiningia* close together with *Mesamia* and *Fitchana* on his chart of deltocephaline genera, suggesting a close relationship. These genera share the depressed and somewhat produced crown and the forewing with numerous extra costal veins with other typical Platymetopiini, and they appear to be the genera most closely related to *Platymetopius*.

Oman (1949) placed *Danbara* Oman, 1949 near *Bandara* and placed *Cetexa* Oman, 1949 near *Eusama*, suggesting close relationships, and DeLong (1967) stated that *Danbara* is related to *Atanus* Oman, 1938 and *Conversana* DeLong, 1967. Therefore, *Danbara* and *Cetexa* are included in Platymetopiini here.

Two of the three described species of *Cahya* Linnavuori, 1959 were included in the analyses of Cao *et al*. (2022), including the type species, *C. chapadensis* (Baker, 1923), and *C. variabilis* (DeLong, 1945). They were both included in the Platymetopiini clade but were not resolved as sister to each other. It appears that a new genus may be needed to accommodate *C. variabilis* and perhaps *C. spinosa* Linnavuori & DeLong, 1979.

In the analyses of Cao *et al.* (2022), *Caranavia separata* Linnavuori & Heller, 1961 was resolved in the Platymetopiini clade, but "*Caranavia* n.sp." was resolved in the Pendarini clade. Re-examination of the female DNA voucher of "*Caranavia* n.sp." from Mexico indicates that, although it is similar to *C. cruentata* Linnavuori, 1959 in size, color and overall structure, the crown of the head is completely shagreen, suggesting that it belongs instead in *Chlorotettix* or a related genus, consistent with its placement on the phylogeny of Cao *et al*. (2022). *Caranavia* spp. have the crown smooth posteriorly. This genus is here included in Platymetopiini but comparison of *C. separata* to the type species, *C. cruentata*, is needed to confirm that these species belong together in the same genus.

Artucephalus DeLong, 1943, *Dampfiana* DeLong & Hershberger, 1948, *Deltorhynchus* DeLong, 1943, *Excavanus* DeLong, 1946, *Lajolla* Linnavuori, 1959, *Onura* Oman, 1938, *Sanuca* DeLong, 1980, and *Tenuisanus* DeLong, 1944 share the depressed and produced crown and usually with numerous extra costal veins that are typical of many Platymetopiini. DeLong (1943a) stated that *Artucephalus* is related to *Aligia*. DeLong & Hershberger (1948) stated that *Dampfiana* DeLong & Hershberger, 1948 is probably related to *Bandara* and *Stoneana* DeLong, 1943. DeLong (1943b, 1944) stated that *Deltorynchus* and *Tenuisanus* are related to *Mesamia*. DeLong (1946, 1980) stated that *Excavanus* and *Sanuca* are related to *Acunasus* DeLong, 1945.

Latinocesa Koçak & Kemal, 2010 appears to be related to *Zabrosa* based on the anteriorly-posteriorly compressed head and strongly convex pronotum. Nielson (1988) stated that *Paracrassana* Nielson, 1988 is closely related to *Crassana* DeLong & Hershberger, 1947.

Distribution

Nearctic, Neotropical, Palearctic.

Newly included genera (all transferred from Athysanini, unless otherwise noted)

Acunasus DeLong, 1945; *Aligia* Ball, 1907; *Alladanus* DeLong & Harlan, 1968; *Ancudana* DeLong & Martinson, 1974*; *Angubahita* DeLong, 1982; *Angulanus* DeLong, 1946; *Aplanus* Oman, 1949; *Aplanusiella* Nielson & Haws, 1992*; *Artucephalus* DeLong, 1943*; *Atanus* Oman, 1938; *Bandara* Ball, 1931; *Bardana* DeLong, 1980; *Benibahita* Linnavuori, 1959; *Bonneyana* Oman, 1949; *Brazosa* Oman, 1938; *Brincadorus* Oman, 1938 (formerly incertae sedis); *Cahya* Linnavuori, 1959; *Caladonus* Oman, 1949*; *Caranavia* Linnavuori, 1959; *Cerrillus* Oman, 1938; *Cetexa* Oman, 1949*; *Cocrassana* Blocker & Larsen, 1991; *Colladonus* Ball, 1936; *Comayagua* Linnavuori & DeLong, 1978; *Conversana* DeLong, 1967; *Costamia* DeLong, 1946; *Cozadanus* DeLong & Harlan, 1968; *Crassana* DeLong & Hershberger, 1947; *Dampfiana* DeLong & Hershberger, 1948*; *Danbara* Oman, 1949*; *Deltorynchus* DeLong, 1943*; *Dolyobius* Linnavuori, 1959; *Duocrassana* Pinedo-Escatel, Zahniser & Dietrich, 2016; *Eusama* Oman, 1949; *Eusceloidia* Osborn, 1923; *Eusora* Oman, 1949; *Eutettix* Van Duzee, 1892; *Excavanus* DeLong, 1946*; *Fitchana* Oman, 1949; *Floridonus* Oman, 1949*; *Fridonus* Oman, 1949*; *Goiattus* Pinedo-Escatel, 2020*; *Idiodonus* Ball, 1936; *Jaacunga* Nielson, 1988; *Lajolla* Linnavuori, 1959*; *Latinocesa* Koçak & Kemal, 2010*; *Mascoitanus* Linnavuori & Heller, 1961 stat. nov.*; *Mesamia* Ball, 1907; *Napo* Linnavuori & DeLong, 1976; *Neocrassana* Linnavuori, 1959; *Neodonus* DeLong & Hershberger, 1948; *Nigridonus* Oman, 1949*; *Norvellina* Ball, 1931; *Nurenus* Oman, 1949*; *Ollarianus* Ball, 1936; *Omansobara* Xing, 2017*; *Onura* Oman, 1938*; *Pachytettix* Linnavuori, 1959; *Paracolladonus* Nielson, 1988*; *Paracrassana* Nielson, 1988*; *Paraganus* Linnavuori, 1955; *Paranurenus* Nielson, 1988*; *Paratanus* Young, 1957; *Platymetopius* Burmeister, 1838; *Pseudalaca* Linnavuori, 1959*; *Pseudaligia* Kramer & DeLong, 1968; *Pseudonapo* Pinedo-Escatel & Dietrich, 2020*; *Pseutettix* DeLong, 1967; *Renonus* DeLong, 1959; *Retusanus* DeLong, 1945; *Saltadorus* Camisão, Zahniser, & Takiya, 2024 (formerly incertae sedis); *Sanuca* DeLong, 1980*; *Spaltumtettix* Pinedo-Escatel & Dietrich, 2020*; *Spinulana* DeLong, 1967; *Stoneana* DeLong, 1943; *Tenuisanus* DeLong, 1944*; *Twiningia* Ball, 1931*; *Usanus* DeLong, 1947; *Zabrosa* Oman, 1949

*These genera were not included in the analyses of Cao *et al*. (2022). Justification for their inclusion is given above. All other non-asterisked genera were included in those analyses and found within the Platymetopiini clade (Fig. 1; Supp. file 2).

Tribe **Scaphoideini** Oman, 1943

Remarks

The expanded taxon sampling and larger data set in the analyses of Cao *et al*. (2022) (Fig. 1; Supp. file 2) showed that Scaphoideini sensu Zahniser & Dietrich (2013) is paraphyletic with respect to Phlepsiina and Drabescina, which were treated previously as separate tribes. The latter taxa were both resolved as monophyletic by Cao *et al*. (2022) with the exceptions that *Phlepsanus* Oman, 1949 should be transferred to Phlepsiina (from Athysanini) and *Nirvanguina* Zhang & Webb, 1996 (previously placed in Paraboloponina Ishihara, 1953) should be placed to Scaphoideini (unplaced to subtribe). Some genera previously included in Scaphoideini (all restricted to the New World) are transferred to other tribes and some other genera are newly placed in it based on these results. The analyses revealed a complex pattern of relationships among Scaphoideini genera which are currently unplaced to subtribe and which form multiple monophyletic groups of genera and phylogenetic grades along the backbone. This pattern of relationships does not provide a convenient opportunity to define a monophyletic group to include these genera. Currently, we consider these genera to be unplaced to subtribe, and the nominotypical subtribe is considered, for now, to include only *Scaphoideus* Uhler, 1889. More detailed analyses that include representatives of other genera and more species from large genera are needed to better understand the relationships within this lineage and to identify morphological characters that may define generic groupings. Given the size and morphological diversity of the tribe as here circumscribed, a diagnosis for the entire group is not given, but diagnoses are given below for the subtribes and for the grouping of Scaphoideina + unplaced genera, and they are included in the key to tribes and subtribes below.

Cao *et al*. (2022) included in their analyses the following genera which were resolved in this lineage and possess some of the diagnostic characters listed below in the diagnosis for Scaphoideina + unplaced genera. These genera are transferred to Scaphoideini (unplaced to subtribe) on the basis of this result, and they are: *Aeternus* Distant, 1918, *Allotapes* Emeljanov, 1964, *Cyanidius* Emeljanov, 1964, *Knullana* DeLong, 1941, *Lineana* Li & Xing, 2024, *Nirvanguina* Zhang & Webb, 1996, *Pingellus* Evans, 1966, and *Poliona* Emeljanov, 1972.

The following genera, not included in the dataset of Cao *et al.* (2022) also possess characters listed in the diagnosis given below and are transferred to Scaphoideini (unplaced to subtribe): *Aparaphysis* Duan & Zhang, 2013, *Jakarellus* Webb, 1980, *Malasiella* Evans, 1954, *Moshkga* Deeming & Webb, 1982, *Scaphetus* Evans, 1966. *Scaphomonoides* Li, 2011, *Scaphytoceps* Dlabola, 1957, *Stenomisella* Evans, 1954, and *Stymphalella* Evans, 1954. *Acacimenus* Dlabola, 1979 shares a long and partly membranous subgenital plate apex with other Scaphoideini. An undescribed species of this genus from Zambia was represented in the phylogenetic analyses of Zahniser & Dietrich (2013) as "Zambia 121", and was consistently resolved in a clade with the scaphoideine genus *Loipothea* Linnavuori, 1968 and an undescribed species, "Zambia 118" which belongs in or near *Mavromoustaca* Dlabola, 1967. *Neoreticulum* Dai, 2009 is placed in Scaphoideini (unplaced to subtribe) based on its similarity to the scaphoideine genera *Madhyabus* Viraktamath *et al*., 2025 and *Mavromoustaca*.

The analyses of Cao *et al*. (2022) showed that some genera previously included in Scaphoideini should be placed to other tribes. These and related genera are listed below with their new placements.

Distribution

Cosmopolitan.

Included subtribes

Drabescina stat. nov., Phlepsiina stat. nov., Scaphoideina.

Newly included genera (Scaphoideini, unplaced to subtribe; all from Athysanini except where noted)

Acacimenus Dlabola, 1979; *Aeternus* Distant, 1918; *Allophleps* Bergroth, 1920; *Allotapes* Emeljanov, 1964; *Aparaphysis* Duan & Zhang 2013; *Cyanidius* Emeljanov, 1964; *Jakarellus* Webb, 1980; *Knullana* DeLong, 1941 (from Cicadulini); *Lineana* Li & Xing, 2024; *Malasiella* Evans, 1954; *Moshkga* Deeming & Webb, 1982; *Neoreticulum* Dai, 2009; *Nirvanguina* Zhang & Webb, 1996 (from Paraboloponina); *Pingellus* Evans, 1966; *Poliona* Emeljanov, 1972; *Scaphetus* Evans, 1966; *Scaphomonoides* Li, 2011; and *Scaphytoceps* Dlabola, 1957; *Stenomisella* Evans, 1954; *Stymphalella* Evans, 1954.

Excluded genera

Caphodus Oman, 1938 (to Pendarini); *Neophlepsius* Linnavuori, 1955 (to Pendarini); *Penthigrampta* Dietrich & Rakitov, 2002 (to Scaphytopiini); *Perugrampta* Kramer, 1965 (to Scaphytopiini); *Perugramptella* Dietrich & Rakitov, 2002 (to Scaphytopiini); *Scaphoidula* Osborn, 1923 (to Pendarini); *Stenogrampta* Dietrich & Rakitov, 2002 (to Scaphytopiini).

Subtribe **Drabescina** Ishihara, 1953 stat. nov.

Drabescina Ishihara, 1953: 6.
Paraboloponini Ishihara, 1953: 5, syn. reinstated.
Bhatiini Linnavuori & Al-Ne'Amy, 1983: 21.

Diagnosis

Medium to large sized, antennae elongate, usually situated near anterodorsal corners of eyes, antennal pits large and often encroaching onto frontoclypeus, anterior margin of the head usually with one to many transverse carinae or striations, male subgenital plates usually without macrosetae, nymph often with apical process on the head and male pygofer with pair of long apical appendages widely separated at the base.

Remarks

Zahniser & Dietrich (2013) recognized separate subtribes Drabescina and Paraboloponina of Drabescini. However, the species of *Drabescus* Stål, 1872 included by Cao *et al*. (2022) were derived from within Paraboloponina, so we follow Dmitriev (2004) in treating these subtribes as synonyms here.

Omanellinus Zhang, 1999 was originally placed in tribe Paraboloponini of subfamily Selenocephalinae (Zhang *et al*. 1999). Zahniser & Dietrich (2013) erroneously listed the genus in Selenocephalini: Selenocephalina. The original description and drawings of this monotypic Oriental genus indicate that it is nearly identical to *Omanella* Merino, 1936 (Drabescina), differing from the two described species of that genus only in having the style apex digitiform rather than broadened and the apex of the connective process decurved rather than curved upward. These features are not sufficiently different from *Omanella* to warrant treating *Omanellinus* as a separate genus and the latter is here considered a junior synonym of *Omanella*. This results in the new combination *Omanella populus* (Zhang, 1999) comb. nov.

Based on the results of the analyses of Cao *et al*. (2022), *Odzalana* Linnavuori, 1969 is transferred to Selenocephalini (unplaced to subtribe) and *Nirvanguina* Zhang & Webb is transferred to Scaphoideini (unplaced to subtribe).

Distribution

Afrotropical, Australian, Oriental, Palearctic.

Confirmed included genera

Fistulatus Zhang, Zhang & Chen, 1997, *Omanella* Merino 1936 (= *Omanellinus* Zhang 1999 syn. nov.).

Excluded genera

Odzalana Linnavuori, 1969 (to Selenocephalini, unplaced to subtribe); *Nirvanguina* Zhang & Webb, 1996 (to Scaphoideini, unplaced to subtribe).

Subtribe **Phlepsiina** Zahniser & Dietrich 2013 stat. nov.

Diagnosis

Medium sized to large, robust, ivory to dark brown leafhoppers, often with brown irrorate markings on the forewing and body, head distinctly narrower than pronotum, antennal ledge carinate, lorum long and large, anteclypeus widening apically, pronotum lateral margin longer than half basal width of eye, profemur row AM sometimes with 1 or more setae basad of AM1, and nymph with short pygofer and with 6 rows of abdominal macrosetae.

Remarks

The phylogenomic analyses of Cao *et al*. (2022) consistently placed all genera previously included in Phlepsiini in a single clade that was sister to the remaining Scaphoideini. The Nearctic genus *Phlepsanus* Oman, 1949 was previously placed in Athysanini but agrees with the tribal diagnosis of Phlepsiini and was nested in a clade comprising *Texananus* Ball, 1918 and *Excultanus* Oman, 1949 in the phylogeny of Cao *et al*. (2022); thus, *Phlepsanus* is here included in Phlepsiina. The recently described genus *Brevivalvala* Dai, Qu & Yang, 2016 is the only representative of the subtribe known from the Oriental region. Further study is needed to clarify if it belongs in Phlepsiina. It possesses carinae at the anterior margin of the head and the subgenital plates lack macrosetae, suggesting it could be related to Drabescina.

Distribution

Afrotropical, Nearctic, Oriental, Palearctic.

Newly included genus

Phlepsanus Oman, 1949.

Subtribe **Scaphoideina** Oman, 1943

Diagnosis (for Scaphoideina + genera unplaced to subtribe)

Medium sized (usually 4–7 mm), ivory, yellowish, ochraceous, or brown leafhoppers, often marked with orange, brown, or black on head, pronotum, or forewings, head narrower than pronotum and sometimes produced, frontoclypeus long and narrow, antennae long, body slender, head and wings often with brown, orange, ochraceous, or ivory markings, forewing with one or more darkly pigmented reflexed veins in vicinity of outer anteapical cell, profemur row AV setae absent or reduced (without stout setae), metatibia macrosetae in row PD long, as long as or longer than 0.5 × length of protibia, male or female pygofer often with dense tufts of long fine or regular setae, subgenital plate apex membranous or long, digitate, and somewhat membranous or weakly sclerotized, subgenital plates with numerous long fine setae laterally and/or dorsally, male genitalia often with processes connected or articulated to base of aedeagus or apex of connective stem.

Remarks

For reasons explained above, only *Scaphoideus* is currently included in subtribe Scaphoideina. The other genera that were placed in Scaphoideini by Zahniser & Dietrich (2013) (with exception of the changes made above) are considered to be placed in Scaphoideini and unplaced to subtribe.

Distribution

Afrotropical, Australian, Nearctic, Oriental, Palearctic.

Tribe **Scaphytopiini** Oman, 1943

Diagnosis

Small to large deltocephalines usually brownish with symmetrical markings that may include paired spots, stripes and/or larger maculae, head usually produced and often strongly so, head width subequal to or less than that of pronotum, gena usually not or only weakly incised below eye (except *Perugrampta*-group) and often extended onto dorsum of head and visible behind eye, anteclypeus strongly expanded distally (except *Perugramptella* Dietrich & Rakitov, 2002), forewing with reflexed costal veins often numerous, crossvein m-cu2 absent, appendix well developed sometimes extended around wing apex, male sternal apodemes weakly developed, connective Y-shaped with arms widely separated, stem often short or absent, first valvula with strigate dorsal sculpture, second valvulae with median dorsal cleft usually well-delimited, distal blades usually with numerous, close-set conical teeth.

Remarks

Zahniser & Dietrich (2013) noted that Old World genera placed in this tribe by previous authors (Oman *et al*. 1990; Webb & Godoy 1993) are only superficially similar to the endemic New World type genus. The analyses of Cao *et al*. (2022) (Fig. 1; Supp. file 2) grouped the type genus with some Neotropical genera placed in Athysanini or Scaphoideini by Zahniser & Dietrich (2013). These genera are here transferred to Scaphytopiini based on the distinctly produced crown and/or broad gena extended onto the dorsal margin of the head behind the eye. The morphologically aberrant genus *Idioceromimus* Dietrich & Rakitov, 2002 has the crown short and rounded to the face but has the gena very broad, as in *Scaphytopius* Ball, 1931. *Perugrampta* and related Neotropical genera have the head strongly and angulately produced but have the gena emarginate below the eye. The unusual morphology of the nymph of *Idioceromimus*, with an unpaired dorsal process and pair of lateral processes on the head, is similar to that of *Nesothamnus* Linnavuori, 1959, also here included in Scaphytopiini. Both genera also share an unusual bright red color pattern (Dietrich & Rakitov 2002). The ovipositor structure of the included genera is variable, but they all share similar strigate dorsal sculpture on the first valvula and the second valvulae are similar to those of other genera belonging to the large, mostly endemic New World clade that includes Bahitini, Pendarini, Platymetopiini and Scaphytopiini.

Distribution

Nearctic, Neotropical.

Newly included genera

Idioceromimus Dietrich & Rakitov, 2002 (from Athysanini); *Nesothamnus* Linnavuori, 1959 (from Athysanini); *Penthigrampta* Dietrich & Rakitov, 2002 (from Scaphoideini); *Perugrampta* Kramer, 1965 (from Scaphoideini); *Perugramptella* Dietrich & Rakitov, 2002 (from Scaphoideini); *Stenogrampta* Dietrich & Rakitov, 2002 (from Scaphoideini).

Excluded genus

Aparaphysis Duan & Zhang 2013 (to Scaphoideini).

Tribe **Selenocephalini** Fieber, 1872

Diagnosis

Medium-sized to large deltocephalines, head with transverse carinae on crown-face transition (Selenocephalina) or without carinae (Bonaspeiina, Hypacostemmina), profemur row AV often with relatively long macrosetae in basal half, male anal tube large and well-sclerotized, connective with arms widely separated and stem short or absent, second valvulae relatively elongate and slender with dorsal teeth restricted to distal third or less.

Remarks

The analysis of Cao *et al*. (2022) (Fig. 1; Supp. file 2) recovered a clade of mostly Afrotropical genera including Bonaspeiini, Hypacostemmini and Selenocephalini sensu Zahniser & Dietrich (2013) but also including several genera currently placed in other tribes including Athysanini, Drabescini, Penthimiini and Stegelytrini. Bonaspeiini as defined by Zahniser & Dietrich (2013) is paraphyletic, having given rise to Selenocephalini. Here we expand Selenocephalini to include subtribes Bonaspeiina and Hypacostemmina, the concepts of which remain the same as those of Zahniser & Dietrich (2013) except for the transfer of *Dagama* Distant, 1910 (previously included in Athysanini) to Bonaspeiina. The Oriental genera *Orientus* DeLong, 1938, *Sychentia* Wei & Webb, 2010, and *Tambocerus* Zhang & Webb, 1996 are transferred to Selenocephalini based on the results of Cao *et al*. (2022) but remain unplaced to subtribe. Similarly, the Afrotropical genera *Musosa* and *Jafar*, previously included in Penthimiini, are also transferred to Selenocephalini (unplaced to subtribe) based on the recent phylogenomic results, as are *Afrovarta* Zahniser, 2013 (previously placed in Athysanini) and *Odzalana* (previously placed in Drabescini). All of these genera except *Afrovarta*. *Sychentia* and *Orientus* resemble Selenocephalina in having the crown-face transition transversely carinate. *Sychentia* has male genitalia that are typical of the crown-group Deltocephalinae (pygofer with basolateral cleft, valve triangular and articulating with pygofer laterally at a short point, connective Y-shaped, style broadly bilobed at base) which differ from the plesiomorphic states present in Stegelytrini, where it was previously placed.

Distribution

Afrotropical, Nearctic (*Orientus ishidae* Matsumura introduced), Oriental, Palearctic.

Included subtribes

Bonaspeiina stat. nov., Hypacostemmina stat. nov., Selenocephalina.

Newly included genera

Afrovarta Zahniser, 2013 (unplaced to subtribe; from Athysanini); *Dagama* Distant, 1910 (to Bonaspeiina; from Athysanini); *Jafar* Kirkaldy, 1903 (unplaced to subtribe; from Penthimiini); *Musosa* Linnavuori, 1977 (unplaced to subtribe; from Penthimiini); *Odzalana* Linnavuori, 1969 (unplaced to subtribe; previously Paraboloponina); *Orientus* DeLong, 1938 (unplaced to subtribe; from Athysanini); *Sychentia* Wei & Webb, 2010 (unplaced to subtribe; from Stegelytrini); *Tambocerus* Zhang & Webb, 1996 (unplaced to subtribe; from Athysanini).

Excluded genera

Omanellinus Zhang, 1999 (to Drabescini).

Subtribe **Selenocephalina** Fieber, 1872

Selenocephalina Fieber, 1872: 10.
Ianeirini Linnavuori, 1978: 43, syn. nov.
Adamini Linnavuori & Al-Ne'amy, 1983: 27, syn. nov.
Dwightiini Linnavuori & Al-Ne'amy, 1983: 23 (invalid due to homonymy of type genus).
Dwightlini McKamey, 2003: 449, syn. nov.

Remarks

Cao *et al*. (2022) resolved a monophyletic clade including Selenocephalina as delimited here. *Dwightla* McKamey, 2003, the only genus of the previously recognized subtribe Dwightlina of Selenocephalini, was derived from within a clade of other genera in Selenocephalina. Therefore, Dwightlina is here considered a new synonym of Selenocephalina. Ianeirina and Adamina are also synonymized with Selenocephalina based on the resolved positions of *Abimwa* Linnavuori, 1978 (previously Ianeirina) and *Adama* Dlabola, 1980 (previously Adamina) with respect to Selenocephalina. Along with *Dwightla*, they share with Selenocephalina the presence of transverse carinae on the anterior margin of the head. Two genera previously placed in Ianeirina, *Ianeira* Linnavuori, 1969 and *Xugyrosus* nom. nov., do not have carinae at the anterior margin of the head but are retained in Selenocephalina based on their apparent similarity to other genera previously placed in Ianeirina (see discussion in Xu & Zhang 2023). *Geelus* Stiller, 2020, originally placed in Bonaspeiini, was resolved as sister the remaining Selenocephalina. Like *Ianeira* and *Xugyrosus*, *Geelus* does not possess carinae on the anterior margin of the head, but its relatively long and slender shape differs markedly from other Bonaspeiina and is similar to genera previously placed in Ianeirina (as discussed by Xu & Zhang 2023). Based on these similarities and its phylogenetic placement, it is transferred here to Selenocephalina. Dlabola (1987) compared *Thanomahia* Dlabola, 1987 to *Selenocephalus* Germar, 1833 and the description shows that this genus belongs in

Selenocephalina based on the carinae on the anterior margin of the head, the connective U-shaped with stem very short or absent, the pygofer dorsally incised to midlength, the pygofer side without macrosetae and dorsally produced to a declivous process, and segment X large and broadly sclerotized dorsally.

Xu & Zhang (2023) described the genus and species *Gyrosus deltodontus* Xu & Zhang, 2023 and placed it in Ianeirina. *Gyrosus* Xu & Zhang, 2023 is preoccupied by *Gyrosus* Gray, 1862 (Suidae; a synonym of *Sus* Linnaeus, 1758). We propose the replacement name *Xugyrosus* nom. nov., resulting in *Xugyrosus deltodontus* (Xu & Zhang, 2023) comb. nov.

Distribution

Afrotropical, Oriental, Palearctic.

Newly included genera

Abimwa Linnavuori, 1978 (formerly Selenocephalini: Ianeirina); *Adama* Dlabola, 1980 (formerly Selenocephalini: Adamina); *Bardera* Linnavuori & Al-Ne'amy, 1983 (formerly Selenocephalini: Ianeirina); *Dwightla* McKamey, 2003 (formerly Selenocephalini: Dwightlina); *Geelus* Stiller, 2020 (formerly Bonaspeiini); *Ianeira* Linnavuori, 1969 (formerly Selenocephalini: Ianeirina); *Kanziko* Linnavuori & Al-Ne'amy, 1983 (formerly Selenocephalini: Ianeirina); *Thanomahia* Dlabola, 1987 (from Athysanini); *Xugyrosus* nom. nov. (formerly Selenocephalini: Ianeirina).

Tribe **Vartini** Zahniser & Dietrich, 2013

Remarks

The analyses of Cao *et al*. (2022) (Fig. 1; Supp. file 2) consistently resolved a monophyletic group including the previous concepts of Vartini and Punctulini, along with several Indomalayan bamboo-feeding genera previously placed in Athysanini or Deltocephalini. This entire clade is treated as Vartini s. lat. here, with included subtribes Punctulina, Vartina, and the newly established subtribe Bambusanina subtribe nov. *Loeia*, previously included in Deltocephalini, was consistently resolved in this lineage but its position with respect to the three subtribes differed among analyses. In the tree presented here (Fig. 1; Supp. file 2), *Loeia* was resolved as sister to the other sampled Punctulina. Dietrich (2025) revised the genus and justified placing it Punctulini, and this placement is followed here, except as subtribe Punctulina of Vartini (see more discussion above, under Deltocephalini). Vartini was resolved as sister to Mukariini, another bamboo-feeding lineage from southeast Asia and Australasia. Vartini encompasses significant morphological diversity and a diagnosis of the entire group is not attempted here. Punctulina and Vartina share a similarly modified male 2S sternal apodeme. Some Bambusanina have enlarged 2S apodemes but not in the same shape and orientation as the other subtribes. More observations of these and related characters in Bambusanina and other Vartini will help to clarify their utility in diagnosing Vartini and its subtribes.

Distribution

Afrotropical, Palearctic, Oriental.

Included subtribes

Bambusanina subtribe nov., Punctulina stat. nov., Vartina.

Subtribe **Bambusanina** subtribe nov.

urn:lsid:zoobank.org:act:C5644A9F-720E-45DA-A216-951416D7A496

Fig. 5

Type genus

Bambusana Anufriev, 1969.

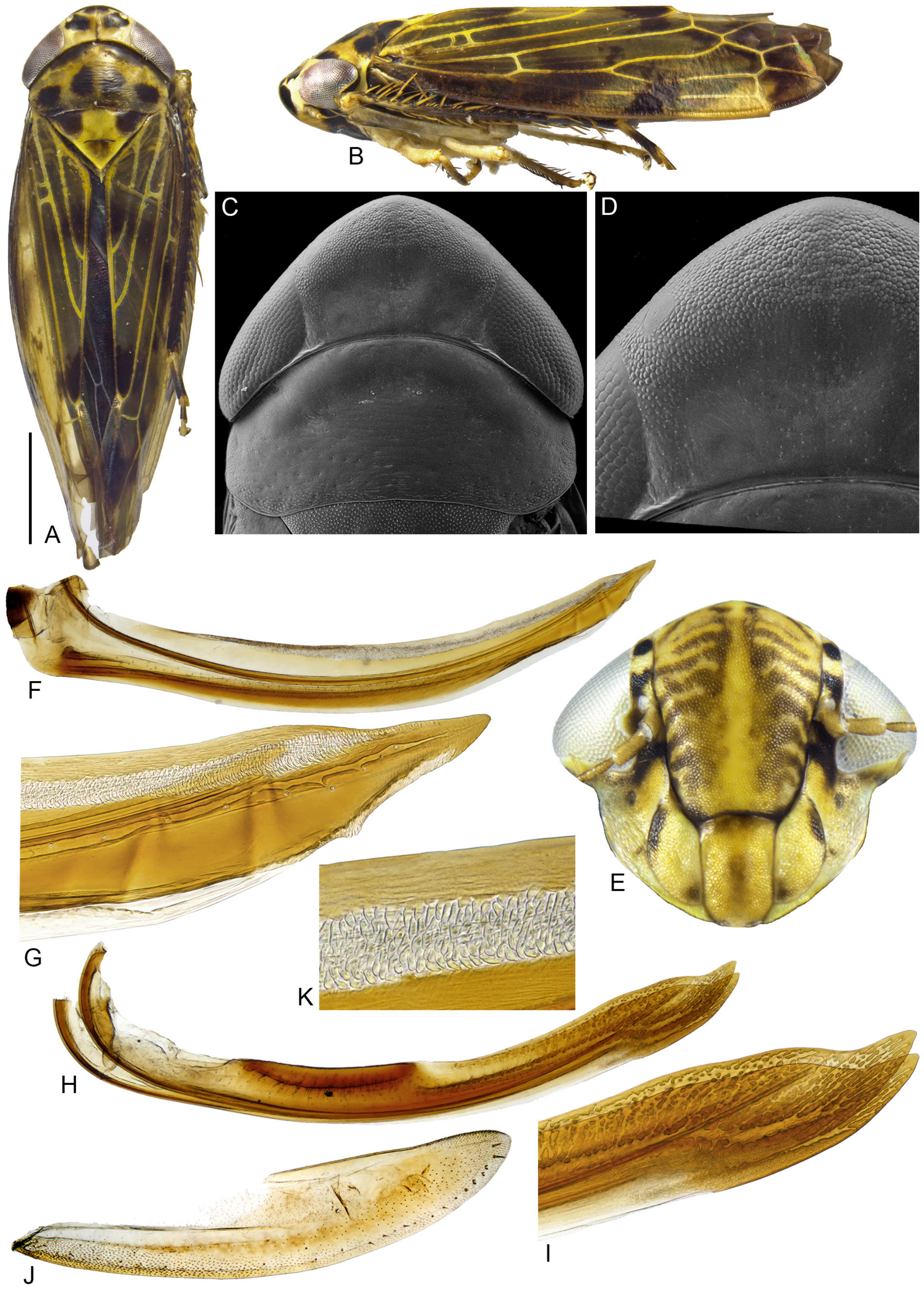

Fig. 5. Vartini Zahniser & Dietrich, 2013: Bambusanina subtribe nov. **A–B, E**. *Bambusana biflaka* Li, 2024 (♂, INHS). **C–D**. *Alishania fodingensis* Xing *et al*., 2010 (♀, INHS). **F–K**. *Abrus digitatus* Dietrich *et al*., 2020 (♀, INHS). **A**. Dorsal habitus. **B**. Lateral habitus. **C**. Head and pronotum, dorsal view, SEM. **D**. Detail of crown, dorsal view, SEM. **E**. Face. **F**. First valvula, lateral view. **G**. Detail of first valvula apex. **H**. Second valvula, lateral view. **I**. Detail of second valvula apex. **J**. Gonoplac, lateral view. **K**. detail of first valvula sculpturing. Scale bar: A = 1 mm.

Description

Small to medium-sized cylindrical or wedge-shaped deltocephalines, color stramineous to brown, with extensive dark brown markings dorsally (rarely green without dark markings), forewing veins usually pale, bordered with brown, head with crown anterior margin broadly rounded to angulately produced, rounded to face, and without transverse carinae, crown between eyes less than 1.5 × eye width, face in anterior view wider than tall and orientation oblique in profile, anteclypeus narrow basally and expanded distally, forewing macropterous and often with supernumerary crossveins and without reflexed costal veins basad of Rs origin, profemur with AM1 near midheight of anterior surface, male abdomen with 2s apodemes enlarged or not and if so usually parallel, not elongate and not divergent or capitate, male pygofer with profuse macrosetae and with one or more sclerotized ventral processes arising preapically and often extended mesad but not articulated with aedeagal atrium, subgenital plate much shorter than pygofer and lateral margins convex and usually with macrosetae scattered or in irregular sublateral rows, connective articulated to aedeagus and with anterior branches parallel or slightly divergent, style with apex usually enlarged and often modified with teeth or branches, membrane laterad of aedeagal atrium with basal or distal branches, ovipositor protruding well beyond pygofer apex, first valvulae dorsal sculpture granulose, areolate, or imbricate, reaching dorsal margin of valvula or with dorsal unsculptured dorsal band, second valvulae with distal teeth short and widely spaced, sometimes absent.

Remarks

This subtribe is here established to include a group of bamboo-associated Oriental genera formerly placed in Athysanini or Opsiini that is sister to Vartina+Punctulina in the phylogenomic results of Cao *et al*. (2022). The dataset of Cao *et al*. (2022) included six genera that are here placed in the new tribe: *Abrus*, *Alishania*, *Bambusana*, *Bambusananus*, *Branchana* and *Neurotettix*). Although these genera lack the more distinctive characteristics of the latter two subtribes, they are similar in having the male pygofer, style and aedeagus often highly modified and in lacking elongate, capitate 2s apodemes.

Distribution

Oriental.

Included genera

Abrus Dai & Zhang, 2002; *Alishania* Vilbaste, 1969; *Bambusana* Anufriev, 1969; *Bambusananus* Li & Xing, 2024; *Branchana* Li, 2024; *Fuscmacula* Yao, Zhang & Xing 2021; *Neurotettix* Matsumura, 1914.

Subtribe **Punctulina** Dai, Zahniser, Viraktamath & Webb, 2017 stat. nov.

Diagnosis

Small to medium-sized black or brownish to ochraceous leafhoppers, texture of dorsum including pronotum, mesonotum, forewings and head often punctate, anterior margin of head sometimes carinate, forewing sometimes with extra crossveins particularly in clavus, apodemes of male abdominal segment II long, divergent, and capitate, male pygofer with paired median sclerotized lobes articulated to sides of aedeagal atrium.

Remarks

This subtribe was first described as separate tribe to include some morphologically peculiar genera from the Indomalayan and Oceanian regions (Dai *et al*. 2017). More recently, Dietrich *et al*. (2020) and Ramaiah *et al.* (2023) included two genera of more ‘normal looking’ Deltocephalinae based on the presence of some unusual traits shared with Punctulina including elongate, capitate male 2S abdominal apodemes. The analysis of Cao *et al*. (2022) supported this broader concept of Punctulina and suggested that *Hecalusina* (previously placed in Hecalini) belongs to this lineage; it is here transferred to this subtribe. The analysis of Cao *et al*. (2022) grouped Punctulina together in a clade comprising two tribes of leafhoppers that are associated with bamboo, Mukariini and Vartini.

Distribution

Oriental.

Newly included genera

Hecalusina He, Zhang & Webb, 2008 (from Hecalini).

Subtribe **Vartina** Zahniser & Dietrich, 2013

Diagnosis

Medium sized to large, somewhat elongate, usually greenish or bluish leafhoppers, usually with red or orange longitudinal stripes and/or spots, head produced and usually sharply pointed, gena usually visible behind the eye in dorsal view, frontoclypeus elongate, lorum distant from genal margin, profemur intercalary row setae thick and extending to or beyond middle of profemur, forewings truncate apically, apodemes of male sternite II long, subrectangular, capitate, and directed posterolaterally, connective with anterior arms appressed, and male segment X tube-like, protruding from pygofer, and often well-sclerotized.

Remarks

Paralampridius Dai *et al*., 2011 was resolved as sister to a clade of genera in Vartina in the analyses of Cao *et al*. (2022). With other Vartina, *Lampridius* and *Paralampridius* share bright orange markings on the dorsum, subgenital plates fused to each other and to valve (present in some Vartina), and apodemes of sternite II long, flared apically, and directed posterolaterally. *Lampridius* has a bifurcate aedeagus, with two shafts, which influenced previous authors to erroneously place it in Opsiini.

Distribution

Afrotropical, Oriental.

Newly included genera

Lampridius Distant, 1918 (from Opsiini); *Paralampridius* Dai, Dietrich & Zhang, 2011 (from Opsiini).

Deltocephalinae incertae sedis

Remarks

Fifty-one genera, most of them previously placed in Athysanini, could not confidently be placed to tribe because they were not sampled in the phylogenomic analyses of Cao *et al*. (2022), could not be closely associated with other genera that were sampled, or were sampled but their resolved phylogenetic position currently does not allow straightforward placement to a tribe described above. These genera are currently considered of uncertain placement to tribe in Deltocephalinae. The genera that were included in the Cao *et al*. (2022) analyses and considered incertae sedis here are discussed above under tribal treatments except for *Loralia* Evans, 1966. This Australian-endemic genus was resolved as sister to *Occinirvana* Evans, 1942, the only genus currently included in Occinirvanini and also endemic to Australia. *Occinirvana* exhibits extremely modified morphology, including an elongated head with foliaceous anterior margin, concave face, long antennae, and ocelli located on the crown. *Loralia* does not share any of these or other known distinctive characters and including it in Occinirvanini would thus render that tribe impossible to diagnose morphologically based on current knowledge. The branches separating these two sister taxa on the molecular phylogenies (Cao *et al*. 2022) are also long, indicating considerable genetic divergence matching their morphological disparities. For now, we prefer to consider *Loralia* as incertae sedis within Deltocephalinae pending further phylogenetic study of the endemic Australian fauna that incorporates other rarely-collected Australian-endemic genera (e.g., *Occiplanocephalus* Evans, 1942).

Newly considered incertae sedis in Deltocephalinae

Anaemotettix Korolevskaya, 1980; *Antoniellus* Linnavuori, 1959; *Argyrilla* Emeljanov, 1972; *Aricanus* Linnavuori, 1959; *Asiotoxum* Emeljanov, 1964; *Asthenotettix* Korolevskaya, 1980; *Baroma* Oman, 1938; *Bolotheta* Kramer, 1963; *Brachylope* Emeljanov, 1962; *Brachypterona* Lindberg, 1954; *Brasilanus* Linnavuori, 1959; *Carelmapu* Linnavuori, 1959; *Chaparea* Linnavuori, 1959; *Chimaerotettix* Dietrich & Rakitov, 2002; *Concepciona* Linnavuori & DeLong, 1977; *Conoscelis* Abdul-Nour, 1988; *Consepusa* Linnavuori & DeLong, 1977; *Cyclevertex* Li & Xing, 2024; *Desertana* DeLong & Martinson, 1973; *Divitiacus* Distant, 1918; *Dlabolaracus* Remane, 1961; *Ephelodes* Emeljanov, 1972; *Euleimonios* Kirkaldy, 1906; *Gunawardenea* Fletcher & Moir, 2008; *Hamulotettix* Dai & Zhang, 2011; *Houtbayana* Linnavuori, 1961; *Huancabamba* Linnavuori, 1959; *Inghamia* Evans, 1966; *Laminacutus* Abdul-Nour, 2002; *Lamprotettix* Ribaut, 1952; *Lascumbresa* Linnavuori & DeLong, 1979; *Laylatina* Abdul-Nour, 1988; *Loralia* Evans, 1966; *Melillaia* Linnavuori, 1971; *Nakaharanus* Ishihara, 1953; *Neohegira* Linnavuori & DeLong, 1978; *Occiplanocephalus* Evans, 1942; *Okaundua* Linnavuori, 1968; *Ophionotum* Emeljanov, 1964; *Oxytettigella* Metcalf, 1952; *Phlepsobahita* Linnavuori, 1959; *Phycotettix* Haupt, 1929; *Pygotettix* Matsumura, 1940; *Rinconada* Linnavuori & DeLong, 1977; *Selachina* Emeljanov, 1962; *Sincholata* DeLong, 1982; *Stenometohardya* Dlabola, 1981; *Streptopyx* Linnavuori, 1958; *Tapetia* Emeljanov, 1964; *Tingolix* Linnavuori & DeLong, 1978; *Yungasia* Linnavuori, 1959.

Key to tribes of Deltocephalinae

1. Connective T-shaped, bar-shaped, or platelike or, if Y-shaped, with arms forming broadly obtuse angle; style more or less linear, not broadly bilobed at base 2
– Connective with anterior arms well-delimited, somewhat or not at all divergent; connective Y- or U-shaped or 'linear' with anterior arms closely appressed; style broadly bilobed at base 6

2. Head much narrower than pronotum; profemur row AM with numerous preapical macrosetae; metatibia dorsal surface with supernumerary macrosetae between rows PD and AD, especially basally; pro- and mesotibia row PD and often row AD with numerous (> 6) macrosetae; forewing appendix often large, extending around apex; Oriental, Palearctic .... **Stegelytrini** Baker, 1915
– Head slightly narrower to wider than pronotum; profemur row AM with not more than 2 preapical macrosetae; metatibia dorsal surface without supernumerary macrosetae; pro- and mesotibia with < 6 macrosetae; forewing appendix reduced or absent 3

3. Anterior margin of head usually with a single distinct transverse carina between ocelli; epistomal suture keeled or evident from change in texture on frontoclypeus; subgenital plates completely or partially fused to each other and/or to valve (if completely articulated then pronotum produced dorsally, with longitudinal crest, *Ikelibeloha* Zahniser & Nielson, 2012); Madagascar .... **Acostemmini** Evans, 1972 (part)
– Anterior margin of head shagreen, glabrous, or with several irregular striae or carinae, without single distinct carina between ocelli; epistomal suture not keeled; subgenital plates not fused, articulated with valve 4

4. Forewing acuminate apically; head narrower than pronotum (exception: *Cariancha* Oman, 1938); connective bar-shaped or plate-like, without well-defined stem; Nearctic, Neotropical .... **Acinopterini** Oman, 1943
– Forewing rounded apically; head as wide as or wider than pronotum; connective with well-developed anterior arms and posterior stem 5

5. Connective with median, darkly sclerotized Y- or T-shaped ridge following stem and arms of connective; forewing central anteapical cell not strongly constricted medially; female pregenital sternite VIII not concealed or folded beneath sternite VII, movably articulated with sternite VII;

Nearctic (*Fieberiella florii* (Stål, 1864) introduced in North America), Palearctic ....**Fieberiellini** Wagner, 1951

– Connective evenly sclerotized throughout; forewing central anteapical cell constricted medially; female pregenital sternite VIII folded beneath and concealed by sternite VII, sternites not articulated with each other; Neotropical .... **Luheriini** Linnavuori, 1959

6. Subgenital plates fused to each other; valve straplike, fused to pygofer laterally or not visible as a separate structure (fused to plates); connective fused with aedeagus 7

– Subgenital plates usually free (exceptions include some Vartina, some Deltocephalini: *Miradeltaphus* Dash & Viraktamath, 1995 and *Yuanamia*); valve usually present, articulated with pygofer laterally and usually articulated with subgenital plates; connective articulated with or fused to aedeagus ... 8

7. Anterior margin of head with a distinct transverse carina between ocelli; forewings tectiform, not overlapping at rest; forewing appendix reduced or absent; valve strap-like, fused to pygofer laterally; Afrotropical (especially Madagascar), Oriental (India) .... **Acostemmini** Evans, 1972 (part)

– Anterior margin of head without transverse carina; forewings, if macropterous, with apices overlapping at rest and appendix extending around wing apex; valve fused to subgenital plates; Afrotropical, Australian, Oriental, Palearctic ....**Goniagnathini** Wagner, 1951

8. Head strongly produced, conical or spatulate; gena acutely incised laterally below eye; profemur intercalary row absent or with few scattered setae; metafemur macrosetal formula 2+0 or 2+1; metatarsomere I shorter than metatarsomeres II and III combined, expanded apically; metatibia straight through most of length and distinctly bent distally in dorsal view 9

– Without above combination of characters; head produced or not; gena obtusely incised or not incised laterally below eye; profemur intercalary row more or less well-delimited and with several to many long fine setae; metafemur macrosetal formula usually 2+2+1; metatarsomere I longer than metatarsomeres II and III combined, usually not expanded apically; metatibia arcuate throughout its length in dorsal view 15

9. Aedeagus movably hinged between base and shaft; connective with anterior arms closely appressed; first valvula dorsal sculpturing maculose to granulose, submarginal; second valvula teeth obtusely triangular, serrate, uniformly shaped; Afrotropical, Australian, Oriental, Palearctic .... **Chiasmini** Distant, 1908 (part, *Listrophora* Boulard, 1971 and some *Chiasmus* Mulsant & Rey, 1855)

– Aedeagus not hinged; connective with anterior arms separate (Y-shaped); first valvula dorsal sculpturing pattern variable; second valvula teeth absent or shape variable if present 10

10. Ocelli on crown 11

– Ocelli on anterior margin of head or absent 12

11. Macropterous; crown encroaching onto eyes; frontoclypeus with median longitudinal carina; Palearctic .... **Eupelicini: Eupelicina** Sahlberg, 1871

– Brachypterous; crown not encroaching onto eyes; frontoclypeus and anteclypeus tumid, without longitudinal carina; Afrotropical (South Africa, Lesotho) .... **Eupelicini: Drakensbergenina** Linnavuori, 1979

12. Macropterous; forewing slender and acuminate, appendix reduced or absent; hindwing submarginal vein evanescent apically; valve fused to pygofer; male pygofer without basolateral cleft; style base connected or articulated with apical part only laterally; Afrotropical, Australian, Oriental, Palearctic .... **Eupelicini: Paradorydiina** Evans, 1936

– Brachypterous, or if macropterous, forewing appendix present and hindwing submarginal vein complete; valve articulated to pygofer; male pygofer with basolateral cleft; style base broadly fused with apical part 13

13. Forewing with veins A1 and A2 separate throughout their length; first valvula without well-delimited ventroapical sculptured area; second valvula with distinct teeth; Palearctic .... **Dorycephalini** Oman, 1943
– Forewing brachypterous (veins A1 and A2 absent) or if macropterous or submacropterous, veins A1 and A2 fused subapically; first valvula with well-delimited ventroapical sculptured area; second valvula without teeth 14

14. Aedeagus with terminal processes; first and second valvulae humpbacked dorsally; Nearctic ....**Hecalini** Distant, 1908 (part, *Attenuipyga* Oman, 1949, *Neoslossonia* Van Duzee, 1909)
– Aedeagus without terminal processes; first and second valvulae not humpbacked dorsally; Neotropical (Argentina) .....**Faltalini** Zahniser & Dietrich, 2010 (part, *Dietrichana* Zahniser, 2021)

15. Aedeagus bifurcate, with two gonopores 16
– Aedeagus not bifurcate, with single gonopore 19

16. Subgenital plates fused throughout their length; Oriental ....**Vartini: Vartina** Zahniser & Dietrich, 2013 (part, *Lampridius*)
– Subgenital plates fused only at base or not at all fused 17

17. Subgenital plates fused at base and with distinct lateral lobate appendages; Oriental ....**Vartini: Bambusanina** subtribe nov. (part, *Alishania*)
– Subgenital plates not fused at base and without lateral lobate appendages 18

18. Connective fused to aedeagus; Oriental .... **Mukariini** Distant, 1908 (part, some *Mukaria*)
– Connective articulated with aedeagus; Cosmopolitan ....**Opsiini** Emeljanov, 1962

19. Robust and squat, dorsally rounded, ventrally flattened leafhoppers; ocelli on crown (rarely on anterior margin or crown not delimited) and distant from eyes; frontoclypeus sometimes inflated anteriorly, texture glabrous or finely shagreen; antennal ledge strong, forming distinct ledge, sometimes continuous with anterior margin of head; protibia dorsal side flat, margins carinate; forewing appendix large, extending around wing apex; Cosmopolitan ....**Penthimiini** Kirschbaum, 1868
– Without the above combination of characters 20

20. Small ovoid or elongated, ventrally flattened leafhoppers; head slightly to strongly produced; face flattened or frontoclypeus inflated medially or anteriorly, horizontal in lateral view; ocelli on anterior margin of head or just above margin, often distant from eye; antennal bases near anterodorsal (upper) corners of eyes; profemur row AV setae absent; outer anteapical cell often confluent with or nearly touching costal vein; inner apical cell often stalked at base; Oriental, feeding on bamboo .... **Mukariini** Distant, 1908 (part)
– Without above combination of characters 21

21. Apodemes of male abdominal sternite II long, slender, directed posterolaterally, capitate or flared apically; male pygofer usually with sclerotized medial lobe articulated to atrium of aedeagus; associated with bamboo 22
– Apodemes of male abdominal sternite II not well developed, or if so, then not long, slender, directed posterolaterally, and capitate or flared apically; male pygofer without sclerotized medial lobe articulated to atrium of aedeagus; usually not associated with bamboo 23

22. Medium to large greenish or bluish leafhoppers with red or orange longitudinal stripes or spots; crown produced, pointed; gena not incised laterally below eye, visible behind the eye in dorsal view; frontoclypeus elongate; lorum distant from genal margin; profemur intercalary row setae thick and extending to or basad of middle of profemur; forewing macropterous, truncate apically; connective with anterior arms closely appressed; male segment X tube-like, extended well posterad of pygofer, often well-sclerotized; Afrotropical, Oriental .... **Vartini: Vartina** Zahniser & Dietrich, 2013
– Small to medium-sized black or brownish to ochraceous leafhoppers without bright red or orange maculae; texture of dorsum, including pronotum, mesonotum, forewings and head often punctate; anterior margin of head sometimes carinate; forewing sometimes with extra crossveins, particularly in clavus; Oriental .... **Vartini: Punctulina** Dai, Zahniser, Viraktamath & Webb, 2017

23. Small to large deltocephalines usually brownish with symmetrical markings that may include paired spots, stripes and/or larger maculae; head usually produced, often strongly so, width subequal to or less than that of pronotum; gena usually not or only weakly incised below eye (except *Perugrampta*-group), often extended onto dorsum of head and visible behind eye; anteclypeus strongly expanded distally (except *Perugramptella*); forewing usually with reflexed costal veins, often numerous, crossvein m-cu2 absent, appendix well developed sometimes extended around wing apex; connective Y-shaped with arms widely separated, stem often short or absent; Nearctic, Neotropical .... **Scaphytopiini** Oman, 1943
– Without the above combination of characters 24

24. Crown and face strongly rugose; body length greater than 7 mm; Neotropical .... **Arrugadini** Linnavuori, 1965
– Crown and face shagreen, glabrous, or striate, not rugose, or if rugose then body less than 7 mm in length 25

25. Connective Y-shaped and fused to aedeagus; male pygofer with one or more pairs of teeth, spines, or processes; pygofer side excavated medially, scoop-like; male segment X long, sclerotized laterally, sometimes sclerotized ventrally and/or dorsally; second valvulae with a median dorsal tooth; Nearctic (western North America) .... **Athysanini: Cochlorhinina** Oman, 1943
– Connective shape variable, but not Y-shaped and fused to aedeagus; male pygofer with or without processes; pygofer side variable, usually not distinctly excavated; male segment X variable; second valvulae usually without dorsal tooth on shaft 26

26. Metatarsomere I with platellae on plantar surface; ocelli distant from eyes, at least 4 × own diameter from adjacent eye; anteclypeus slender, elongate, tapered, produced apically and extended well beyond lower margin of gena 27
– Metatarsomere I without platellae on plantar surface; ocelli usually close to eyes (exceptions: some Chiasmini and Faltalini); anteclypeus truncate with apex not or only slightly produced beyond lower margin of gena 29

27. Head not produced anteriorly; crown rounded to face or anterior margin of head carinate, not foliaceous; Oriental, Nearctic, Palearctic (*Grypotes puncticollis* introduced to northeastern North America) ....**Athysanini: Koebeliina** Baker, 1897 (part, *Grypotes* Fieber, 1866 group)
– Head strongly produced, foliaceous anteriorly 28

28. Ocelli on face; antennae shorter than head width; forewing veins pustulate, appendix absent; Nearctic (western North America) ....**Athysanini: Koebeliina** Baker, 1897 (part, *Koebelia* Baker, 1897)
– Ocelli on crown; antennae longer than head width; forewing veins not pustulate, appendix present; Australian (Western Australia) .... **Occinirvanini** Evans, 1966

29. Anteclypeus parallel-sided or tapering toward apex; connective with distinct stem, with anterior arms closely appressed or sometimes separate anteriorly, articulated with aedeagus; aedeagus often hinged at base; ovipositor usually protruding far beyond pygofer apex; first valvula with dorsal sculpturing maculose to granulose, with distinct unsculptured band on dorsal margin, without distinct ventroapical sculptured area; second valvula with obtusely triangular and serrated teeth; Cosmopolitan .... **Chiasmini** Distant, 1908 (part)
– Without the above combination of characters 30

30. Crown narrow, width between eyes less than or equal to median width of eye; crown completely shagreen to base; anteclypeus usually extending beyond normal curve of gena; pronotum lateral margin without carina; male pygofer declivous, directed posteroventrally, with few macrosetae, basolateral cleft absent or not membranous; Cosmopolitan ....
....**Eupelicini: Stenometopiina** Baker, 1923
– Without the above combination of characters 31

31. Dorsoventrally depressed or flattened leafhoppers; head strongly or sometimes weakly produced, median length usually at least 2 × length next to eye; crown broad, more or less parabolically shaped; crown to face transition acutely angled; anterior margin sometimes foliaceous; face lying slightly obliquely to horizontal plane; lateral margin of pronotum long, nearly as long or longer than least width of eye; first valvula dorsal sculpturing maculose to granulose, distinctly submarginal, with unsculptured band on dorsal margin (except *Glossocratus* Fieber, 1866); second valvula without dorsal teeth (except *Glossocratus*) 32
– Not dorsoventrally depressed or flattened; head not strongly produced; crown broad or not, rarely parabolically shaped; crown to face transition less acute; face usually lying in a more upright plane; lateral margin of pronotum usually shorter than least width of eye; first valvula dorsal sculpturing variable; second valvula with dorsal teeth 33

32. Ocelli close to eyes, closer to eyes than lateral frontal sutures; male apodemes of abdominal sternite I long, narrow, as long as apodemes of sternite II; male apodemes of abdominal sternite II large, spatulate; first and second valvulae humpbacked dorsally (except *Glossocratus*); second valvula concave ventrally (except *Glossocratus*); Cosmopolitan ....**Hecalini** Distant, 1908 (part)
– Ocelli relatively distant from eyes, usually 3–4 × their diameter from eye or more (except some *Faltala* Oman, 1938 and *Bonamus* Oman, 1938), sometimes absent or obscure; male apodemes of abdominal sternite I and II short or undeveloped; first and second valvulae not strongly humpbacked dorsally; second valvula not concave ventrally; Nearctic, Neotropical ....
....**Faltalini** Zahniser & Dietrich, 2010 (part)

33. Anteclypeus parallel-sided or tapering apically; lorum relatively small, well-separated from genal margin; connective with anterior arms closely appressed anteriorly, linear, triangular, or racket-shaped 34
– Anteclypeus shape variable, but often widening toward apex; lorum usually relatively larger; connective with anterior arms usually well-separated, Y- or U-shaped 37

34. Connective fused to aedeagus 35
– Connective usually articulated with aedeagus (exceptions: *Cabrulus*; some *Flexamia* spp.) 36

35. Body elongate, somewhat depressed; anterior margin of head with transverse carinae; first valvula dorsal sculpturing pattern maculose to granulose and distinctly submarginal, with distinctly delimited ventroapical sculptured area; second valvula without dorsal teeth; ovipositor protruding far beyond pygofer apex; Nearctic (Mexico), Neotropical ....
....**Faltalini** Zahniser & Dietrich, 2010 (part, *Tenucephalus* DeLong, 1944)

– Body not elongate or depressed; crown rounded to face, anterior margin shagreen; first valvula sculpturing pattern imbricate, scale-like, and reaching dorsal margin, without distinct apicoventral sculptured area; second valvula with irregular teeth; ovipositor not protruding far beyond pygofer; Cosmopolitan ....**Deltocephalini** Fieber, 1869

36. Subgenital plates fused with valve, apex of plate with sharply pointed process; connective articulated posteriorly with a pair of long processes; female sternite VII ovate, sometimes elongate; Afrotropical, Palearctic .... **Tetartostylini** Wagner, 1951

– Subgenital plates articulated with valve, apices usually not produced into sharply pointed processes; processes of connective present or absent; female sternite VII not ovate or elongate; Cosmopolitan .... **Paralimnini** Distant, 1908

37. Macropterous, forewing with 2 anteapical cells; usually small, slender leafhoppers; male segment X not sclerotized; Cosmopolitan ....**Macrostelini** Kirkaldy, 1906

– Macropterous to brachypterous, if macropterous then usually with 3 anteapical cells; if with 2 anteapical cells, then larger, more robust leafhoppers and male segment X usually sclerotized at least laterally or ventrally 38

38. Small to medium sized, slender, elongate leafhoppers; usually yellow, ochraceous, or pale green, often with paired black or brown markings or spots on head; subgenital plate often with row of macrosetae distant from lateral margin, with numerous long fine setae laterally; male pygofer incised dorsally nearly to base, often with differentiated dorsal and ventral lobes each of which may be produced into conical, triangular, or spine-like process; male segment X elongate and sclerotized dorsally; Nearctic, Neotropical, Palearctic ....**Cicadulini** Van Duzee, 1892

– Size and color variable; subgenital plate macrosetae variable, with or without long fine setae; male pygofer dorsal incision variable; male segment X usually not elongate and strongly sclerotized 39

39. Body usually broad and robust; forewings usually shortened, brachypterous to submacropterous; hindwings usually narrowed antero-posteriorly when outstretched or otherwise reduced in size; connective U- or sometimes Y- shaped with stem very short or absent; male segment X broad and sclerotized; ovipositor usually distinctly protruding beyond pygofer apex; Afrotropical (South Africa) .... **Selenocephalini: Bonaspeiina** Zahniser & Dietrich, 2013

– Body shape variable; forewings usually macropterous; hindwings not narrowed anteriorly-posteriorly when outstretched; connective variable; male segment X variable; ovipositor usually not protruding far beyond pygofer apex 40

40. Small to medium sized leafhoppers, usually with symmetrical dark markings; head distinctly wider than pronotum; anteclypeus parallel-sided or tapered apically; phragma sclerotized dorsad of aedeagal atrium, membranously connected to segment X, forming a dorsal connective; male pygofer dorsal margin thickened, declivous, and often ending in ventrally directed curved hook or spine; Australian, Nearctic, Oriental, Palearctic ....**Limotettigini** Baker, 1915

– Without the above combination of characters 41

41. Large, yellow to greenish species; forewing veins greenish; forewing venation highly reticulated apically; forewing resting orientation tectiform, appendix reduced; style apex footlike; Afrotropical (South Africa) ....**Selenocephalini: Hypacostemmina** Linnavuori & Al-Ne'amy, 1983

– Without the above combination of characters 42

42. Medium-sized robust leafhoppers with symmetrical markings consisting of spots, stripes, bands or large unicolorous areas, often with ivory, orange, brown, and/or black coloration; head usually wider

than pronotum; crown usually with transverse preapical groove; crown-face transition often with one or more transverse carinae; clypellus widening toward apex or sometimes inflated and tapered toward apex; forewing usually with reflexed costal veins; Nearctic, Neotropical .... **Bahitini** Zahniser & Dietrich, 2013
– Without the above combination of characters 43

43. Medium sized to large and robust; usually ivory to brown or dark brown; head distinctly narrower than pronotum; antennal ledges carinate; lorum long, relatively large; anteclypeus long, widening apically; pronotum lateral margin long, longer than half basal width of eye; forewing often with brown irrorate markings; profemur row AM sometimes with one or more thick setae basad of AM1; nymph with pygofer short, with 6 rows of abdominal macrosetae; Afrotropical, Nearctic, Oriental, Palearctic .... **Scaphoideini: Phlepsiina** Zahniser & Dietrich, 2013
– Without the above combination of characters 44

44. Anterior margin of head with two or more distinct transverse carinae 45
– Crown to face transition rounded, angulate, or foliaceous, but anterior margin of head usually without transverse carinae (rarely with single carina present) 46

45. Antennae long; antennal bases situated near upper corners of eyes; antennal pits often large, encroaching onto frontoclypeus; profemur row AM without any additional thick setae basad of AM1; male pygofer usually with numerous macrosetae; subgenital plates usually without thick setae, usually with only fine, hairlike setae; Afrotropical, Australian, Oriental, Palearctic .... **Scaphoideini: Drabescina** Ishihara, 1953
– Antennae short; antennal bases situated near middle of eyes; antennal pits not large, not encroaching onto frontoclypeus; profemur row AM often with one or more thick setae basad of AM1; male pygofer usually without or with reduced number of macrosetae; subgenital plates usually with thick, often relatively short, setae laterally; Afrotropical, Oriental, Palearctic .... **Selenocephalini: Selenocephalina** Fieber, 1872

46. *With some combination of the following characters: head narrower than pronotum, produced anteriorly; frontoclypeus long, narrow; antennae long, longer than width of head; body slender; head and wings often with brown, orange, ochraceous, or ivory markings; forewing with one or more darkly pigmented reflexed costal veins; profemur row AV setae absent or reduced (not stout); metatibia row PD macrosetae long, as long as or longer than 0.5 × length of protibia; male or female pygofer with dense tufts of long fine or regular setae; subgenital plate apex sometimes membranous or long, digitate, somewhat membranous or weakly sclerotized; subgenital plates with numerous long fine setae laterally; basal processes of aedeagus or connective often present, connected or articulated to base of aedeagus or apex of connective stem; Cosmopolitan .... **Scaphoideini: Scaphoideina** Oman, 1943 + genera unplaced to subtribe
– Without some combination of the above characters 47

*This group is difficult to define morphologically due to its size and morphological diversity. The most common and distinctive characters that are usually present are the head narrower than the pronotum, the long antennae, and the long metatibia row PD setae. If two or more of these characters and one or more of the additional stated characters are present, it likely belongs to this group.

47. Moderately large relatively robust leafhoppers; ground color usually tan, head with crown rounded to face, frontoclypeus relatively broad; anteclypeus usually parallel-margined or tapering toward apex; first valvula with dorsal sculpturing areolate or granulose with elements of sculpture not organized into distinct rows; second valvulae usually with one or two dorsal teeth on basal fused section; Nearctic, Palearctic ....**Athysanini: Athysanina** Van Duzee, 1892
– Without the above combination of characters 48

48. Medium sized to large ochraceous, yellowish, greenish, or brownish leafhoppers, sometimes with irregular brown irrorate markings or ramose pigment lines; crown usually relatively short and broad, convex, wider than pronotum, width between eyes distinctly greater than eye width, anterior margin usually rounded to face, texture often entirely shagreen; anteclypeus parallel-sided or broadened distally; forewing costal margin without extra crossveins basad of Rs fork; nymph with head produced more strongly than in adult, with medial longitudinal carina on upper part of face, pygofer lobes attenuate and parallel to each other; Nearctic, Neotropical .... **Pendarini** Dmitriev, 2009
– Without the above combination of characters 49

49. Color stramineous to brown, with extensive dark brown markings dorsally (rarely green without dark markings), forewing veins usually pale, bordered with brown; head with crown anterior margin broadly rounded to angulately produced, rounded to face, without transverse carinae, crown between eyes less than 1.5 × eye width; forewing macropterous, often with supernumerary crossveins, without reflexed costal veins basad of Rs origin; male abdomen with 2s apodemes enlarged, usually parallel, not divergent or capitate; male pygofer with one or more sclerotized ventral processes arising preapically, often extended mesad but not articulated with aedeagal atrium; subgenital plate much shorter than pygofer, lateral margins convex, usually with macrosetae scattered or in irregular sublateral rows; style with apex usually enlarged and often modified with teeth or branches; membrane laterad of aedeagal atrium with basal or distal branches; Oriental, associated with bamboo .... **Vartini: Bambusanina** subtribe nov.
– Coloration various but often with bold symmetrical contrasting dark and pale markings dorsally, crown often with paired black spots on anterior margin and forewing usually with numerous round white translucent spots; crown usually depressed; anterior margin of head usually well-defined and crimped, forming distinct angle with face in profile, slightly to strongly produced and angulate in dorsal view, texture of posterior region glabrous or finely striate, not entirely shagreen; forewing costal margin usually with extra crossveins basad of Rs fork; Nearctic, Neotropical, Palearctic ......
.... **Platymetopiini** Haupt, 1929

Discussion

The classification changes made here are based on the largest and most well-supported phylogenetic estimate of Deltocephalinae to date (Cao *et al*. 2022) that included 730 terminal taxa and > 160 000 nucleotide positions. All tribes recognized here are monophyletic with respect to the taxon sampling of Cao *et al*. (2022) (Fig. 1). The classification recognizes 30 tribes and 24 subtribes, 16 of which are non-nominotypical subtribes. Several large lineages were resolved in those analyses that are recognized as tribes here (including Pendarini, Platymetopiini, Scaphoideini, Selenocephalini, and Vartini). Each of these tribes comprise a substantial amount of morphological diversity and they are therefore difficult to define based on individual unique and universally shared morphological characters. This is also true for some other large, well-established monophyletic tribes of Deltocephalinae (e.g., Chiasmini, Deltocephalini, Macrostelini, Opsiini; see discussion in Zahniser & Dietrich 2013). However, these groups are recognizable through combinations of characters that are relatively stable at higher levels. We conclude that the strongly supported results of the phylogenomic analyses, in combination with morphological observations and justification, necessitate the classification changes made here. Further, more detailed analyses of individual lineages including more taxa and exploration of more morphological characters will be needed to refine the classification in the future.

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Supplementary files

Supp. file 1. Classification of the tribes, subtribes, and genera of Deltocephalinae Fieber, 1869. https://doi.org/10.5852/ejt.2026.1035.3171.14099

Supp. file 2. The consensus maximum likelihood tree of Deltocephalinae Fieber, 1869 from Fig. 1, expanded and with labeled tips. https://doi.org/10.5852/ejt.2026.1035.3171.14101