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An updated classification of the jumping plant-lice (Hemiptera: Psylloidea) integrating molecular and morphological evidence

Daniel BURCKHARDT [1,*], David OUVRARD [2] & Diana M. PERCY [3]

[1] Naturhistorisches Museum, Augustinergasse 2, 4001 Basel, Switzerland.
[2] ANSES, Plant Health Laboratory, Entomology and invasive plants unit, 755 avenue du campus Agropolis, CS 30016, 34988 Montferrier-sur-Lez Cedex, France.
[3] Department of Botany, University of British Columbia, 6270 University Boulevard, Vancouver V6T 1Z4, Canada.

[*] Corresponding author: daniel.burckhardt@bs.ch
[2] Email: david.ouvrard@anses.fr
[3] Email: diana.percy@ubc.ca

[1] urn:lsid:zoobank.org:author:2FA5C7E5-D28E-4220-9796-02717E892B1D
[2] urn:lsid:zoobank.org:author:2748132A-5D53-4BBA-9E33-F2723DCAAF19
[3] urn:lsid:zoobank.org:author:84F3C908-9927-40A6-BBBF-6951B7736278

Abstract. The classification of the superfamily Psylloidea is revised to incorporate findings from recent molecular studies, and to integrate a reassessment of monophyla primarily based on molecular data with morphological evidence and previous classifications. We incorporate a reinterpretation of relevant morphology in the light of the molecular findings and discuss conflicts with respect to different data sources and sampling strategies. Seven families are recognised of which four (Calophyidae, Carsidaridae, Mastigimatidae and Triozidae) are strongly supported, and three (Aphalaridae, Liviidae and Psyllidae) weakly or moderately supported. Although the revised classification is mostly similar to those recognised by recent authors, there are some notable differences, such as *Diaphorina* and *Katacephala* which are transferred from Liviidae to Psyllidae. Five new subfamilies and one new genus are described, and one secondary homonym is replaced by a new species name. A new or revised status is proposed for one family, four subfamilies, four tribes, seven subtribes and five genera. One tribe and eight genera / subgenera are synonymised, and 32 new and six revised species combinations are proposed. All recognised genera of Psylloidea (extant and fossil) are assigned to family level taxa, except for one which is considered a nomen dubium.

Keywords. Sternorrhyncha, systematics, new taxa, new combinations, nomenclature.

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Introduction

Jumping plant-lice or psyllids constitute the superfamily Psylloidea Latreille, 1807 of the hemipterous Sternorrhyncha Duméril, 1806 with world-wide about 4000 described and at least as many undescribed species (Burckhardt & Queiroz 2020). As with related aphids, scale insects and whiteflies, psyllids feed exclusively on plant sap but, unlike these, are generally highly specialised with respect to the plant taxa on which they develop (Hollis 2004; Ouvrard 2020). Host plants belong mostly to the eudicots (e.g., Fabaceae Juss., Myrtaceae Juss. and Sapindales Juss. ex Bercht. & J.Presl) and, to a lesser extent, to the Magnoliales Bromhead; only a few species are associated with monocots and conifers (Ouvrard *et al*. 2015). Psyllids occur in all biogeographical regions of the world except for Antarctica. Their greatest diversity is in the tropics and south temperate regions (Hollis 2004). The Afrotropical and Neotropical biogeographical realms are probably particularly species-rich but also constitute the least known faunas (Burckhardt & Queiroz 2020).

Classifications are efficient tools for organising and communicating biodiversity data especially when they are composed of rigorously tested monophyletic taxa. For a long time, psyllid classifications were dominated by studies of the adult morphology of north temperate taxa lacking well-defined analytical methods which resulted in highly artificial classifications (e.g., Bekker-Migdisova 1973). Several revisions of tropical and south temperate taxa and the study of immatures using phenetic and cladistic methodology culminated in the seminal paper of White & Hodkinson (1985) who proposed a classification comprising eight families. This paper also summarises the history of psyllid systematics. White & Hodkinson's (1985) paper triggered a series of mostly morphological studies testing their groupings. The results of these revisions were summarised in the revised classification by Burckhardt & Ouvrard (2012).

Recently, the results of comprehensive molecular phylogenetic analyses of Psylloidea were published (Percy *et al*. 2018) based on around 400 of the 4000 described species. A subsequent study comprising 56 species focused on east Palaearctic/Oriental taxa (Cho *et al*. 2019). While these analyses confirmed many of the previously recognised taxa (at family, subfamily or genus level), there are some notable differences with respect to the most recent classification by Burckhardt & Ouvrard (2012), and in some instances the molecular data resolved taxa which were previously recognised as polyphyletic.

Here, we present a revised classification addressing the family group levels. We assign all genus group names to the appropriate family, subfamily, tribe or subtribe. We also redefine a few genera in cases where this helps to understand the family level classification and reflect systematic information supported by the molecular data.

Material and methods

The scope of the classification proposed here follows that by Burckhardt & Ouvrard (2012), i.e., it includes all published family and genus-group names of extant and fossil taxa of true Psylloidea (Ouvrard *et al.* 2010). The mesozoic family Liadopsyllidae Martynov, 1926, which is considered the stem-group (Burckhardt & Poinar 2019) or sister-group (Drohojowska *et al*. 2020) of true Psylloidea, is not considered here.

The genera are organised alphabetically according to family and, where present, subfamily and tribe. No attempt is made to list all citations and ranks of family-group names published in the literature. Moreover, misspellings are not listed systematically either. This information can be found in Psyl'list (Ouvrard 2020). Synonyms, including new ones, of family-group names are listed under the respective valid name. For each valid family, subfamily or tribe, differences to the concept of Burckhardt & Ouvrard (2012) are discussed and new taxa are diagnosed with a formal description to satisfy the provisions of International Commission on Zoological Nomenclature (1999, 2012; thereafter ICZN 1999/2012). All valid genus-group names are listed with author and year. Synonyms, including new ones, are listed in parentheses after the valid genus name without authors or dates. More information is available on the

Psyl'list website (Ouvrard 2020). The data of specimen illustrated on Figs 2–3, 5–8 is provided in the Suppl. file 1.

This revised classification reflects, as well as possible, the phylogenies presented by Percy *et al*. (2018) and Cho *et al*. (2019). The taxa (families, subfamilies, tribes, subtribes or genera) included in these molecular analyses are marked with an asterisk. Those taxa not included in the molecular analyses are attributed to higher taxa following Burckhardt & Ouvrard's (2012) classification or, if new morphological evidence is available, placed with diagnostic characters given. The phylogenies by Percy *et al*. (2018) and Cho *et al*. (2019) are largely congruent. Significant differences between the two studies are discussed under the relevant taxa. In a few cases with contradictory evidence between analyses, we took an arbitrary decision, to choose the grouping that needed the least changes, i.e., the one that was closest to the classification of Burckhardt & Ouvrard (2012), or that was supported by the phylogenies by Percy *et al*. (2018) in favour of those by Cho *et al*. (2019) as the former was based on a more comprehensive sampling of taxa.

Representatives of almost all described psyllid genera and large amounts of undescribed material, including new genera, were examined mostly from the following institutions: Natural History Museum, London (BMNH); Naturhistorisches Museum, Basel (NHMB); Muséum d'histoire naturelle, Genève (MHNG); National Museum of Natural History, Washington, DC. Additional material was also examined from the Zoological Institute of the Russian Academy of Sciences, St. Petersburg; the Agricultural University, Beijing; the Australian National Insect Collection, Canberra; the New Zealand Arthropod Collection, Auckland; the Muséum national d'histoire naturelle, Paris; the Moravian Museum, Brno and the Museum für Naturkunde, Berlin.

Results

Taxonomy

Class Insecta Linnaeus, 1758
Order Hemiptera Linnaeus, 1758
Suborder Sternorrhyncha Duméril, 1806

Superfamily **Psylloidea** Latreille, 1807

Percy *et al*. (2018) presented two mitogenome (mtg) phylogenies that we refer to here as the AN tree ('all-nucleotide' tree) and the CC tree ('conserved-codon' tree), as well as a much reduced taxon sampling using a nuclear genome analysis, and a combined mitochondrial and nuclear data analysis. Due to the greater taxon sampling for the mitogenome analyses, we refer mostly to these results here. The results of Cho *et al*. (2019) are similar to the AN tree. In the main, analyses in Percy *et al*. (2018) and Cho *et al.* (2019) had considerable congruence, with notable exceptions discussed below. Both mtg trees are similar and recover the same crown groups. The major difference lies in the basal groupings. The Aphalaridae Löw, 1879, as defined here, is a paraphyletic basal assemblage in the AN tree (also paraphyletic in Cho *et al*. 2019) and a poorly supported monophylum in the CC tree. Carsidaridae Crawford, 1911 (including *Pachypsylla*) and Homotomidae Heslop-Harrison, 1958 form a poorly supported sister group in the AN tree and a paraphyletic, basal assemblage in the CC tree. The former hypothesis (i.e., sister family relationship between Carsidaridae (without Pachypsyllinae Crawford, 1914) and Homotomidae) is supported by two putative morphological synapomorphies (Hollis & Broomfield 1989) and is recovered with stronger support in the nuclear genome data in Percy *et al*. (2018) as well as combined data in Cho *et al*. (2019). In both mtg trees, the Mastigimatinae Bekker-Migdisova, 1973 constitutes the sister group to a well supported (94%) clade comprising the Liviidae Löw, 1879, as defined here, and the PTCD clade (Psyllidae, Triozidae Löw, 1879, Calophyinae Vondráček, 1957 sensu Burckhardt &

Ouvrard (2012), *Diaphorina* Löw,1880 and *Katacephala* Crawford, 1914). This grouping differs from that of Burckhardt & Ouvrard (2012) who included Mastigimatinae in their artificial Calophyidae. For this reason, Mastigimatinae is removed from Calophyidae and given family rank here. This move is supported by Cho *et al*. (2019) although the phylogenetic placement of Mastigimatinae is not identical. The Liviidae, as defined here, is a poorly supported monophylum in the AN tree and paraphyletic in the CC tree. It is also recovered as paraphyletic in combined data analyses in both Percy *et al.* (2018) and Cho *et al*. (2019). In both mtg trees, the PTCD clade is very strongly supported (100%) (consistent with Cho *et al*. 2019), and Calophyidae Vondráček, 1957 (without Mastigimatinae) constitutes the sister taxon of the remainder of taxa in the PTCD clade with good (AN tree) or poor support (CC tree); notably, an alternative placement of Calophyidae as sister to Triozidae (albeit with mixed support) in combined data analyses in both Percy *et al*. (2018) and Cho *et al*. (2019) serves to emphasise that phylogenetic placement within the PTCD clade awaits robust confirmation. The support of the monophyly of Psyllidae (including *Diaphorina* and *Katacephala*) is good (AN tree) or poor (CC tree) and that of Triozidae very strong in both trees (99%). Again, due to ambiguity in the placement of *Diaphorina* in the combined data analysis in Percy *et al*. (2018), additional analyses will be required for robust confirmation. In summary, not all taxonomic groups recognized here are strongly supported as monophyla in all or any of the molecular analyses, in some cases we have erred on the side of providing a practical and stable classification, particularly where ambiguity in molecular analyses remains. A summary of family interrelationships adopted here is shown in Fig. 1.

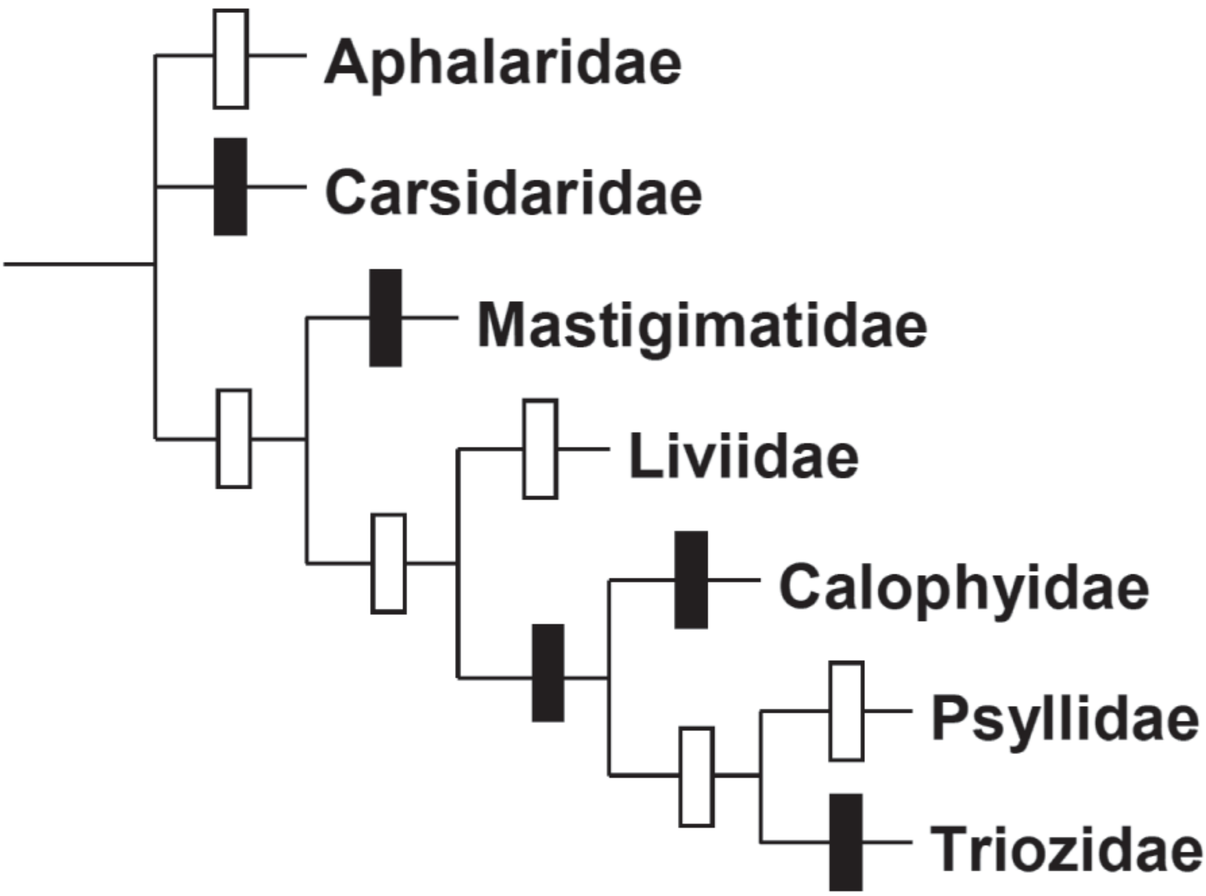

Fig. 1. Cladogram representation of the classification of Psylloidea Latreille, 1807 adopted here, node symbols indicate families with poor to moderate support (white), or strong support (black) in molecular analyses (Percy *et al*. 2018).

Family ***Aphalaridae** Löw, 1879

Comments

In both mtg trees, Aphalaridae contains six strongly supported monophyla which we rank as subfamilies: Aphalarinae, Microphyllurinae subfam. nov., Phacopteroninae Heslop-Harrison, 1958 stat. nov., Rhinocolinae Vondráček, 1957, Spondyliaspidinae Schwarz, 1898 and a clade of seven undescribed species from New Caledonia representing an unnamed genus and subfamily. This last subfamily is not further treated here and will be described in another paper (Percy, unpublished). There is evidence (from multiple molecular analyses) that these six subfamilies are likely not collectively monophyletic, however, there is still insufficient data to clarify the phylogenetic placement of each monophyletic subfamily with respect to the others, and therefore, rather than recognize each as a separate family, we have retained them as subfamilies within Aphalaridae "sensu lato" pending further analyses. In Aphalaridae, we also place Togepsyllinae Bekker-Migdisova, 1973 and Cecidopsyllinae Li, 2011 stat. nov. which were not included in the molecular analyses by Percy *et al*. (2018) but representatives were analysed by Cho *et al*. (2019). A morphological character shared by all constituent subfamilies, and putative synapomorphy for the family, is the tarsal arolium of the immatures which is either completely absent or forms a lobe lacking an unguitractor (Burckhardt & Ouvrard 2012).

Apart from strong support of the sister group relationship of Microphyllurinae subfam. nov. (as "*Parapaurocephala*" in Percy *et al*. 2018) and Phacopteroninae stat. nov., there are no consistent and well-supported relationships between the subfamilies in the molecular analyses by Percy *et al*. (2018). A putative morphological synapomorphy grouping the Rhinocolinae, Spondyliaspidinae and Togepsyllinae is the tubercular or knob-like meracanthus rather than horn-shaped as in the other aphalarid subfamilies and most other Psylloidea. Luo *et al.* (2017) listed some putative synapomorphies suggesting a close relationship of Rhinocolinae and Togepsyllinae, a relationship which was also shown in Drohojowska's (2015) trees based on an analysis of the thorax morphology, and recovered in the molecular data set of Cho *et al*. (2019).

Aphalaridae, in the present definition, differs from that of Burckhardt & Ouvrard (2012) in the positions of Cecidopsyllinae, Microphyllurinae subfam. nov., Pachypsyllinae and Phacopteroninae. *Cecidopsylla* Kieffer, 1905, was assigned to Calophyidae (Mastigimatinae) and is transferred here to Aphalaridae (Cecidopsyllinae). *Microphyllurus* Li, 2002, the only member of Microphyllurinae subfam. nov., was treated as a junior synonym of *Peripsyllopsis* Enderlein, 1926 (Liviidae: Euphyllurinae: Diaphorinini) by Burckhardt & Ouvrard (2012), whereas the "'*Paurocephala*' *longicella* group", which we consider here a synonym of *Microphyllurus* (see below), was referred to Aphalaridae (Rhinocolinae). Pachypsyllinae was part of Aphalaridae and is transferred here to Carsidaridae. Phacopteroninae was considered a family of basal position within Psylloidea, and a basal position for Phacopteronidae as sister to the remaining Psylloidea was strongly supported in Cho *et al*. (2019); this is one of the notable differences with analyses in Percy *et al*. (2018). It may be that the different taxon sampling strategies were critical in determining these results, but here we have elected to adopt the placement using the more comprehensive taxon sampling in Percy *et al*. (2018).

Subfamily ***Aphalarinae** Löw, 1879

Comments

The Aphalarinae is strongly supported as a monophylum in molecular analyses (Percy *et al*. 2018; Cho *et al*. 2019), morphologically (Loginova 1964; Brown & Hodkinson 1988; Burckhardt & Queiroz 2013; Ouvrard *et al*. 2013) and by the pattern of sperm formation (Labina *et al*. 2014). The subfamily includes two monophyletic tribes: the extant Aphalarini and the extinct Paleopsylloidini†.

Tribe ***Aphalarini** Löw, 1879

Caillardiini Loginova, 1964: 447.
Coelocarinae Li, 2011: 351.
Colposceniini Bekker-Migdisova, 1973: 109.
Eumetoecini Li, 2011: 356.
Gyropsyllini White & Hodkinson, 1985: 270.
Stigmaphalarini Vondráček, 1957: 140, nomen nudum, no included genera, recognised by Loginova (1974).
Xenaphalarini Loginova, 1964: 447.

Comments

Aphalarini comprises the extant members of the subfamily and is probably monophyletic. It has been diagnosed by Loginova (1964), Brown & Hodkinson (1988) and Burckhardt & Queiroz (2013). The phylogenetic relationships between the 16 recognised genera were analysed by Burckhardt & Queiroz (2013). In the molecular analyses of Percy *et al*. (2018) six of the genera were included. The molecular analyses share with the morphological tree by Burckhardt & Queiroz (2013) the basal position of *Colposcenia* and the sister group relationship of *Aphalara* and *Craspedolepta* (the latter was recovered also by Cho *et al*. 2019).

Included genera

**Aphalara* Foerster, 1848 (syn. *Pseudaphorma*, *Rumicita*); *Brachystetha* Loginova, 1964; *Caillardia* de Bergevin, 1931; **Colposcenia* Enderlein, 1929 (syn. *Phanerostigma*, *Stigmaphalara*); **Craspedolepta* Enderlein, 1921 (syn. *Anomocera*, *Cerna*, *Loginovia*, *Magnaphalara*, *Neocraspedolepta*, *Paracraspedolepta*, *Tetrafollicula*, *Xanioptera*); *Crastina* Loginova, 1964 (syn. *Eustigmatia*); *Epheloscyta* Loginova, 1976; *Eumetoecus* Loginova, 1961; *Eurotica* Loginova, 1962; *Gyropsylla* Brèthes, 1921 (syn. *Metaphalara*, *Coelocara* sensu Li nec Tuthill); *Hodkinsonia* Burckhardt *et al*., 2004 (replacement name for *Burckhardtia* Brown & Hodkinson nec Frech); **Lanthanaphalara* Tuthill, 1959; **Limataphalara* Hodkinson, 1992; **Neaphalara* Brown & Hodkinson, 1988; *Rhodochlanis* Loginova, 1964 (syn. *Rhombaphalara*); *Xenaphalara* Loginova, 1961.

Tribe **Paleopsylloidini**† Bekker-Migdisova, 1985

Palaeoaphalarinae† Klimaszewski in Klimaszewski & Popov, 1993: 14.

Comments

The poorly defined Paleopsylloidini† comprises seven Eocene genera. Ouvrard *et al*. (2013) suggested that the tribe may be paraphyletic with respect to Aphalarini which includes only recent representatives.

In an overview of Hemiptera represented in the Insect Limestone (latest Eocene) of the Isle of Wight, UK, Szwedo *et al*. (2019) listed the tribes Aphalarini and Palaeoaphalarini†. They placed *Paleopsylloides*† Bekker-Migdisova, 1985, type genus of Palaeoaphalarini†, in the former tribe rather than in the latter, which is an obvious oversight.

Included genera

Carsidarina† Bekker-Migdisova, 1985 (syn. *Palaeoaphalara*†); *Catopsylla*† Scudder, 1890 (syn. *Psyllites*†); *Eogyropsylla*† Klimaszewski, 1993 (syn. *Parascenia*†); *Lapidopsylla*† Klimaszewski in Klimaszewski and Popov, 1993; *Necropsylla*† Scudder, 1890; *Paleopsylloides*† Bekker-Migdisova, 1985; *Proeurotica*† Bekker-Migdisova, 1985 (syn. *Plesioaphalara*†).

Subfamily **Cecidopsyllinae** Li, 2011 stat. rev. et nov.

Comments

The monotypic Cecidopsyllinae was diagnosed by Li (2011); for diagnoses of *Cecidopsylla* see also Burckhardt (1991b) and Yang *et al*. (2009). In the study of Cho *et al*. (2019), *Cecidopsylla* forms the sister taxon to all other psyllids, except for *Pseudophacopteron* (Phacopteroninae). For this reason, we transfer it to Aphalaridae and remove Cecidopsyllinae from synonymy with Mastigimatinae (Burckhardt & Ouvrard 2012). Within the Mastigimatinae as defined by Burckhardt *et al*. (2018b), *Cecidopsylla* resembles *Synpsylla* in the shape of the head, antennae and forewings but there are no detailed synapomorphies suggesting that the two are phylogenetically close. Awaiting new evidence, we leave the latter in the Mastigimatidae (see discussion there).

Included genus

Cecidopsylla Kieffer, 1905.

Subfamily ***Microphyllurinae** subfam. nov.
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Fig. 2

Type genus

Microphyllurus Li, 2002.

Diagnosis

Adult

Head with subtrapezoidal vertex smoothly passing into genae that lack processes. Frons triangular. Antenna about as long as head width. Clypeus flattened, triangular. Propleurites with subequal epimeron and episternum. Tibiae distinctly longer than femora; metacoxa with small pointed meracanthus and small membranous lobe on metatrochanteral cavity; metatibia without genual spine, bearing an open crown of 8–9 densely spaced, sclerotised, apical spurs; metabasitarsus with 2 spurs. Forewing weakly coriaceous, covered in surface spinules; costal break and pterostigma developed; veins R and M+Cu subequal, branches of vein M, and vein Cu_{1a} very long; anal break close to apex of vein Cu_{1b}. Hindwing with costal setae not grouped; vein R+M developed. Male proctiger one-segmented; in profile, with large posterior lobe in basal half. Female terminalia cuneate.

Description

Adult

Head, in profile, inclined at 45° from longitudinal body axis (Fig. 2A). Vertex subtrapezoidal, passing smoothly into genae which are not produced into processes; coronal suture fully developed (Fig. 2C); frons triangular with median ocellus situated at dorso-median edge (Fig. 2D). Antenna 10-segmented, filiform, about as long as head width. Clypeus flattened, triangular (Fig. 2D), not visible in profile. Rostrum very short, hardly exceeding procoxae. Thorax moderately arched dorsally; pronotum transversely ribbon-shaped, longer medially than laterally; mesopraescutum in longitudinal body axis shorter than mesoscutum which is strongly bulged; propleurites with subequal epimeron and episternum. Legs (Fig. 2B) moderately slender, tibiae distinctly longer than femora; metacoxa with small pointed meracanthus and small membranous lobe on metatrochanteral cavity (Fig. 2B: lobe); metatibia without genual spine, bearing an open crown of 8–9 densely spaced, sclerotised, apical spurs; metabasitarsus with 2 spurs (Fig. 2B). Forewing weakly coriaceous, membrane semitransparent, covered in surface spinules; costal break and pterostigma developed; veins R and M+Cu subequal, branches of vein M, and vein Cu_{1a} very long; anal break close to apex of vein Cu_{1b}. Hindwing slightly shorter than forewing, membranous; costal setae not grouped; vein R+M developed. Male proctiger one-segmented; in profile, with large posterior lobe in basal half. Male subgenital plate semiglobular. Paramere shorter than proctiger. Female terminalia cuneate. Circumanal ring oval.

Immature

Unknown.

Comments

In describing *Paurocephala longicella* Tuthill (1943a) noted that the forewing venation differs from other known species of *Paurocephala* Crawford, 1913. In a review of *Rhinocola* Foerster, 1848 and associated genera, Heslop-Harrison (1952) discussed *P. longicella* for which he erected '*Parapaurocephala*' but failed to provide a description. The name is, therefore, a nomen nudum and not available (ICZN 1999/2012: article 13.1.1). Burckhardt & Basset (2000) referred to the taxon as "'*Paurocephala*' *longicella* group". Based on a single male, Li (2002) described *Microphyllurus longicellus* Li, 2002, from Hainan (China). We have examined the holotype of *Microphyllurus longicellus* (DB, 31 Aug. 2009) and material identified as *Paurocephala longicella* from Fiji and Samoa (MHNG, 9 Jul. 2018). We conclude that the samples are congeneric but represent different species, one each in China, Fiji and Samoa, respectively, and suggest the following nomenclatorial acts:

Microphyllurus Li, 2002, stat. rev., removed from synonymy with *Peripsyllopsis*.
Microphyllurus longicellus (Tuthill, 1943) comb. nov. from *Paurocephala*.
Microphyllurus lii nom. nov. for *Microphyllurus longicellus* Li, 2002, nec Tuthill (1943a).

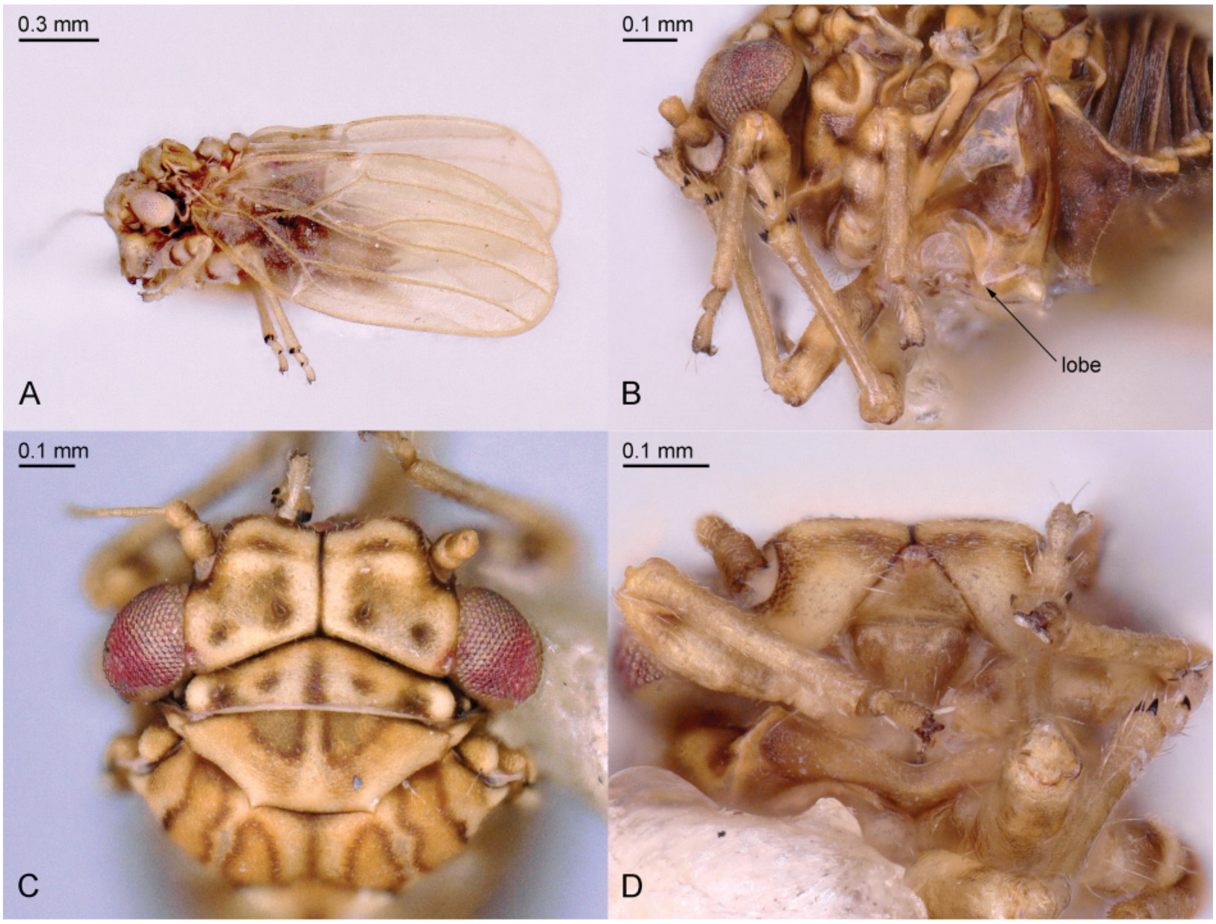

Fig. 2. Microphyllurinae subfam. nov.: *Microphyllurus* sp. **A**. Habitus, in profile view. **B**. Legs. **C**. Head, dorsal view. **D**. Head, ventral view.

Included genus

**Microphyllurus* Li, 2002 (syn. *Microphyllura*, misspelling, Li, 2011; *Parapaurocephala* Heslop-Harrison, nomen nudum; '*Paurocephala*' *longicella* group sensu Burckhardt & Basset, 2000).

Subfamily *****Phacopteroninae** Heslop-Harrison, 1958 stat. nov.

Phacoseminae Kieffer, 1906: 387 (the substitute name Phacopteronidae is maintained according to the ICZN 1999/2012, article 40.2).
Pseudophacopterini Bekker-Migdisova, 1973: 103.
Pseudophacopteroninae Li, 2011: 233.

Comments

The Phacopteroninae is strongly supported as a monophylum in both mtg trees and morphologically (Heslop-Harrison 1958; White & Hodkinson 1985). The subfamily corresponds to the concept of Burckhardt & Ouvrard (2012). The genera are poorly defined and their phylogenetic relationships are unknown.

Included genera

**Cornegenapsylla* Yang & Li, 1982 (syn. *Neophacopteron*); *Phacopteron* Buckton, 1896 (syn. *Phacosema*); *Phacosemoides* Costa Lima & Guitton, 1962; **Pseudophacopteron* Enderlein, 1921 (syn. *Chineura*); *Sulciana*† Klimaszewski, 1998.

Subfamily *****Rhinocolinae** Vondráček, 1957

Anomalopsyllinae Vondráček, 1963: 263.
Apsyllini Bekker-Migdisova, 1973: 107.

Comments

The Rhinocolinae is strongly supported as a monophylum in both mtg trees, morphologically (Burckhardt & Lauterer 1989; Burckhardt & Basset 2000; Burckhardt & Queiroz 2017) and, to a certain extent, by the pattern of sperm formation (Labina *et al.* 2014). It corresponds to the concept of Burckhardt & Ouvrard (2012). The phylogenetic relationships within the subfamily have been analysed by Burckhardt & Lauterer (1989), Burckhardt & Basset (2000), and Ouvrard *et al.* (2010).

Included genera

Agonoscena Enderlein, 1914; *Ameroscena* Burckhardt & Lauterer, 1989; *Anomalopsylla* Tuthill, 1952; **Apsylla* Crawford, 1912; *Cerationotum* Burckhardt & Lauterer, 1989; *Crucianus* Burckhardt & Lauterer, 1989; *Leurolophus* Tuthill, 1942; *Lisronia* Loginova, 1976 (syn. *Pseudotingidiforma* Heslop-Harrison, 1952 nomen nudum [no type designated] syn. nov., *Rhachistoneura*); *Megagonoscena* Burckhardt & Lauterer, 1989; *Moraniella* Loginova, 1972; *Notophyllura* Hodkinson, 1986; *Protoscena*† Klimaszewski, 1997; **Rhinocola* Foerster, 1848; *Rhusaphalara* Park & Lee, 1982 (syn. *Koreaphalara*); *Tainarys* Brèthes, 1920 (syn. *Vicinilura*†).

Subfamily *****Spondyliaspidinae** Schwarz, 1898

Livillinae Scott, 1882: 462, unavailable, stem genus not included.

Comments

The Spondyliaspidinae is strongly supported as a monophylum in both mtg trees, morphologically (Burckhardt 1991a) and by the pattern of sperm formation (Labina *et al*. 2014). The concept of the subfamily is the same as that by Burckhardt & Ouvrard (2012). In the mtg analyses there is a well-supported basal split between *Ctenarytaina* Ferris & Klyver, 1932 and the remainder of the subfamily (*Anoeconeossa* Taylor, 1987, *Australopsylla* Tuthill & Taylor, 1955, *Blastopsylla* Taylor, 1985, *Boreioglycaspis* Moore, 1964, *Cardiaspina* Crawford, 1911, *Creiis* Scott, 1882, *Cryptoneossa* Taylor, 1990, *Glycaspis* Taylor, 1960, *Lasiopsylla* Froggatt, 1900 and *Platyobria* Taylor, 1987).

Tribe *Ctenarytainini** White & Hodkinson, 1985, stat. rev., sensu novo

Comments

Burckhardt (1991a) suggested that the tribe Ctenarytainini sensu White & Hodkinson (1985) and Taylor (1990) is probably not monophyletic. The mtg analyses confirm this. Here we define the tribe in a new sense by the presence in the adult of a longitudinal comb of bristles on the mesotibia and a knob-like meracanthus, the latter character probably being a symplesiomorphy.

Included genera

**Ctenarytaina* Ferris & Klyver, 1932 (syn. *Bosellius*, *Eurhinocola*, *Euryopsylla*, *Loginoviana* Mathur nomen nudum, *Papiana*); *Syncarpiolyma* Froggatt, 1901.

Tribe ***Spondyliaspidini** Schwarz, 1898

Comments

The mtg analyses strongly support the monophyly of a group of ten genera which lack, in the adult, a longitudinal comb of bristles on the mesotibia and a proper meracanthus. The latter character probably constitutes a synapomorphy. Within the tribe there is a strong support for a clade embracing *Australopsylla*, *Cardiaspina*, *Creiis*, *Glycaspis* and *Lasiopsylla* and the sister group relationship of *Anoeconeossa* and *Cryptoneossa*. The sister group relationship of *Creiis* and *Lasiopsylla* (as currently defined) is only weakly supported with *Creiis* paraphyletic with respect to *Lasiopsylla*. The two genera differ morphologically only in the shape of the forewing. There are another 11 genera which are not included in the molecular analyses.

Included genera

Agelaeopsylla Taylor, 1990; **Anoeconeossa* Taylor, 1987; **Australopsylla* Tuthill & Taylor, 1955; **Blastopsylla* Taylor, 1985; *Blepharocosta* Taylor, 1992; **Boreioglycaspis* Moore, 1964; **Cardiaspina* Crawford, 1911 (replacement name for *Cardiaspis* Schwarz nec Amyot, nec Saunders, syn. *Pennapsylla* Froggatt nomen nudum); **Creiis* Scott, 1882; **Cryptoneossa* Taylor, 1990; *Dasypsylla* Froggatt, 1900 (syn. *Callistochermes*); *Eriopsylla* Froggatt, 1901; *Eucalyptolyma* Froggatt, 1901; **Glycaspis* Taylor, 1960; *Hyalinaspis* Taylor, 1960; *Kenmooreana* Taylor, 1984; **Lasiopsylla* Froggatt, 1900 (syn. *Uhleria*); *Leptospermonastes* Taylor, 1987; *Phellopsylla* Taylor, 1960 (replacement name for *Thea* Scott nec Mulsant); *Phyllolyma* Scott, 1882 (syn. *Cometopsylla*); **Platyobria* Taylor, 1987; *Spondyliaspis* Signoret, 1879 (syn. *Scenitopsylla*, *Spondytora*).

Subfamily **Togepsyllinae** Bekker-Migdisova, 1973

Hemipteripsyllinae Yang & Li, 1981: 186.

Comments

This small, probably monophyletic subfamily comprising two highly modified genera in South and East Asia as well as in the Neotropics (Brown & Hodkinson 1988; Hodkinson 1990; Luo *et al*. 2017) was not included in the molecular study of Percy *et al*. (2018). Its assignement to the Aphalaridae by Burckhardt & Ouvrard (2012) is supported by the molecular study of Cho *et al*. (2019).

Included genera

Syncoptozus Enderlein, 1918; *Togepsylla* Kuwayama, 1931 (syn. *Hemipteripsylla*, *Tingidiforma* Heslop-Harrison nomen nudum).

Family *__Calophyidae__ Vondráček, 1957

Comments

Burckhardt & Ouvrard (2012) admitted the artificial nature of their Calophyidae comprising five subfamilies. Two of these, Calophyinae and Mastigimatinae were included in the molecular analyses of Percy *et al*. (2018) and Cho *et al*. (2019), which both confirmed nonmonophyly of Calophyidae. The Mastigimatinae is removed here from Calophyidae and raised to family status. The other four subfamilies lack all metabasitarsal spurs. In addition, Atmetocraniinae Becker-Migdisova, 1973, Calophyinae and Metapsyllinae Kwon, 1983 bear an internal comb of apical metatibial spurs suggesting they may be closely related. Atmetocraniinae and Calophyinae share also the one-segmented asymmetric antennal flagellum in immatures (Burckhardt & Mifsud 2003; Burckhardt & Ouvrard 2012). With this, admittedly weak, evidence we keep the four subfamilies in the Calophyidae awaiting evidence to the contrary.

Subfamily **Atmetocraniinae** Becker-Migdisova, 1973

Comments

The subfamily was diagnosed by Burckhardt & Ouvrard (2012).

Included genus

Atmetocranium Tuthill, 1952.

Subfamily *__Calophyinae__ Vondráček, 1957

Microceropsyllini Bekker-Migdisova, 1973: 104.
Strogylocephalidae Li, 2011: 1257.

Comments

The subfamily was diagnosed by Burckhardt & Ouvrard (2012).

Included genera

**Calophya* Löw, 1879 (syn. *Calophya* (*Neocalophya*), *Holotrioza*, *Microceropsylla*, *Paracalophya*, *Pelmatobrachia*); *Pseudoglycaspis* Brown & Hodkinson, 1988; **Strogylocephala* Crawford, 1917 (syn. *Synaphalara*).

Subfamily **Metapsyllinae** Kwon, 1983

Comments

The subfamily was diagnosed by Burckhardt & Ouvrard (2012).

Included genus

Metapsylla Kuwayama, 1908.

Subfamily **Symphorosinae** Li, 2002

Comments

The subfamily was diagnosed by Li (2002). Burckhardt & Ouvrard (2012) pointed out the similarity of the male subgenital plate of *Symphorosus* and *Cecidopsylla* (classified here in Aphalaridae: Cecidopsyllinae) but did not list detailed synapomorphies between the two genera.

Included genus

Symphorosus Li, 2002.

Family ***Carsidaridae** Crawford, 1911, sensu novo

Comments

In both mtg trees the monophyly of Carsidaridae and *Pachypsylla* is strongly or very strongly supported. Carsidaridae+*Pachypsylla* (Pachypsyllinae) and Homotomidae form a poorly supported sister group in the AN tree and both families are included in an unresolved basal assemblage in the CC tree. In the molecular analyses by Cho *et al*. (2019), *Celtisaspis* (Pachypsyllinae) is recovered as weakly supported sister-group of Homotomidae, rather than Carsidaridae, and the monophyly of Carsidaridae, *Celtisaspis* and Homotomidae is well supported. Hollis & Broomfield (1989) listed two putative morphological synapomorphies to link Carsidaridae and Homotomidae: 1) the presence of a pair of large tubercles on the metapostnotum, and 2) all three ventral sense organs of the metafemur in a basal position. These characters are present also in Pachypsyllinae, though the tubercles on the metapostnotum are relatively small in *Celtisaspis*. Cho *et al*. (2019) mention the bipartite male proctiger as a putative synapomorphy of Homotomidae+Pachypsyllinae. As in Aphalaridae, the three taxa discussed here form, depending on the type of analysis, an unresolved basal (paraphyletic) assemblage or a monophylum with contradicting relationships between the constituent groups. For reasons of consistency, we include the three groups in the single family Carsidaridae. The concept of Carsidaridae by Burckhardt & Ouvrard (2012) is broadened here to include also Homotomidae and Pachypsyllinae which is transferred from Aphalaridae.

Subfamily ***Carsidarinae** Crawford, 1911

Prionocnemidae Scott, 1882: 466, invalid as not derived from an included genus name.
Tenaphalarini Heslop-Harrison, 1958: 577–578.
Mesohomotomini Bekker-Migdisova, 1973: 101.

Comments

In both mtg trees the monophyly of the subfamily is very strongly supported. Hollis (1987) provided a morphological diagnosis and analysed the intra-subfamily relationships. In the mtg analyses, with five of the eight recognised genera included, *Mesohomotoma* is in a moderately supported basal position, whereas in the morphological tree it is the sister taxon of *Paracarsidara*; and apart from a reasonably well supported clade comprising *Protyora*+*Tenaphalara*+*Paracarsidara*, the relationships between the other genera are only poorly supported.

Included genera

**Allocarsidara* Hollis, 1987; *Carsidara* Walker, 1869 (syn. *Eustigmia*, *Thysanogyna*); *Epicarsa* Crawford, 1911; **Mesohomotoma* Kuwayama, 1908 (syn. *Udamostigma*); **Paracarsidara* Heslop-Harrison, 1960; **Protyora* Kieffer, 1906 (syn. *Neocarsidara*); **Tenaphalara* Kuwayama, 1908; *Tyora* Walker, 1869 (syn. *Carsidaroida*, *Nesiope*).

Subfamily ***Homotominae** Heslop-Harrison, 1958, stat. rev.

Comments

The subfamily and its constituent tribes and subtribes were diagnosed by Hollis & Broomfield (1989) (treated as family, subfamilies and tribes) who also analysed the generic relationships of the family using morphological evidence; the three subfamilies (here tribes) were represented in a trifurcation in their cladogram. The molecular analyses, in which only three genera were included, reflect this morphological tree but sampled only two subfamilies (here tribes). Following Ouvrard (2002), the classification of Burckhardt & Ouvrard (2012) differs from that of Hollis & Broomfield (1989) in the inclusion of *Phytolyma* Scott, 1882 in the Macrohomotominae White & Hodkinson, 1985 (Phytolymini) rather than in the Aphalarinae. The classification presented here reflects that of Burckhardt & Ouvrard (2012) though with reduced ranks.

Tribe Dynopsyllini Bekker-Migdisova, 1973, stat. rev.

Subtribe **Diceraopsyllina** Hollis & Broomfield, 1989, stat. nov.

Included genus

Diceraopsylla Crawford, 1912.

Subtribe **Dynopsyllina** Bekker-Migdisova, 1973, stat. rev.

Triozamiini Bekker-Migdisova, 1973: 114.

Included genera

Afrodynopsylla Hollis & Broomfield, 1989; *Austrodynopsylla* Hollis & Broomfield, 1989; *Dynopsylla* Crawford, 1913 (syn. *Crawfordella*, *Sphingocladia*); *Triozamia* Vondráček, 1963.

Tribe *Homotomini Heslop-Harrison, 1958, stat. rev.

Subtribe ***Homotomina** Heslop-Harrison, 1958, stat. nov.

Psausiini Bekker-Migdisova, 1973: 102.

Included genus

**Homotoma* Guérin-Méneville, 1844 (syn. *Anisostropha*, *Austrohomotoma*, *Caenohomotoma*, *Harrisonella*, *Heterohomotoma*, *Labobrachia*, *Metapsausia*, *Psausia* Enderlein, 1914, *Psausia* Yang & Li, 1984).

Subtribe **Synozina** Bekker-Migdisova, 1973, stat. nov.

Synoziini White & Hodkinson, 1985: 162 (misspelling).

Included genus

Synoza Enderlein, 1918.

Tribe *Macrohomotomini White & Hodkinson, 1985, stat. rev.

Subtribe ***Edenina** Bhanotar, Ghosh & Ghosh, 1972, stat. nov.

Included geneus

**Mycopsylla* Froggatt, 1901 (syn. *Edenus*).

Subtribe ***Macrohomotomina** White & Hodkinson, 1985, stat. nov.

Included genera

**Macrohomotoma* Kuwayama, 1908; *Pseudoeriopsylla* Newstead, 1911.

Subtribe **Phytolymina** White & Hodkinson, 1985, stat. nov.

Comments

Differs from other subtribes in the Macrohomotomini in the presence of a costal break in the forewing and small tubercles on the metapostnotum (Burckhardt *et al*. 2018a). In Cho *et al*. (2019), *Moriphila* is nested in *Homotoma*.

Included genera

Moriphila Burckhardt & Cho in Burckhardt *et al*., 2018a; *Phytolyma* Scott, 1882.

Subfamily ***Pachypsyllinae** Crawford, 1914

Comments

The subfamily was diagnosed by Tuthill (1943b) and White & Hodkinson (1985).

Included genera

Celtisaspis Yang & Li, 1982; **Pachypsylla* Riley, 1885 (syn. *Blastophysa*); *Tetragonocephala* Crawford, 1914.

Family ***Liviidae** Löw, 1879

Comments

In both mtg trees, this poorly supported monophyletic or paraphyletic family contains two strongly supported monophyla and one monotypic taxon which we rank as subfamilies: Euphyllurinae, Liviinae and Neophyllurinae subfam. nov. There is no strong support for any particular sister group relationship, although in a backbone constraint analysis in Percy *et al*. (2018), Neophyllurinae subfam. nov. grouped more strongly with Liviinae than Euphyllurinae Crawford, 1914. The family as defined here differs from that of Burckhardt & Ouvrard (2012) in that it lacks the Diaphorinini (minus *Megadicrania* and *Psyllopsis*, which are included here in the Euphyllurinae). Adults of Liviidae often have a crown of densely spaced apical spurs and immatures have multiple lanceolate or sectasetae.

Subfamily ***Euphyllurinae** Crawford, 1914

Psyllopsiini Vondráček, 1951: 128.
Pachypsylloidini Loginova, 1964: 457.
Strophingiinae White & Hodkinson, 1985: 270.

Comments

The Euphyllurinae as defined here is strongly supported as a monophylum in both mtg trees, morphologically it is, however, more difficult to diagnose. All species included here have immatures with a fan-shaped tarsal arolium bearing an unguitractor. Hosts are, as far as known, Ericaceae (Ericales), Oleaceae (Lamiales), Polygonaceae (Caryophyllales), Rutaceae and Sapindaceae (Sapindales), and Salvadoraceae (Brassicales). Its present concept, which is not further subdivided into tribes, embraces the constituents of the tribes Euphyllurini (except *Neophyllura*), Pachypsylloidini and Strophingiini of Burckhardt & Ouvrard (2012), as well as *Megadicrania*, *Peripsyllopsis* and *Psyllopsis* (from Diaphorinini).

The molecular analyses clearly show that the Diaphorinini of Burckhardt & Ouvrard (2012) is polyphyletic though only three of 13 genera were analysed. Of the 13 genera, only *Megadicrania* Loginova, 1976, *Peripsyllopsis* Enderlein, 1926 and *Psyllopsis* Löw, 1879, remain in Euphyllurinae. The other genera are transferred to Psyllidae: *Caradocia*, *Epipsylla* and *Geijerolyma* to Ciriacreminae, *Diaphorina* and *Parapsylla* to Diaphorininae, *Katacephala*, *Lautereropsis*, *Notophorina* and *Tuthillia* to Katacephalinae subfam. nov. and *Cornopsylla* to Psyllinae.

Included genera

Brachyphyllura Li, 2011; *Crytophyllura* Li, 2011; *Eremopsylloides* Loginova, 1964; **Euphyllura* Foerster, 1848 (syn. *Platystigma*); *Ligustrinia* Loginova, 1973; *Megadicrania* Loginova, 1976; *Pachypsylloides* de Bergevin, 1927; *Peripsyllopsis* Enderlein, 1926; **Psyllopsis* Löw, 1879; **Strophingia* Enderlein, 1914; *Shaerqia* Kemal & Koçak, 2009 (replacement name for *Acaerus* Loginova nec Pascoe; syn. *Sureaca*); *Syringilla* Loginova, 1967.

Subfamily ***Liviinae** Löw, 1879

Paurocephalini Vondráček, 1963: 277.
Diclidophlebiini Bekker-Migdisova, 1973: 100.
Camarotosceninae Li, 2011: 381.
Sinuonemopsyllinae Li, 2011: 373.

Comments

The monophyly of Liviinae is strongly supported in both mtg trees and also morphologically (Burckhardt & Mifsud 2003). The concept of the subfamily is the same as that by Burckhardt & Ouvrard (2012). Both morphologically and in the molecular analyses *Diclidophlebia* Crawford, 1920 and *Paurocephala* are closely related. Whereas each of the genera was recovered as monophyletic in a morphological study (Burckhardt & Mifsud 2003), in the molecular analyses *Diclidophlebia* is paraphyletic with respect to *Paurocephala*.

Included genera

Aphorma Hodkinson, 1974 (syn. *Leprostictopsylla*); *Camarotoscena* Haupt, 1935; **Diclidophlebia* Crawford, 1920 (replacement name for *Heteroneura* Crawford nec Fallén; syn. *Aconopsylla*, *Gyroza*, *Haplaphalara*, *Paraphalaroida*, *Sinuonemopsylla*, *Woldaia*); **Livia* Latreille, 1802 (syn. *Diraphia* Illiger, *Neolivia* replacement name for *Diraphia* Waga nec Illiger, *Vailakiella*); **Paurocephala* Crawford, 1913 (syn. *Marpsylla*, *Paurocephala* (*Thoracocorna*), *Pauroterga*); **Syntomoza* Enderlein, 1921 (syn. *Anomoterga*, *Homalocephala*).

Subfamily *Neophyllurinae subfam. nov.
urn:lsid:zoobank.org:act:2CB3C7BB-1F3C-4C9E-A8B0-F5AB5B6C537A
Fig. 3

Type genus

Neophyllura Loginova, 1973.

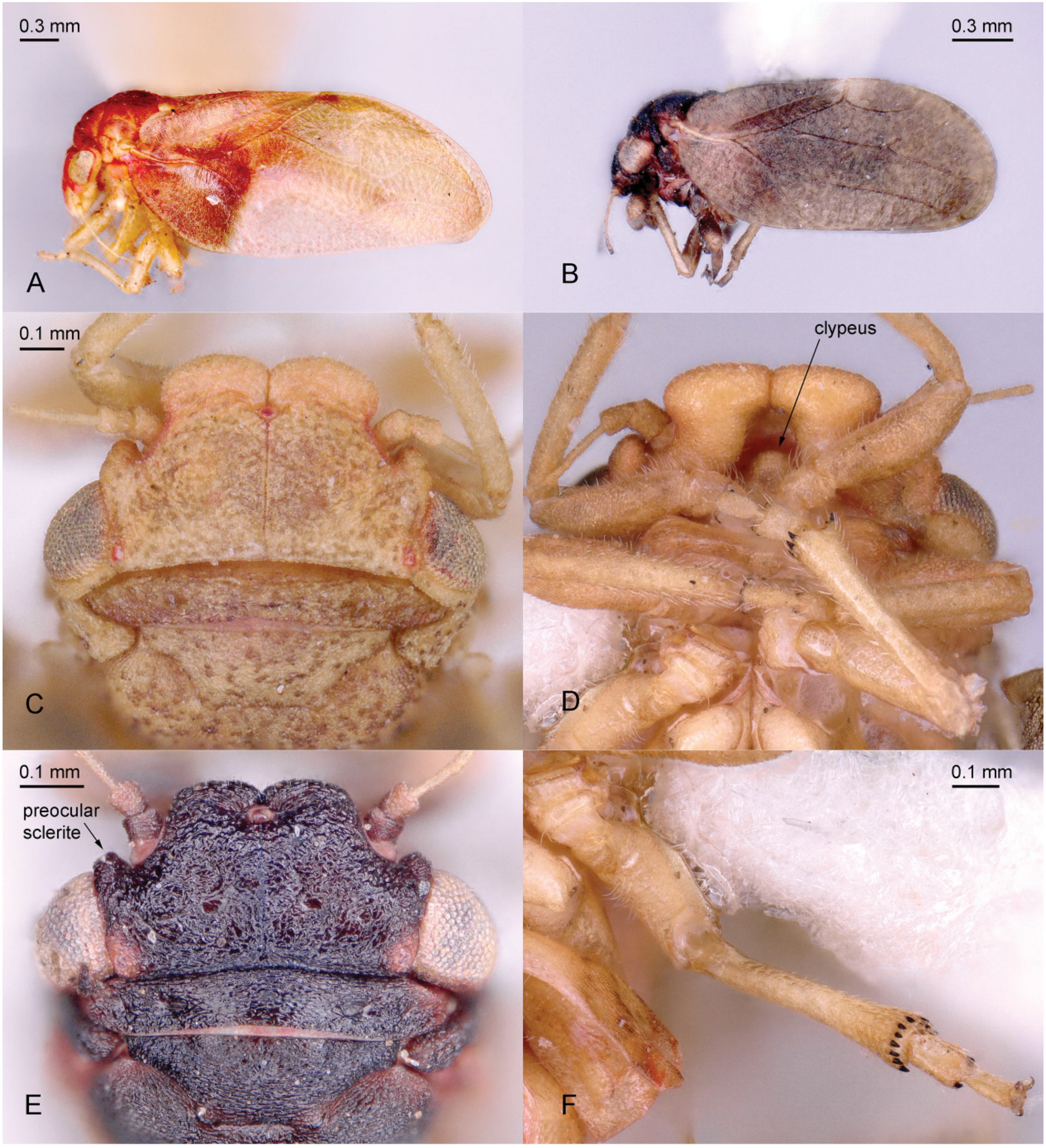

Fig. 3. Neophyllurinae subfam. nov.: *Neophyllura* spp. **A**. *Neophyllura arbuticola* (Crawford, 1914), habitus, in profile view. **B**. *Neophyllura* sp., habitus, in profile view. **C–D, F**. *Neophyllura arctostaphyli* (Schwarz, 1904). **E**. *Neophyllura* sp. **C, E**. Head, dorsal view. **D**. Head, ventral view. **F**. Hind leg.

Diagnosis

Adult

Head with subtrapezoidal vertex that is separated from genae by incomplete transverse suture; genae forming transverse ridges; frons oval, almost completely covered by median ocellus; preocular sclerite developed, forming large tubercle. Thorax strongly arched dorsally; propleurites with subequal epimeron and episternum. Parapteron elongate, rectangular, much larger than tegula. Metacoxa with moderately large, blunt meracanthus and inconspicuous membranous tubercle on metatrochanteral cavity; metatibia without genual spine, bearing an open crown of 8–9 irregularly spaced, sclerotised, apical spurs; metabasitarsus with 2 spurs. Forewing membrane coriaceous, more or less rugose; costal break developed, pterostigma absent or indistinct; branches of vein M relatively long; anal break close to apex of vein Cu_{1b}.

Fifth instar immature

Caudal plate with additional pore fields.

Description

Adult

Head, in profile, strongly inclined at almost 90° from longitudinal body axis (Fig. 3A–B). Vertex subtrapezoidal, separated from genae by incomplete transverse suture; genae forming transverse ridges; coronal suture fully developed; frons oval, almost completely covered by median ocellus; preocular sclerite developed, forming large tubercle (Fig. 3C, E). Antenna 10-segmented, filiform, about as long as head width. Clypeus pear-shaped, visible in profile (Fig. 3D). Rostrum very short, hardly exceeding procoxae. Thorax strongly arched dorsally; pronotum transversely ribbon-shaped (Fig. 3C, E); mesopraescutum in longitudinal body axis shorter than mesoscutum which is strongly bulged; propleurites with subequal epimeron and episternum. Parapteron elongate, rectangular, much larger than tegula. Legs relatively short, tibiae slightly longer than femora; basitarsi not much longer than broad; metacoxa with moderately large, blunt meracanthus and inconspicuous membranous tubercle on metatrochanteral cavity; metatibia without genual spine, bearing an open crown of 8–9 irregularly spaced, sclerotised, apical spurs; metabasitarsus with 2 spurs (Fig. 3F). Forewing oval or rhomboidal, membrane coriaceous, more or less rugose; costal break developed, pterostigma absent or indistinct; vein R shorter than M+Cu or both veins subequal, branches of vein M relatively long; anal break close to apex of vein Cu_{1b}. Hindwing almost as long as forewing, membranous; costal setae grouped; vein R+M developed. Male proctiger one-segmented; in profile, tubular. Male subgenital plate subglobular. Paramere lamellar. Female terminalia cuneate. Circumanal ring oval.

Fifth instar immature

Caudal plate bearing additional pore fields. Tarsal arolium short, fan-shaped with unguitractor.

Included genus

**Neophyllura* Loginova, 1973 (syn. *Arbutophila*).

Family ***Mastigimatidae** Bekker-Migdisova, 1973, stat. nov.

Bharatianinae White & Hodkinson, 1985: 272.

Comments

The taxon was diagnosed by Burckhardt & Ouvrard (2012) and Burckhardt *et al*. (2018b). The former suggested the following sister group relationships: *Bharatiana*+*Mastigimas* and *Cecidopsylla*+*Synpsylla*, and Burckhardt *et al*. (2018b) indicated that *Toonapsylla* may be closely related to the former clade. Cho *et al*. (2019) showed that *Cecidopsylla* and *Toonapsylla* are not closely related and that the former has a basal position within Psylloidea. For this reason we transfer *Cecidopsylla* to Aphalaridae. *Toonapsylla* shares a series of morphological characters with *Bharatiana*+*Mastigimas* (Burckhardt *et al*. 2018b), supporting the monophyly of the three genera. *Synpsylla* resembles *Cecidopsylla* in the shape of the head, antennae and forewings but there are also important differences such as absence/presence of submedian ridges on the metapostnotum or number and arrangement of the apical metatibial spurs. Awaiting new evidence, we leave *Synpsylla* in the Mastigimatidae.

Included genera

Bharatiana Mathur, 1973; **Mastigimas* Enderlein, 1921 (syn. *Coelocara*); *Synpsylla* Yang, 1984; *Toonapsylla* Burckhardt, 2018 in Burckhardt *et al*. (2018b).

Family ***Psyllidae** Latreille, 1807

Comments

The monophyly of Psyllidae is well (AN tree) or only moderately (CC tree) supported in the molecular analyses. The two mtg trees share the same internal topology with most clades strongly supported (Fig. 4). The composition of Psyllidae proposed here differs from the Psyllidae of Burckhardt & Ouvrard (2012) in the addition of *Diaphorina* and *Katacephala* (from Liviidae, Euphyllurinae) as two distinct, basal clades, though inclusion of *Diaphorina* in Psyllidae requires further testing (Percy *et al*. 2018). The molecular analyses further suggest that the subfamily Psyllinae of Burckhardt & Ouvrard (2012) is polyphyletic. Here we remove *Amorphicola* and *Platycorypha* and assign them each to a new subfamily. An unnamed taxon from Madagascar, also warranting subfamily status, is not further treated here as it contains no described genus and species.

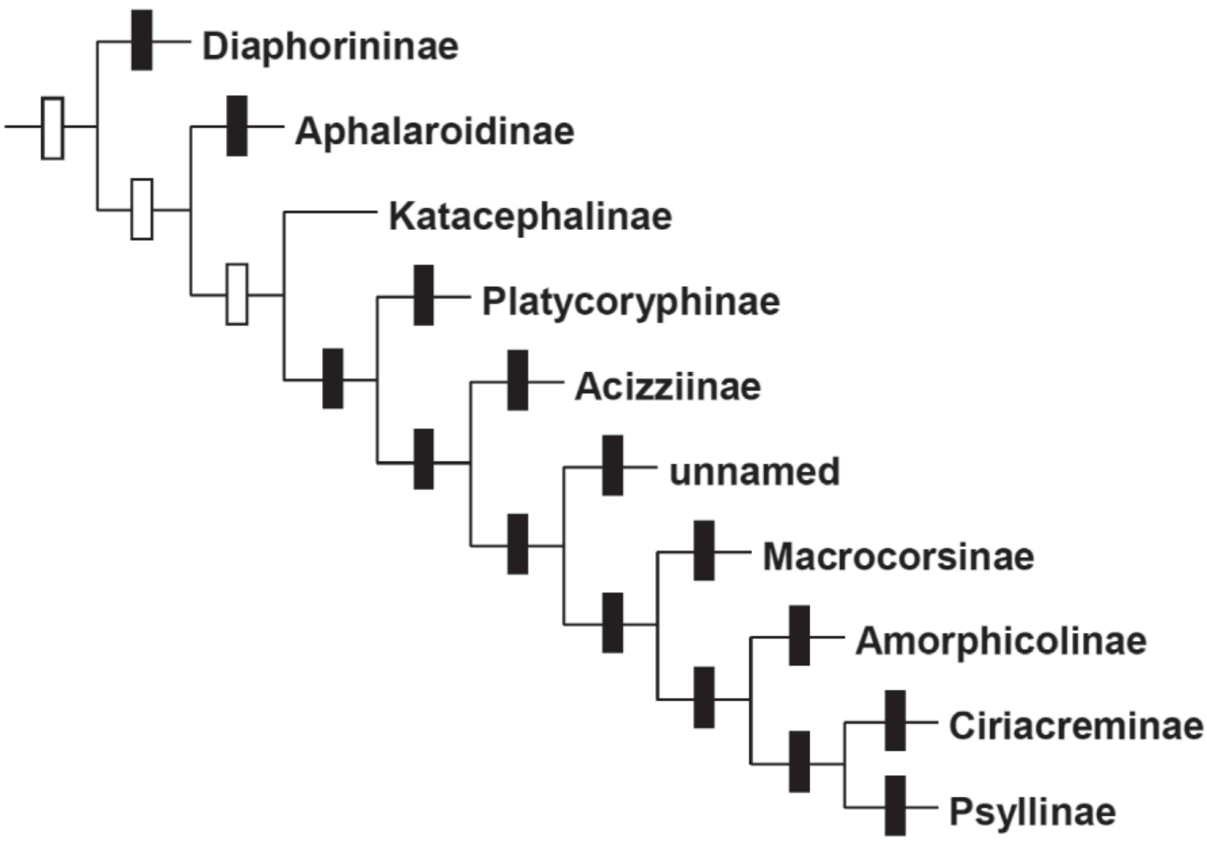

Fig. 4. Cladogram representation of the classification of Psyllidae Latreille, 1807 adopted here, node symbols indicate subfamilies with poor to moderate support (white), or strong support (black) in molecular analyses (Percy *et al*. 2018). For Katacephalinae subfam. nov. no node symbol is given as only a single species was included in the analyses.

Subfamily *Acizziinae White & Hodkinson, 1985

Comments

The monophyly of Acizziinae is strongly supported in both mtg trees.

Included genus

**Acizzia* Heslop-Harrison, 1961 (replacement name for *Neopsylla* Heslop-Harrison nec Wagner; syn. *Neoacizzia* Park & Taylor nomen nudum [no included species] syn. nov., *Neoacizzia* Li, 2011)

Subfamily ***Amorphicolinae** subfam. nov.
urn:lsid:zoobank.org:act:3F17DEF8-6E82-4586-9AA8-ED1325E5D087
Fig. 5

Type genus

Amorphicola Heslop-Harrison, 1961.

Diagnosis

Adult

Vertex separated from genae by transverse suture; genae forming conical processes; coronal suture fully developed; frons oval, almost completely covered by median ocellus; anteorbital tubercle and

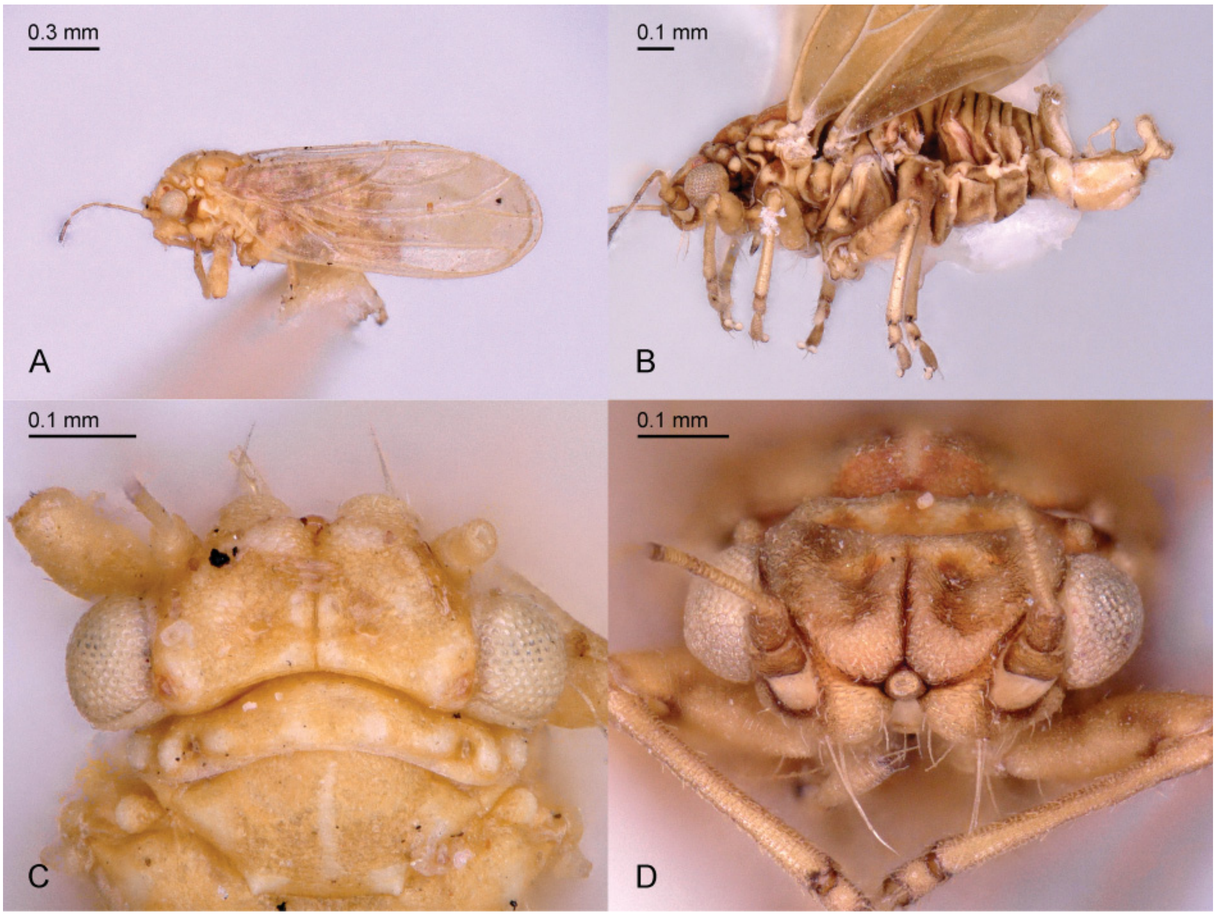

Fig. 5. Amorphicolinae subfam. nov.: *Amorphicola* sp. **A**. Habitus, in profile view. **B**. Legs and terminalia. **C**. Head, dorsal view. **D**. Head, frontal view.

preocular sclerite absent. Antenna with segment 3 longer than segments 7 or 8. Thorax moderately arched dorsally; propleurites with subequal epimeron and episternum. Metatibia without genual spine, bearing 4 irregularly spaced, sclerotised, apical spurs; metabasitarsus with 2 spurs. Forewing rhomboidal, broadly rounded apically; membrane semitransparent; costal break developed, pterostigma large; anal break close to apex of vein Cu_{1b}. Hindwing with grouped costal setae; vein M+Cu developed. Male proctiger one-segmented; in profile, tubular. Paramere complex, in profile axe or hammer-shaped with several sclerotised peg setae on the inner face.

Fifth instar immature

Body flattened, broadly oval. Antenna 7-segmented, beset with a few short club-shaped setae. Forewing pad lacking humeral lobes, bearing short marginal club-shaped setae. Margin of hindwing pad with club-shaped or capitate setae. Tarsal arolium lacking pedicel. Caudal plate with 4+4 marginal sectasetae and some moderately long club-shaped setae. Anus in ventral position; circumanal ring heart-shaped, consisting of a single row of pores, lacking additional pore fields.

Description

Adult

Head, in profile, weakly to moderately inclined at 30–45° from longitudinal body axis (Fig. 5A–B). Vertex subtrapezoidal, separated from genae by transverse suture; genae forming conical processes which are separated or contiguous at base; coronal suture fully developed; frons oval, almost completely covered by median ocellus; anteorbital tubercle and preocular sclerite not developed (Fig. 5C–D). Antenna 10-segmented, filiform, 1.0–1.5 times as long as head width, segment 3 longer than segments 7 or 8. Clypeus pear-shaped, slightly flattened, hardly visible in profile. Rostrum short, distinctly exceeding procoxae. Thorax moderately arched dorsally (Fig. 5A–B), slightly narrower than head; pronotum ribbon-shaped; mesopraescutum in longitudinal body axis about as long as mesoscutum; propleurites with subequal epimeron and episternum. Legs moderately long, tibiae slightly longer than femora; basitarsi not much longer than broad; metacoxa with moderately large, horn-shaped meracanthus; metatibia without genual spine, bearing 4 irregularly spaced, sclerotised, apical spurs; metabasitarsus with 2 spurs (Fig. 5B). Forewing rhomboidal, broadly rounded apically (Fig. 5A); membrane semitransparent, covered in irregularly spaced surface spinules; costal break developed, pterostigma large; vein R longer than M+Cu; anal break close to apex of vein Cu_{1b}. Hindwing almost as long as forewing, membranous; costal setae grouped; vein M+Cu developed. Male proctiger one-segmented; in profile, tubular. Male subgenital plate subglobular or elongate. Paramere complex, in profile hammer-shaped (Fig. 5B) with several sclerotised peg setae on the inner face. Female terminalia cuneate. Circumanal ring oval.

Fifth instar immature

Body flattened, broadly oval. Antenna 7-segmented, beset with a few short club-shaped setae; bearing a single subapical rhinarium on each of segments 3 and 5, and 2 rhinaria on segment 7. Forewing pad lacking humeral lobes, bearing short marginal club-shaped setae. Margin of hindwing pad with club-shaped or capitate setae. Legs bearing club-shaped or capitate setae; tarsal arolium longer than claws, fan-shaped with unguitractor but lacking pedicel. Caudal plate developed, semi-circular; margin with 4+4 sectasetae and some moderately long club-shaped setae. Anus in ventral position; circumanal ring heart-shaped, consisting of a single row of pores, without additional pore fields.

Included genus

**Amorphicola* Heslop-Harrison, 1961.

Subfamily ***Aphalaroidinae** Vondráček, 1963

Arepuniinae White & Hodkinson, 1985: 271 (misspelling).

Comments

The monophyly of Aphalaroidinae as understood here is strongly supported in both mtg trees and it is well circumscribed morphologically (Burckhardt 1987). The molecular analyses place *Telmapsylla*, which was previously included in the Aphalaroidinae (Burckhardt & Ouvrard 2012), in Ciriacreminae; we therefore transfer this genus to Ciriacreminae. Burckhardt & Ouvrard (2012) treated *Primascena*† as a synonym of *Diclidophlebia* (Liviidae: Liviinae). However, the presence of metabasitarsal spurs and a crown of spaced apical spurs on the metatibia in *P. subita*† Klimaszewski, 1998, the type species of *Primascena*†, indicate a relationship to Aphalaroidinae, as suggested by Burckhardt & Mifsud (2003). We follow the latter authors and recognise *Primascena*†, stat. rev., as a valid genus in the Aphalaroidinae.

The internal phylogenetic relationships were discussed by Burckhardt (1987, 2005) but there is no explicit, testable hypothesis. In the molecular analyses, where only three of the 13 currently recognised genera were included, the sister group relationship between *Aphalaroida* and *Russelliana* is only poorly supported.

Included genera

**Aphalaroida* Crawford, 1914; *Baccharopelma* Burckhardt *et al*., 2004 (replacement name for *Neopelma* Burckhardt nec Sclater, *Burckhardtia* Straube & Meritzki nec Frech, nec Brown & Hodkinson); *Connectopelma* Šulc, 1914 (replacement name for *Delina* Blanchard nec Robineau-Desvoidy); *Ehrendorferiana* Burckhardt, 2005; **Freysuila* Aleman, 1887 (syn. *Indana*); *Pachyparia* Loginova, 1967; *Panisopelma* Enderlein, 1910; *Primascena*† Klimaszewski, 1998, stat. rev.; *Prosopidopsylla* Burckhardt, 1987; **Russelliana* Tuthill, 1959 (syn. *Arepuna*); *Sphinia* Blanchard, 1852; *Yangus* Fang, 1990 (syn. *Pallipsylla*); *Zonopelma* Burckhardt, 1987.

Subfamily ***Ciriacreminae** Enderlein, 1910

Comments

The monophyly of Ciriacreminae is strongly supported in both mtg trees and its circumscription corresponds mostly to that of Burckhardt & Ouvrard (2012) with the addition of *Telmapsylla* Hodkinson, 1992, *Caradocia* Laing, 1923, *Epipsylla* Kuwayama, 1908 and *Geijerolyma* Froggatt, 1903 which are included here. However, all five Old World and two additional New World genera listed by Burckhardt & Ouvrard (2012) are not included in the molecular analyses. In both mtg trees, the monophyly of *Auchmerina*, *Euceropsylla*+*Heteropsylla*, of *Telmapsylla*+‘*Limbopsylla*’ *laguncularioe* and of *Mitrapsylla*+‘*Limbopsylla*’ *nigrivenis*, as well as the sister group relationship of the first two groups is very strongly supported.

The artificial nature of *Limbopsylla* was acknowledged by Brown & Hodkinson (1988) when erecting the genus. The type species is a member of Platycoryphinae subfam. nov. (see there for more details). Two species of ‘*Limbopsylla*’ included in the molecular analysis are placed in the Ciriacreminae: ‘*Limbopsylla*’ *laguncularioe* and ‘*Limbopsylla*’ *nigrivenis*. We transfer here the former to *Telmapsylla* and assign the second to the new genus *Hollisiana* gen. nov. (see Table 1 and description below).

‘*Limbopsylla*’ *laguncularioe* (Brown & Hodkinson, 1988) comb. nov. and *Telmapsylla minuta* Hodkinson, 1992 constitute a very strongly supported monophyletic clade in both mtg trees. Morphologically, the two species share the head with a trapezoidal vertex, the lack of anteorbital tubercles, the hemispherical, adpressed eyes, the conical, apically pointed genal processes, the large cu_1 cell of the forewing, the

Table 1. Species in Psyllidae originally assigned to *Limbopsylla* Brown & Hodkinson, 1988 and their current generic placement.

Species list	Valid generic assignment	Authority
Limbopsylla beeryi (Caldwell, 1944)	*Apsyllopsis mexicana* (Crawford, 1914)	Burckhardt & Queiroz (2020)
Limbopsylla boquetensis Brown & Hodkinson, 1988	*Heteropsylla boquetensis* (Brown & Hodkinson, 1988)	Muddiman *et al*. (1992)
Limbopsylla campanellai Brown & Hodkinson, 1988	*Euphalerus campanellai* (Brown & Hodkinson, 1988)	Hollis & Martin (1997)
Limbopsylla caradociforma Brown & Hodkinson, 1988	*Hollisiana caradociforma* (Brown & Hodkinson, 1988) comb. nov.	comb. nov.
Limbopsylla chirui Brown & Hodkinson, 1988	not congeneric with *L. nata* (placement to be determined)	
Limbopsylla estribii Brown & Hodkinson, 1988	not congeneric with *L. nata* (placement to be determined)	
Limbopsylla laguncularíae Brown & Hodkinson, 1988	*Telmapsylla laguncularíae* (Brown & Hodkinson, 1988) comb. nov.	comb. nov.
Limbopsylla nata Brown & Hodkinson, 1988	type species of *Limbopsylla*	Brown & Hodkinson (1988)
Limbopsylla nigrivenis Brown & Hodkinson, 1988	*Hollisiana nigrivenis* (Brown & Hodkinson, 1988) comb. nov.	comb. nov.
Limbopsylla tumidicosta Brown & Hodkinson, 1988	not congeneric with *L. nata* (placement to be determined)	
Limbopsylla sp. A of Brown & Hodkinson, 1988	not congeneric with *L. nata* (placement to be determined)	

presence of a M+Cu vein in the hindwing, the grouped apical metatibial spurs and the short female terminalia in the adult; and immatures with 7-segmented antenna, fan-shaped tarsal arolium with an unguitractor and a short petiole, and 4+4 marginal sectasetae on the caudal plate. Despite many morphological differences between the two species, such as antennal length, absence/presence of a genual spine and details of the male terminalia in the adult, and the number of rows of pores in the circumanal ring, we consider them congeneric and propose the following new combination: *Telmapsylla laguncularíae* (Brown & Hodkinson, 1988) comb. nov. from *Limbopsylla*.

Here, we move three genera which were not treated in the molecular analyses from Liviidae: Euphyllurinae (Diaphorinini) to the Ciriacreminae. *Caradocia*, *Epipsylla* and *Geijerolyma* constitute together a putative monophyletic group based on the presence of long genal processes, very long antennae, metatibia lacking a genual spine but bearing an open crown of densely spaced apical spurs, and two sclerotised spurs on the metabasitarsus. According to White & Hodkinson (1985), immatures of *Epipsylla* lack sectasetae on the abdominal margin. While we confirm this for an Asian species (Thailand, NHMB), this is not the case for Afrotropical taxa (material examined from Cameroon, NHMB), where the immatures are similar to those of *Mitrapsylla* with four sectasetae present on the abdominal margin, two grouped together and each situated on a small tubercle, and with the circumanal ring extending to the abdominal dorsum and consisting of several rows of wax pores. The combination of the last two characters can be found only in the Ciriacreminae.

Included genera

**Auchmerina* Enderlein, 1918; *Auchmeriniella* Brown & Hodkinson, 1988; *Caradocia* Laing, 1923; *Ciriacremum* Enderlein, 1910 (syn. *Bunoparia*); *Epipsylla* Kuwayama, 1908; **Euceropsylla* Boselli, 1929 (syn. *Aremica*); *Geijerolyma* Froggatt, 1903; **Heteropsylla* Crawford, 1914; **Hollisiana* gen. nov.; *Insnesia* Tuthill, 1964; *Isogonoceraia* Tuthill, 1964; *Jataiba* Burckhardt & Queiroz, 2020; *Kleiniella* Aulmann, 1912 (syn. *Desmiostigma*, *Syndesmophlebia*); *Manapa* Brown & Hodkinson, 1988; **Mitrapsylla* Crawford, 1914; *Queiroziella* Burckhardt, 2021; *Palmapenna* Hollis, 1976; **Telmapsylla* Hodkinson, 1992; *Trigonon* Crawford, 1920.

Genus ***Hollisiana*** gen. nov.
urn:lsid:zoobank.org:act:2DDCB705-CCB8-442F-8EAC-B3050DF0192A
Fig. 6

Type species

Limbopsylla nigrivenis Brown & Hodkinson, 1988; by present designation. Gender feminine.

Etymology

This genus is dedicated to David Hollis for his outstanding contribution to psyllid systematics.

Description

Adult

See also Brown & Hodkinson 1988: figs 63–64 for illustrations. Moderately large psyllids, 2.5–5.0 mm long. Head about as wide as mesonotum, inclined at 45° from longitudinal body axis (Fig. 6A–B). Vertex trapezoidal, about 1.8 times as wide as long along midline, weakly indented around foveae; passing smoothly into genae not separated by transverse suture; genae produced into long conical processes which are covered in conspicuous long setae; median suture complete, reaching hind margin of head; lateral ocelli on small tubercles; frons forming small rhomboid sclerite, delimited by vertex and genae, almost completely covered by median ocellus; compound eyes relatively small, hemispherical, stalked on large preocular sclerite and occiput (Fig. 6C–D). Clypeus hidden by genae in lateral view, pear-shaped; rostrum short, only apex visible in lateral view. Antenna filiform, longer than forewing, 10-segmented, in some species flagellum getting thinner towards apex; flagellum beset with long conspicuous bristles; segment 3 shorter than segments 7 or 8, with a single subapical rhinarium on each of segments 4, 6, 8, and 9; terminal setae shorter than segment 10. Thorax weakly arched dorsally; lacking macroscopic setae. Pronotum transversely ribbon-shaped.

Propleurites about as broad as high, slightly oblique; proepimeron as big as or larger than episternum. Forewing oval, broadly, irregularly rounded apically, transparent, more than twice as long as wide; pterostigma lacking; costal break present, indistinct; cells m_1 and cu_1 large; anal break close to apex of vein Cu_{1b}. Hindwing slightly shorter than forewing; costal setae grouped; vein R and M+Cu. Metacoxa with large, horn-shaped, pointed meracanthus; metafemur slightly shorter than metatibia; metatibia bearing genual spine and 1+3+1 apical spurs. Metabasitarsus with two lateral spurs. Male proctiger unipartite, tubular or with posterior lobe. Subgenital plate elongate. Paramere slender, lamellar or digitiform. Aedeagus long and thin; distal segment shorter than paramere, inflated in apical third; sclerotised end tube of ductus ejaculatorius short, slightly sinuous. Female terminalia, in profile, cuneate, moderately short to relatively long. Circumanal ring oval, consisting of two subequal rows of pores. Valvulae triangular and lacking serrations.

Fifth instar immature (Fig. 6E–H)

Body elongate, about twice as long as wide (Fig. 6G–H). Antenna 9-segmented, sparsely beset with a few short setae; bearing a single subapical rhinarium on each of segments 4, 6, 8 and 9. Forewing pad small, lacking humeral lobes, bearing short marginal club-shaped setae. Margin of hindwing pad with short bristles. Legs long, with at least one moderately long capitate seta on tibiae; tarsal arolium about twice as long as claws, fan-shaped with unguitractor and pedicel. Abdomen slender; caudal plate weakly sclerotised; abdominal margin with 6+6 sectasetae, the two at the rear close together and each on a small tubercle and, in some species, distinctly larger than the remainder. Anus in terminal position; circumanal ring extending to the abdominal dorsum and consisting of several rows of wax pores.

Distribution

Neotropical.

Host plant and biology

Guatteria spp. (Annonaceae). Immatures secrete long wax threads from sectasetae at the abdominal apex. In a species from Brazil (Roraima) and Costa Rica, these terminal wax threads form two conspicuous spiral filaments (Fig. 6E–H) (Hanson & Nishida 2016: 89; Burckhardt 2017: 34).

Comments

Hollisiana gen. nov. is similar to *Mitrapsylla* from which it differs in the absence of a pterostigma in the adults; and the narrow abdomen with 6+6 marginal sectasetae (rather than 4+4) in the fifth instar immature.

Two species are included in the new genus: *Hollisiana caradociforma* (Brown & Hodkinson, 1988) gen. et comb. nov. and *Hollisiana nigrivenis* (Brown & Hodkinson, 1988) gen. et comb. nov., both from *Limbopsylla*. The two species differ in the forewing pattern (colourless or fumate versus conspicuously dark veins), male proctiger (absence versus presence of a posterior lobe), female terminalia (long versus

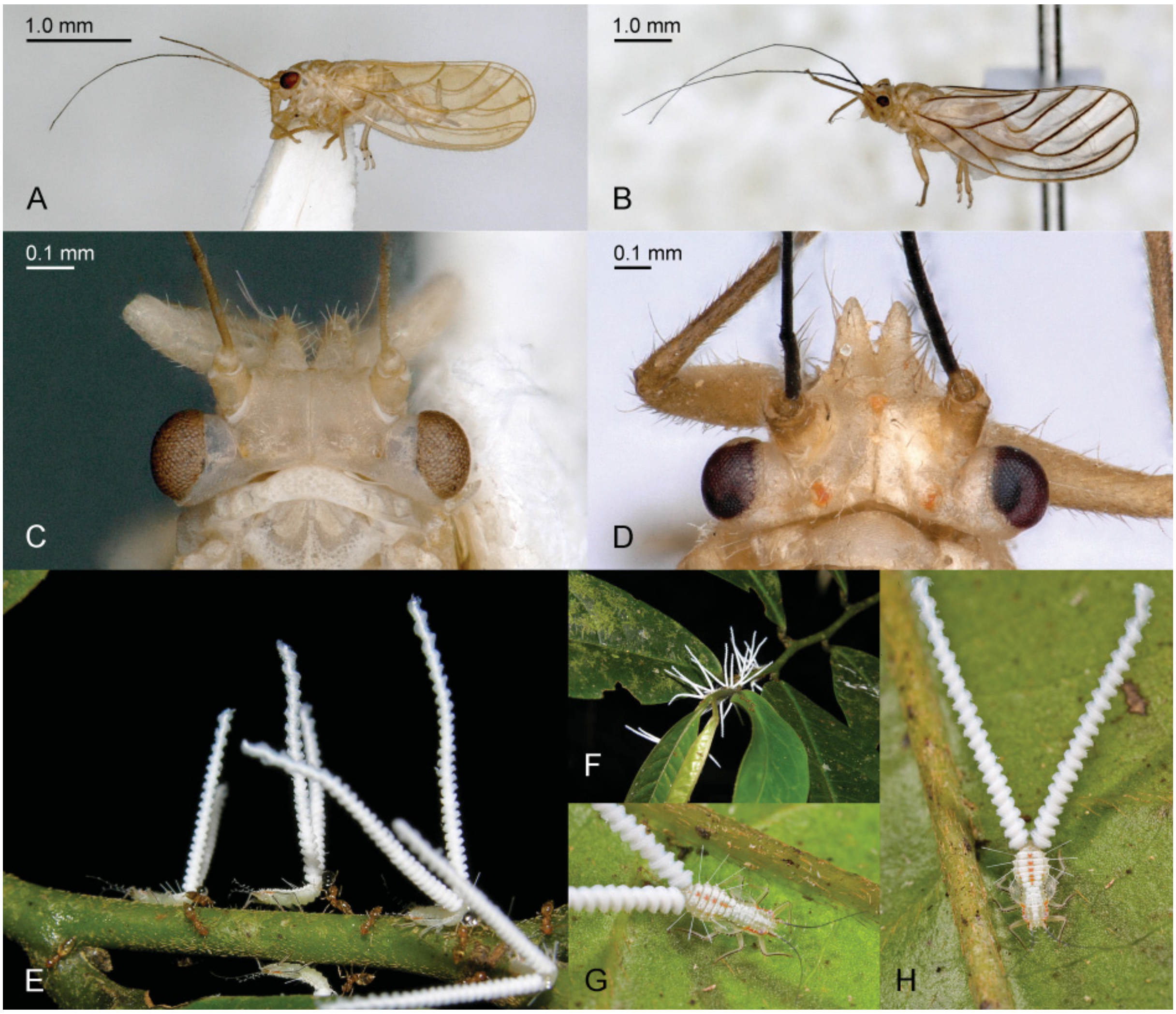

Fig. 6. Ciriacreminae Enderlein, 1910: *Hollisiana* spp. **A, C**. *Hollisiana caradociforma* (Brown & Hodkinson, 1988) gen. et comb. nov. **B, D**. *Hollisiana* sp. from Brazil. **E–H**. *Hollisiana* sp. from Costa Rica. **A–B**. Habitus, in profile view. **C–D**. Head, dorsal view. **E**. Immatures tended by ants. **F–H**. Immatures with spiral filaments. (Photos E–F by Kenji Nishida; G–H by Piotr Naskrecki).

short), abdomen of immatures (elongate oval versus narrow almost parallel-sided). The two species each represent a species group with more undescribed species in tropical America (BMNH, NHMB data).

Subfamily ***Diaphorininae** Vondráček, 1951

Comments

The AN tree (but not the CC tree) shows reasonably strong support for a sister group relationship of *Diaphorina* to the remainder of Psyllidae, and, as noted earlier, reduced taxon nuclear genome and combined data analyses by Percy *et al*. (2018) place *Diaphorina* outside Psyllidae and sister to Triozidae. Increased taxon sampling and more analyses are required to robustly resolve this ambiguity, and therefore erection of a separate family is currently rejected in favour of inclusion in Psyllidae at this time. Based on the morphology of head, forewings and male terminalia we consider *Parapsylla* the sister group of *Diaphorina* and include it in the Diaphorininae.

Included genera

**Diaphorina* Löw, 1880 (replacement name for *Diaphora* Löw nec Stephens, syn. *Brachypsylla*, *Gonanoplicus*, *Pennavena*, *Eudiaphorina*); *Parapsylla* Heslop-Harrison, 1961 (syn. *Agmapsylla*).

Subfamily ***Katacephalinae** subfam. nov.
urn:lsid:zoobank.org:act:DE4F5C17-6685-47B9-9659-CEFD8828244D
Fig. 7

Type genus

Katacephala Crawford, 1914.

Diagnosis

Adult

Head with genae forming conical to lobular processes; preocular sclerite developed. Antenna 10-segmented, 0.9–2.2 times as long as head width, segment 3 usually longer than segments 7 or 8. Metatibia usually without genual spine, bearing an open crown of 6–19 evenly spaced, sclerotised, apical spurs; metabasitarsus usually with 2 spurs. Forewing with costal break and large pterostigma; anal break close to apex of vein Cu_{1b}. Hindwing almost as long as forewing. Male proctiger one-segmented, in profile, often with posterior lobes. Paramere usually simple with stout setae on the inner face.

Fifth instar immature

Body often bearing lanceolate setae or sectasetae but lacking capitate setae. Antenna 7–10 segmented with 4 rhinaria. Tarsal arolium fan-shaped, unguitractor developed.

Description

Adult

Head, in profile, hardly to strongly (Fig. 7A–F) inclined at 0–90° from longitudinal body axis. Vertex trapezoidal (Fig. 7J) to almost subrectangular (Fig. 7L), separated from genae by transverse suture; genae forming conical to lobular processes which are separated or contiguous medially; coronal suture usually fully developed (Fig. 7G, I–L) but sometimes reduced (Fig. 6H); frons small, almost completely covered by median ocellus; anteorbital tubercle rarely developed (Fig. 7L: arrow); preocular sclerite always present (Fig. 7J: arrow). Antenna 10-segmented, filiform, 0.9–2.2 times as long as head width, segment 3 ususally longer than segments 7 or 8 (except for some species of *Tuthillia*). Clypeus pear-shaped, flattened in *Tuthillia*; hardly or not visible in profile. Rostrum short, distinctly exceeding procoxae. Thorax weakly (Fig. 7F) to strongly (Fig. 7B) arched dorsally, as wide as or wider than head; pronotum transversely ribbon-shaped; mesopraescutum in longitudinal body axis slightly to distinctly

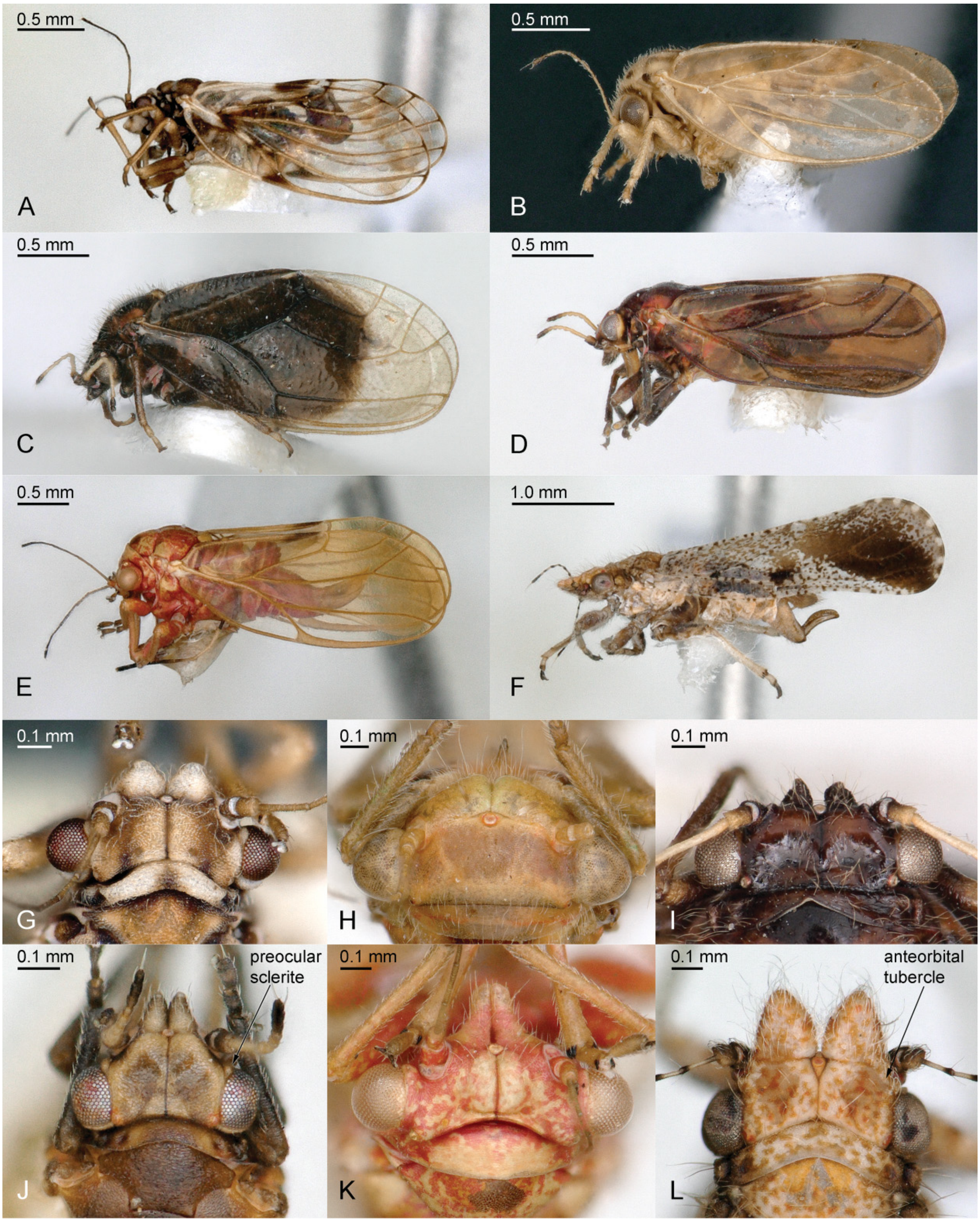

Fig. 7. Katacephalinae subfam. nov. **A, G**. *Katacephala longiramis* (Burckhardt, 1987). **B**. *Katacephala tenuipennis* Tuthill, 1944. **C, I**. *Lautereropsis* sp. **D, J**. *Notophorina brevicornis* Burckhardt, 1987. **E, K**. *Notophorina* sp. **F, L**. *Tuthillia* sp. **H**. *Katacephala* sp. **A–F**. Habitus, in profile view. **G–L**. Head, dorsal view.

shorter than mesoscutum; propleurites narrow or broad, relative sizes of epimeron and episterum variable. Legs moderately long, tibiae longer than femora; basitarsi slightly longer than to about twice as long as broad; metacoxa with large, horn-shaped meracanthus; metatibia without genual spine (exception *Notophorina vitripennis* Burckhardt, 1987), bearing an open crown of 6–19 evenly spaced, sclerotised, apical spurs; metabasitarsus with 2 spurs (exception *Notophorina monocentra* Burckhardt, 1987). Forewing oval (Fig. 7B), somewhat rectangular, rhomboidal or very elongate (Fig. 7F), narrowly (Fig. 7B) to broadly rounded apically (Fig. 7C); membrane semitransparent, sometimes with pattern; costal break developed, pterostigma large; anal break close to apex of vein Cu_{1b}. Hindwing almost as long as forewing, membranous; costal setae indistinctly to clearly grouped; vein R+M+Cu branching into veins R+M and Cu or R and M+Cu. Male proctiger one-segmented, in profile, often with posterior lobes. Male subgenital plate subglobular or elongate. Paramere usually simple with stout setae on the inner face. Female terminalia cuneate or falcate. Circumanal ring oval.

Fifth instar immature

Body oval to elongate, fairly robust; surface often covered in lanceolate setae or sectasetae but lacking capitate setae. Antenna 7–10 segmented with 4 rhinaria. Dorsal thoracic sclerites varying from small to large. Tarsal arolium fan-shaped, unguitractor developed, pedicel absent or present. Forewing-pads often with large humeral lobes. Anus in ventral or terminal position. Circumanal ring variable.

Comments

The four genera included in the new subfamily were assigned by Burckhardt & Ouvrard (2012) to the polyphyletic tribe Diaphorinini (Euphyllurinae) along with other genera referred here to Euphyllurinae (Liviidae), Ciriacreminae, Diaphorininae and Psyllinae (Psyllidae). Putative autapomorphies of the new subfamily are the open crown of densely spaced metatibial spurs and the posteriorly lobed male proctiger in adults, as well as the presence of lanceolate setae and the lack of capitate setae in immatures. Hosts of the Oriental *Lautereropsis* Burckhardt & Malenovský, 2003 are unknown. The other three genera are associated entirely or partially with Myrtaceae and are mostly Neotropical.

Included genera

**Katacephala* Crawford, 1914 (syn. *Jenseniella*); *Lautereropsis* Burckhardt & Malenovský, 2003; *Notophorina* Burckhardt, 1987; *Tuthillia* Hodkinson, Brown & Burckhardt, 1986.

Subfamily ***Macrocorsinae** Vondráček, 1963

Euphalerini Bekker-Migdisova, 1973: 112.

Comments

The monophyly of Macrocorsinae is very strongly supported in both mtg analyses. The four genera treated in the analyses are also assigned to this subfamily by Burckhardt & Ouvrard (2012) who included another eight genera. Meanwhile, *Euphaleropsis* and *Peregrinivena* were synonymised (Burckhardt *et al*. 2018b). *Trisetipsylla* was placed in the Macrocorsinae by Cho *et al*. (2019) rather that in Psyllinae (Burckhardt & Ouvrard 2012). At least some species of *Trisetipsylla* have immatures with extra pore fields on the caudal plate, supporting this placement.

Otroacizzia† Klimaszewski, 1996 contains the following species: *O. muta*† Klimaszewski, 1996 (type species), *O. prosapia*† Klimaszewski, 1996, *O. soriae*† Peñalver & García-Gimeno, 2006 and *O. tertia*† Klimaszewski, 1996. Burckhardt & Ouvrard (2012) synonymised *Otroacizzia* with *Euryconus*.

A reevaluation of the status of the four fossil species by Klimaszewski (1996) and Peñalver & García-Gimeno (2006) showed that *Otroacizzia* is a species mix referrable to *Colophorina* (*O. muta*) and to *Euryconus* (other species). Whereas the antennae are short and a genual spine is lacking in *O. muta*, the antennae are long and the genual spine is developed in the other three species. Thus, *O. muta* shows the characteristics of *Colophorina*, making *Otroacizzia*† a junior synonym of the former. The other three species of *Otroacizzia*† conform with the diagnosis of *Euryconus* and are transferred there. The following new synonymy and new combinations are proposed here:

Colophorina Capener, 1973 = *Otroacizzia*† Klimaszewski, 1996, syn. nov.
Colophorina muta† (Klimaszewski, 1996) comb. nov. from *Otroacizzia*†
Euryconus prosapia† (Klimaszewski, 1996) comb. nov. from *Otroacizzia*†
Euryconus soriae† (Peñalver & García-Gimeno, 2006) comb. nov. from *Otroacizzia*†
Euryconus tertia† (Klimaszewski, 1996) comb. nov. from *Otroacizzia*†

Included genera

Apsyllopsis Burckhardt & Queiroz, 2020; *Brinckitia* Heslop-Harrison, 1961; **Colophorina* Capener, 1973 (syn. *Otroacizzia*†, syn. nov.); **Epiacizzia* Li, 2002; *Euphaleropsis* Li, 2004 (syn. *Peregrinivena*); **Euphalerus* Schwarz, 1904; *Euryconus* Aulmann, 1912; *Macrocorsa* Vondráček, 1963; **Paraphyllura* Yang, 1984; *Pugionipsylla* Li in Li *et al.*, 2006; *Retroacizzia* Heslop-Harrison, 1961; *Tridencopsylla* Li, 2002; *Trisetipsylla* Yang & Li, 1984.

Subfamily ***Platycoryphinae** subfam. nov.

urn:lsid:zoobank.org:act:B8BF6738-548A-4042-A942-7A21085A3973
Fig. 8

Type genus

Platycorypha Tuthill, 1945.

Diagnosis

Adult

Head with oval frons, which is almost completely covered by median ocellus. Clypeus pear-shaped, in profile hidden by genae and not visible. Propleurites with episternum subequal to or smaller than epimeron. Metacoxa with large, pointed, horn-shaped meracanthus; metatibia with large genual spine, bearing 4–5 irregularly spaced, sclerotised, apical spurs; metabasitarsus with 2 spurs. Forewing rhomboidal; costal break and pterostigma developed; cell cu_1 large; anal break close to apex of vein Cu_{1b}. Male proctiger one-segmented.

Fifth instar immature

Body broadly oval, lacking capitate setae. Antenna with 4 rhinaria. Meso and metathoracic sclerites small. Forewing pad lacking humeral lobes. Margin of hindwing pad usually with one sectaseta. Legs lacking capitate setae; tarsal arolium fan-shaped with unguitractor and pedicel. Caudal plate developed, semi-circular; margin with up to 3+3 sectasetae.

Description

Adult

Head, in profile, weakly to strongly inclined at 30–90° from longitudinal body axis (Fig. 8A, C, E, G). Vertex subrectangular to transversely subtrapezoidal (Fig. 8B, D, F, H); separated from genae sometimes by transverse or oblique suture, sometimes passing smoothly into genae; genae smoothly rounded (Fig. 8D, H) or forming short (Fig. 7F) or long conical processes (Fig. 8B); coronal suture fully developed or completely reduced; frons oval, almost completely covered by median ocellus; anteorbital tubercle sometimes developed (Fig. 8D: arrow). Antenna 10-segmented, filiform, ranging from slightly longer than head width to distinctly longer than forewing, segment 3 shorter or longer than segments 7 or 8. Clypeus pear-shaped, in profile hidden by genae and not visible. Rostrum usually short, only tip exceeding procoxae, sometimes longer (in some *Platycorypha* spp.). Thorax weakly (Fig. 7G) to strongly (Fig. 8A) arched dorsally, about as wide as head; pronotum weakly or very strongly inclined from longitudinal body axis; propleurites narrow to broad, with episternum subequal to or smaller than epimeron. Legs moderately long, tibiae often shorter than femora, sometimes subequal or longer; basitarsi not much longer than broad; metacoxa with large, pointed, horn-shaped meracanthus; metatibia with large genual spine, bearing 4–5 irregularly spaced, sclerotised, apical spurs; metabasitarsus with 2 spurs. Forewing rhomboidal, broadest in apical third or in the middle, narrowly rounded or angular apically; membrane semitransparent, covered in surface spinules; costal break and pterostigma developed; vein C+Sc weakly or strongly widened; vein R longer than M+Cu; cell cu_1 large; caudal break close to apex of vein Cu_{1b}. Hindwing slightly shorter than forewing, membranous; costal setae ungrouped or grouped;

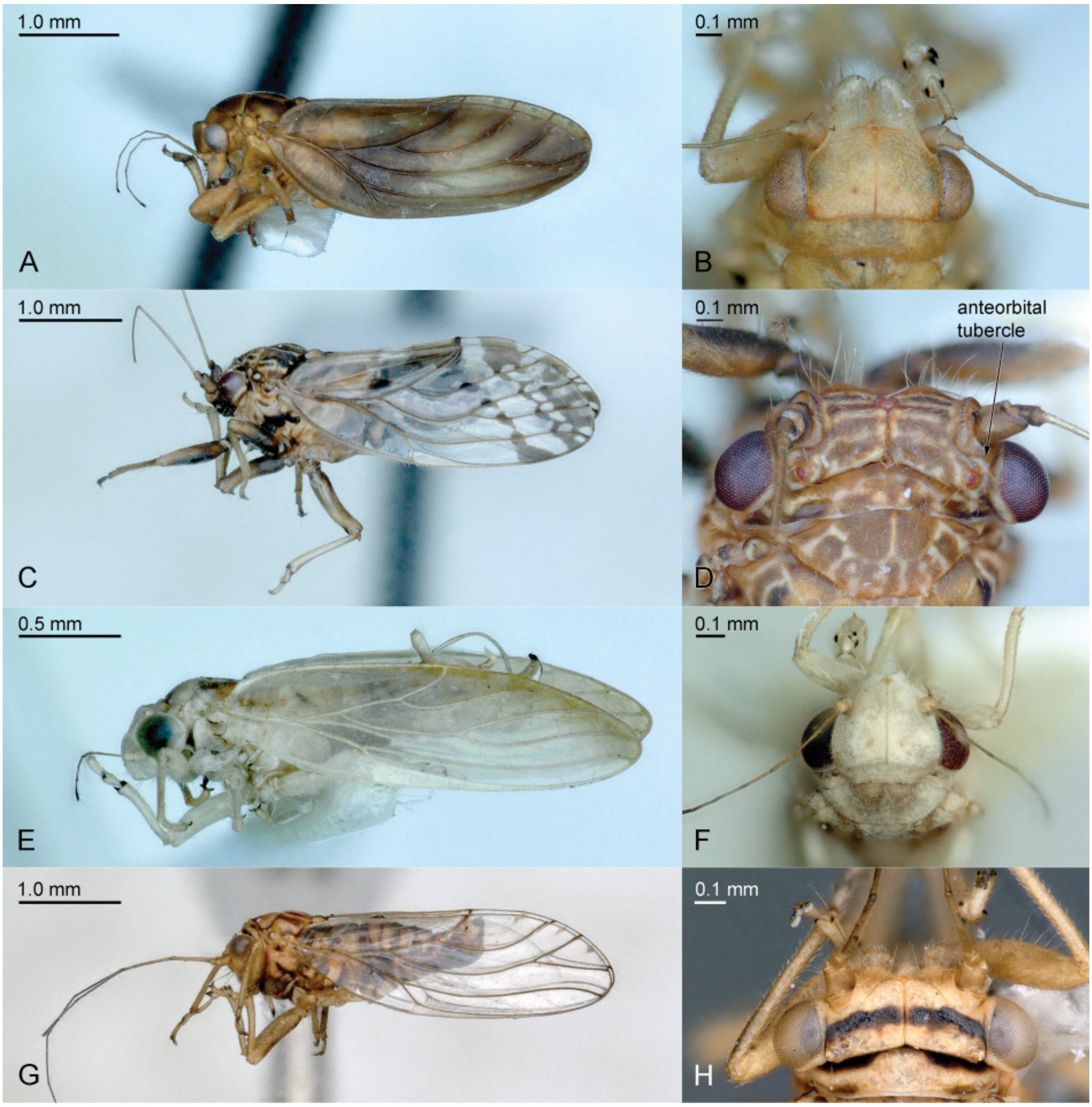

Fig. 8. Platycoryphinae subfam. nov. **A–B**. *Allophorina* sp. **C–D**. *Limbopsylla nata* Brown & Hodkinson, 1988. **E–F**. *Padaukia macrolobii* Burckhardt & Queiroz, 2018. **G–H**. *Platycorypha nigrivirga* Burckhardt, 1987. **A, C, E, G**. Habitus, in profile view. **B, D, F, H**. Head, dorsal view.

vein R+M+Cu indistinctly trifurcating or splitting into R and M+Cu. Male proctiger one-segmented; in profile, tubular or with posterior lobe. Male subgenital plate subglobular or elongate. Paramere lamellar or complex. Female terminalia short or moderaly long; proctiger often with dorsal hump.

Fifth instar immature

Body broadly oval, lacking capitate setae. Antenna 7, 9 or 10-segmented, with 4 rhinaria. Meso and metathoracic sclerites small. Forewing pad lacking humeral lobes. Margin of hindwing pad usually with one sectaseta. Legs lacking capitate setae; tarsal arolium shorter or longer than claws, fan-shaped with unguitractor and pedicel. Caudal plate developed, semi-circular; margin with up to 3+3 sectasetae. Anus in ventral or terminal position; circumanal ring small heart-shaped to large undulate, restricted to ventral side or extended to dorsal side; consisting of a single row or multiple rows of pores, without additional pore fields.

Comments

Brown & Hodkinson (1988) created *Limbopsylla* as a polyphyletic holding place for ten "species of the subfamilies Acizziinae and Ciriacreminae which cannot be placed in existing genera". Three species have been removed previously and three species are transferred here (Table 1). Based on adult and immature material of an undescribed species from Brazil associated with *Tachigali rugosa* (Fabaceae) (NHMB) which is congeneric with *L. nata*, the type species of *Limbopsylla*, we conclude that *Limbopsylla* is a valid genus closely related to *Platycorypha*, and that the other species included in *Limbopsylla* (Table 1) are not congeneric with the type species.

Included genera

Allophorina Hodkinson, 1991; *Limbopsylla* Brown & Hodkinson, 1988; *Padaukia* Hollis & Martin, 1993 (syn. *Peltapaurocephala* Heslop-Harrison nomen nudum, no description); *Platycorypha* Tuthill, 1945 (syn. *Neopsyllia*).

Subfamily ***Psyllinae** Latreille, 1807

Arytainini Crawford, 1914: 106.
Alloeoneurini Vondráček, 1951: 127.
Anomoneurini Klimaszewski, 1963: 92.
Cyamophilini Loginova, 1976: 596.
Cacopsyllinae Li, 2011: 744.
Cornopsyllinae Li, 2011: 532. **Syn. nov.**

Comments

In both trees, the monophyly of Psyllinae and the division into three monophyletic subgroups is very strongly supported. The most basal clade consists of a single Asian species, viz. *Cacopsylla eriobotryae* (Yang, 1984). The second clade contains four West Palaearctic genera associated with faboid Fabaceae: *Arytaina* Foerster, 1848, *Arytainilla* Loginova, 1972, *Arytinnis* Percy, 2003 and *Livilla* Curtis, 1835. The first three are monophyletic, the last is paraphyletic with respect to *Arytainilla* and *Arytinnis*, as previously shown by Percy (2003). *Livilla ulicis* Curtis, 1836, the type species of *Livilla*, belongs to a very strongly supported clade which is sister group to a poorly supported *Arytainilla*. *Livilla blandula* (Horváth, 1905), a species closely related to *Livilla pyrenaea* (Mink, 1859), the type species of *Floria* Löw, 1879, and *Livilla radiata* (Foerster, 1848), the type species of *Alloeoneura* Löw, 1879, belong to a clade which is sister group to the very strongly supported *Arytinnis*. To split *Livilla* s. lat. into two monophyletic genera, viz. *Livilla* s. str. and *Floria* (syn. *Alloeoneura*), respectively, is not practicable at the moment as only a quarter of the known species (see Ouvrard 2020 for a complete list of species) were included in the molecular analyses and no morphological characters are known reflecting these groupings. The third clade comprises a very strongly supported group of North American species associated with *Ceanothus* L. (Rhamnaceae) (= *Ceanothia* Heslop-Harrison, 1961 and *Nyctiphalerus* Bliven, 1955, see Table 2), previously referred to the genera *Ceanothia*, *Euglyptoneura* Heslop-Harrison, 1961 and *Nyctiphalerus*, which is sister group to a poorly supported clade comprising one clade represented by a single species (*Pexopsylla cercocarpi* Jensen, 1957) and four very strongly supported clades: 1. holarctic species of *Cacopsylla* Ossiannilsson, 1970 associated with Elaeagnaceae, Lardizabalaceae, Rosaceae and Salicaceae (= *Cacopsylla* s. str.); 2. holarctic species associated with Betulaceae (= *Psylla* s. str., Table 3), previously referred to *Baeopelma* Enderlein, 1926, *Cacopsylla*, *Chamaepsylla* Ossiannilsson, 1970 and *Psylla*; 3. palaearctic species associated with *Buxus* (Buxaceae) (= *Spanioneura* Foerster, 1848, see Table 4), previously referred to *Psylla* and *Spanioneura*; 4. North American species associated with *Cercocarpus* and *Purshia* (Rosaceae) (= *Purshivora* Heslop-Harrison, 1961, see Table 2), previously referred to *Cacopsylla*, *Ceanothia*, *Nyctiphalerus* and *Purshivora*. Cho *et al*. (2019) transferred *Psylla longicauda* Konovalova, 1986, an Asian species associated with *Prunus*, to *Spanioneura* and provided morphological adult characters to define *Psylla* s.str. and *Spanioneura*.

Similar to *Arytaina*, *Arytainilla*, *Arytinnis* and *Livilla*, associated with brooms (Fabaceae), which constitute a species-rich clade endemic to the Western Palaearctic, a group of Psyllinae radiated in Western North America on *Ceanothus* (Rhamnaceae) as well as *Cercocarpus* and *Purshia* (Rosaceae). North America authors (Crawford 1914; Tuthill 1943b; Jensen 1956, 1957a, 1957b; Bliven 1956, 1958) assigned these species to the genera *Arytaina*, *Euphalerus* and *Psylla*, rendering these genera very artificial, and to two monotypic genera *Nyctiphalerus* and *Pexopsylla*. Heslop-Harrison (1961) discussed the North American genera previously referred to *Arytaina* and, rightly, concluded that they are not congeneric with *Arytaina spartii* (Hartig, 1841) (= *A. genistae* (Latreille, 1804)), the type species of *Arytaina*. He erected the four genera *Amorphicola* Heslop-Harrison, 1961, *Ceanothia*, *Euglyptoneura* and *Purshivora*. His descriptions are not diagnostic and he also mixed up the figures (fig. 2 concerns *Ceanothia* and fig. 3 *Amorphicola*, and not vice versa). Whereas *Amorphicola* (see Amorphicolinae subfam. nov.) is well characterised by its paramere morphology and by its host associations (Fabaceae), the other three genera are not. Hollis & Martin (1997) redefined *Euphalerus* Schwarz, 1904 and suggested that the Nearctic species are not congeneric with *Euphalerus nidifex* Schwarz, 1904, the type species, or with most of the Neotropical species. Percy *et al*. (2012) transferred these species to *Nyctiphalerus*. The molecular analyses shed much needed light on the phylogenetic relationships in this group. There are monophyletic clades associated with Rhamnaceae (*Ceanothus*) and with Rosaceae (*Cercocarpus*, *Purshia*). The former is characterised by immatures with a terminal anus and a large circumanal ring which extends onto the dorsum of the caudal plate, the latter has immatures with a ventral anus and a smaller circumanal ring restricted to the venter of the caudal plate. The clade of *Ceanothus* comprises one group with the genal processes in a lower plane to that of the vertex and lacking a genual metatibial spine (type species of *Ceanothia* and *Euglyptoneura*), and another group with genal processes and vertex flattened and in the same plane and bearing a genual metatibial spine (type species of *Nyctiphalerus*). The Rosaceae clade also splits into two groups: one bearing metatarsal spurs (type species of *Purshivora*) and one lacking metatarsal spurs (type species of *Pexopsylla*). Here we suggest that *Ceanothia*, *Nyctiphalerus*, *Pexopsylla* and *Purshivora* are good genera, and that *Euglyptoneura* syn. nov. is a junior synonym of *Ceanothia* (Table 2).

The Oriental genus *Cornopsylla* is transferred here from Liviidae, Euphyllurinae, Diaphorinini to Psyllidae, Psyllinae. The position of *Cornopsylla* within Psyllidae is supported by morphological (Luo *et al*. 2013) and molecular characters (Cho *et al*. 2019); in both papers, *Cornopsylla* was treated as a member of Psyllinae.

Psyllinae is a species-rich subfamily (ca 800 spp., Ouvrard 2020) with many species referred to *Cacopsylla* s. str. and *Psylla* s. str. that do not fit the restricted concepts of these genera provided above. Awaiting more studies on these species, we leave them in *Cacopsylla* s. lat. and *Psylla* s. lat.

Table 2 (continued on next page). North American species in Psyllidae Latreille, 1807 associated with *Ceanothus* (Rhamnaceae) as well as *Cerocarpus* and *Purshia* (Rosaceae) referrable to *Ceanothia* Heslop-Harrison, 1961; *Nyctiphalerus* Bliven, 1955; *Purshivora* Heslop-Harrison, 1961; and *Pexopsylla* Jensen, 1957. Taxa sampled in Percy *et al*. (2018) are indicated with an asterisk.

Valid combination	Previous combinations	Comments
Host: *Ceanothus* (Rhamnaceae)		
Ceanothia* **Heslop-Harrison, 1961, type-species *Arytaina ceanothae* Crawford, 1914, by original designation = *Euglyptoneura* Heslop-Harrison, 1961: 434, type-species *Arytaina minuta* Crawford, 1914, by original designation, syn. nov.		
Ceanothia assimilis (Crawford, 1914)	*Arytaina assimilis* Crawford, 1914	transferred by Hodkinson & Hollis (1987)
Ceanothia bicolor (Jensen, 1957)	*Arytaina bicolor* Jensen, 1957	transferred by Hodkinson & Hollis (1987)
Ceanothia boharti (Jensen, 1957)	*Arytaina boharti* Jensen, 1957	transferred by Hodkinson & Hollis (1987)
**Ceanothia ceanothae* (Crawford, 1914)	*Arytaina ceanothae* Crawford, 1914	= *Arytaina ceanothi*, unjustified emendation by Tuthill (1943b)
Ceanothia essigi (Jensen, 1957)	*Arytaina essigi* Jensen, 1957	transferred by Hodkinson & Hollis (1987)
Ceanothia fuscipennis (Crawford, 1914)	*Arytaina fuscipennis* Crawford, 1914; *Euglyptoneura fuscipennis* (Crawford, 1914)	comb. nov.
**Ceanothia insolita* (Tuthill, 1943)	*Arytaina insolita* Tuthill, 1943	transferred by Hodkinson & Hollis (1987)
**Ceanothia minuta* (Crawford, 1914)	*Arytaina minuta* Crawford, 1914; *Euglyptoneura minuta* (Crawford, 1914)	comb. nov.
Ceanothia mitella (Jensen, 1957)	*Arytaina mitella* (Jensen, 1957)	transferred by Hodkinson & Hollis (1987)
**Ceanothia robusta* (Crawford, 1914)	*Arytaina robusta* Crawford, 1914; *Euglyptoneura robusta* (Crawford, 1914)	comb. nov.
Ceanothia tardiuscula (Bliven, 1958)	*Arytaina tardiuscula* Bliven, 1958	transferred by Hodkinson (1988)
***Nyctiphalerus** **Bliven, 1955**, type-species *Nyctiphalerus lynceus*, Bliven, 1955, by original designation		
Nyctiphalerus dubius (Caldwell, 1944)	*Euphalerus dubius* Caldwell, 1944	transferred by Percy *et al*. (2012)
Nyctiphalerus jugovenosus (Tuthill, 1937)	*Euphalerus jugovenosus* Tuthill, 1937	transferred by Percy *et al*. (2012)
Nyctiphalerus lynceus Bliven, 1955		
Nyctiphalerus nepos (Bliven, 1956)	*Euphalerus nepos* Bliven, 1956	transferred by Percy *et al*. (2012)
Nyctiphalerus propinquus (Crawford, 1914)	*Euphalerus propinquus* Crawford, 1914	transferred by Percy *et al*. (2012)
**Nyctiphalerus rugipennis* (Crawford, 1914)	*Euphalerus rugipennis* Crawford, 1914	transferred by Percy *et al*. (2012)
**Nyctiphalerus vermiculosus* (Crawford, 1914)	*Euphalerus vermiculosus* Crawford, 1914	transferred by Percy *et al*. (2012)
Host: *Cercocarpus* and *Purshia* (Rosaceae)		
***Purshivora** **Heslop-Harrison, 1961**, type-species *Arytaina chelifera*, Crawford, 1914, by original designation		
**Purshivora aculeata* (Crawford, 1914)	*Arytaina aculeata* Crawford, 1914; *Ceanothia aculeata* (Crawford, 1914)	comb. nov.
Purshivora acuminata (Jensen, 1956)	*Psylla acuminata* Jensen, 1956; *Cacopsylla acuminata* (Jensen, 1956)	comb. nov.
Purshivora adusta (Tuthill, 1937)	*Euphalerus adustus* Tuthill, 1937; *Nyctiphalerus adustus* (Tuthill, 1937)	comb. nov.
**Purshivora brevistigmata* (Patch, 1912)	*Psylla brevistigmata* Patch, 1912; *Cacopsylla brevistigmata* (Patch, 1912)	comb. nov.
Purshivora cercocarpi (Jensen, 1957)	*Euphalerus cercocarpi* Jensen, 1957; *Nyctiphalerus cercocarpi* (Jensen, 1957)	comb. nov.

Table 2 (continued).

Valid combination	Previous combinations	Comments
	Host: *Cercocarpus* and *Purshia* (Rosaceae)	
Purshivora chelifera (Crawford, 1914)	*Arytaina chelifera* Crawford, 1914	transferred by Heslop-Harrison (1961)
Purshivora coryli (Patch, 1912)	*Psylla coryli* Patch, 1912; *Cacopsylla coryli* (Patch, 1912)	comb. nov.
Purshivora difficilis (Tuthill, 1943)	*Psylla difficilis* Tuthill, 1943; *Cacopsylla difficilis* (Tuthill, 1943)	comb. nov.
**Purshivora hirsuta* (Tuthill, 1938)	*Arytaina hirsuta* Tuthill, 1938; *Psylla hirsuta* (Tuthill, 1938); *Psylla* (*Hepatopsylla*) *hirsuta* (Tuthill, 1938); *Cacopsylla hirsuta* (Tuthill, 1938)	comb. nov.
Purshivora idahoensis (Jensen, 1946)	*Euphalerus idahoensis* Jensen, 1946; *Nyctiphalerus idahoensis* (Jensen, 1946)	comb. nov.
Purshivora insignita (Tuthill, 1943)	*Psylla insignita* Tuthill, 1943; *Cacopsylla insignita* (Tuthill, 1943)	comb. nov.
Purshivora maculata (Crawford, 1914)	*Psylla maculata* Crawford, 1914; *Cacopsylla maculata* (Crawford, 1914)	comb. nov.
Purshivora magna (Crawford, 1914)	*Psylla brevistigmata magna* Crawford, 1914; *Psylla* (?*Thamnopsylla*) *magna* (Crawford, 1914); *Cacopsylla magna* (Crawford, 1914)	comb. nov.
Purshivora media (Tuthill, 1943)	*Psylla media* Tuthill, 1943; *Cacopsylla media* (Tuthill, 1943)	comb. nov.
**Purshivora minuta* (Crawford, 1914)	*Psylla minuta* Crawford, 1914; *Psylla* (?*Hepathopsylla*) *minuta* (Crawford, 1914); *Cacopsylla minuta* (Crawford, 1914)	comb. nov.
Purshivora nigranervosa (Jensen, 1956)	*Psylla nigranervosa* Jensen, 1956; *Cacopsylla nigranervosa* (Jensen, 1956)	comb. nov.
Purshivora pubescens (Crawford, 1914)	*Arytaina pubescens* Crawford, 1914	transferred by Heslop-Harrison (1961)
Purshivora tantilla (Tuthill, 1937)	*Euphalerus tantillus* Tuthill, 1937; *Nyctiphalerus tantillus* (Tuthill, 1937)	comb. nov.
****Pexopsylla* Jensen, 1957**, type-species *Pexopsylla cercocarpi*, Jensen, 1957, by original designation		
**Pexopsylla cercocarpi* Jensen, 1957		

Included genera

Anomoneura Schwarz in Uhler, 1896; **Arytaina* Foerster, 1848 (syn. *Amblyrhina*, *Ataenia*, *Psyllopa*); **Arytainilla* Loginova, 1972 (syn. *Hispaniola* Ramírez Gómez, 1956 nomen nudum [type species not designated], *Lindbergia* Heslop-Harrison, 1951 nomen nudum [no included species], *Lindbergiella* Heslop-Harrison, 1961 nomen nudum [type species not designated], *Spartina*); **Arytinnis* Percy, 2003; *Astragalita* Loginova, 1976; **Cacopsylla* Ossiannilsson, 1970 (syn. *Edentatipsylla*, *Hepatopsylla*, *Osmopsylla*, *Thamnopsylla*, *Psyllia* Kirkaldy, 1905 nomen nudum); **Ceanothia* Heslop-Harrison, 1961 (syn. *Euglyptoneura* Heslop-Harrison, 1961, syn. nov.); *Cornopsylla* Li, 1994; *Cyamophila* Loginova, 1976; *Cyamophiliopsis* Li, 2011; *Cylindropsylla* Li, 2011; *Gelonopsylla* Li, 1992; **Livilla* Curtis, 1835 (syn. *Alloeoneura*, *Floria*, *Floriella*); *Mecistoneura* Li, 2011; **Nyctiphalerus* Bliven, 1955; *Palaeolindbergiella* Heslop-Harrison, 1961; **Pexopsylla* Jensen, 1957; *Pseudacanthopsylla* Samy, 1972; **Psylla* Geoffroy, 1762 (syn. *Baeopelma* syn. nov., *Chamaepsylla* syn. nov., *Psylla* (*Labyrinthopsylla*) syn. nov., *Asphagis* Enderlein, 1921); **Purshivora* Heslop-Harrison, 1961; **Spanioneura* Foerster, 1848 (*Asphagidella* Enderlein, 1921 syn. nov.).

Table 3. Holarctic species in Psyllinae Latreille, 1807 associated with Betulaceae referrable to *Psylla* Geoffroy, 1762. Taxa sampled in Percy *et al*. (2018) are indicated with an asterisk.

Valid combination	Original combination	Comments
***Psylla* Geoffroy, 1762**: 482, type-species: *Chermes alni* Linnaeus, 1758, by subsequent designation under the plenary powers of the ICZN Opinion 731 (1965); = *Asphagis* Enderlein, 1921: 120, type-species *Chermes fusca* Zetterstedt, 1828, by original designation, synonymised by Tuthill (1943b); *Baeopelma* Enderlein, 1926: 399, type-species *Psylla colorata* Löw, 1888, by original designation and monotypy, syn. nov.; *Chamaepsylla* Ossiannilsson, 1970: 140, type-species: *Psylla hartigii* Flor, 1861, by original designation and monotypy, syn. nov.; *Psylla* (*Labyrinthopsylla*) Ossiannilsson, 1970: 140, type-species: *Psylla foersteri* Flor, 1861, by original designation and monotypy, syn. nov.		
Host: *Alnus*		
**Psylla alni* (Linnaeus, 1758)	*Chermes alni* Linnaeus, 1758	
Psylla alnicola Li, 1992		
Psylla alnifasciata Li, 2011		
Psylla alniformosanaesuga Lauterer *et al*., 1988		
Psylla alpina Foerster, 1848		
Psylla borealis Horváth, 1908		
Psylla caudata Crawford, 1914		
Psylla cordata Tamanini, 1977		
**Psylla floccosa* Patch, 1909		
**Psylla foersteri* Flor, 1861		comb. rev. from *Baeopelma*
Psylla fusca (Zetterstedt, 1828)	*Chermes fusca* Zetterstedt, 1828	
Psylla magnifera Kuwayama, 1908		
Psylla viridescens (Provancher, 1872)	*Diraphia viridescens* Provancher, 1872	
Host: *Betula*		
Psylla ancylocaula Li, 2011		
Psylla betulae (Linnaeus, 1758)	*Chermes betulae* Linnaeus, 1758	
Psylla betulaenanae Ossiannilsson, 1970		
Psylla betulibetuliae Li, 2011		
**Psylla hartigii* Flor, 1861		comb. rev. from *Chamaepsylla*
Psylla huabeialnia Li, 2011		
Psylla kotejai Drohojowska & Klimaszewski, 2006		
**Psylla striata* Patch, 1911		comb. rev. from *Cacopsylla*
Host: *Carpinus*		
Psylla carpinicola Crawford, 1914		
Host: *Corylus*		
Psylla diloncha (Caldwell, 1938)	*Psyllia diloncha* Caldwell, 1938	comb. rev. from *Cacopsylla*
Host: *Ostrya*		
**Psylla colorata* Löw, 1888		comb. rev. from *Baeopelma*

Psyllidae incertae sedis

Comments

Klimaszewski (1997) erected the poorly diagnosed genera *Indepsylla*†, *Parapsyllopsis*† and *Paropsylla*† from Dominican amber. Burckhardt & Ouvrard (2012) synonymised the first with *Limbopsylla* Brown & Hodkinson, 1988 and the two others with *Platycorypha* Tuthill, 1945. A reevaluation of *Limbopsylla* and

Table 4. Holarctic species in Psyllinae Latreille, 1807 associated with *Buxus* (Buxaceae) and *Prunus* (Rosaceae) referrable to *Spanioneura* Foerster, 1848. Taxa sampled in Percy *et al*. (2018) are indicated with an asterisk.

Valid combination	Previous combinations	Comments
***Spanioneura* Foerster, 1848**: 94; = *Asphagidella* Enderlein, 1921: 120, type-species *Chermes buxi* Linnaeus, 1758, by original designation, syn. nov.		
Host: *Buxus* (Buxaceae)		
*_Spanioneura buxi_ (Linnaeus, 1758)	*Chermes buxi* Linnaeus, 1758; *Psylla buxi* (Linnaeus, 1758); *Asphagidella buxi* (Linnaeus, 1758); *Psylla* (*Asphagidella*) *buxi* (Linnaeus, 1758); *Psylla* (*Baeopelma*) *buxi* (Linnaeus, 1758)	comb. rev.; transferred by Loginova (1964)
Spanioneura chujoi (Miyatake, 1982)	*Psylla chujoi* Miyatake, 1982	comb. nov.
Spanioneura caucasica Loginova, 1968		
*_Spanioneura fonscolombii_ Foerster, 1848		
Host: *Prunus* (Rosaceae)		
Spanioneura longicauda (Konovalova, 1986)	*Psylla longicauda* Konovalova, 1986	transferred by Cho *et al*. (2019)
Spanioneura morimotoi (Miyatake, 1963)	*Psylla morimotoi* Miyatake 1963	comb. nov.
Spanioneura omogoensis (Miyatake, 1963)	*Psylla omogoensis* Miyatake, 1963	comb. nov.
Spanioneura pechai (Klimaszewski & Lodos, 1977)	*Amblyrhina pechai* Klimaszewski & Lodos, 1977	transferred by Hodkinson & Hollis (1987)
Spanioneura persica Burckhardt & Lauterer, 1993		
Spanioneura sanguinea (Provancher, 1872)	*Diraphia sanguinea* Provancher, 1872; *Psylla sanguinea* (Provancher, 1872)	comb. nov.
Spanioneura turkiana (Klimaszewski & Lodos, 1977)	*Amblyrhina turkiana* Klimaszewski & Lodos, 1977	transferred by Hodkinson & Hollis (1987)
Spanioneura yasumatsui (Miyatake, 1963)	*Psylla yasumatsui* Miyatake, 1963	comb. nov.
Spanioneura ziozankeana (Kuwayama, 1908)	*Psylla ziozankeana* Kuwayama, 1908	comb. nov.

Platycorypha suggests that they are not closely related to these two genera. Here, we reinstate the three genera as incertae sedis in the Psyllidae:

Indepsylla† Klimaszewski, 1996, stat. rev.
Parapsyllopsis† Klimaszewski, 1996, stat. rev.
Paropsylla† Klimaszewski, 1996, stat. rev.

Family ***Triozidae** Löw, 1879

Asiotriozinae Li, 2011: 1512.
Bactericerini Heslop-Harrison, 1958: 577–578.
Carsitriinae Li, 2011: 1303.
Epitriozini Kwon, 1983: 79.
Eutriozini Loginova, 1964: 473.
Hemischizocraniini Bekker-Migdisova, 1973: 115.
Leptinopterinae (sic) Bekker-Migdisova, 1973: 104.
Metatriozidinae Li, 2011: 1513.
Neolithinae White & Hodkinson, 1985: 273.
Neotriozidae Li, 2011: 1307.
Paracomecini Bekker-Migdisova, 1973: 115.

Pauropsyllinae Crawford, 1914: 42.
Rhinopsyllidae Klimaszewski, 1993: 65.
Siphonaleyrodinae Takahashi, 1932: 48.
Trichochermini Kwon, 1983: 82.
Triozopsinae Li, 2011: 1383.

Comments

With around 70 genera and over 1000 species (Ouvrard 2020), the Triozidae constitutes the second largest family of Psylloidea. Many of the genera are poorly defined and *Trioza* Foerster, 1848 with over 400 described species has long been recognised as polyphyletic (Hollis 1984). The molecular analyses confirm the polyphyly of *Trioza* and the artificial nature of genera such as *Kuwayama* Crawford, 1911. For a more stable and improved classification, most of the genera have to be redefined and several new genera have to be described to establish monophyletic clades, where no generic name is currently available. This task is beyond the scope of the present paper and awaits further studies.

Included genera

**Aacanthocnema* Tuthill & Taylor, 1955; *Acanthocasuarina* Taylor in Taylor *et al.* (2011); *Afrotrioza* Hollis, 1984; **Anomocephala* Tuthill, 1942; *Asiotrioza* Li, 2011; **Bactericera* Puton, 1876 (syn. *Allotrioza*, *Carsitria*, *Eubactericera*, *Bactericera* (*Klimaszewskiella*) replacement name for *Smirnovia* Klimaszewski nec Lučnic, *Paratrioza*, *Rhinopsylla*); **Baeoalitriozus* Li, 2011; *Berchemitrioza* Li, 2011; **Calinda* Blanchard, 1852; **Casuarinicola* Taylor in Taylor *et al.* 2010; **Cecidotrioza* Kieffer, 1908 (syn. *Homotrioza*); **Ceropsylla* Riley, 1885; **Cerotrioza* Crawford, 1918; *Chouitrioza* Li, 1989; *Colopelma* Enderlein, 1926; *Conicotrioza* Li, 2005; **Crawforda* Caldwell, 1940; *Dolichotrioza* Li, 2002; **Dyspersa* Klimaszewski, 1968; *Egeirotrioza* Boselli, 1931 (syn. *Evegeirotrioza*); *Engytatoneura* Loginova, 1972; *Eotrioza* Konovalova, 1987 (syn. *Trachotrioza* Li, 2011); *Epitrioza* Kuwayama, 1910; *Eryngiofaga* Klimaszewski, 1968; *Eutrioza* Loginova, 1964; *Furcitrioza* Li, 2011; *Genotriozus* Li, 2011; **Hemischizocranium* Tuthill, 1956; **Hemitrioza* Crawford, 1914; **Heterotrioza* Dobreanu & Manolache, 1960 (syn. *Trioza* (*Halotrioza*), *Triozidus*); **Hevaheva* Kirkaldy, 1902; *Hippophaetrioza* Conci & Tamanini, 1984 (syn. *Hippophaetrioza* (*Maculatrioza*)); *Izpania* Klimaszewski, 1962; **Kuwayama* Crawford, 1911 (replacement name for *Epitrioza* Crawford nec Kuwayama, syn. *Succinopsylla*†); **Lauritrioza* Conci & Tamanini, 1986; **Leptotrioza* Miyatake, 1972; **Leptynoptera* Crawford, 1919; **Leuronota* Crawford, 1914 (syn. *Paracomeca*); *Levidea* Tuthill, 1938; **Megatrioza* Crawford, 1915; *Metatrioza* Tuthill, 1939; *Myotrioza* Taylor, in Taylor *et al*. 2016; *Neolithus* Scott, 1882; *Neotrioza* Kieffer, 1905; *Neotriozella* Crawford, 1911 (replacement name for *Neotrioza* Crawford nec Kieffer); *Nothotrioza* Burckhardt in Carneiro *et al*., 2013; *Ozotrioza* Kieffer, 1905; *Parastenopsylla* Yang, 1984 (syn. *Indotrioza*); **Pariaconus* Enderlein, 1926; **Pauropsylla* Rübsaamen, 1899 (syn. *Neotrioza* sensu Li, 2011 nec Kieffer, 1905, misinterpretation, *Sympauropsylla*); *Paurotriozana* Caldwell, 1940; *Petalolyma* Scott, 1882; **Phylloplecta* Riley, 1884 (syn. *Choricymoza*, *Sinitrioza*); **Powellia* Maskell, 1879; *Pseudotrioza* Miyatake, 1972; *Rhegmoza* Enderlein, 1918; *Rhinopsyllida*† Klimaszewski, 1997; **Schedoneolithus* Tuthill, 1959; **Schedotrioza* Tuthill & Taylor, 1955; *Siphonaleyrodes* Takahashi, 1932; **Spanioza* Enderlein, 1926; **Stenopsylla* Kuwayama, 1910 (syn. *Cryptotrioza*, *Dasymastix*, *Eustenopsylla*, *Philippinocarsia*); **Stevekenia* Percy, 2017; **Swezeyana* Caldwell, 1940; *Torulus* Li, 1991; **Trichochermes* Kirkaldy, 1904 (replacement name for *Trichopsylla* Thomson nec Kolenati); *Trioacantha*† Klimaszewski, 1998; **Trioza* Foerster, 1848 (syn. *Metatriozidus*, *Triozopsis*); **Triozoida* Crawford, 1911 (syn. *Myrmecephala*, *Optomopsylla*); *Trisetitrioza* Li, 1995 (syn. *Neorhinopsylla*).

Psylloidea incertae sedis

Nomina dubia

Labicria Enderlein, 1918: 348; type-species: *Labicria barbata* Enderlein, 1918 by original designation and monotypy.

Comments

The type of the Brazilian *Labicria barbata* is destroyed (D. Burckhardt, unpubl.) and we have not seen any fresh material fitting the original description.

Unavailable names

Cephalopsyllini Heslop-Harrison, 1960: 160; nomen nudum, no included genera.

Stigmaphalarini Vondráček, 1957: 140; nomen nudum, no included genera; syn. of Aphalarini Löw, 1879.

Dentotriza Park & Taylor, 1996a: 177; nomen nudum, no included species.

Hispaniola Ramírez Gómez, 1956: 76; nomen nudum, type species not designated; syn. of *Arytainilla* Loginova, 1972.

Lindbergia Heslop-Harrison, 1951: fig. 2a–b; nomen nudum, no included species, syn. of *Arytainilla* Loginova, 1972.

Lindbergiella Heslop-Harrison, 1961: 509; nomen nudum, type species not designated; syn. of *Arytainilla* Loginova, 1972.

Loginoviana Mathur, 1975: 230; nomen nudum, no type designated and no description; syn. of *Ctenarytaina* Ferris & Klyver, 1932.

Metapaurocephala Heslop-Harrison, 1952: 966; nomen nudum, no type designated.

Neoacizzia Park & Taylor, 1996b: 177; nomen nudum, no included species; syn. of *Acizzia* Heslop-Harrison, 1961.

Parapaurocephala Heslop-Harrison, 1952: 962; nomen nudum, no description; syn. of *Microphyllurus* Li, 2002.

Paraphyllolyma Heslop-Harrison, 1952: 966; nomen nudum, no type designated.

Peltapaurocephala Heslop-Harrison, 1952: 966; nomen nudum, no description; syn. of *Padaukia* Hollis & Martin, 1993.

Pennapsylla Froggatt, 1923: pl. 2, fig. 11, nomen nudum, no type designated; syn. of *Cardiaspina* Crawford, 1911.

Phacopteronella Heslop-Harrison, 1960: 504; nomen nudum, no description, no type designated.

Pseudotingidiforma Heslop-Harrison, 1952: 966; nomen nudum, no type designated; syn. of *Lisronia* Loginova, 1976.

Psyllia Kirkaldy, 1905: 268; nomen nudum, no description; syn. of *Cacopsylla* Ossiannilsson, 1970.

Tingidiforma Heslop-Harrison, 1951: 27; nomen nudum; syn. of *Togepsylla* Kuwayama, 1931.

Nomenclatorial acts and changes

New taxa

Amorphicolinae subfam. nov.

Katacephalinae subfam. nov.

Microphyllurinae subfam. nov.

Neophyllurinae subfam. nov.

Platycoryphinae subfam. nov.

Hollisiana gen. nov.

New synonymies

Psyllinae Latreille, 1807 = Cornopsyllini Li, 2011, syn. nov.

Ceanothia Heslop-Harrison, 1961 = *Euglyptoneura* Heslop-Harrison, 1961, syn. nov.

Colophorina Capener, 1973 = *Otroacizzia*† Klimaszewski, 1996, syn. nov.

Lisronia Loginova, 1976 = *Pseudotingidiforma* Heslop-Harrison, 1952, nomen nudum, syn. nov.

Acizzia Heslop-Harrison, 1961 = *Neoacizzia* Park & Taylor, 1996b, nomen nudum, syn. nov.

Psylla Geoffroy, 1762 = *Baeopelma* Enderlein, 1926, syn. nov.

Psylla Geoffroy, 1762 = *Chamaepsylla* Ossiannilsson, 1970, syn. nov.

Psylla Geoffroy, 1762 = *Psylla* (*Labyrinthopsylla*) Ossiannilsson, 1970, syn. nov.

Spanioneura Foerster, 1848 = *Asphagidella* Enderlein, 1921, syn. nov.

New combinations

Ceanothia fuscipennis (Crawford, 1914) comb. nov. from *Arytaina*

Ceanothia minuta (Crawford, 1914) comb. nov. from *Arytaina*

Ceanothia robusta (Crawford, 1914) comb. nov. from *Arytaina*

Colophorina muta† (Klimaszewski, 1996) comb. nov. from *Otroacizzia*†

Euryconus prosapia† (Klimaszewski, 1996) comb. nov. from *Otroacizzia*†

Euryconus soriae† (Peñalver & García-Gimeno, 2006) comb. nov. from *Otroacizzia*†

Euryconus tertia† (Klimaszewski, 1996) comb. nov. from *Otroacizzia*†

Hollisiana caradociforma (Brown & Hodkinson, 1988) gen. et comb. nov. from *Limbopsylla*

Hollisiana nigrivenis (Brown & Hodkinson, 1988) gen. et comb. nov., from *Limbopsylla*

Microphyllurus longicellus (Tuthill, 1943) comb. nov. from *Paurocephala*

Purshivora aculeata (Crawford, 1914) comb. nov. from *Arytaina*

Purshivora acuminata (Jensen, 1956) comb. nov. from *Psylla*

Purshivora adusta (Tuthill, 1937) comb. nov. from *Euphalerus*

Purshivora brevistigmata (Patch, 1912) comb. nov. from *Psylla*

Purshivora cercocarpi (Jensen, 1957) comb. nov. from *Euphalerus*

Purshivora coryli (Patch, 1912) comb. nov. from *Psylla*

Purshivora difficilis (Tuthill, 1943) comb. nov. from *Psylla*

Purshivora hirsuta (Tuthill, 1938) comb. nov. from *Arytaina*

Purshivora idahoensis (Jensen, 1946) comb. nov. from *Euphalerus*

Purshivora insignita (Tuthill, 1943) comb. nov. from *Psylla*

Purshivora magna (Crawford, 1914) comb. nov. from *Psylla*

Purshivora maculata (Crawford, 1914) comb. nov. from *Psylla*

Purshivora media (Tuthill, 1943) comb. nov. from *Psylla*

Purshivora minuta (Crawford, 1914) comb. nov. from *Psylla*

Purshivora nigranervosa (Jensen, 1956) comb. nov. from *Psylla*

Purshivora tantilla (Tuthill, 1937) comb. nov. from *Euphalerus*

Spanioneura chujoi (Miyatake, 1982) comb. nov. from *Psylla*

Spanioneura morimotoi (Miyatake, 1963) comb. nov. from *Psylla*

Spanioneura omogoensis (Miyatake, 1963) comb. nov. from *Psylla*

Spanioneura sanguinea (Provancher, 1872) comb. nov. from *Diraphia*

Spanioneura ziozankeana (Kuwayama, 1908) comb. nov. from *Psylla*

Telmapsylla laguncularíae (Brown & Hodkinson, 1988) comb. nov. from *Limbopsylla*

Revived combinations

Psylla colorata Löw, 1888 comb. rev. from *Baeopelma*

Psylla diloncha (Caldwell, 1938) comb. rev. from *Cacopsylla*

Psylla foersteri Flor, 1861 comb. rev. from *Baeopelma*

Psylla hartigii Flor, 1861 comb. rev. from *Chamaepsylla*

Psylla striata Patch, 1911 comb. rev. from *Cacopsylla*

Spanioneura buxi (Linnaeus, 1758), comb. rev. from *Psylla*

Replacement name

Microphyllurus lii, nom. nov. for *Microphyllurus longicellus* Li, 2002, nec Tuthill (1943a)

New and revived status

Family Mastigimatidae Bekker-Migdisova, 1973, stat. nov.

Subfamily Cecidopsyllinae Li, 2011, stat. rev. et nov.

Subfamily Homotominae Heslop-Harrison, 1958, stat. rev.

Subfamily Phacopteroninae Heslop-Harrison, 1958, stat. nov.

Tribe Ctenarytainini White & Hodkinson, 1985, stat. rev.

Tribe Dynopsyllini Bekker-Migdisova, 1973, stat. rev.

Tribe Homotomini Heslop-Harrison, 1958, stat. rev.

Tribe Macrohomotomini White & Hodkinson, 1985, stat. rev.

Subtribe Diceraopsyllina Hollis & Broomfield, 1989, stat. nov.

Subtribe Dynopsyllina Bekker-Migdisova, 1973, stat. rev.

Subtribe Edenina Bhanotar, Ghosh & Ghosh, 1972, stat. nov.

Subtribe Macrohomotomina White & Hodkinson, 1985, stat. nov.

Subtribe Homotomina Heslop-Harrison, 1958, stat. nov.

Subtribe Phytolymina White & Hodkinson, 1985, stat. nov.

Subtribe Synozina Bekker-Migdisova, 1973, stat. nov.

Indepsylla† Klimaszewski, 1996, stat. rev.

Microphyllurus Li, 2002, stat. rev.

Parapsyllopsis† Klimaszewski, 1996, stat. rev.

Paropsylla† Klimaszewski, 1996, stat. rev.

Primascena† Klimaszewski, 1998, stat. rev.

Discussion

The revised classification presented here is similar to that of Burckhardt & Ouvrard (2012) but with some notable differences. The Carsidaridae, Homotomidae, Phacopteronidae and Triozidae remain unchanged in terms of circumscription and content but the first three are sunk to subfamilies. Also, the circumscription of the following well-defined subfamilies is identical in the two classifications: Aciziinae, Aphalarinae, Atmetocraniinae, Calophyinae, Liviinae, Metapsyllinae, Pachypsyllinae, Rhinocolinae, Spondyliaspidinae, Symphorosinae and Togepsyllinae. Their assignment to families remains unchanged except for Pachypsyllinae which is transferred from Aphalaridae to Carsidaridae, along with Homotomidae which is sunk to subfamily. From the Calophyidae of Burckhardt & Ouvrard (2012), the Mastigimatinae is removed and given family status, except for *Cecidopsylla* which is assigned to the Cecidopsyllinae within Aphalaridae. The most fundamental change concerns the Diaphorinini (Euphyllurinae) of Burckhardt & Ouvrard (2012), representing a polyphyletic assemblage of 13 genera. Apart from *Megadicrania*, *Peripsyllopsis* and *Psyllopsis*, which remain in Euphyllurinae, all genera are transferred to Psyllidae: *Caradocia*, *Epipsylla* and *Geijerolyma* to Ciriacreminae, *Cornopsylla* to Psyllinae, *Diaphorina* and *Parapsylla* to Diaphorininae and *Lautereropsis*, *Katacephala*, *Notophorina* and *Tuthillia* to Katacephalinae subfam. nov. *Microphyllurus* is removed from synonymy with *Peripsyllopsis* and moved as a separate subfamily to Aphalaridae. The Euphyllurinae as conceived here, is not further subdivided into tribes, but includes the three genera mentioned above and the constituent of the tribes Euphyllurini, Pachypsylloidini and Strophingiini of Burckhardt & Ouvrard (2012), but with *Neophyllura* removed into a separate subfamily. The Psyllidae as defined here differ from the previous concept in the addition of Diaphorininae and Katacephalinae subfam. nov. as well as slightly changed subfamily circumscriptions. The Amorphicolinae subfam. nov. and Platycoryphinae subfam. nov. are separated from Psyllinae, and a few genera and species are moved between subfamilies.

Future research should address the following aspects. The monophyly of the weakly supported family level taxa and weakly supported or unresolved relationships between these should be tested by including additional informative taxa not previously included and by analysing additional genes. The current placement of some taxa not previously included in the molecular analyses should be tested such as the placement of the Atmetocraniinae, Metapsyllinae and Symphorosinae in the Calophyidae; that of *Caradocia*, *Epipsylla* and *Geijerolyma* in the Ciriacreminae; that of *Lautereropsis*, *Notophorina* and *Tuthillia* in the Katacephalinae subfam. nov.; as well as that of *Allophorina*, *Limbopsylla* and *Padaukia* in the Platycoryphinae subfam. nov. In Psyllinae, several genera are poorly defined and more morphological and molecular work is required. The internal classification of Triozidae is not addressed here, as the entire generic classification of the family needs to be reexamined, a task beyond the scope of this paper. Finally, many new species and genera represented in collections (BMNH, MHNG, NHMB, USNM, etc.) await description and poorly known faunas, such as the Afrotropical and Neotropical regions, should be explored with targeted field work.

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Supp. file 1: The data of specimens illustrated on Figs 2–3, 5–8.
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