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

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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.
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 Magnoliidae 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 Palaeartic/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, Trichoza 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 Mastigimatae in their artificial Calophyidae. For this reason, Mastigimatae is removed from Calophyidae and given family rank here. This move is supported by Cho et al. (2019) although the phylogenetic placement of Mastigimatae 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 Vondrácik, 1957 (without Mastigimatae) 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, Spondylaspiddinae 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, Spondylaspiddinae 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 (Mastigimatae) 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 Paleopsylioidini†.
Tribe *Aphalarini* Löw, 1879

Caillardiini Loginova, 1964: 447.
Coelocarinae Li, 2011: 351.
Colposceniini Bekker-Migdisova, 1973: 109.
Eumetecini 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*, *Paracrasspedolepta*, *Tetrafollicula*, *Xanioptera*); *Crastina* Loginova, 1964 (syn. *Eustigmatia*); *Epheloscyta* Loginova, 1976; *Eumetoeus* 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 *Paleopsylloidites*† 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; *Paleopsylloidites*† 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.

*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

*Corregenapsylla* 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*, *Spondytorra*).

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 metabasitarcal 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 & Misfud 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

**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), Celsiaspis (Pachypsyllinae) is recovered as weakly supported sister-group of Homotomidae, rather than Carsidaridae, and the monophyly of Carsidaridae, Celsiaspis 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 Celsiaspis. 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 *Homotinae* 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; *Australdynopsylla* 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.

Psauusiini 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 genus**

*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 Diaphorini (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

Psyllopisiini 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 Diaphoriniini).

The molecular analyses clearly show that the Diaphoriniini 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 Diaphorinae, Katacephala, Lautereropsis, Notophorina and Tuthillia to Katacephalinae subfam. nov. and Cornopsylla to Psyllinae.

Included genera

Brachyphyllura Li, 2011; Crytophyllura Li, 2011; Ereomopsyllidoides Loginova, 1964; *Euphyllura Foerster, 1848 (syn. Platy stigma); Ligustrinia Loginova, 1973; Megadicrania Loginova, 1976; Pachypsylloidoides 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.
Sinuonomopsyllinae 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, Sinuonomopsylla, 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.

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**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 Cu₁₁b.

**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 Cu₁₁b. Hind wing 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*+*Synopsylla*, 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. *Synysylla* 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 *Synysylla* in the Mastigimataidae.

**Included genera**

*Bharatiana* Mathur, 1973; *Mastigimas* Enderlein, 1921 (syn. *Coelocara*); *Synysylla* 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.

![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.](image)

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

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

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preocular sclerite absent. Antenna with segment 3 longer than segments 7 or 8. Thorax moderately arched dorsally; propopleurites 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 Cu₁b. 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; anteoorbital 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; propopleurites 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 Cu₁b. 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* Hodgkinson, 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*’ lagunculariae 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*’ lagunculariae 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*’ lagunculariae(Brown & Hodkinson, 1988) comb. nov. and *Telmapsylla minuta* Hodgkinson, 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 antorbital tubercles, the hemispherical, adpressed eyes, the conical, apically pointed genital processes, the large cu₁ cell of the forewing, the
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 lagunculariae* (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; *Isogonocerea* 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.

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**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 chirai* Brown & Hodkinson, 1988     | not congeneric with *L. nata* (placement to be determined) |                                                 |
| *Limbopsylla esribii* Brown & Hodkinson, 1988    | not congeneric with *L. nata* (placement to be determined) |                                                 |
| *Limbopsylla lagunculariae* Brown & Hodkinson, 1988| *Telmapsylla lagunculariae* (Brown & Hodkinson, 1988) comb. nov. | comb. nov.                                   |
| *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) |                                                 |
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 procoecial 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 and cu large; anal break close to apex of vein Cu_{i3}. Hindwing slightly shorter than forewing; costal setae grouped; vein R and M+Cu. Metacoxa with large, horn-shaped, pointed meracanthus; metasternum slightly shorter than metatibia; metatibia bearing genual spine and 1+3+1 apical spurs. Metatarsals with two lateral spurs. Male metaptergite 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 unguicultrator 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.

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BURCKHARDT D. *et al.*, Updated classification of the jumping plant-lice
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* Vondrácék, 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. *Brachysylla*, *Gonanoplicus*, *Pennavena*, *Eudiaphorina*); *Parapsylla* Heslop-Harrison, 1961 (syn. *Agmapsylla*).

Subfamily *Katacephalinae* subfam. nov.

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 Cu1b. 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; antorbital 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 usually 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. Lauterropsis 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 \emph{Notophorina vitripennis} Burckhardt, 1987), bearing an open crown of 6–19 evenly spaced, sclerotised, apical spurs; metatarsiarsus with 2 spurs (exception \emph{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, unguinactor 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 \emph{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. \emph{Jenseniella}); \emph{Lautereropsis} Burckhardt & Malenovský, 2003; \emph{Notophorina} Burckhardt, 1987; \emph{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, \emph{Euphaleropsis} and \emph{Peregrinivena} were synonymised (Burckhardt \emph{et al.} 2018b). \emph{Trisetipsylla} was placed in the Macrocorsinae by Cho \emph{et al.} (2019) rather that in Psyllinae (Burckhardt & Ouvrard 2012). At least some species of \emph{Trisetipsylla} have immatures with extra pore fields on the caudal plate, supporting this placement.

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

A reevaluation of the status of the four fossil species by Klimaszewski (1996) and Peñalver & Garcia-Gimeno (2006) showed that \emph{Otroacizzia} is a species mix referable to \emph{Colophorina} (\emph{O. muta}) and to \emph{Euryconus} (other species). Whereas the antennae are short and a genual spine is lacking in \emph{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.**

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**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 cu₁ large; anal break close to apex of vein Cu₁b. Male proctiger one-segmented.

**Fifth instar immature**

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

**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 cu1 large; caudal break close to apex of vein Cu1b. 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 moderary 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

*Artytainini* Crawford, 1914: 106.
*Allooneurini* Vondráček, 1951: 127.
*Anomoneurini* Klimaszewski, 1963: 92.
*Cymophilini* 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: *Artytina* Foerster, 1848, *Artytainilla* Loginova, 1972, *Arytinnis* Percy, 2003 and *Livilla* Curtis, 1835. The first three are monophyletic, the last is paraphyletic with respect to *Artytainilla* 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 \textit{Ceanothus} L. (Rhamnaceae) (= \textit{Ceanothia} Heslop-Harrison, 1961 and \textit{Nyctiphalerus} Bliven, 1955, see Table 2), previously referred to the genera \textit{Ceanothia}, \textit{Euglyptoneura} Heslop-Harrison, 1961 and \textit{Nyctiphalerus}, which is sister group to a poorly supported clade comprising one clade represented by a single species (\textit{Pexopsylla cercocarpi} Jensen, 1957) and four very strongly supported clades: 1. holarctic species of \textit{Cacopsylla} Ossiannilsson, 1970 associated with Elaeagnaceae, Lardizabalaceae, Rosaceae and Salicaceae (= \textit{Cacopsylla} s. str.); 2. holarctic species associated with Betulaceae (= \textit{Psylla} s. str., Table 3), previously referred to \textit{Baeopelma} Enderlein, 1926, \textit{Capopsylla}, \textit{Chamaepsylla} Ossiannilsson, 1970 and \textit{Psylla}; 3. palaearctic species associated with \textit{Buxus} (Buxaceae) (= \textit{Spanioneura} Foerster, 1848, see Table 4), previously referred to \textit{Psylla} and \textit{Spanioneura}; 4. North American species associated with \textit{Cercocarpus} and \textit{Purshia} (Rosaceae) (= \textit{Purshivora} Heslop-Harrison, 1961, see Table 2), previously referred to \textit{Cacopsylla}, \textit{Ceanothia}, \textit{Nyctiphalerus} and \textit{Purshivora}. Cho et al. (2019) transferred \textit{Psylla longicauda} Konovalova, 1986, an Asian species associated with \textit{Prunus}, to \textit{Spanioneura} and provided morphological adult characters to define \textit{Psylla} s.str. and \textit{Spanioneura}.

Similar to \textit{Arytaina}, \textit{Arytainilla}, \textit{Arytainnis} and \textit{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 \textit{Ceanothus} (Rhamnaceae) as well as \textit{Cercocarpus} and \textit{Purshia} (Rosaceae). North America authors (Crawford 1914; Tuthill 1943b; Jensen 1956, 1957a, 1957b; Bliven 1956, 1958) assigned these species to the genera \textit{Arytaina}, \textit{Euphalerus} and \textit{Psylla}, rendering these genera very artificial, and to two monotypic genera \textit{Nyctiphalerus} and \textit{Pexopsylla}. Heslop-Harrison (1961) discussed the North American genera previously referred to \textit{Arytaina} and, rightly, concluded that they are not congeneric with \textit{Arytaina spartii} (Hartig, 1841) (= \textit{A. genistae} (Latreille, 1804)), the type species of \textit{Arytaina}. He erected the four genera \textit{Amorphicola} Heslop-Harrison, 1961, \textit{Ceanothia}, \textit{Euglyptoneura} and \textit{Purshivora}. His descriptions are not diagnostic and he also mixed up the figures (fig. 2 concerns \textit{Ceanothia} and fig. 3 \textit{Amorphicola}, and not vice versa). Whereas \textit{Amorphicola} (see \textit{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 \textit{Euphalerus} Schwarz, 1904 and suggested that the Nearctic species are not congeneric with \textit{Euphalerus nidifex} Schwarz, 1904, the type species, or with most of the Neotropical species. Percy et al. (2012) transferred these species to \textit{Nyctiphalerus}. The molecular analyses shed much needed light on the phylogenetic relationships in this group. There are monophyletic clades associated with Rhamnaceae (\textit{Ceanothus}) and with Rosaceae (\textit{Cercocarpus}, \textit{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 \textit{Ceanothus} comprises one group with the genal processes in a lower plane to that of the vertex and lacking a genal metatibial spine (type species of \textit{Ceanothia} and \textit{Euglyptoneura}), and another group with genal processes and vertex flattened and in the same plane and bearing a genal metatibial spine (type species of \textit{Nyctiphalerus}). The Rosaceae clade also splits into two groups: one bearing metatarsal spurs (type species of \textit{Purshivora}) and one lacking metatarsal spurs (type species of \textit{Pexopsylla}). Here we suggest that \textit{Ceanothia}, \textit{Nyctiphalerus}, \textit{Pexopsylla} and \textit{Purshivora} are good genera, and that \textit{Euglyptoneura} syn. nov. is a junior synonym of \textit{Ceanothia} (Table 2).

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

\textit{Psyllinae} is a species-rich subfamily (ca 800 spp., Ouvarard 2020) with many species referred to \textit{Cacopsylla} s. str. and \textit{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 \textit{Cacopsylla} s. lat. and \textit{Psylla} s. lat.
Table 2 (continued on next page). North American species in Psyllidae Latreille, 1807 associated with *Ceanothus* (Rhamnaceae) as well as *Cercocarpus* and *Purshia* (Rosaceae) referable 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 ceanothi*, unjustified emendation by Tuthill (1943b)

| Ceanothia fuscipennis (Crawford, 1914) | Arytaina fuscipennis Crawford, 1914; *Euglyptoneura fuscipennis* (Crawford, 1914) | comb. nov. |
| Ceanothia tardiuscula (Bliven, 1958) | *Arytaina tardiuscula* Bliven, 1958 | transferred by Hodkinson (1988) |

*Nyctiphalerus* Bliven, 1955, type-species *Nyctiphalerus lyncus*, 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 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

| Nyctiphalerus verniculosus (Crawford, 1914) | Euphalerus verniculosus 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)

| Purshivora cercocarpi (Jensen, 1957) | *Euphalerus cercocarpi* Jensen, 1957; *Nyctiphalerus cercocarpi* (Jensen, 1957) | comb. nov. |
Included genera

Anomoneura Schwarz in Uhler, 1896; *Arytaina* Foerster, 1848 (syn. *Amblyrhina*, *Ataenia*, *Psylla*);
*Arytainilla* Loginova, 1972 (syn. *Hispaniola* Ramirez 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* Kirkaldy, 1905 nomen nudum; *Arytininis* Percy, 2003; *Astragalita* Loginova, 1976; *Cyamophila* Loginova, 1976; *Cyamophiliopsis* Li, 2011; *Cylindropsylla* Li, 2011; *Gelonopsylla* Li, 1992; *Livilla* Curtis, 1835 (syn. *Alloeoneura*, *Floria*, *Floriella*); *Mecistoneura* Li, 2011; *Palaeolindbergiella* Heslop-Harrison, 1961; *Psylla* Geoffroy, 1762 (syn. *Baeopelma* syn. nov., *Chamaepsylla* syn. nov., *Psylla* (Labyrinthopsylla) syn. nov., *Asphagis* Enderlein, 1921); *Pexopsylla* Jensen, 1957, type-species *Pexopsylla cercocarpi*, Jensen, 1957, by original designation

*Burckhardt D. et al.*, Updated classification of the jumping plant-lice

Table 2 (continued).

| Valid combination | Previous combinations | Comments |
|-------------------|-----------------------|----------|
| 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 difficileis (Tuthill, 1943) | Psylla difficileis Tuthill, 1943; Cacopsylla difficileis (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 (?)Hepatopsylla 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

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

| Valid combination | Original combination | Comments |
|-------------------|----------------------|----------|
| *Psylla* Geoffroy, 1762 | *Chermes alni* Linnaeus, 1758 | by subsequent designation under the plenary powers of the ICZN Opinion 731 (1965); *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. |
| *Psylla alni* (Linnaeus, 1758) | *Chermes alni* Linnaeus, 1758 | comb. rev. from *Baeopelma* |
| *Psylla alnifasciata* Li, 2011 | | |
| *Psylla alpina foersteri* Horváth, 1908 | | |
| *Psylla caudata* Crawford, 1914 | | |
| *Psylla cordata* Tamanini, 1977 | | |
| *Psylla floccosa* Patch, 1909 | | |
| *Psylla foersteri* Flor, 1861 | | |
| *Psylla fusca* (Zetterstedt, 1828) | *Chermes fusca* Zetterstedt, 1828 | |
| *Psylla magnifera* Kuwayama, 1908 | | |
| *Psylla viridescens* (Provancher, 1872) | *Diraphia viridescens* Provancher, 1872 | |
| *Psylla ancylocaula* Li, 2011 | | |
| *Psylla betulacola* (Linnaeus, 1758) | *Chermes betulacola* Linnaeus, 1758 | |
| *Psylla betulaenae* Ossiannilsson, 1970 | | |
| *Psylla betulibetulae* 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* |
| *Psylla carpinicola* Crawford, 1914 | | |
| *Psylla diloncha* (Caldwell, 1938) | *Psyllia diloncha* Caldwell, 1938 | comb. rev. from *Cacopsylla* |
| *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* | | |
| *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) |
| **Host: Buxus (Buxaceae)** | | |
| *Spanioneura chujo* (Miyatake, 1982) | *Psylla chujo* 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 pechui* (Klimaszewski & Lodos, 1977) | *Amblyrhina pechui* 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.
Carsitrini Li, 2011: 1303.
Epitriozini Kwon, 1983: 79.
Eutriozini Loginoiva, 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. 
Siphonaleyroidea Takahashi, 1932: 48. 
Trichochermini Kwon, 1983: 82. 
Trizopsinae 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 *Triozoa* Foerster, 1848 with over 400 described species has long been recognised as polyphyletic (Hollis 1984). The molecular analyses confirm the polyphyly of *Triozoa* 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**

*†Acanthocnema* Tuthill & Taylor, 1955; *Acanthocasuarina* Taylor in Taylor et al. (2011); *Afrotrioza* Hollis, 1984; *†Anomocepha* Tuthill, 1942; *Asiotrioza* Li, 2011; *†Bactericera* Puton, 1876 (syn. *Allotrioza*, *Carsiria*, *Eubactericera*, *Bactericera* (Klimaszewski) replacement name for *Smirnovia* Klimaszewski nec Lučnic, *Paratrioza*, *Rhinopsylla*); *Baeolitriozus* Casuarinicola, 1991; *†Ceropsysylla* Riley, 1885; *†Cerotrioza* Crawford, 1918; *Choutrioza* Li, 1989; *Colopelma* Enderlein, 1926; *Conicotreioza* Li, 2005; *Crawforda* Caldwell, 1940; *Dolichotrioza* Li, 2002; *†Dyspersa* Klimaszewski, 1968; *Egeirotrioza* Bosselli, 1931 (syn. *Evegiotrioza*); *Engytatoneura* Loginova, 1972; *Eotrioza* Konovalova, 1987 (syn. *Trachotrioza* Li, 2011); *Epitrioza* Kuwayama, 1910; *Eryngiofaga* Klimaszewski, 1968; *Eutrioza* Loginova, 1964; *Furcitrioza* Li, 2011; *Genotrioza* Li, 2011; *†Hemischizocranium* Tuthill, 1956; *†Hemitrioza* Crawford, 1914; *†Heterotrioza* Dobreau & Manolache, 1960 (syn. *Triozia* (Halotrioza), *Triozidus*); *†Hevaheva* Kirkaldy, 1902; *†Hippopaetrioza* Conci & Tamanini, 1984 (syn. *Hippopaetrioza* (Maculatrioza)); *Ipania* Klimaszewski, 1962; *†Kuwayama* Crawford, 1911 (replacement name for *Eptipioza* 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; *Neolitthis* Scott, 1882; *Neotrioza* Kieffer, 1905; *Neotrizella* Crawford, 1911 (replacement name for *Neotrioza* Crawford nec Kieffer); *Nothotrioza* Burckhardt in Carneiro et al., 2013; *Ozotrioza* Kieffer, 1905; *Parastenopsylla* Yang, 1984 (syn. *Indotrioza*); *†Paraiconus* Enderlein, 1926; *†Pauropsylla* Rübsaamen, 1899 (syn. *Neotrioza* sensu Li, 2011 nec Kieffer, 1905, misinterpretation, *Sympauropsylla*); *Paurotirozana* Caldwell, 1940; *Petalolyma* Scott, 1882; *†Phyllopecta* Riley, 1884 (syn. *Choricymoza*, *Sinotrioza*); *†Powellia* Maskell, 1879; *Pseudotrioza* Miyatake, 1972; *Rhegunia* 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; *†Triosa* 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 Cienarytaina 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 chujo (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 lagunculariae (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.
Parapsylla† 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, Liviniae, Metapsyllinae, Pachypsyllinae, Rhinocolinae, Spondylaspisidae, Symphorosinae and Togephyllinae. 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 (Euphylurinae) of Burckhardt & Ouvrard (2012), representing a polyphyletic assemblage of 13 genera. Apart from Megadicrania, Peripsyllopsis and Psyllopsis, which remain in Euphylurinae, 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 Tuthilla to Katacephalinae subfam. nov. Microphyllurus is removed from synonymy with Peripsyllopsis and moved as a separate subfamily to Aphalaridae. The Euphylurinae as conceived here, is not further subdivided into tribes, but includes the three genera mentioned above and the constituent of the tribes Euphylurini, 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 Diaphorinini 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 Atmetocranini, Metapsyllinae and Symphorosinae in the Calophyidae; that of Caradocia, Epipsylla and Geijerolyma in the Ciriacreminae; that of Lautereropsis, Notophorina and Tuthilla 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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