

**Phylogenetic relationships within the subfamily Aphalarinae
including a revision of *Limataphalara*
(Hemiptera: Psylloidea: Aphalaridae)**

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BURCKHARDT D. & QUEIROZ D. L. 2013: Phylogenetic relationships within the subfamily Aphalarinae including a revision of *Limataphalara* (Hemiptera: Psylloidea: Aphalaridae). In: KMENT P., MALENOVSKÝ I. & KOLIBÁČ J. (eds.): Studies in Hemiptera in honour of Pavel Lauterer and Jaroslav L. Stehlík. *Acta Musei Moraviae, Scientiae biologicae* (Brno) **98(2)**: 35–56. – The hitherto monotypic Neotropical genus *Limataphalara* Hodkinson, 1992 is revised and three new species are described and illustrated: *Limataphalara eucosma* sp.nov. from Brazil associated with *Nectandra lanceolata* (Lauraceae), *L. hollisi* sp.nov. from Costa Rica associated with *N. membranacea*, and *L. lautereri* sp.nov. from Brazil associated with *N. cuspidata*. Based on the new species the generic diagnosis is revised and the presumed host association with *Nectandra* is confirmed. For the first time larvae of the genus are described and the phylogenetic relationships of all known genera within Aphalarinae are analysed with cladistic methodology using 16 morphological characters. The analysis resulted in three most parsimonious trees which differ considerably from previously published phylogenetic schemes resulting in the following new family level synonymies: Aphalarinae Löw, 1879 (= Caillardini Loginova, 1964, syn.nov.; Coelocarinae Li, 2011, syn.nov.; Colposceniini Bekker-Migdisova, 1973, syn.nov.; Craspedoleptini Klimaszewski, 2001, syn.nov.; Eumetoecini Li, 2011, syn.nov.; Gyropsyllini White & Hodkinson, 1985, syn.nov.; Rhombaphalarini Klimaszewski, 1987, syn.nov.; Stigmaphalarini Vondráček, 1957, nomen nudum, syn.nov.; Xenaphalarini Loginova, 1964, syn.nov.), and the following new genus level synonymy: *Rhodochlanis* Loginova, 1964 (= *Rhombaphalara* Loginova, 1964, syn.nov.). The following revised or new combinations are proposed: *Rhodochlanis* Klimaszewski, 1967, stat. rev. (from *Rhombaphalara*); *Rhodochlanis halocnemi* (Loginova, 1964), comb.nov. (from *Rhombaphalara*); *Rhodochlanis halostachidis* (Loginova, 1970), comb.nov. (from *Rhombaphalara*); *Rhodochlanis insolita* (Burckhardt & Mifsud, 1998), comb.nov. (from *Rhombaphalara*). Identification keys are provided for adults of the world genera of Aphalarinae and for adults and larvae of the known *Limataphalara* species.

Keywords. Psyllids, Aphalarinae, taxonomy, new species, phylogeny, host plants, Neotropical Region

Introduction

Psyllids or jumping plant-lice are phloem-feeding Sternorrhyncha resembling minute cicadas. They are generally highly host specific on woody dicotyledonous plants and display their largest species diversity in the tropics (BURCKHARDT 2005, HOLLIS 2004). The subfamily Aphalarinae (Aphalaridae) is atypical in this respect as two thirds of its constituent genera occur in North temperate biomes and the two largest genera, *Aphalara* Foerster, 1848, and *Craspedolepta* Enderlein, 1921, are associated with herbaceous plants of the Asteraceae, Polygonaceae and several other families (Table 1). *Aphalara* and *Craspedolepta* are predominantly Holarctic in distribution; *Crastina*

Loginova, 1964, and *Colposcencia* Enderlein, 1929, occur in the Palaearctic, Oriental and Afrotropical Regions; *Brachystetha* Loginova, 1964, *Caillardia* de Bergevin, 1931, *Epheloscyta* Loginova, 1976, *Eumetoecus* Loginova, 1961, *Eurotica* Loginova, *Rhodochlanis* Loginova, 1964, and *Xenaphalara* Loginova, 1961, are restricted to the Palaearctic; the monotypic genera *Hodkinsonia* Burckhardt *et al.*, 2004, *Lanthanaphalara* Tuthill, 1959, *Limataphalara* Hodkinson, 1992, and *Neaphalara* Brown & Hodkinson, 1988, are endemic to the Neotropical Region; and *Gyropsylla* Brèthes, 1921, occurs in the Neotropical, Nearctic and Oriental Regions.

Table 1. Host plants of aphalarine genera.

Psyllid genus	Host genus
<i>Aphalara</i>	Polygonaceae (Caryophyllales) and other families; herbaceous plants
<i>Brachystetha</i>	<i>Nitraria</i> (Nitrariaceae, Sapindales)
<i>Caillardia</i>	<i>Anabasis</i> , <i>Haloxylon</i> (Amaranthaceae, Caryophyllales)
<i>Colposcencia</i>	<i>Tamarix</i> (Tamaricaceae, Caryophyllales)
<i>Craspedolepta</i>	Asteraceae (Asterales) and other families; herbaceous plants
<i>Crastina</i>	<i>Myricaria</i> , <i>Tamarix</i> (Tamaricaceae, Caryophyllales)
<i>Epheloscyta</i>	<i>Kalopanax</i> (Araliaceae, Apiales)
<i>Eumetoecus</i>	<i>Kochia</i> (Amaranthaceae, Caryophyllales)
<i>Eurotica</i>	<i>Eurotia</i> (Amaranthaceae, Caryophyllales)
<i>Hodkinsonia</i>	<i>Aralia</i> (Araliaceae, Apiales)
<i>Gyropsylla</i>	<i>Ilex</i> (Aquifoliaceae, Aquifoliales)
<i>Lanthanaphalara</i>	<i>Dunalia</i> (Solanaceae, Solanales)
<i>Limataphalara</i>	<i>Nectandra</i> (Lauraceae, Laurales)
<i>Neaphalara</i>	Araliaceae (Apiales)
<i>Rhodochlanis</i>	Amaranthaceae (Caryophyllales)
<i>Xenaphalara</i>	<i>Ceratocarpus</i> (Amaranthaceae, Caryophyllales)

Based on adult characters of the Palaearctic taxa LOGINOVA (1964a, b) subdivided the Aphalarinae into the four tribes Aphalarini, Caillardiini, Colposceniini and Xenaphalarini. WHITE & HODKINSON (1985), in their classification of the world fauna, adopted to a large extent Loginova's classification. They analysed adult and larval characters but included only six genera referred to this subfamily. They added the tribes Gyropsyllini for *Gyropsylla* and transferred the Phytolymini erected by BEKKER-MIGDISOVA (1973) for *Phytolyma* Scott, 1882, from the Anomalopsyllinae (Aphalaridae) to the Aphalarinae. The Phytolymini was later moved to the Homotomidae by OUVARD (2002). KLIMASZEWSKI (1983, 1987) used a phenetic approach to analyse the Palaearctic taxa. He split *Craspedolepta* s. l. into several genera and subgenera and proposed a classification of six tribes which resembled that of WHITE & HODKINSON (1985) but differed in the erection of the Rhombaphalarini for three genera previously assigned to the Caillardiini. Klimaszewski's classification was discussed by BURCKHARDT & LAUTERER (1997) who pointed out methodological shortcomings and mistakes in the

observation of some characters. KLIMASZEWSKI (2001) further developed his previous classifications and split off the Craspedoleptini from the Aphalarini. BURCKHARDT & OUVARD (2012) recognised in their revised psyllid classification the extant tribes Aphalarini, Caillardiini, Colposceniini, Gyropsyllini and Xenaphalarini, suggesting that the subfamily in its present definition is likely to be monophyletic but that the constituent tribes may not be. In addition to the recent taxa, several fossil Aphalarinae have been described which are referred to the extinct tribe Paleopsylloidiini (OUVRARD *et al.* 2013). The fossil tribe is not discussed here. In summary, none of the previous classifications of Aphalarinae used cladistic methodology nor included all genera in their assessments thus making them difficult to test.

HODKINSON (1980, 1989, 1992) suggested that the majority of Aphalarinae is of Palearctic origin, and that *Aphalara* and *Craspedolepta* migrated to North America across a Beringia connection. The Neotropical taxa, however, represent relict forms of a much larger fauna. Hodkinson (1992) pointed out that the small or monotypic Neotropical genera appear taxonomically isolated from each other but that the host plant, i.e. *Nectandra* (Lauraceae), could represent a shared character between related taxa. HOLLIS & MARTIN (1997) presented an overview of psyllids associated with Lauraceae and listed the following New World Aphalarinae from *Nectandra*: *Gyropsylla cannella* (Crawford, 1925) from ?*Nectandra* sp. (Brazil), *Limataphalara brevicephala* Hodkinson, 1992, from *N. coriacea* (Belize, USA: Florida), and a new species of an unidentified genus from *N. membranacea* (Costa Rica). During recent field work in Brazil we found another two undescribed species similar to the last one, also associated with *Nectandra*.

Here we describe the new taxa from *Nectandra*, analyse their phylogenetic relationships within the Aphalarinae, test previous classifications of Aphalarinae and discuss host plant and biogeographic relationships.

Material and methods

Material was examined or is listed from following institutions:

LEEF	Laboratório Entomológico, Embrapa Florestas, Colombo, PR, Brazil
MHNG	Muséum d'histoire naturelle, Genève, Switzerland
MZSP	Museu de Zoologia, Universidade de São Paulo, SP, Brazil
NHMB	Naturhistorisches Museum, Basel, Switzerland
BMNH	Natural History Museum, London, UK
USNM	United States National Museum collections, Beltsville, MD, USA

Morphological terminology follows HOLLIS (1976, 2004), BROWN & HODKINSON (1988), OSSIANNILSSON (1992), and YANG *et al.* (2009). The morphological studies were made with a Leica MZ12 stereo microscope and a Leica DMLB (with phase contrast and Nomarski differential interference contrast) compound microscope. The drawings were made with a drawing tube from permanent mounts in Canada balsam of dissected specimens previously cleared in KOH and washed in H₂O. Measurements were taken from slide mounted material and are given in millimeters (mm).

A cladistic analysis was performed with NONA version 2.0 (GOLOBOFF 1999) and WINCLADA 1.00 (NIXON 2002). The following parameters were used: maximum trees to keep = 10 000; number of replications = 5; starting trees per replication = 5; random seed = 0; search strategy = multiple TBR (tree-bisection-reconnection) + TBR; unconstrained search. For constructing a consensus tree the command Nelsen (collapse + consensus) was chosen.

Phylogenetic analysis

For analysing the phylogenetic relationships among extant aphalarine genera we performed a cladistic analysis using 16 adult characters, six of which concern the head and its appendages, two the thorax, one the forewing, five the hind legs and two the aedeagus (Tables 2 and 3). Most characters are binary except for four, which are treated as unordered. *Tainarys* Brèthes, 1920 (Aphalaridae, Rhinocolinae) was included in the analysis as outgroup. The analysis resulted in 3 most parsimonious trees (Fig. 1, consensus tree) of 31 steps with a consistency index = 0.67 and retention index = 0.83.

The anteriorly displaced eyes and enlarged postorbital ridges (characters 1 and 2, Table 2) in *Eurotica* and *Xenaphalara* were used by LOGINOVA (1964a) to group them

Table 2. Characters and states used in the cladistic analysis (*cf.* Table 3, Fig. 1).

1. Eyes in normal position (0); displaced anteriorly (1)
2. Post-orbital ridges (in longitudinal body axis) short (0); long (1)
3. Vertex length > half width (0); equal or < half width (1)
4. Frons large, triangular (0); small, very short, parallel-sided (1); small, triangular (2); narrow, long, ribbon-shaped (3)
5. Clypeus flattened, heart-shaped (0); produced, spherical or tubular (1)
6. Rhinarium on antennal segment 7 absent (0); present (1)
7. Propleurites divided by a vertical suture (0); by an oblique suture (1)
8. Mesosternum subrectangular, rounded laterally (0); narrowed in the middle, with rim antero-laterally (1); very short, transverse (2)
9. Pterostigma of forewing present (0); absent (1)
10. Metacoxa with area beneath meracanthus straight (0); bearing a swelling (1)
11. Metatibia length/femur length ratio < 1.4 (0); > 1.5 (1)
12. Long stout bristles on apex of metafemur and base of metatibia lacking (0); present (1)
13. Apical metatibial spurs moderately dense, short (0); very dense, long (1); hardly sclerotised (2)
14. Metatarsus moderately long (0); very short (1)
15. Apex of aedeagus simple, weakly inflated (0); simple, strongly inflated (1); strongly inflated, with anterior sclerotised hook and posterior membranous lobe (2)
16. Joint of distal segment of aedeagus at base (0); set some way from base (1)

Phylogenetic relationships within Aphalarinae and revision of *Limataphalara*

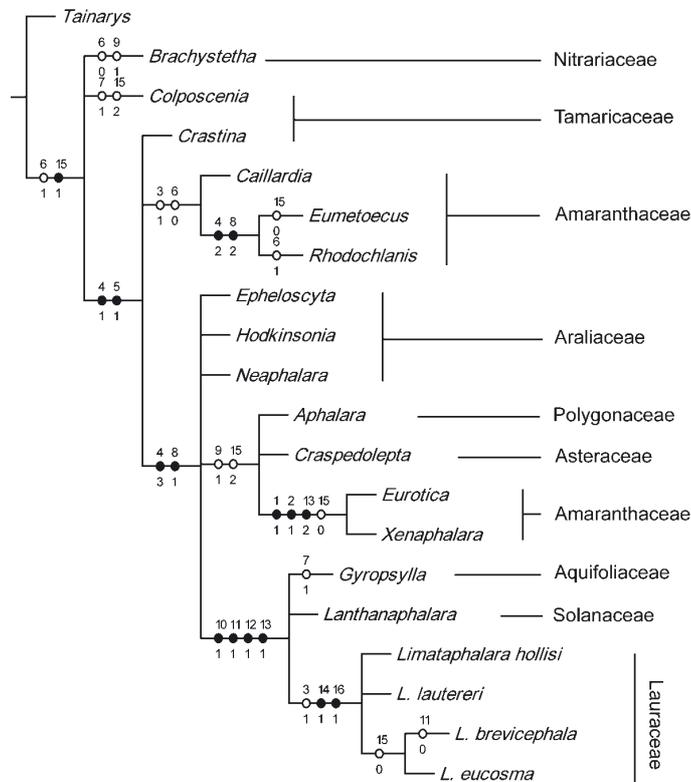


Fig. 1. Cladogram illustrating phylogenetic and host plant relationships of Aphalarinae. *Tainarys* (Rhinocolinae) was chosen as outgroup. Characters (numbers above dots) and character states are listed in Table 2, the character matrix in Table 3. Black dots represent synapomorphies, white dots homoplasies.

together in the Xenaphalarini. This group is also recovered in our analysis. KLIMASZEWSKI (1987) and LOGINOVA (1964a) split the subfamily into two groups based on the relative vertex length (character 3), short in the Caillardiini *sensu* Loginova and long in the other tribes. LOGINOVA (1964a) did not mention which state she thought was derived. KLIMASZEWSKI (1987) suggested, with doubts, that the short vertex is derived but he did not include the character in his cladogram. The Caillardiini *sensu* Loginova is also monophyletic in our analysis. A previously not considered character concerns the frons (character 4). In *Tainarys* (outgroup), *Brachystetha* and *Colposcencia* the frons is large and triangular suggesting that this is the plesiomorphic state. In *Caillardia* and *Crastina* the frons is very short and parallel-sided, in *Eumetoecus* and *Rhodochlanis* small and triangular, and in the remaining genera narrow, long and ribbon-shaped. The last two states define a monophyletic group each. The former corresponds to the Rhombaphalarini *sensu* KLIMASZEWSKI (1987), the latter to the tribes Aphalarini, Gyropsyllini and

Table 3. Matrix for Aphalarinae (cf. Table 2, Fig. 1).

<i>Tainarys</i>	0000000000000000
<i>Aphalara</i>	0003110110000020
<i>Brachystetha</i>	0000000010000010
<i>Caillardia</i>	0011100000000010
<i>Colposcения</i>	0000011000000020
<i>Craspedolepta</i>	0003110110000020
<i>Crastina</i>	0001110000000010
<i>Epheloscyta</i>	0003110100000010
<i>Eumetoecus</i>	0012100200000000
<i>Eurotica</i>	1103110110002000
<i>Hodkinsonia</i>	0003110100000010
<i>Gyropsylla</i>	0003111101111010
<i>Lanthanaphalara</i>	00031101011110?0
<i>Limataphalara brevicephala</i>	0013110101011101
<i>Limataphalara eucosma</i>	0013110101111101
<i>Limataphalara hollisi</i>	0013110101111111
<i>Limataphalara lautereri</i>	0013110101111111
<i>Neaphalara</i>	0003110100000010
<i>Rhodochlanis</i>	0012110200000010
<i>Xenaphalara</i>	1103110110002000

Xenaphalarini *sensu* WHITE & HODKINSON (1985). The clypeus (character 5) can be flattened as in *Tainarys* (outgroup), *Brachystetha* and *Colposcения*, spherical or tubular. KLIMASZEWSKI (1987) used the clypeus in his analysis. The four states he distinguished are not clear and he may have miscoded some taxa. For example, *Aphalara* and *Brachystetha* are said to have a rounded forward directed clypeus, which is true for *Aphalara* but not *Brachystetha* where it is flattened. Most aphalarines have a single subapical rhinarium on each of segments 4–9 (character 6) but in *Brachystetha*, *Caillardia* and *Eumetoecus* those on segments 7 and sometimes 4 are reduced. KLIMASZEWSKI (1987) suggested that the presence of six rhinaria is primitive within Aphalarinae and that reductions occurred several times independently. This is confirmed by our study. The propleurites (character 7) are divided by a vertical suture in all genera except for *Colposcения* and *Gyropsylla* where the suture is oblique. According to LOGINOVA (1964a) and WHITE & HODKINSON (1985) the suture is diagonal in *Crastina* but this is not the case. KLIMASZEWSKI (1987) suggested that this character is of little use to elucidate relationships in Aphalarinae which is confirmed by our analysis. The mesosternum (character 8) is subrectangular and rounded laterally in its plesiomorphic state. In *Eumetoecus* and *Rhodochlanis* it is very short and transverse. In the *Epheloscyta*–*Limataphalara*-clade it is narrowed in the middle with an antero-lateral rim. Several forewing characters have been used by previous authors in their analyses. KLIMASZEWSKI (1987) defined the Caillardiini *sensu* Loginova by forewings which ‘are thickened and half-cuticular’. This character is difficult to define and variable within some genera, and we consider it unsuitable for phylogenetic purposes. Similarly the

presence or absence of a ‘nodal-line’, a character which was used by previous authors, is sometimes difficult to determine. The suggested presence in *Crastina* by LOGINOVA (1964a) and WHITE & HODKINSON (1985) could not be substantiated. The same goes for the lack of a costal break in *Aphalara* and *Craspedolepta* mentioned by WHITE & HODKINSON (1985) which is erroneous. The presence/absence of a pterostigma (character 9) is equally problematical. It is absent in *Aphalara*, *Brachystetha* and *Craspedolepta* but present in the other genera though very narrow in some cases. In *Gyropsylla*, e.g. it is short and broad in *G. cannella* (Crawford, 1925) but long and very narrow in *G. spagazziniana* (Lizer, 1919). The clade *Gyropsylla*–*Limataphalara* is characterised by the metacoxa with the area beneath the meracanthus bearing a swelling (character 10). HODKINSON (1992) suggested that also *Neaphalara* bears this large swelling but this is not the case. The clade *Gyropsylla*–*Limataphalara* is further characterised by very long metafemora (character 11), the presence of long stout bristles on the apex of the metafemur and base of metatibia (character 12), and very dense, long apical metatibial spurs (character 13). In *Eurotica* and *Xenaphalara* the apical metatibial spurs are hardly sclerotised. Autapomorphic for *Limataphalara* is the very short metatarsus (character 14). KLIMASZEWSKI (1987) used the shape of the apex of the distal segment of the aedeagus which we use here in a slightly simplified way (character 15). The analysis suggests that this character shows a lot of homoplasy. Autapomorphic for *Limataphalara* is the joint of the distal segment of aedeagus which is set some way from base (character 16). No larval characters could be found suitable for the cladistic analysis mostly due to insufficient material.

Key to world genera of Aphalarinae (adults)

- 1 Metacoxa with area beneath meracanthus strongly swollen. 2
- Metacoxa with area beneath meracanthus almost straight. 4
- 2 Clypeus tubular, extended perpendicularly to lower head surface, with shoulder-like constriction medially. On *Ilex* (Aquifoliaceae). *Gyropsylla*
- Clypeus short, subspherical. 3
- 3 Vertex, along midline, longer than half its width, bearing a large anterior lobe on either half. On *Dunalia* (Solanaceae). *Lanthanaphalara*
- Vertex, along midline, shorter than half its width, smoothly passing into genae anteriorly not bearing anterior lobes. On *Nectandra* (Lauraceae). *Limataphalara*
- 4 Eyes displaced anteriorly. Postorbital ridges large. Apical metatibial spurs light-coloured, hardly sclerotised. 5
- Posterior eye margin almost level with posterior head margin. Postorbital ridges narrow. Apical metatibial spurs dark brown or almost black, strongly sclerotised. 6

- 5 Clypeus acute apically. Forewing with long, slender pterostigma, vein Rs sinuous relative to fore margin. On *Eurotia* (Amaranthaceae). ***Eurotica***
- Clypeus rounded apically. Forewing without pterostigma, vein Rs convex relative to fore margin. On *Ceratocarpus* (Amaranthaceae). ***Xenaphalara***
- 6 Frons small, at most as long as longitudinal diameter of frontal ocellus, broad, parallel-sided. 7
- Frons larger, more than twice as long as longitudinal diameter of frontal ocellus. 8
- 7 Head inclined almost 90° from longitudinal body axis. On *Anabasis* and *Haloxylon* (Amaranthaceae). ***Caillardia***
- Head inclined about 45° from longitudinal body axis. On *Myricaria* and *Tamarix* (Tamaricaceae). ***Crastina***
- 8 Frons widening towards base, more or less triangular, short or long. 9
- Frons narrowly ribbon-shaped, often narrowed towards base, long. ... 12
- 9 Clypeus adpressed, flattened. Vertex more than half as long as wide, ending in flat lobes anteriorly. 10
- Clypeus sticking out, subglobular or tubular. Vertex less than half as long as wide, rounded to genae anteriorly. 11
- 10 Propleurites with subequal proepisternum and epimeron, divided by perpendicular suture. Forewing lacking pterostigma. On *Nitraria* (Nitrariaceae). ***Brachystetha***
- Propleurites with small proepisternum and large epimeron, divided by diagonal suture. Forewing bearing distinct pterostigma. On *Tamarix* (Tamaricaceae). ***Colposcения***
- 11 Preocular sclerite large, posteriorly reaching to base of vertex. A subapical rhinarium present on each of antennal segments 4, 6, 8 and 9. On *Kochia* (Amaranthaceae). ***Eumetoecus***
- Preocular sclerite small, posteriorly reaching at most to the middle of vertex. A subapical rhinarium present on each of antennal segments 4–9. On various Amaranthaceae. ***Rhodochlanis* (= *Rhombaphalara* syn.nov.)**
- 12 Forewing lacking pterostigma. 13
- Forewing with membranous pterostigma. 14
- 13 Clypeus tubular, often very long. Vertex angular anteriorly, separated from genae by narrow groove. On herbaceous Polygonaceae and other families. ***Aphalara***

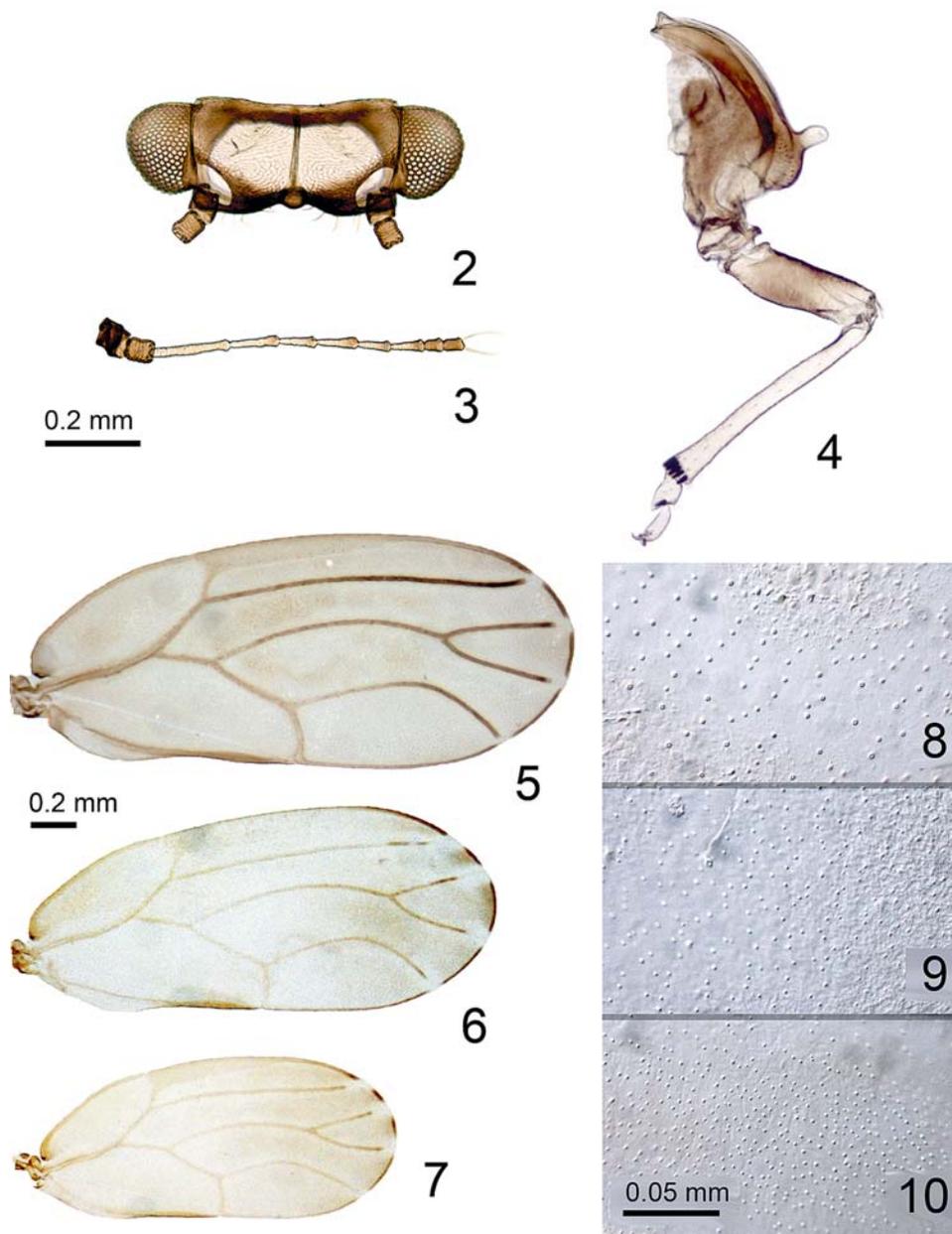
- Clypeus spherical. Vertex usually rounded anteriorly, passing smoothly into genae. On herbaceous Asteraceae and other families. *Craspedolepta*
- 14 Pterostigma long, ending at about apical fifth of vein Rs. Palaearctic. On *Kalopanax* (Araliaceae). *Epheloscyta*
- Pterostigma short, ending at about the middle or apical third of vein Rs. Neotropical. 15
- 15 Genae with distinct tubercle on lower head surface between antennal insertion and eye. Clypeus short, in profile hardly visible. On *Aralia* (Araliaceae). *Hodkinsonia*
- Genae lacking tubercle on lower head surface between antennal insertion and eye. Clypeus long, tubular, in profile clearly visible. On Araliaceae. *Neaphalara*

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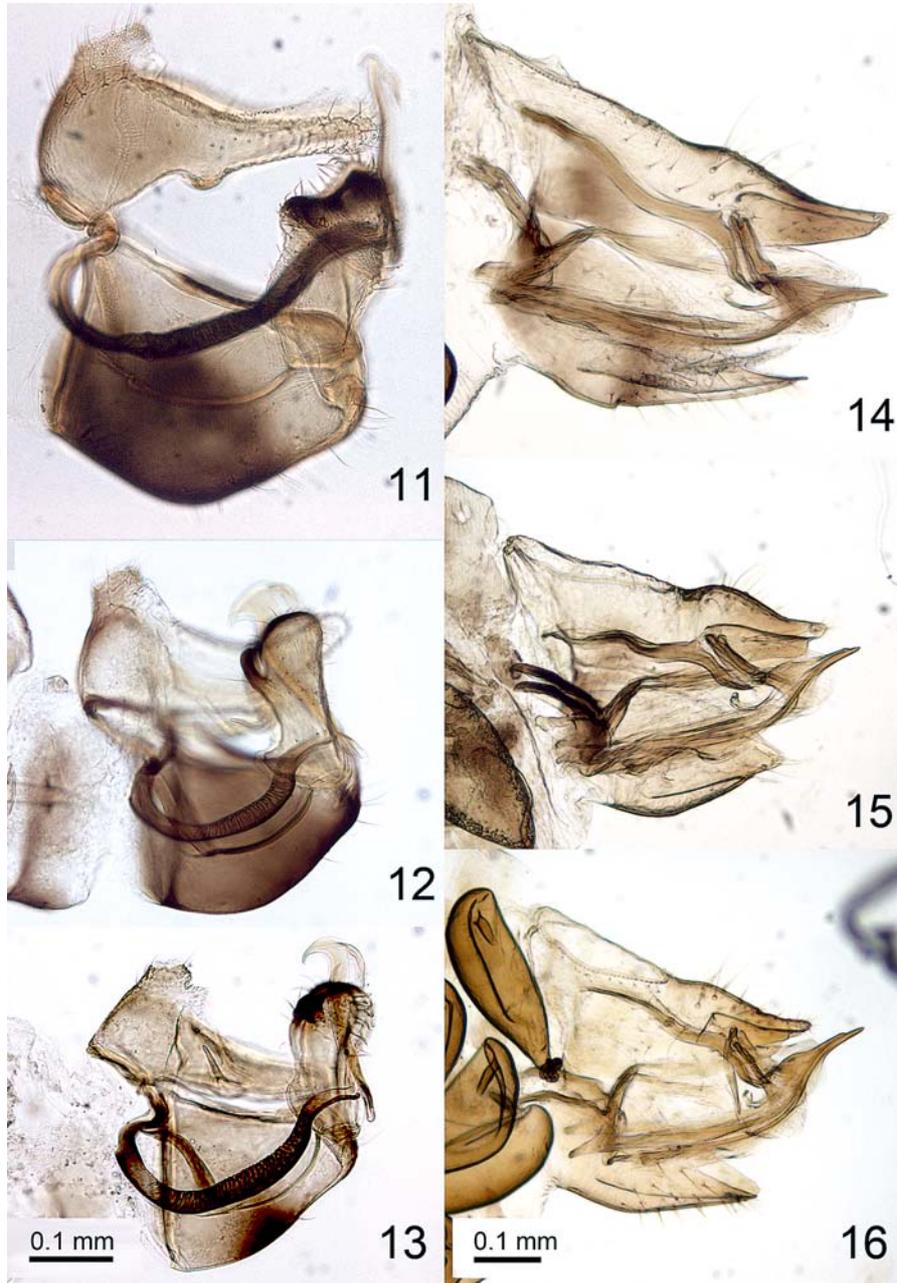
Limataphalara Hodkinson, 1992

Limataphalara Hodkinson, 1992: 84. Type species *Limataphalara brevicephala* Hodkinson, 1992, by original designation and monotypy.

Diagnosis. Adult. Head (Fig. 2) only little inclined from longitudinal body axis, moderately to very short. Vertex trapezoidal, two foveae distinct, coronal suture fully developed; anteriorly smoothly passing into genae; lateral ocelli situated adjacent to the eye. Frons forming narrow, elongate sclerite. Eyes hemispherical. Preocular sclerite developed at anterior half of eye, small or large. Antenna (Fig. 3) 10-segmented, 1.0–1.2 times as long as head width, segment 3 the longest, with a single large rhinarium on each of segments 4 to 9; terminal setae on segment 10 longer than segment, pointed. Clypeus small, pear-shaped, not extended anteriorly. Thorax weakly arched dorsally, with short, collar-like pronotum. Propleurites subrectangular, with subequal proepisternum and proepimeron, suture vertical with two dorsal branches. Mesoscutellum and metascutellum raised, knob-like. Mesosternum subrectangular, narrowed in the middle, with antero-lateral rim. Forewing (Figs 5–7) oblong-oval, with pterostigma and costal break, anal break vein adjacent to apex of vein Cu_{1b} ; vein R and M+Cu subequal, vein Rs almost straight, cell m_1 smaller than cu_1 which is large; marginal vein and apices of veins Rs, M_{1+2} , M_{3+4} and Cu_{1a} conspicuously lighter than rest of veins and membrane; wing membrane semitransparent, veins concolorous or darker, particularly apically; surface spinules (Figs 8–10) covering all cells, leaving spinule-free stripes along veins, fine densely spaced, sometimes forming irregular transverse rows or rings. Hindwing membranous, slightly shorter than forewing; furcation of vein R+M+Cu into R, M and Cu indistinct; costal setae grouped. Hind leg (Fig. 4) with metacoxa bearing a short, stout and apically rounded meracanthus and a rounded swelling between the meracanthus and the trochanter's insertion; metafemur apically and sometimes metatibia basally with stout long bristles; metatibia 1.2–1.9 times as long as metafemur, lacking genual spine,



Figs 2–10. Morphological details of *Limataphalara* spp. 2–4, 6, 9 – *L. hollisi* sp.nov. 5, 8 – *L. eucosma* sp.nov. 7, 10 – *L. lautereri* sp.nov. 2 – Head; 3 – antenna; 4 – hind leg; 5–7 – forewing; 8–10 – surface spinules in the apical third of cell m₁. Scale for Figs 2–4: 0.2 mm; Figs 5–7: 0.2 mm; Figs 8–10: 0.05 mm.



Figs 11–16. Terminalia of *Limataphalara* spp. 11, 14 – *L. eucosma* sp.nov. 12, 15 – *L. hollisi* sp.nov. 13, 16 – *L. lautereri* sp.nov. 11–13 – Male terminalia, lateral view; 14–16 – female terminalia, lateral view. Scale for Figs 11–13: 0.1 mm; Figs 14–16: 0.1 mm.

with 7–10 strongly sclerotised apical spurs forming an open crown. Metabasitarsus very short, bearing two strongly sclerotised lateral spurs. Male proctiger (Figs 11–13) with moderately long, sinuous posterior processes usually bearing an inner, weakly sclerotised hook-like process; subgenital plate subglobular or elongate. Paramere (Figs 17–19) elongate, with a claw or thumb-like strongly sclerotised inner process situated between the basal and apical thirds of the anterior margin. Distal portion of aedeagus (Figs 20–22) articulated some way from base, bearing small or large subapical hook and long sclerotized end tube of ductus ejaculatorius with saw-shaped or denticulate dorsal margin. Female terminalia (Figs 14–16) cuneate; proctiger, in profile, arched distal to circumanal ring which consists of two rows of pores, the outer longitudinal to margin, the inner ones diagonal. Subgenital plate ranging from about half as long to almost as long as proctiger, ventral margin weakly curved or angled, pointed or incised apically.

Fifth instar larva (Figs 26, 27, 29–31). Body oval, strongly flattened. Dorsal surface and margin densely covered in elongate tubercles bearing a lanceolate seta each; marginal tubercles longer than dorsal ones. Antenna 1- or indistinctly 2-segmented, covered in tubercles each bearing a single normal or lanceolate seta; one rhinarium clearly visible in basal part corresponding to adult scape, flagellar rhinaria indistinct (perhaps partially reduced). Clypeus with a pair of moderately long simple setae. Forewing bud with humeral lobe extending anteriorly to the middle of the eye. Thoracic tergites large. Caudal plate pointed posteriorly. Anus ventral, at some distance from the abdominal hind margin; circumanal ring small, lens-shaped, outer ring consisting of a single row of elongate pores. Tarsal arolium trapezoidal, shorter than claws, with short unguitactor, lacking petiole.

Egg (Figs 23–25, 28). Oval with short lateral pedicel, widest in basal third, narrowing towards apex which bears a long filament which is almost as long as egg.

Host plants. *Limataphalara* spp. appear monophagous on species of *Nectandra* Rol. ex Rottb. (Lauraceae).

Distribution. Neotropical from the USA (Florida) in the north to Brazil (Paraná) in the south reflecting the distribution of its host genus *Nectandra* (ROHWER 1993).

Key to *Limataphalara* species: adults

- 1 Head, pro and mesothorax, legs and marginal half of forewing cell c+sc dark brown or almost black, rest of body and forewings amber-coloured. Metatibia/metafemur length ratio < 1.4. Belize, USA (Florida). On *N. coriacea*. ***L. brevicephala* Hodkinson**
- Body coloration different; vertex yellowish, ochreous or light brown; marginal area of forewing cell c+sc not significantly darker than remainder of wing (Figs 5–7). Metatibia/metafemur length ratio > 1.5. 2

- 2 Thorax dark brown or black dorsally with lighter longitudinal stripes on mesopraescutum and scutum and white spots. Body dimensions large: head width > 0.8 mm, forewing length > 2.3 mm. Paramere relatively massive with dense thick long setae along dorsal margin, and thick short claw-like process in the middle of the anterior margin (Figs 11, 17). Distal portion of aedeagus slender, styliform with small apical hook and serrate sclerotised end tube of ductus ejaculatorius (Fig. 20). Female subgenital plate pointed apically (Fig. 14). Brazil (Paraná). On *N. lanceolata*. ***L. eucosma* sp.nov.**
- Thorax ochreous or yellow dorsally with more or less expanded, dark brown or black median longitudinal stripe or band. Body dimensions smaller: head width < 0.8 mm, forewing length < 2.3 mm. Paramere relatively slender with sparse fine long setae along dorsal margin, and slender, long thumb-like process in the middle of the anterior margin (Figs 12, 13, 18, 19). Distal portion of aedeagus club-shaped with large apical hook and sclerotised end tube of ductus ejaculatorius bearing a single denticle (Figs 21, 22). Female subgenital plate incised apically (Figs 15, 16). 3
- 3 Body dimensions larger: head width > 0.6 mm, forewing length > 1.9 mm. Paramere and distal portion of aedeagus as in Figs 12, 18. Female subgenital plate short: proctiger/subgenital plate ratio = 2.0; apical incision on subgenital plate long and wide. Costa Rica. On *N. membranacea*. ***L. hollisi* sp.nov.**
- Body dimensions smaller: head width < 0.6 mm, forewing length < 1.9 mm. Paramere and distal portion of aedeagus as in Figs 13, 19. Female subgenital plate long: proctiger/subgenital plate ratio = 1.6; apical incision on subgenital plate short and narrow. Brazil (Mato Grosso, Pará). On *N. cuspidata*. ***L. lautereri* sp.nov.**

Key to *Limataphalara* species: fifth instar larvae

[larvae of *L. brevicephala* and *L. hollisi* unknown]

- 1 Forewing pad long, antenna length/forewing pad length ratio < 0.5. Setae on antenna shorter than diameter of antenna; lanceolate setae on margins of head, wing pads and caudal plate shorter than tubercles on which they are situated. ***L. eucosma* sp.nov.**
- Forewing pad short, antenna length/forewing pad length ratio > 0.5. Setae on antenna longer than diameter of antenna; lanceolate setae on margins of head, wing pads and caudal plate longer than tubercles on which they are situated. ***L. lautereri* sp.nov.**

List of species

Limataphalara brevicephala Hodkinson, 1992

Limataphalara brevicephala Hodkinson, 1992: 86; holotype ♂, USA: Florida, Miami, 13.iv.1982, *Nectandra coriacea* (USNM; not examined).

Material examined. **Belize:** 1 ♂, Cayo, Chiquibul Forest, Las Cuevas, 21.iii.1995, Fog 10, *Cedrela*, D. Hollis et al. leg.; 1 ♀, same but iii–iv.1999, C. Minty leg. (MT) (BMNH, dry mounted).

Description. Adult. Described by HODKINSON (1992).

Fifth instar larva. Unknown.

Host plant. *Nectandra coriacea* (Sw.) Griseb. (Lauraceae).

Distribution. USA (Florida) (HODKINSON 1992), Belize (HOLLIS & MARTIN 1997).

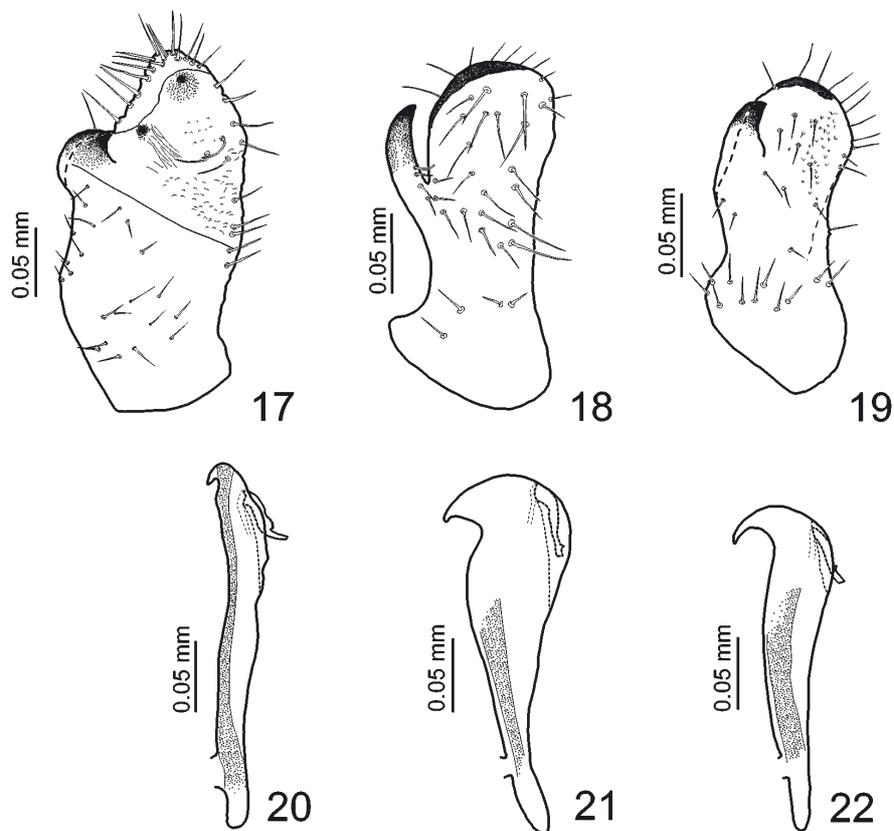
Limataphalara eucosma sp.nov. (Figs 5, 8, 11, 14, 17, 20, 23, 26, 28–31)

Type material. Holotype: ♂, **Brazil: Paraná:** Colombo, S25°19.078' W49°09.116', 930 m, 24.v.2013, *Nectandra lanceolata*, D. L. Queiroz leg. (MZSP, slide mounted). Paratypes: **Brazil: Paraná:** 1 ♂, 3 ♀♀, 3 larvae, 3 parasitised larval cases, same data as holotype. 1 ♂, 2 ♀♀, same but 17.vii.2013, S25°19.096' W49°09.100', D. L. Queiroz leg., #542. Rio Grande do Sul: 1 ♂, RS, Passo Fundo, 27.vi.2013, S28°13.195' W52°24.714, 630 m, D. L. Queiroz leg. #517 (LEEF, MZSP, NHMB, slide mounted, and preserved in 70% ethanol).

Description. Adult. Coloration. Ochreous with brown, black and white patches and dots. Vertex light brown, darker anteriorly, anterior margin white, anterior delimitation to genae and occiput black. Eyes grey, ocelli reddish. Lower head surface brown to black. Antenna yellowish, segments 1 and 2 brown, segments 4–8 with dark apices, segments 9 and 10 dark brown or black. Thorax dark brown or black dorsally with lighter longitudinal stripes on mesopraescutum and scutum and white spots as follows: six on pronotum, and two each on posterior margin of mesoprascutum, meso and metascutellum. Thorax laterally and ventrally straw-coloured with dark margins of sclerites. Forewing with yellowish or light brown, transparent membrane and basally yellow and otherwise brown to black veins, apices of veins Rs, M_{1+2} , M_{3+4} and Cu_{1a} white. Hindwing whitish, transparent. Legs yellowish to brown. Abdominal sclerites including terminalia ochreous to dark brown, intersegmental membrane yellow.

Structure. Body dimensions large. Surface spinules of forewing (Fig. 8) arranged in irregular transverse rows. Terminalia as in Figs 11, 14, 17, 20. Male subgenital plate elongate, ventral margin, in profile, angular. Paramere relatively broad with a claw-like hook slightly above the middle of the fore margin, a sclerotised rim near apical margin and an inward directed sclerotised point near apex on the inner face; inner face in apical third of posterior half with tubercular microsculpture; dorsal margin with long, dense setae. Distal segment of aedeagus slender with small apical hook and moderately long, sinuous sclerotised end tube of the ductus ejaculatorius which is serrate on its dorsal side. Female subgenital plate long, pointed apically.

Measurements and ratios in Table 4.



Figs 17–22. Male genital organs of *Limataphalara* spp. 17, 20 – *L. eucosma* sp.nov. 18, 21 – *L. hollisi* sp.nov. 19, 22 – *L. lautereri* sp.nov. 17–19 – Paramere, inner face; 20–22 – distal portion of aedeagus. Scale: 0.05 mm.

Fifth instar larva. Coloration. Ochreous with dark brown spines. Eyes grey. Antenna yellow with dark tip.

Structure. Lanceolate setae on antenna shorter than antennal diameter. Marginal tubercles longer than associated lanceolate seta. Tubercles on thoracic and abdominal dorsum in average about twice as long as their base. Forewing pad long.

Measurements and ratios in Table 5.

Etymology. From Greek εὐκοσμος = ornate, referring to the attractive adult colour pattern.

Host plant. *Nectandra lanceolata* Nees & Mart. (Lauraceae).

Distribution. Brazil (Paraná).

Table 4. Measurements (in mm) and ratios of adult *Limataphalara* spp. (n = 1 ♂, 1 ♀/ species).

	head width (HW)	antenna length (AL)	forewing length (WL)	metatibia length (TL)	♂ proctiger length (MP)	paramere length (PL)	aedeagus distal sgmt length	♀ proctiger length (FP)
<i>eucosma</i> ♂	0.80	0.80	2.30	0.70	0.18	0.25	0.25	
<i>eucosma</i> ♀	0.88	0.90	2.63	0.78				0.70
<i>hollisi</i> ♂	0.65	0.75	2.00	0.55	0.15	0.20	0.25	
<i>hollisi</i> ♀	0.73	0.78	2.30	0.60				0.50
<i>lautereri</i> ♂	0.55	0.60	1.53	0.48	0.13	0.18	0.20	
<i>lautereri</i> ♀	0.60	0.60	1.78	0.50				0.45

	AL/ HW	WL/ HW	WL/ forewing breadth	TL/ HW	TL/ metafemur length	MP/ HW	FP/ HW	FP/ circumanal ring length	FP/ ♀ subgenital plate
<i>eucosma</i> ♂	1.00	2.88	2.30	0.88	1.87	0.22			
<i>eucosma</i> ♀	1.03	3.00	2.19	0.89	1.63		0.80	2.80	1.56
<i>hollisi</i> ♂	1.15	3.08	2.29	0.85	1.83	0.23			
<i>hollisi</i> ♀	1.07	3.17	2.30	0.83	1.71		0.69	1.82	2.00
<i>lautereri</i> ♂	1.09	2.77	2.18	0.86	1.73	0.23			
<i>lautereri</i> ♀	1.00	2.96	2.09	0.83	1.67		0.75	2.00	1.06

***Limataphalara hollisi* sp.nov.**

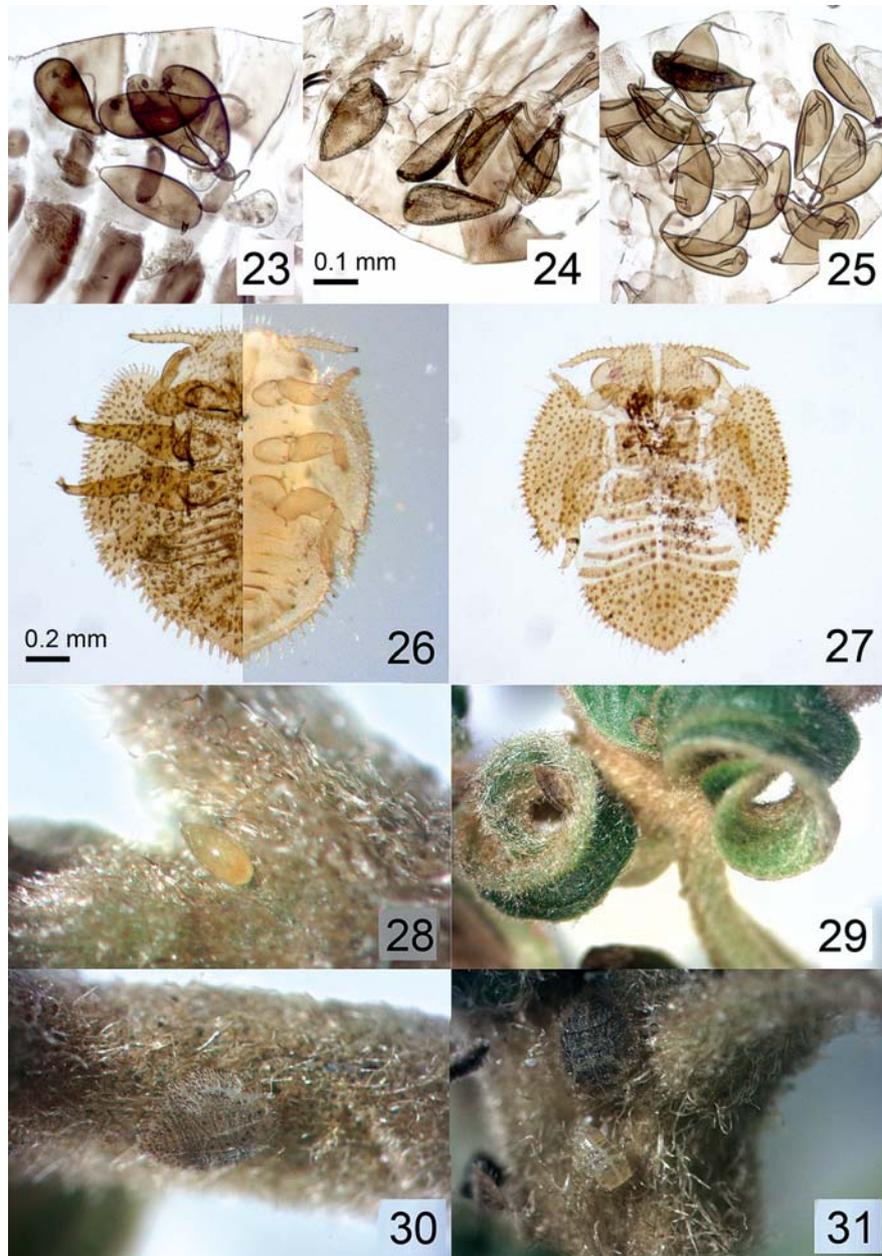
(Figs 2–4, 6, 9, 12, 15, 18, 21, 24)

Psyllidae Aphalarinae genus and species n., HOLLIS & MARTIN 1997: 471, table 1.

Type material. Holotype: ♂, **Costa Rica:** San José, 2–4 km East of San Jeronimo, 1500 m, 4.ii.1993, *Nectandra membranacea*, D. Hollis leg. (BMNH, dry mounted). Paratypes: **Costa Rica:** 1 ♂, 2 ♀♀, same data as holotype; 1 ♂, 1 ♀, same data as holotype but 26.i.–4.ii.1993 (BMNH, NHMB, dry and slide mounted).

Description. Adult. Coloration. Yellow or straw-coloured dorsally, brown or dark brown ventrally. Antennal segments 1 and 2 ochreous or brown, 3–7 yellow, 4–8 dark brown apically, 9 and 10 almost black. Clypeus yellow. Meso- and metanotum with more or less expanded dark brown median longitudinal stripe. Forewing semi-transparent, with greyish membrane and concolorous veins except for apical region where veins are almost black, strongly contrasting with the membrane and apices of veins Rs, M_{1+2} , M_{3+4} and Cu_{1a} , which are white. Hindwing colourless. Femora and metacoxae dark brown. Abdominal sclerites dark brown, membranes yellow. Male proctiger ochreous. Female terminalia yellow. Younger specimens with less expanded dark colour.

Structure. Body dimensions intermediate between those of *L. eucosma* and *lautereri*. Surface spinules of forewing (Fig. 9) arranged in irregular rings. Terminalia as in Figs 12, 15, 18, 21. Male subgenital plate subglobular, ventral margin, in profile, broadly rounded. Paramere relatively slender with long thumb-like process in apical third of the fore margin and sclerotised apical margin; inner face in apical third of posterior half lacking tubercular microsculpture; dorsal margin with moderately long, spaced setae. Distal



Figs 23–31. Eggs and larvae of *Limataphalara* spp. 23, 26, 28–31 – *L. eucosma* sp.nov. 24 – *L. hollisi* sp.nov. 25, 27 – *L. lautereri* sp.nov. 23–25 – Eggs in female abdomen; 26, 27 – fifth instar larva (26 – left dorsal, right ventral view); 28 – egg on branchlet of *Nectandra lanceolata*; 29 – deformation induced on *N. lanceolata*; 30, 31 – larvae on branchlet of *Nectandra lanceolata*. Scale for Figs 23–25: 0.1 mm; Figs 26, 27: 0.2 mm.

Table 5. Measurements (in mm) and ratios of fifth instar larvae of *Limataphalara* spp. (n: *L. eucosma* = 1; *L. lautereri* = 2).

	body length (BL)	antenna length (AL)	BL/body breadth (BB)	BB/ caudal plate breadth (CPB)	AL/ forewing pad length	caudal plate length / CPB	CPB/ circumanal ring breadth
<i>eucosma</i>	1.53	0.38	1.05	1.61	0.40	4.00	6.55
<i>lautereri</i>	1.40–1.48	0.34–0.44	1.18–1.19	1.62–1.72	0.53–0.78	3.00–5.00	5.27–7.25

segment of aedeagus thick with large apical hook and moderately long, sinuous sclerotised end tube of the ductus ejaculatorius, which bears a tubercle on its dorsal side. Female subgenital plate short, with deep, wide incision apically.

Measurements and ratios in Table 4.

Fifth instar larva unknown.

Etymology. Dedicated to David Hollis who collected the type material.

Host plant. *Nectandra membranacea* (Sw.) Griseb. (Lauraceae).

Distribution. Costa Rica.

***Limataphalara lautereri* sp.nov.** (Figs 7, 10, 13, 16, 19, 22, 25, 27)

Type material. Holotype: ♂, **Brazil: Pará:** Belém, Embrapa campus, S1°24.9–26.6' W48°25.3–26.6', 20 m, 8–15.iv.2013, *Nectandra cuspidata*, edge of Amazonian forest, D. Burckhardt & D. L. Queiroz leg., #99(2) (MZSP, dry mounted). Paratypes: **Brazil: Mato Grosso:** 2 ♀♀, Tabaporã, Fazenda Crestani, S11°18.8/20.2' W55°57.7/58.5', 330–380 m, 6–8.xi.2012, transitional forest near river, forest edges, farm land, parc vegetation, D. Burckhardt & D. L. Queiroz leg., #62; 1 ♀, same but Tabaporã, S11°20.0' W55°50.5', 430 m, 8.xi.2012, forest edge along unpaved road, D. Burckhardt & D. L. Queiroz leg., #63. 1 ♂, 4 larvae, 1 skin, Sinop, 28.viii.2013, S11°52.250' W55°35.747', 350 m, D. L. Queiroz leg., #566; 2 ♂♂, same but 29.viii.2013, S11°52.967' W55°38.420', 320 m, #569; 2 ♀♀, same but 30.viii.2013, S11°52.252' W55°35.746', 360 m, #571; 2 ♂♂, 2 ♀♀, same but S11°52.164' W55°35.804', #572; 2 ♂♂, 4 ♀♀, 19 imm, 14 skins, Ponta Pora, 12.ix.2013, S21°59.940' W55°33.814', 585 m, Fazenda Mariana, D. L. Queiroz leg., #576; 1 ♀, Bonito, 19.ix.2013, S21°10.282' W56°26.457', 290 m, Hotel Cabanas ground, D. L. Queiroz leg., #585; 1 ♂, 1 ♀ same but S21°10.345' W56°26.533', 320 m, #586. **Pará:** 119 ♂♂, 92 ♀♀, 2 larvae, 3 parasitised larval cases, same data as holotype; 8 ♂♂, 14 ♀♀, 4 larvae, Pará, Belém, Jardim Botânico Bosque Rodrigues Alves, S1°25.8' W48°27.2', 30 m, 14.iv.2013, *Nectandra cuspidata*, edge of Amazonian forest; sweeping vegetation, D. Burckhardt & D. L. Queiroz leg., #103(2) (LEEF, MHNG, MZSP, HNMB, BMNH, USNM; dry and slide mounted and preserved in 70% and 100% ethanol).

Description. Adult. Coloration. Ochreous. Head black ventrally. Antennal segments 1 and 2 brown, 3 entirely yellow, 4–8 yellow basally and brown apically, 9 and 10 almost black. Pronotum yellow; thorax with black longitudinal median stripe extending from mesoscutum to metascutellum. Forewing semi-transparent, ochreous, veins only slightly darker than membrane, apices of veins Rs, M₁₊₂, M₃₊₄ and Cu_{1a} white. Hindwing colourless, transparent. Abdominal sternites in male dark brown or black.

Structure. Body dimensions small. Surface spinules of forewing (Fig. 10) irregularly, densely arranged. Terminalia as in Figs 13, 16, 19, 22. Male subgenital plate

subglobular, ventral margin, in profile, weakly curved. Paramere relatively slender with short thumb-like process in apical third of the fore margin and sclerotised apical margin; inner face in apical third of posterior half with tubercular microsculpture; dorsal margin with moderately long, spaced setae. Distal segment of aedeagus moderately thick with large apical hook and moderately long, sinuous sclerotised end tube of the ductus ejaculatorius which bears a tubercle on its dorsal side. Female subgenital plate short, with shallow, narrow incision apically.

Measurements and ratios in Table 4.

Fifth instar larva. Coloration. Yellowish, spines slightly darker.

Structure. Lanceolate setae on antenna longer than antennal diameter. Marginal tubercles much shorter than associated lanceolate seta. Tubercles on thoracic and abdominal dorsum in average about as long as their base. Forewing pad short.

Measurements and ratios in Table 5.

Etymology. Dedicated to Pavel Lauterer.

Host plant. *Nectandra cuspidata* Nees & Mart. (Lauraceae).

Distribution. Brazil (Mato Grosso, Pará).

Discussion and conclusions

Apart from the monotypic Gyropsyllini, following previously defined groupings appear also in our cladistic analysis (Fig. 1, Tables 2 and 3): the Xenaphalarini, the Caillardiini *sensu* LOGINOVA (1964a) and the Rhombaphalarini of previous authors (KLIMASZEWSKI 1987, 2001, LOGINOVA 1964a, WHITE & HODKINSON 1985). Otherwise our analysis is considerably different suggesting the tribes Aphalarini, Craspedoleptini and Stigmaphalarini of previous classifications are paraphyletic or polyphyletic. This is mostly due to the position of *Brachystetha* and *Crastina*. The former differs from *Aphalara* and close relatives in the large, triangular frons, the flattened clypeus and the subrectangular, laterally rounded mesosternum. The latter differs from *Colposcения* in the small, parallell-sided frons, the subglobular clypeus and the vertical propleural suture. The relationships of *Brachystetha* and *Colposcения* with respect to the remaining genera are not resolved in our analysis. The clades *Crastina*–*Limataphalara*, *Eumetoecus*+*Rhodochlanis*, *Epheloscyta*–*Limataphalara*, *Eurotica*+*Xenaphalara* and *Gyropsylla*–*Limataphalara* are well supported. There are no characters, apart from the common host family Araliaceae, to group the two Central American genera *Hodkinsonia* and *Neaphalara* as well as the eastern Asian *Epheloscyta* together. The two Central American genera do not, however, form a distinct group with the other Neotropical members of the subfamily (*Gyropsylla*, *Lanthanaphalara* and *Limataphalara*).

Applying a formal tribal classification would result in at least two monotypic tribes, depending on where the level is set, which would be of no practical use. We therefore synonymise all extant tribes: Aphalarinae Löw, 1879: 606 (= Caillardiini Loginova, 1964: 447, syn.nov.; Coelocarinae Li, 2011: 351, syn.nov.; Colposceniini Bekker-Migdisova, 1973: 109, syn.nov.; Craspedoleptini Klimaszewski, 2001: 196, syn.nov.; Eumetoecini

Li, 2011: 356, syn.nov.; Gyropsyllini White & Hodkinson, 1985: 270, syn.nov.; Rhombaphalarini Klimaszewski, 1987: 228, syn.nov.; Stigmaphalarini Vondráček, 1957: 140, nomen nudum, syn.nov.; Xenaphalarini Loginova, 1964: 447, syn.nov.).

CONCI & TAMANINI (1984) and BURCKHARDT (1989) discussed *Rhodochlanis* and *Rhombaphalara* and suggested that they may be congeneric. They did not, however, formally synonymise them awaiting an analysis of the phylogenetic relationships within the subfamily. In our analysis we found no morphological differences between the two and formally synonymise them here: *Rhodochlanis* Loginova, 1964 (= *Rhombaphalara* Loginova, 1964, type species *Rhombaphalara halocnemi* Loginova, 1964, by original designation and monotypy, syn.nov.). The following revised or new combinations are proposed: *Rhodochlanis achaetae* Klimaszewski, 1967, stat. rev. (from *Rhombaphalara*); *Rhodochlanis halocnemi* (Loginova, 1964), comb.nov. (from *Rhombaphalara*); *Rhodochlanis halostachidis* (Loginova, 1970), comb.nov. (from *Rhombaphalara*); *Rhodochlanis insolita* (Burckhardt & Mifsud, 1998), comb.nov. (from *Rhombaphalara*).

HODKINSON (1980) suggested the presence of *Aphalara* and *Craspedolepta* in the Nearctic region may be due to immigration from the Palaearctic region across a Beringia connection. On the other hand *Gyropsylla*, *Hodkinsonia* and *Neaphalara* were regarded by HODKINSON (1989) as an old Neotropical group. A Palaearctic origin for *Aphalara* and *Craspedolepta* is in accordance with our cladistic analysis. The biogeographical relationships of the other three New World genera seem more complicated but without a fully resolved phylogeny little can be concluded at present. *Gyropsylla* has an interesting distribution that includes both the Neotropics and China. The phylogenetic relationships of the Araliaceae feeding genera *Epheloscyta*, *Hodkinsonia* and *Neaphalara* are unresolved. If these genera should prove to be monophyletic as a group then this would be another case of a Neotropical–eastern Asian distribution.

The host relationships within the Aphalarinae are visualised in Fig. 1. Five genera are associated with Amaranthaceae, three with Araliaceae, two with Tamaricaceae and the rest with a single plant family each. Neither the genera associated with Amaranthaceae nor those with Tamaricaceae form a monophyletic group, suggesting that the two plant families were colonised by psyllids more than once. As the phylogenetic relationships of the three psyllid genera associated with Araliaceae are not resolved nothing can be concluded. The host of *Gyropsylla cannella* has been reported as possibly *Nectandra* sp. This could not be substantiated, however, as we found a series of *G. cannella*, adults and larvae, on *Ilex microdonta* during recent field work in Brazil (Burckhardt & Queiroz, unpublished data). This host is more plausible as the other *Gyropsylla* species with known host plants all develop on *Ilex*.

Acknowledgements

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