

Research article

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Another puzzle piece in the systematics of the chewing louse genus *Myrsidea*, with a description of a new genus *Apomyrsidea*

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Abstract. A new avian chewing louse genus *Apomyrsidea* gen. nov. is described based on species parasitizing birds in the family Formicariidae. Diagnostic characteristics and phylogenetic analyses were used to evaluate and confirm the generic status and merit its recognition as unique and different from *Myrsidea* Waterston, 1915. Three species previously belonging to the genus *Myrsidea* are placed in the new genus *Apomyrsidea* gen. nov. and are discussed: *Apomyrsidea circumsternata* (Valim & Weckstein, 2013) gen. et comb. nov., *Apomyrsidea isacantha* (Valim & Weckstein, 2013) gen. et comb. nov. and *Apomyrsidea klimesi* (Sychra in Sychra *et al.*, 2006) gen. et comb. nov.

Keywords. Phthiraptera, *Apomyrsidea*, *Myrsidea*, morphology, phylogeny.

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Introduction

Chewing lice (Psocodea Hennig, 1966: Phthiraptera Haeckel, 1896) are obligate permanent ectoparasites, meaning they live their entire life cycle on their hosts (Clayton *et al.* 2015). Many are microhabitat specialists, often occupying specific body parts on the host (Johnson *et al.* 2012). The species parasitizing birds feed on feathers, dead skin, skin secretions, and in some cases blood (Price *et al.* 2003). At high prevalence, they can cause significant harm to feathers, skin irritation and even possible secondary infections that decrease the fitness of the bird hosts (Møller *et al.* 1990; Mullen & Durden 2002).

In the past, the taxonomy of chewing lice was based on morphology (Clay 1966; Price *et al.* 2003); however, in the last two decades, molecular and phylogenetic studies have helped to resolve the

systematics of this diverse group (Johnson *et al.* 2004; Smith *et al.* 2011). The chewing lice genus *Myrsidea* Waterston, 1915 is among the most diverse and host specific genera within the parasitic lice (Phthiraptera), with more than 380 species described worldwide (Kolencik & Sychra, unpublished data). While there are 49 species of *Myrsidea* described from Neotropical suboscine birds (Kolencik *et al.* 2018), only three have been described from birds of the family Formicariidae Gray, 1840 (Sychra *et al.* 2006; Valim & Weckstein 2013). These three species show a set of characteristics that are unique among all species of *Myrsidea* to the extent that Sychra *et al.* (2006) and Valim & Weckstein (2013) suggested that they may be placed outside of *Myrsidea*. Here, we evaluate both morphological and molecular data of these three species along with representatives of the major clades in *Myrsidea*. We find that the combination of differences found from both morphological and molecular data is strong enough to merit their recognition in a separate genus here named as *Apomyrsidea* gen. nov.

Material and methods

Morphology

All the morphological descriptions and characters as well as the terminology of chaetotaxy were taken from or follow those from Clay (1961, 1962, 1966, 1969), Sychra *et al.* (2006) and Valim & Weckstein (2013). Taxonomy and nomenclature of the birds follows IOC Bird World List ver. 10.1 (Gill *et al.* 2020).

Phylogenetic reconstruction

For the phylogenetic reconstruction we used a fragment of the mitochondrial gene cytochrome oxidase I (COI, 379bp). We amplified and sequenced this fragment from *Apomyrsidea klimesi* (Sychra in Sychra *et al.*, 2006) (3 nymphs ex *Formicarius analis* (d'Orbigny & Lafresnaye, 1837) from Zona Protectora Las Tablas on the Pacific slope of the Cordillera de Talamanca, 8°54' N, 82°47' W; 1300 m a.s.l.; identical sequences; GenBank accession number: MW381016) using the technique described by Martinu *et al.* (2015). All other sequences were downloaded from GenBank (Table 1) and aligned in SeaView ver. 4.7 (Gouy *et al.* 2010) using Clustal Omega (Sievers *et al.* 2011) and checked visually. In total, we aligned 50 sequences from seven chewing lice genera from the suborder Amblycera Kellogg, 1896 and two sequences from the suborder Ischnocera Kellogg, 1896 as the outgroups. To determine the best model fit to our data we used PartitionFinder ver. 2.1.1 (PF; Lanfear *et al.* 2016) and compared all models using the corrected Akaike Information Criterion (AICc). We selected two different approaches for a phylogenetic reconstruction to examine the similarity among the methods. First, the randomly accelerated maximum likelihood (RAxML ver. 8.2.12; Stamatakis 2014) method was used with three partitions and the model GTR+I+G for each and estimated 1000 bootstrap trees. Second, MrBayes ver. 3.2 (Ronquist & Huelsenbeck 2003) was used for Bayesian analysis with GTR+I+G model for two partitions and HKY+G for the third. We conducted two parallel runs for 20 000 000 generations with four Markov chains (Huelsenbeck & Bollback 2001), which were sampled every 1000 generations with a total of 20 000 parameter points estimates. Markov chains were examined in Tracer ver. 1.7.1 (Rambaut *et al.* 2018) to determine that the chains had reached stationarity and 10% of trees were removed as burnin. A 50% majority rule consensus tree with posterior probabilities was generated. The outgroup ischnoceran genus *Philopterus* Nitzsch, 1818 was used for rooting in both trees.

Institutional abbreviations

FMNH	=	Field Museum of Natural History, Chicago, USA
INBio	=	Instituto Nacional de Biodiversidad, Costa Rica
MMBC	=	Moravian Museum, Brno, Czech Republic
MZUSP	=	Museum of Zoology of the University of São Paulo, Brazil
NSF	=	National Science Foundation, USA

Table 1 (continued on next page). List of the louse species included in our phylogenetic analyses, with their hosts and GenBank accession numbers. * = in GenBank as species of *Myrsidea*; † = a new sequence.

Lice species	Host species	GenBank number
<i>Actornithophilus ceruleus</i>	<i>Anous tenuirostris</i>	AF545666
<i>Actornithophilus erinaceus</i>	<i>Rostratula benghalensis</i>	AF545667
<i>Actornithophilus piceus</i>	<i>Larus</i> sp.	AF545668
<i>Apomyrsidea circumsternata</i> *	<i>Formicarius colma</i>	KF048105
<i>Apomyrsidea isacantha</i> *	<i>Chamaeza nobilis</i>	KF048115
<i>Apomyrsidea klimesi</i> †	<i>Formicarius analis</i>	MW381016
<i>Colpocephalum fregili</i>	<i>Corvus albus</i>	MF443951
<i>Colpocephalum indi</i>	<i>Ictinia mississippiensis</i>	MF443945
<i>Colpocephalum napiforme</i>	<i>Buteo lagopus</i>	MF443947
<i>Colpocephalum polybori</i>	<i>Caracara cheriway</i>	MF443950
<i>Colpocephalum subzerafae</i>	<i>Falco berigora</i>	MF443946
<i>Colpocephalum turbinatum</i>	<i>Circus approximans</i>	MF443944
<i>Dennyus bartoni</i>	<i>Aerodramus mearnsi</i>	DQ139300
<i>Dennyus carljonesi carljonesi</i>	<i>Aerodramus v. vestitus</i>	DQ139294
<i>Dennyus carljonesi forresteri</i>	<i>Aerodramus elaphrus</i>	DQ139297
<i>Dennyus carljonesi forresteri</i>	<i>Aerodramus francicus</i>	DQ139296
<i>Dennyus kristinae</i>	<i>Aerodramus s. spodiopygius</i>	DQ139305
<i>Dennyus mimiogregororum</i>	<i>Aerodramus papuensis</i>	DQ139301
<i>Dennyus singhi</i>	<i>Aerodramus assimilis</i>	DQ139307
<i>Menacanthus alaudae</i>	<i>Calamonastes fasciolatus</i>	MG682392
<i>Menacanthus alaudae</i>	<i>Plocepasser mahali</i>	MG682398
<i>Menacanthus camelinus</i>	<i>Lanius collaris</i>	MG682399
<i>Menacanthus eurysternus</i>	<i>Curruca subcoerulea</i>	MG682400
<i>Menacanthus eurysternus</i>	<i>Prinia flavicans</i>	MG682401
<i>Menacanthus eurysternus</i>	<i>Turdus libonyana</i>	MG682393
<i>Menacanthus eurysternus</i>	<i>Melaenornis silens</i>	MG682384
<i>Menacanthus eurysternus</i>	<i>Turdus merula</i>	KJ730692
<i>Menacanthus</i> sp.	<i>Lagonosticta rara</i>	DQ887248
<i>Menacanthus</i> sp.	<i>Pogoniulus chrysoconus</i>	MG682396
<i>Menacanthus takayamai</i>	<i>Locustella luscinioides</i>	KJ730535
<i>Myrsidea alexanderi</i>	<i>Pheugopedius maculipectus</i>	MF563536
<i>Myrsidea argentina</i>	<i>Spinus magellanicus</i>	KY113129
<i>Myrsidea ceciliae</i>	<i>Ramphastos culminatus</i> × <i>ariel</i>	KF048126
<i>Myrsidea</i> cf. <i>bubalornithis</i>	<i>Bubalornis niger</i>	MG682394
<i>Myrsidea</i> cf. <i>textoris</i>	<i>Ploceus ocularis</i>	MG682397
<i>Myrsidea cinnamomei</i>	<i>Attila citriniventris</i>	KF048110
<i>Myrsidea contopi</i>	<i>Leptopogon amaurocephalus</i>	MF563537
<i>Myrsidea cruickshanki</i>	<i>Chlorothraupis carmioli</i>	GQ454449
<i>Myrsidea icterocephalae</i>	<i>Tangara icterocephala</i>	KF048103
<i>Myrsidea incerta</i>	<i>Catharus ustulatus</i>	FJ171268
<i>Myrsidea seminuda</i>	<i>Thraupis palmarum</i>	KF048116
<i>Myrsidea valimi</i>	<i>Euphonia anneae</i>	GQ454450

Table 1 (continued). List of the louse species included in our phylogenetic analyses, with their hosts and GenBank accession numbers. * = in GenBank as species of *Myrsidea*; † = a new sequence.

Lice species	Host species	GenBank number
<i>Myrsidea violaceae</i>	<i>Euphonia hirundinacea</i>	KY113137
<i>Ricinus mugimaki</i>	<i>Cossypha dichroa</i>	KF768816
<i>Ricinus</i> sp.	<i>Atila spadiceus</i>	AF545762
<i>Ricinus</i> sp.	<i>Cyanocopsa parellina</i>	AF545763
<i>Ricinus</i> sp.	<i>Ficedula hyperythra</i>	AF545764
<i>Ricinus</i> sp.	<i>Fringillaria tahapisi</i>	MG682387
<i>Ricinus</i> sp.	<i>Platysteira laticincta</i>	MK032013
<i>Ricinus</i> sp.	<i>Terpsiphone batesi</i>	KU187311
<i>Ricinus</i> sp.	<i>Terpsiphone viridis</i>	KY359404
Outgroups		
<i>Philopterus solus</i>	<i>Rhinopomastus cyanomelas</i>	MG682416
<i>Traihoriella laticeps</i>	<i>Andigena nigrirostris</i>	AY149398

Results

Here, we find that species of *Apomyrsidea* gen. nov. are unique and morphologically distinct from all species of *Myrsidea*. Specifically, the simple combination of the presence of the posterior dorsal head seta (*dhs*) 23 and the dorso-central pronotal setae (*dps*) 2 (Fig. 3), sternite I lying inside the wide notch of sternite II (Fig. 5) and different type of fusion in the terminal sternites – male abdominal sternite VIII and female sternite VII both at least partially but conspicuously separated from the subgenital plate, which is formed by a single sternite IX (in the male; Fig. 2) or fusion of sternites VIII and IX (in the female; Fig. 1), make these species distinct. These characters were further defined in Clay (1966), Sychra *et al.* (2006) and Valim & Weckstein (2013).

This separation is also supported with the present phylogenetic analyses of 379bp fragment of COI from 50 amblyceran species across 6 genera: *Actornithophilus* Ferris, 1916, *Colpocephalum* Nitzsch, 1818, *Dennyus* Neumann, 1906, *Myrsidea* (including all three species of *Myrsidea* occurring on formicariid hosts that are here placed in *Apomyrsidea* gen. nov.), *Menacanthus* Neumann, 1912 and *Ricinus* De Geer, 1778, and with two ischnoceran lice, *Traihoriella laticeps* (Piaget, 1888) and *Philopterus solus* (Tendeiro, 1962), as outgroups (Fig. 10). Both Bayesian analysis and Maximum Likelihood analysis (Appendix) resulted in trees with a similar topology, differing in some intra-generic relationships. However, both trees coincide in topology of our main focus, ‘*Myrsidea* from Formicariidae’ – *Apomyrsidea* gen. nov., and place it sister to all other species of *Myrsidea*.

Class Insecta Linnaeus, 1758
 Superorder Psocodea Hennig, 1966
 Order Phthiraptera Haeckel, 1896
 Suborder Amblycera Kellogg, 1896
 Family Menoponidae Mjöberg, 1910

Genus *Apomyrsidea* gen. nov.

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Myrsidea Waterston, 1915: 12 (in partim).

Type species

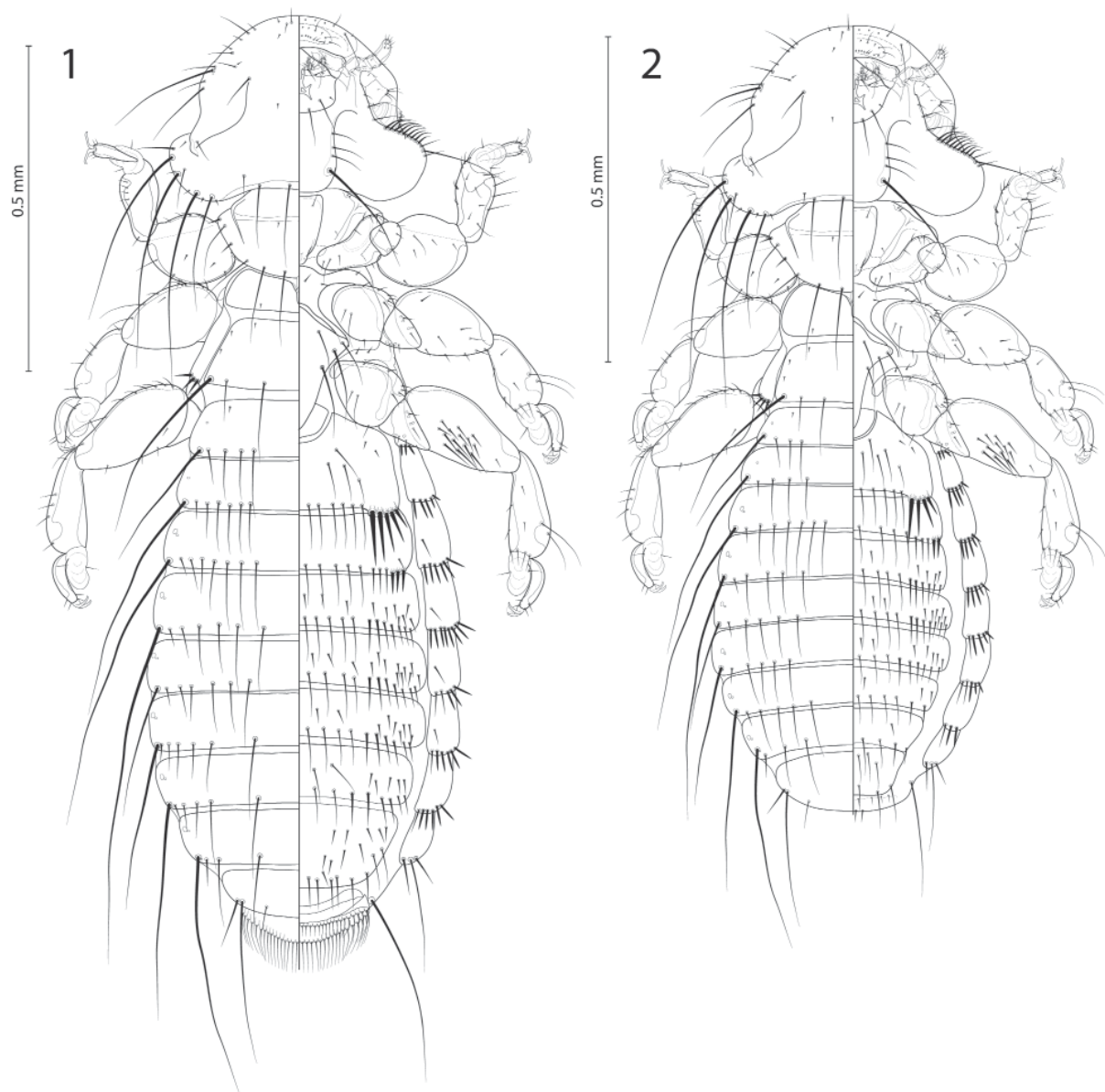
Apomyrsidea klimesi (Sychra in Sychra *et al.*, 2006: 55) gen. et comb. nov.

Diagnosis

Apomyrsidea can be characterized and distinguished from all other menoponid chewing lice genera with the combination of following characteristics:

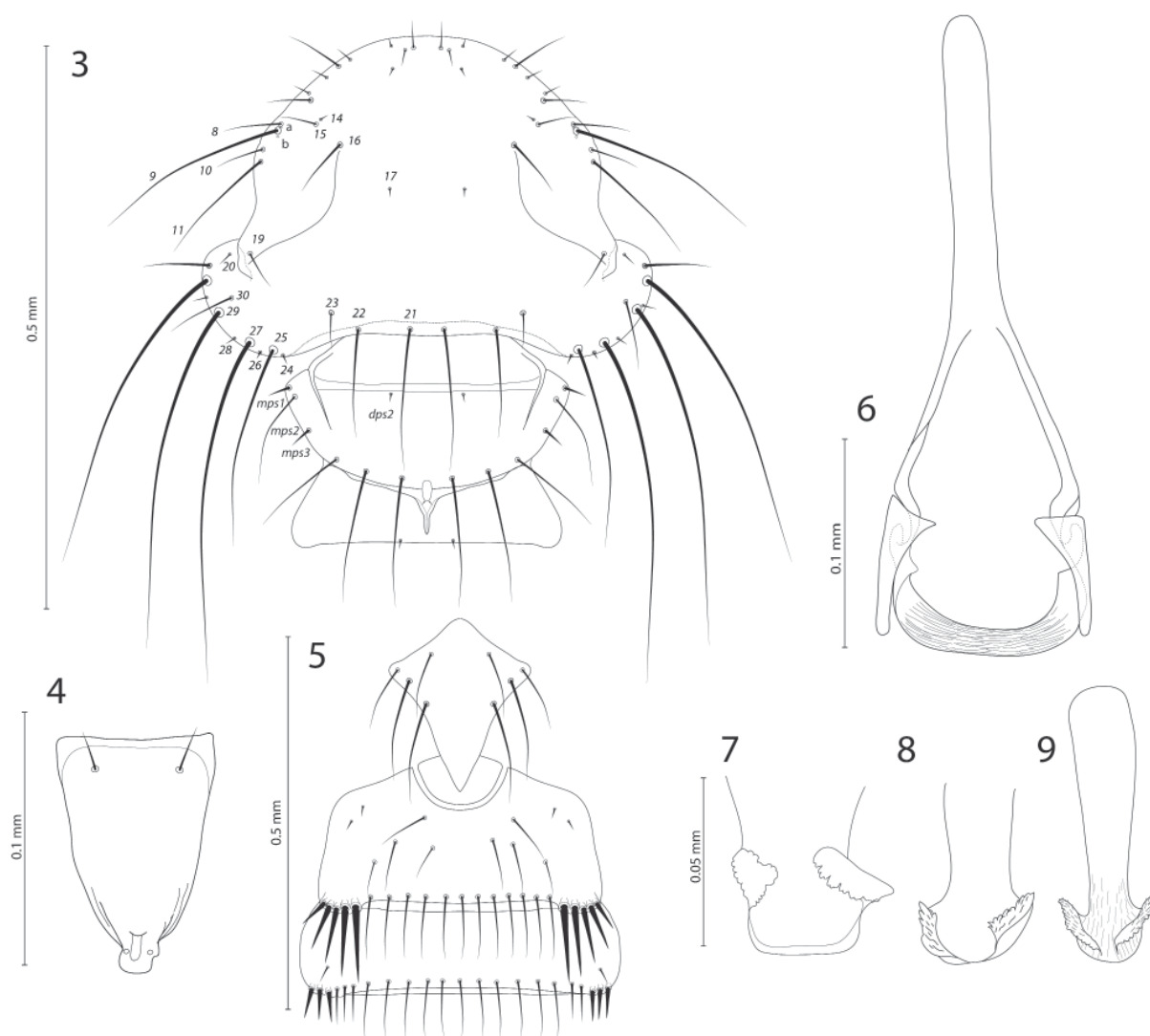
Head

- rounded anteriorly, lacking lateral slit or notch, without sclerotized processes (oral spines) arising near the base of maxillary palpi (Figs 1–3);



Figs 1–2. Dorso-ventral view of *Apomyrsidea klimesi* (Sychra in Sychra *et al.*, 2006) gen. et comb. nov. (CR15). 1. ♀. 2. ♂.

- alveoli of dorsal head setae (*dhs*; marginal temporal setae by Clay 1969) 26 and 27 not closely associated (Fig. 3);
- *dhs* 18 (outer mid-dorsal head seta by Clay (1966) or dorsal head seta „d“ by Clay (1962) is missing;
- *dhs* 22 (outer occipital seta by Valim & Weckstein 2013 or posterior dorsal head seta „f“ by Clay 1962) approximately as long as *dhs* 21 (inner occipital seta by Valim & Weckstein 2013), both surpassing pronotal carina;
- *dhs* 23 (posterior dorsal head seta “e” in Clay 1962) present and anteriorly to line of bases of *dhs* 21 and 22 (Fig. 3);
- head sensilla 3–5 sensu Clay (1961) or c–e sensu Clay (1969) absent;
- characteristic gular plate with the greater length and thickness of the posterior pair of setae compared to the rest ones (Figs 1–2).



Figs 3–9. 3–6. *Apomyrsidea klimesi* (Sychra in Sychra *et al.*, 2006) gen. et comb. nov. (CR15). 3. Dorsal view of head, prothorax and mesothorax of female. 4. Prosternal plate of female. 5. Metasternal plate and sternites I–III of female. 6. Male genitalia. – 7–9. Male genital sac sclerites. 7. *A. klimesi* gen. et comb. nov. 8. *A. circumsternata* (Valim & Weckstein, 2013) gen. et comb. nov. 9. *A. isacantha* (Valim & Weckstein, 2013) gen. et comb. nov. Abbreviations: a–b = head sensilla; *dps* = dorso-central pronotal setae; *mps* = marginal prothoracic setae; 8–30 = dorsal head setae. Figs 7–9 are drawn to the same scale.

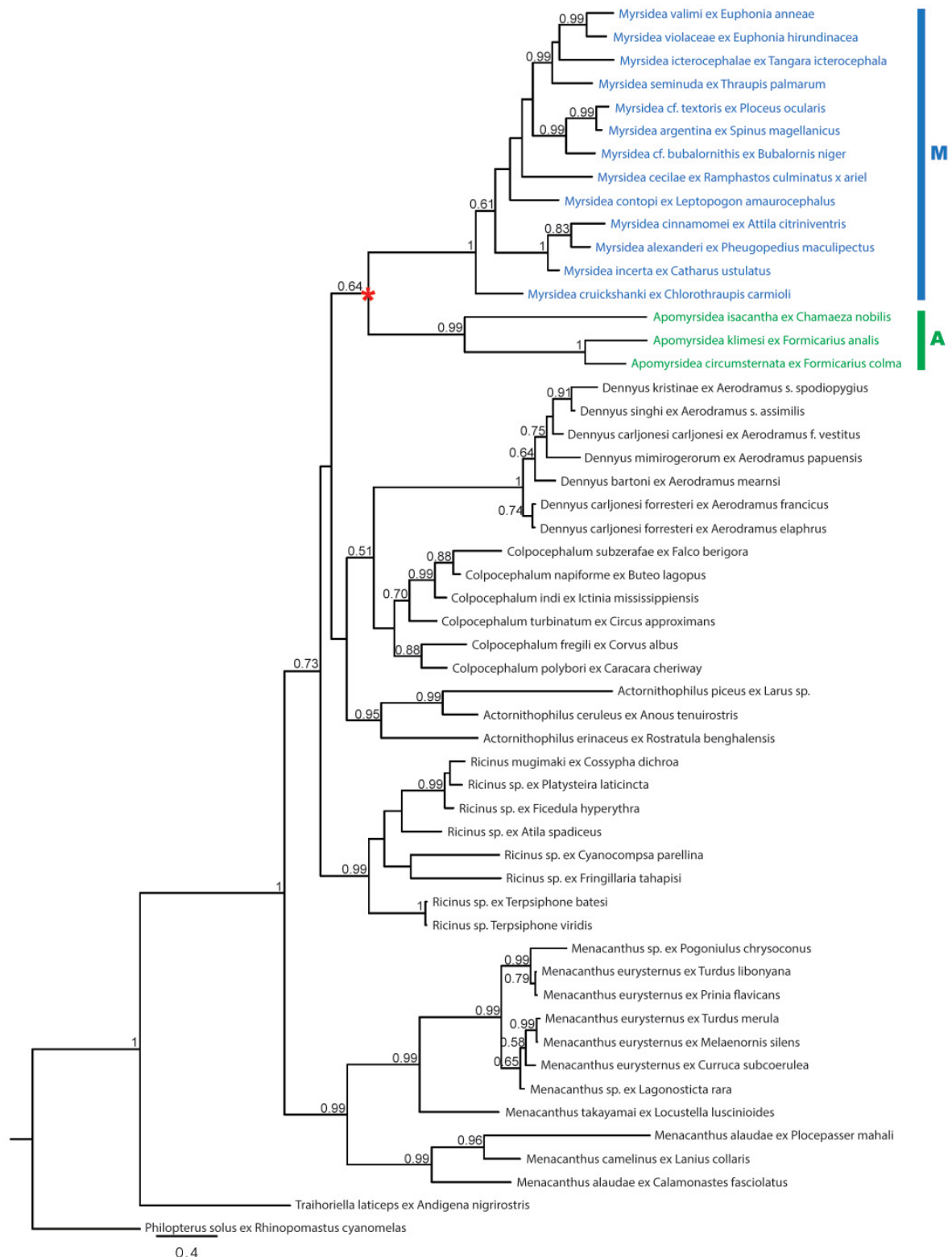


Fig. 10. Bayesian phylogenetic tree of selected amblyceran genera and species based on partial mitochondrial gene COI. Tree is rooted with outgroup species *Philopterus solus* (Tendeiro, 1962). Posterior probability values are shown above the nodes (values <50% are not shown). Blue colour indicates species of *Myrsidea* Waterston, 1915 (M); green colour indicates species of *Apomyrsidea* gen. nov. (A); * symbol indicates a node between *Myrsidea* and *Apomyrsidea*.

Thorax

- prosternal plate well developed with straight anterior margin and two anterior setae (Fig. 4);
- pronotum with one pair of minute dorso-central pronotal setae lying near the transverse carina (*dps* 2 by Clay 1962) (Fig. 3);
- pronotum with anterolateral pronotal setae (marginal prothoracic setae 1–3, *mps* 1–3 in Clay 1962) in following arrangement: *mps* 1 and *mps* 3 spine-like, *mps* 2 fine and long; *mps* 1 and *mps* 2 located on each lateral corner of pronotum, with *mps* 3 posteriorly to *mps* 2 on pronotal margin (Fig. 3);
- mesonotum well defined with only two anterior setae;
- mesonotum without median division, but with a Y-shaped line just below postnotum, not forming a suture or even splitting mesonotum (Fig. 3). This Y-shaped line slightly less evident, but also discernible in good specimens from other host families;
- strongly sclerotized ring-like mesothorax – mesothorax with sternum, pleura and tergum fused to form strongly sclerotized ring round the body;
- femur III without combs of spine-like setae but with thick or sparse brushes of setae.

Abdomen

- sternite I mostly surrounded by sternite II (it lies inside the wide notch of sternite II) (Fig. 5);
- sternite II enlarged with a clutch of heavy spine-like setae at each posterior-lateral margin called aster;
- male genitalia as in Fig. 6.
- male genital sac sclerite with two roughly serrated spiculated lateral arms (Figs 7–9);
- female vulva with smooth posterior margin (Fig. 1);
- female ventral anal margin without lateral seta-bearing processes (see Clay 1969);
- sternite VII fused with VIII+IX+X, forming female subgenital plate, although with a distinct transverse fenestra distinctly enclosed at lateral sides of subgenital plate where seventh and eighth segments fused (in *A. circumsternata* and *A. isacantha*; see Valim & Weckstein 2013: fig. 11); in the case of *A. klimesi* – male abdominal sternite VIII and female sternite VII both separated from the subgenital plate, which is formed by a single sternite IX (in the male) or fusion of sternites VIII and IX (in the female) (Figs 1–2).

Etymology

The generic name *Apomyrsidea* is formed by a combination of Greek word ‘*Apo*’ = ‘from’ and *Myrsidea*, referring that it is separated from the genus *Myrsidea*, where it was originally placed. The gender is feminine.

Included species

Three species are included in the *Apomyrsidea* gen. nov., all are restricted to formicariid hosts:

Apomyrsidea circumsternata (Valim & Weckstein, 2013) gen. et comb. nov.

Apomyrsidea isacantha (Valim & Weckstein, 2013) gen. et comb. nov.

Apomyrsidea klimesi (Sychra in Sychra *et al.*, 2006) gen. et comb. nov.

Descriptions of all three species are well presented in the original papers (Sychra *et al.* 2006; Valim & Weckstein 2013). Valim & Weckstein (2013) also presented a key to their identification.

***Apomyrsidea circumsternata* (Valim & Weckstein, 2013) gen. et comb. nov.**

Figs 8, 10

Myrsidea circumsternata Valim & Weckstein, 2013: 383, figs 3–4, 13–15, 17, 19, 22 (type host: *Formicarius colma* Boddaert, 1783).

Material examined

Holotype

BRAZIL • ♀; Rio Acanauí, Município Japurá, Amazonas; 2°01'38" S; 66°40'28" W; 20 Jul. 2007; Weckstein leg.; ex *Formicarius colma* Boddaert, 1783; MZUSP 2314.

Paratypes (2 ♀♀, 3 ♂♂)

BRAZIL • 1 ♂; same collection data as for holotype; FMNH-INS 94002 • 1 ♀; same collection data as for holotype; DNA voucher Mysp.Foco.1.4.2011.3; FMNH-INS 94003 • 2 ♂♂; same collection data as for holotype; MZUSP 2316, MZUSP 2317 • 1 ♀; same collection data as for holotype; MZUSP 2315.

Apomyrsidea isacantha (Valim & Weckstein, 2013) gen. et comb. nov.
Figs 9–10

Myrsidea isacantha Valim & Weckstein, 2013: 381, figs 1–2, 11–12, 16, 18, 20–21 (type host: *Chamaeza nobilis* Gould, 1855).

Material examined

Holotype

BRAZIL • ♀; Rio Acanauí, Município Japurá, Amazonas; 2°01'38" S, 66°40'28" W; 18 Jul. 2007; Weckstein leg.; ex *Chamaeza nobilis* Gould, 1855; MZUSP 2310.

Paratypes (2 ♀♀, 3 ♂♂)

BRAZIL • 1 ♂; same collection data as for holotype; FMNH-INS 94000 • 1 ♀; same collection data as for holotype; DNA voucher Mysp.Chno.1.4.2011.4; FMNH-INS 94001 • 2 ♂♂; same collection data as for holotype; MZUSP 2312, MZUSP 2313 • 1 ♀; same collection data as for holotype; MZUSP 2311.

Apomyrsidea klimesi (Sychra in Sychra *et al.*, 2006) gen. et comb. nov.
Figs 1–7, 10

Myrsidea klimesi Sychra in Sychra *et al.*, 2006: 55, figs 10–11, 14–15 (type host: *Formicarius analis* (d'Orbigny & Lafresnaye, 1837)).

Material examined

Holotype

COSTA RICA • ♀; Hitoy Cerere BR, Provincia Limón; 9°40' N, 85°27' W; 100 m a.s.l.; 27 Aug. 2004; Literak, Capek and Havlicek leg.; ex *Formicarius analis* (d'Orbigny & Lafresnaye, 1837); INBio O.Sychra CR15.

Allotype

COSTA RICA • ♂; same collection data as for holotype; INBio O.Sychra CR15.

Paratypes (1 ♀, 1 ♂)

COSTA RICA • 1 ♀, 1 ♂; same collection data as for holotype; 27 and 31 Aug. 2004; INBio O.Sychra CR14, CR16.

Other material

COSTA RICA • 1 ♂; Zona Protectora Las Tablas on the Pacific slope of the Cordillera de Talamanca; 8°54' N, 82°47' W; 1300 m a.s.l.; 21. Aug. 2010; Sychra and Literak leg.; ex *Formicarius analis*; MMBC O.Sychra CR226.

Discussion

In the key to the genera of the Menoponidae Mjöberg, 1910 of Clay (1969), *Apomyrsidea* gen. nov. would key to couplet 33 being closest to *Myrsidea* and *Oculomenopon* Price & Hellenthal, 2005. All three genera share unique diagnostic characters including: characteristic gular plate with the greater length and thickness of the posterior pair of setae compared to the other ones; missing *dhs* 18; well-developed prosternal plate with two anterior setae; strongly sclerotized ring-like mesothorax – mesothorax with sternum, pleura and tergum fused to form strongly sclerotized ring round the body; and general shape of male genitalia. Moreover, enlarged sternite II with aster of heavy setae at each posterior corner is a common feature of *Apomyrsidea* gen. nov. and *Myrsidea*, while presence of *dhs* 23 and the similar size of *dhs* 21 and *dhs* 22 is shared between *Apomyrsidea* gen. nov. and *Oculomenopon* (Price & Hellenthal 2005).

The most important key characters useful for separating *Apomyrsidea* gen. nov. from all species of *Myrsidea* and *Oculomenopon* are: the presence of *dps* 2, sternite I lying inside the wide notch of sternite II and different type of fusion in the terminal sternites – male abdominal sternite VIII and female sternite VII both at least partially but conspicuously separated from the subgenital plate, which is formed by a single sternite IX (in the male) or fusion of sternites VIII and IX (in the female).

Here, we provide a key for these three genera that modifies and extends the first part of couplet 33 of the Clay's (1969) key as follows:

- 33. Prosternum with 2 central setae 33a
- 33a. *Dps* 2 present; sternite I mostly surrounded by sternite II (it lies inside the wide notch on anterior margin of sternite II) ***Apomyrsidea*** gen. nov.
- Both *dps* absent; sternite I lies above the sternite II that has straight anterior margin without notch 33b
- 33b. *Dhs* 23 absent ***Myrsidea*** Waterston, 1915
- *Dhs* 23 present ***Oculomenopon*** Price & Hellenthal, 2005

Valim & Weckstein (2013) also discussed the presence of *dps* 2 and stated that, according to Clay (1966), the absence of dorso-central pronotal setae (*dps* 1 and *dps* 2) is one of defining characteristics of the genus *Myrsidea*. They wrongly interpreted Clay (1969), when writing: “Clay (1969) presented data showing that some species of *Myrsidea* could have at least one pair of dorso-central pronotal setae (see couplet 32)”. When we checked couplet 32 in the key by Clay (1969), there is a note “not more than one pair of dorso-central pronotal setae”. Moreover, Clay (1969: 11) wrote: “There are usually two pairs of dorso-central pronotal setae (*dps*) lying on or near the transverse carina, but in some species-groups (Clay 1962: 237) or genera (*Myrsidea*) they are reduced to one pair or absent.” We have examined many slides across groups and species of *Myrsidea* and can confirm that *dps* are absent apart from the newly erected *Apomyrsidea*.

Another interesting character is the presence of a cluster of heavy setae on each side of sternite III (Fig. 5). These setae are not as long as the aster, but they are heavier than spine-like setae on the lateral sides of other sternites and they are more conspicuous on females than on males. Despite this, it cannot be used as a basic character of the genus, because it is present only in two species – *A. circumsternata* gen. et comb. nov. and *A. klimesi* gen. et comb. nov. An unusual cluster of three spine-like setae situated on one side of sternite III was described by Klockenhoff (1984) from only one female of *M. serini* (Séguy, 1944). To our knowledge, no other author referred to such a structure on sternite III and we have not found it in any other examined *Myrsidea*.

A partial division of terminal sternites in females is known for example in some *Myrsidea* from bulbuls (Pycnonotidae G.R. Gray, 1840; Hellenthal & Price 2003), or *Myrsidea abbreviata* Eichler, 1951 from *Ramphastos dicolorus* Linnaeus, 1766 (Piciformes Meyer & Wolf, 1810: Ramphastidae Vigors, 1825; Price *et al.* 2004). However, this partial division is noticeable only at the lateral margins of the sternites of these species. A medial division or totally divided terminal sternites are only found in species of *Apomyrsidea*. According to Clay (1969), this is not necessarily a generic character, but in our opinion, it can be useful for separating *Apomyrsidea* gen. nov. from *Myrsidea*.

Another interesting character is the length of *dhs* 21 and *dhs* 22. While Clay (1966) considered the short length of *dhs* 22 compared with the long *dhs* 21 as one of the determining characteristics for the genus *Myrsidea*, *Apomyrsidea* gen. nov. shows *dhs* 22 as long as *dhs* 21 and both exceed the pronotal carina. Interestingly, the enigmatic genus *Ramphasticola* Carriker, 1949, which has been difficult to place, with different authors suggesting it should be nested within *Myrsidea* (Hopkins & Clay 1952; Price *et al.* 2003), has both species with long and short *dhs* 22, further suggesting a molecular phylogenetic analysis is needed to validate the placement of this genus.

The presence of an aster of heavy setae at each posterior corner of sternite II in *Apomyrsidea* gen. nov. and *Myrsidea* may bring some new challenges to determinations. The aster is one of the most visible features of many species of *Myrsidea*, and easily seen even under a stereoscope. However, in some species of *Myrsidea* it can be reduced (e.g., some species of Ramphastidae), while in species of *Apomyrsidea* gen. nov. it is always present. This changes the defining characteristic of the aster as the determining morphological feature for *Myrsidea* and broadens the use of this characteristic to a second genus. Henceforth, if no aster is present in a louse, this does not necessarily mean that it is not a *Myrsidea*, but the presence of asters will narrow the selection to two genera: *Myrsidea* and *Apomyrsidea* gen. nov. This further supports this character as an important one for morphological identifications.

Beside unique morphological characteristics, Valim & Weckstein (2013) referred to these species as “*Myrsidea* from Formicariidae” and suggested they would be phylogenetically distinct from nearly all other species of *Myrsidea*. Therein, instead of describing the new genus, the authors decided to broaden the set of diagnostic characters used to define the genus *Myrsidea*. However, in their phylogenetic tree *Myrsidea* sp. (GenBank KF048123) from *Myiarchus panamensis* Lawrence, 1861 (the avian family Tyrannidae Vigors, 1825), appears to be in the same clade with both species of *Apomyrsidea* gen. nov. used in the analysis (Valim & Weckstein 2013). This may be a misidentification of the sample and needs validation. Further, when this sequence was compared to all other COI sequences (a 379bp fragment of mitochondrial gene cytochrome oxidase subunit I) in GenBank, the highest match was *Menacanthus* sp. (GenBank AF545726) from the tyrannid *Attila spadiceus* (Gmelin J.F., 1789), with a p-distance of only 0.79%, and *Menacanthus* sp. (GenBank KJ730539) from the parid *Poecile* sp. with a p-distance of 1.31%. A comparison between these two species of *Menacanthus* showed the p-distance to be 1.05%, which is likely low enough to confirm it as the same species. On the basis of these facts, we believe that sequence KF048123 is potentially an untrustful sequence and we excluded it from our analysis.

When we used a broader range of genera in our study, *Apomyrsidea* gen. nov. shows a similar pattern creating a well separated clade from all other species of *Myrsidea* (Fig. 10). The familiar issue with lower support values (mostly in basal nodes) is often present when using only a single gene fragment (e.g., Kolencik *et al.* 2017). Unfortunately, the sequences, and their quality, for amblyceran species submitted to the GenBank database are limited and mostly only for a 379bp fragment of COI and/or a 347bp fragment of nuclear EF-1a (elongation factor 1 alpha) gene. Besides that, in many cases both sequences for the same specimen did not overlap; moreover, all three species of *Apomyrsidea* gen. nov. have only data for COI. Thus, it leaves a 379bp COI's fragment as the only one eligible for this study. The COI topology shows that *A. klimesi* gen. et comb. nov. is sister to *A. circumsternata* gen. et

comb. nov., in accordance with their morphology, which was also used in the key for their identification by Valim & Weckstein (2013).

In conclusion, the combination of unique morphological characteristics and the well-separated clade in the phylogenetic tree are strong enough to confirm *Apomyrsidea* gen. nov. as a new genus, and a sister taxon to *Myrsidea*.

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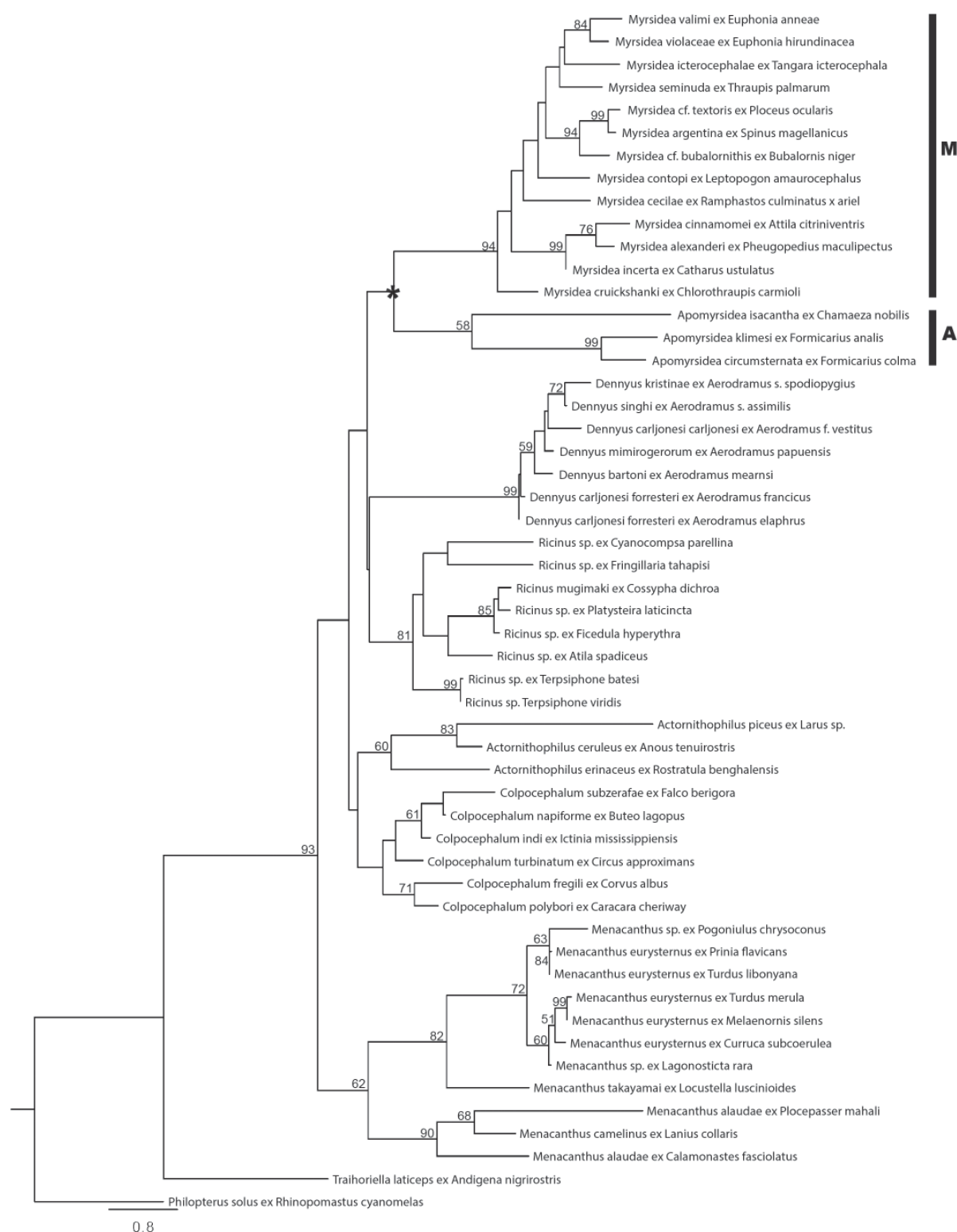
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Appendix

Maximum Likelihood phylogenetic tree of selected amblyceran genera and species on the basis of partial mitochondrial gene COI, with GTR+I+G model of molecular evolution. Bootstraps values are next to the nodes (values below 50% are not shown). M = species of *Myrsidea*; A = species of *Apomyrsidea* gen. nov.; * = a node between *Myrsidea* and *Apomyrsidea* gen. nov.



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