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A new ripiphorid beetle from Upper Cretaceous Burmese amber sheds light on early evolution of the extant subfamily Ripidiinae (Coleoptera: Ripiphoridae)

Un nouveau scarabée ripiphoride d'ambre birman Crétacé supérieur met en lumière l'évolution précoce de la sous-famille Ripidiinae (Coleoptera: Ripiphoridae)

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ABSTRACT

Fossils belonging to Ripidiinae are rare. Here, we describe and figure a remarkable new genus and species of Ripidiinae, *Protoripidius burmiticus* gen. et sp. nov., from the Upper Cretaceous amber of Myanmar. *Protoripidius* can be placed in the extant subfamily Ripidiinae based on the widely separated and abbreviated elytra (in male), unfolded hind wings, simple claws and the absence of tibial spurs. *Protoripidius* bears many transitional features shedding new light on the relationships of the two extant tribes of Ripidiinae. The discovery also highlights the palaeodiversity of the subfamily Ripidiinae in the mid-Cretaceous.

RÉSUMÉ

Les Ripidiinae fossiles sont rares. Nous décrivons et figurons un remarquable genre et espèce nouveaux de cette sous-famille, *Protoripidius burmiticus* gen. et sp. nov., de l'ambre Crétacé supérieur du Myanmar. *Protoripidius* peut être placé dans cette sous-famille actuelle sur la base des élytres largement séparés et raccourcis (chez le mâle), des ailes postérieures non pliables, des griffes simples et de l'absence des éperons tibiaux. *Protoripidius* possède plusieurs structures de « transition » apportant une lumière nouvelle sur les liens de parenté entre les deux tribus modernes de Ripidiinae. Cette découverte illustre aussi la paléodiversité de la sous-famille Ripidiinae au milieu du Crétacé.

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1. Introduction

The tenebrionoid family Ripiphoridae (or wedge-shaped beetles) is a widely distributed group currently including 38 genera and over 400 species (Lawrence et al., 2010). Ripiphorids are very peculiar in terms of their lifestyles as parasitoids, which are uncommon among beetles (Grimaldi and Engel, 2005). The family Ripiphoridae is currently divided into five extant subfamilies:

- Ptilophorinae;
- Pelecotominae;
- Hemirhipidiinae;
- Ripidiinae;
- Ripiphorinae (Bouchard et al., 2011; Falin, 2003; Lawrence et al., 2010).

Recent studies based on molecular data suggested that Ripiphoridae is probably not a monophyletic group with respect to the allied Mordellidae (Batelka et al., 2016a). In addition, the close relationship between Meloidae and Ripiphoridae was not supported based on molecular evidence (Batelka et al., 2016a; McKenna et al., 2015).

Probably due to the peculiar behaviour and a short lifespan of the adults, fossil ripiphorids are scarce, and most of them are confined to the Cenozoic (see summary in Kaupp et al., 2001). Subsequently, several taxa of described ripiphorids have been reinterpreted (Batelka et al., 2006, 2011; Falin and Engel, 2010; Perrichot et al., 2004) and a number of putative ripiphorid larvae have been reported from the Upper Cretaceous Burmese amber (Batelka et al., 2016b; Beutel et al., 2016; Grimaldi et al., 2005). Adults of ripiphorids from Mesozoic deposits are comparatively rare. Recently, Hsiao et al. (2017) reported the oldest representative of Ripiphoridae, *Archaeoripiphorus nuwa* Hsiao, Yu and Deng, from the Middle Jurassic Daohugou beds (ca. 165 Ma) in Inner Mongolia, northeastern China. *Archaeoripiphorus* shares characters belonging to two basal ripiphorid subfamilies, i.e. Pelecotominae and Ptilophorinae (Hsiao et al., 2017). Other Mesozoic ripiphorids, represented by four valid fossil species, are all from the mid-Cretaceous ambers of Myanmar and France (Batelka et al., 2016b; Cockerell, 1917; Falin and Engel, 2010; Perrichot et al., 2004). Among these amber-entombed species, two (*Cretaceoripidius burmiticus* (Cockerell) and *Paleoripiphorus deploegi* Perrichot, Nel and Néraudeau) were firmly placed in the extant derived subfamily Ripidiinae (Batelka et al., 2016b). In the present paper, we report a remarkable new genus belonging to Ripidiinae, also from the mid-Cretaceous Burmese amber.

2. Material and methods

The new genus and species is known from a single adult preserved in a clear piece of Burmese amber, which is derived from amber deposits named Noije Bum, near Tanai in the Hukawng Valley of northern Myanmar. A general introduction of the amber deposit and its geological settings can be found in Grimaldi et al. (2002) and Ross et al. (2010). Recent U-Pb zircon dating constrained the Burmese amber to a maximum age of 98.79 ± 0.62 Ma (Earliest Cenomanian; Shi et al., 2012). The type specimen is deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. Observations and photographs were made using a Zeiss Discovery V20 stereo microscope and a Zeiss Axio Imager 2 light microscope with a digital camera attached respectively. Photomicrographs with green background are taken using green fluorescence as light source attached to a Zeiss Axio Imager 2 light microscope. For the descriptions of thoracic structures, we follow the terminology of Zaragoza Caballero (1991), although certain structures are doubted by Batelka et al. (2011).

3. Systematic palaeontology

Order Coleoptera Linnaeus, 1758

Family Ripiphoridae Gemminger and Harold, 1870 [1853]

Subfamily Ripidiinae Gerstaecker, 1855

Tribe Ripidiini Gerstaecker, 1855

Genus ***Protoripidius* gen.** nov.

Type species. *Protoripidius burmiticus* gen. et sp. nov.

Diagnosis. The genus (based on male) can be separated from all other ripiphorids by a combination of the following characters: antennae filiform, with ten antennomeres; scape and pedicel short, third antennomere elongate; eyes large, not forming unbroken ring around head; mouthparts reduced; mandibles not developed; maxillary palpi three-segmented, gradually shortened and narrowed toward apex; labrum elongate; pronotum subtriangular, lacking grooves or impressions; metanepisternum broad, lacking anterior lobe; elytra short, each elytron distant from one another for the entire length; abdomen with seven visible sternites; all tibial spurs absent; tarsal formula 5-5-4; and first metatarsomere shorter than three remaining combined.

Etymology. The new genus-group name is a combination of the Greek πρωτο- (prōto-), meaning 'first', and *Ripidius*, the type genus of the extant tribe Ripidiini. The name is masculine in gender.

Remarks. *Protoripidius* clearly belongs to the superfamily Tenebrionoidea due to its characteristic 5–5–4 tarsal formula. The new genus is placed in Ripiphoridae based on its general body habitus (except the filiform antennae) similar to many brachypterus members of the family, such as Ripidiinae and Ripiphorinae. We include *Protoripidius* in the subfamily Ripidiinae based on the following combination of characters:

- abdominal sternite II visible externally, similar to sternite III;
- eyes coarsely facetted;
- elytra abbreviated in male, widely separated;
- hind wings not folded transversely;
- tibial spurs completely absent;
- claws simple;
- body densely clothed with short setae (Falin and Engel, 2010).

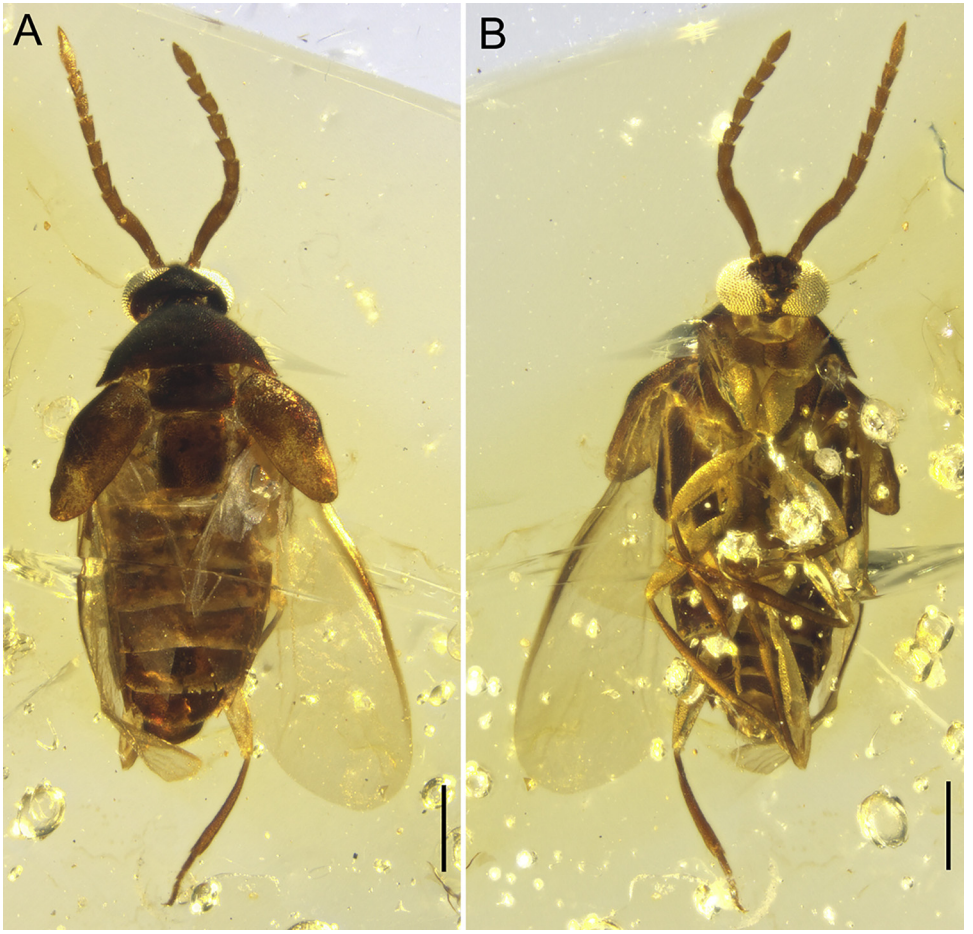

Fig. 1. Microphotographs of holotype (NIGP166155) of *Protoripidius burmiticus* gen. et sp. nov. from Upper Cretaceous amber from Myanmar, under normal reflected light. A. Dorsal view. B. Ventral view. Scale bars: 500 μm.
Fig. 1. Microphotographies de l'holotype (NIGP166155) de *Protoripidus burmiticus* gen. et sp. nov. de l'ambre Crétacé supérieur de Myanmar sous lumière réfléchie normale. A. Vue dorsale. B. Vue ventrale. Barres d'échelle : 500 μm.

Currently, the Ripidiinae comprise two extant tribes:

- Eorhipidiini;
- Ripidiini.

Eorhipidiini can be separated from Ripidiini by the unmodified antennomeres, well-developed mandibles, metanepisternum lacking an anterior lobe and abdomen with six visible sternites (Falin and Engel, 2010). *Protoripidius* appears to intermingle characters of these two extant tribes. It shares with Eorhipidiini the filiform (unmodified) antennae, metanepisternum lacking an anterior lobe and well-developed labrum (although labrum is absent in some *Pterydrias* species); with Ripidiini the absence of mandibles, three-segmented maxillary palpi (four-segmented in Eorhipidiini), each elytron distant from one another for the entire length and abdomen with seven visible sternites. It is plausible that the new genus likely represents a stem group of the derived Ripidiini and we tentatively place *Protoripidius* in Ripidiini based on the putative synapomorphies of the tribe, including the highly reduced mouthparts and the widely separated elytra.

Protoripidius burmiticus sp. nov.
(Figs. 1 and 2).

Etymology. The specific epithet *burmiticus* refers to the occurrence of the new species in burmite (Burmese amber).

Material. Holotype, NIGP166155, male; lowermost Cenomanian, Hukawng Valley, northern Myanmar; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Diagnosis. As for the genus (*vide supra*).

Description. Male. Body small, 2.85 mm long, slightly narrowed anteriorly and posteriorly; dorsum slightly convex. Vestiture consisting of short hairs, not forming pattern.

Head (Fig. 2A) rounded, width 0.64 mm across eyes, length 0.56 mm from posterior margin of head to apex of labrum, slightly declined, with mouthparts directed ventrally, gradually narrowing posteriorly to form narrow neck and short temples. Occipital region without median endocarina; transverse occipital ridge broadly rounded and above plane of pronotum, abutting anterior edge of pronotum and concealing neck from above. Eyes (Fig. 2A, B) slightly emarginate and hypertrophied, but separated

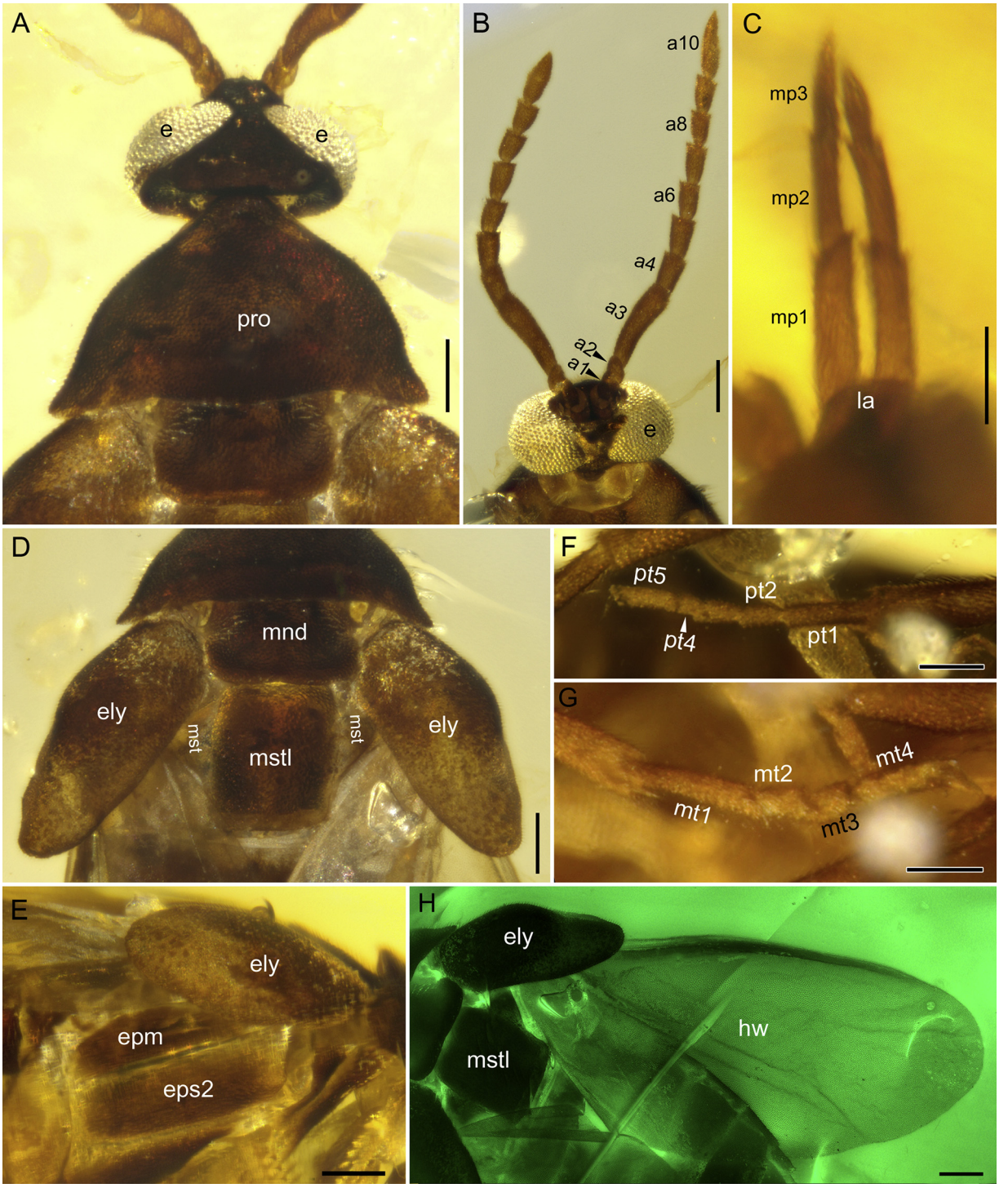

Fig. 2. Enlargements of holotype (NIGP166155) of *Protoripidius burmiticus* gen. et sp. nov. A–G. Under normal reflected light. H. Under green fluorescence. A. Dorsal view of head and prothorax, showing dorsally separated eyes. B. Antennae, ventral view. C. Maxillary palpi. D. Meso- and metathorax. E. Lateral view of thorax. F. Right protarsus. G. Left metatarsus. H. Right elytron and hind wing. Abbreviations: a1–10: antennomeres 1–10; e: eye; ely, elytron; epm: metepimeron; eps2: metanepisternum; hw: hind wing; la: labrum; mnd: mesonotal disc; mp1–3: maxillary palpomeres 1–3; mst: metascutum; mstl: metascutellum; mt1–4: metatarsomeres 1–4; pro: pronotum; pt1–5: protarsomeres 1–5. Scale bars: 200 μm in A, B, D, E and H, 100 μm in C, F and G.

Fig. 2. Agrandissements de l'holotype (NIGP166155). *Protoripidus burmiticus* gen. et sp. nov. A–G. Sous lumière réfléchie normale. H. Sous fluorescence verte. A. Vue dorsale de la tête et du protothorax, montrant dorsalement les yeux séparés. B. Antennes en vue ventrale. C. palpes maxillaires ; méso et métathorax. E. Vue latérale du thorax. F. Protarse droit. G. Métatarse gauche. H. Élytre droit et aile arrière. Abréviations : a1–10 : antennomères 1–10 ; e : œil ; ely, élytre ; epm :métépiméron ; eps2 : méranepiosternum ; hw : aile arrière ; la, labrum ; mnd : disque mésonotal ; mpl–3 palpomères 1–3 du maxillaire ; mst metascutum ; mstl metascutellum ; mtl1–4 métatarsomères 1–4 ; pro : pronotum ; pt1–5 : protarsomères 1–5. Barres d'échelle : 200 μm pour A, B, D, E et H, 100 μm pour C, F et G.

both dorsally and ventrally, coarsely facetted without interfacetal setae. Antennal insertions slightly concealed from above, narrowly separated; subantennal grooves absent. Labrum (Fig. 2C) elongate, anterior margin slight curved. Antennae (Fig. 2B) 10-segmented, filiform; antennomere 1 short, 0.11 mm long; antennomere 2 shorter than antennomere 1, 0.08 mm long, apical margin oblique; antennomere 3 longest, 0.31 mm long; antennomeres 4–9 almost in same width, length of antennomeres 4–10 being 0.13 mm, 0.15 mm, 0.14 mm, 0.15 mm, 0.13 mm, and 0.14 mm; antennomere 10 fusiform, 0.25 mm long. Mandibles and maxillae absent; maxillary palpi (Fig. 2C) 3-segmented, palpomere 1 broad and longest, 0.18 mm long; palpomere 2 slightly narrower and shorter than palpomere 1, 0.11 mm long; palpomere 3 short, 0.09 mm long, pointed at apex.

Pronotum (Fig. 2A) transverse, widest at base and narrowing anteriorly, 1.03 mm wide and 0. 66 mm long. Posterior edge sinuate. Prosternum in front of coxae shorter than mid length of procoxal cavity, apparently with median groove. Prosternal process absent. Procoxae long and projecting. Mesonotal disc (Fig. 2D) rectangular, posterior margin slightly sinuate; metascutellum (Fig. 2D and H) large, subquadrate. Elytra (Fig. 2D, E and H) short, 0.91 mm long and each 0.41 mm wide, exposing much of hind wing, abdomen and pterothorax, widest near middle; elytral apices rounded; disc not costate; epipleura absent. Mesocoxal cavities open laterally. Metaventrite convex; exposed portion of metanepisternum (Fig. 2E) broad, lateral sides nearly parallel, with indistinct punctuation; metepimeron (Fig. 2E) broadly exposed, narrower than metanepisternum, with dorsal margin curved. Hind wing (Fig. 2H) exposed, not folded beneath elytra.

Legs slender; trochanterofemoral joint strongly oblique with femora and well-separated from coxae; protibiae longer than protarsi; lacking tibial spurs; all tarsomeres simple; pro- and mesotarsi 5-segmented; protarsomere 1 elongate, as long as protarsomeres 2–4 combined, protarsomere 5 elongate, as long as protarsomeres 3–4 combined (Fig. 2F); mesotarsi 5-segmented, as long as protarsi; metatarsi 4-segmented, metatarsomere 1 elongate, slightly longer than metatarsomeres 2 and 3 combined, metatarsomere 3 slightly longer than metatarsomere 2, metatarsomere 4 elongate, slightly longer than metatarsomere 1 (Fig. 2G). Pretarsal claws simple, not dentate.

Abdomen with seven free ventrites; postcoxal lines absent. Apical margin of terminal sternite distinctly concave.

4. Discussion

The most remarkable character of *Protoripidius* attributes to the filiform antennae. Among all ripidiine males, this type of antennal form is only found in the putative basal tribe Eorhipidiini (Batelka and Hájek, 2009, 2010), although similar antennal type also occurs in *Ivierhipidius* Barclay, an enigmatic Neotropical genus currently not assigned to any known subfamilies (Barclay, 2015). The antennae of typical ripidiine males are usually uniflabellate (Lawrence et al., 2010). However, in *Pterydrias* Reitter, the sole genus of Eorhipidiini, the antennae possess 11 antennomeres (Batelka and Hájek, 2009), whereas the antennae are 10-segmented in *Protoripidius*. Up to now, only four Ripidiinae genera have been known to embody 10-segmented antennae in males (Batelka, 2011), i.e. *Paleoripiphorus* Perrichot, Nel, and Néraudeau from mid-Cretaceous French amber, *Cretaceoripidius* Falin and Engel from Burmese amber, *Olemehliella* Batelka from Eocene Baltic amber (Batelka, 2017), and extant genus *Blattivorus* Chobaut. The antennal morphology of *Protoripidius* looks quite peculiar, because the filiform type is plesiomorphic (as in Eorhipidiini), while the reduced antennal segmentation is probably a derived character state.

The eyes of *Protoripidius* appear to represent a transitional form between Eorhipidiini and Ripidiini: the eyes of the males of Ripidiini are expanded, almost holoptic (forming unbroken ring around head, apomorphy), whereas they are not expanded but hemispherical in Eorhipidiini (plesiomorphy). The mouthparts of *Protoripidius* appears to be transitional as well: the mandibles of *Protoripidius* are absent as in the Ripidiini, whereas its labrum is present, unlike most members of Ripidiini. Among Ripidiinae, a labrum is only present in *Pterydrias* (Eorhipidiini), *Riekella* Selander, *Paleoripiphorus* and the new genus *Protoripidius*. Many other highly derived characters of *Protoripidius*, such as expanded mesoscutellar shield, widely separated elytra, and 7-segmented abdomen, are supportive of the placement of the genus in the extant Ripidiini, rather than the Eorhipidiini.

Prior to this study, the Burmese amber has yielded three genera of Ripiphoridae: *Flabellotoma* Batelka, Prokop and Engel as the Mesozoic representative of the primitive subfamily Pelecotominae (Batelka et al., 2016b); and *Cretaceoripidius* (Cockerell) and *Paleoripiphorus*, both belonging to the Ripidiinae (Batelka et al., 2016b). Our discovery of a new genus reveals a potentially high palaeodiversity of Ripidiinae in the Cretaceous.

All extant ripiphorids have a life cycle known as endoparasitic on immature stages of other insects at some point in their development (Lawrence et al., 2010). Members of ripidiines parasitize nymphs of cockroaches (Lawrence et al., 2010; Riek, 1955) and Eorhipidiini might be parasitoids of termites (Batelka and Hájek, 2009). The morphologically specialized *Protoripidius* from mid-Cretaceous likely had a similar life style to their extant counterparts. Possible hosts of *Protoripidius*, such as cockroaches or termites, have also been known from the same amber deposit in northern Myanmar (e.g., Engel et al., 2016; Šmídová and Lei, 2017).

5. Conclusions

Our discovery of an interesting new ripidiine genus from the Upper Cretaceous amber of Myanmar adds to the palaeodiversity of Ripiphoridae in the Cretaceous ecosystem. *Protoripidius* bears a number of transitional features that shed new light on the relationships of the two extant tribes and early evolution of Ripidiinae. It also suggests that Rhipidiinae had already diversified and comparatively widespread by at least the mid-Cretaceous, as evidenced

by recent fossil discoveries (Batelka et al., 2016b; Falin and Engel, 2010; Perrichot et al., 2004). *Protoripidius* bears many important morphological characters which would be helpful for future phylogenetic reconstruction of the relationships of the subfamily Ripidiinae.

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References

Barclay, M.V., 2015. *Ivierhipidius*, an enigmatic new Neotropical genus of Ripiphoridae (Coleoptera: Tenebrionoidea) with four new species. Acta Entomologica Musei Nationalis Pragae 55 (2), 691–701.

Batelka, J., 2011. *Olemehlia krali*, a new genus and species of Ripidiinae from Baltic Amber (Coleoptera: Ripiphoridae). Ann. Soc. Entomol. Fr. 47 (3–4), 361–364.

Batelka, J., 2017. A replacement name for the Baltic amber ripidiine genus *Olemehlia* (Coleoptera: Ripiphoridae). Novitates Paleoentomologicae 20, 1–2.

Batelka, J., Hájek, J., 2009. A taxonomic review of the genus *Eorhipidius* (Coleoptera: Ripiphoridae: Ripidiinae), with descriptions of three new species from Asia. Acta Entomol. Musei Nationalis Pragae 49 (2), 769–782.

Batelka, J., Hájek, J., 2010. Taxonomy and distribution of the genus *Pterydrias* Reitter and confirmation of its synonymy with *Eorhipidius* Iablokoff-Khnzorian (Coleoptera: Ripiphoridae: Ripidiinae). Zootaxa 2566, 64–68.

Batelka, J., Collomb, F.M., Nel, A., 2006. *Macrosiagon deuvei* n. sp (Coleoptera: Ripiphoridae) from the French Eocene amber. Ann. Soc. Entomol. Fr. 42 (1), 75–78.

Batelka, J., Engel, M.S., Falin, Z.H., Prokop, J., 2011. Two new ripidiine species in Dominican amber with evidence of aggregative behaviour of males "frozen" in the fossil record (Coleoptera: Ripiphoridae). Eur. J. Entomol. 108 (2), 275–286.

Batelka, J., Kundrata, R., Bocak, L., 2016a. Position and relationships of Ripiphoridae (Coleoptera: Tenebrionoidea) inferred from ribosomal and mitochondrial molecular markers. Ann. Zool. 66 (1), 113–123.

Batelka, J., Prokop, J., Engel, M.S., 2016b. New ripiphorid beetles in mid-Cretaceous amber from Myanmar (Coleoptera: Ripiphoridae): first Pelecotominae and possible Mesozoic aggregative behaviour in male Ripidiinae. Cretaceous Res. 68, 70–78.

Beutel, R.G., Zhang, W.W., Pohl, H., Wappler, T., Bai, M., 2016. A miniaturized beetle larva in Cretaceous Burmese amber: reinterpretation of a fossil "strepsipteran triungulin". Insect Syst. Evol. 47 (1), 83–91.

Bouchard, P., Bousquet, Y., Davies, A.E., Alonso-Zarazaga, M.A., Lawrence, J.F., Lyal, C.H.C., Newton, A.F., Reid, C.A.M., Schmitt, M., Ślipiński, S.A., Smith, A.B.T., 2011. Family-group names in Coleoptera (Insecta). ZooKeys 88, 1–972.

Cockerell, T.D.A., 1917. Fossil insects. Ann. Entomol. Soc. Am. 10 (1), 1–22.

Engel, M.S., Barden, P., Riccio, M.L., Grimaldi, D.A., 2016. Morphologically specialized termite castes and advanced sociality in the Early Cretaceous. Curr. Biol. 26 (4), 522–530.

Engel, Z.H., 2003. Phylogenetic analysis and revision of the genera and subfamilies of the Ripiphoridae (Coleoptera). (Unpublished PhD Dissertation). University of Kansas, Lawrence (xxiv + 535 pp.).

Falin, Z.H., Engel, M.S., 2010. Notes on Cretaceous Ripidiini and revised diagnoses of the Ripidiinae, Ripidiini and Eorhipidiini (Coleoptera: Ripiphoridae). Alavesia 3, 35–42.

Gemminger, M., Harold, B., 1870. Catalogus coleopterorum hucusque descriptorum synonymicus et systematicus, 7. Sumptu E. H. Gummi, Munich, Germany, pp. 1801–2180.

Gerstaecker, C.E.A., 1855. Rhipiphoridum coleopterorum familiae dispositio systematica. Frederici Nicolai, Berlin, Germany (36 pp., + 1 pl.).

Grimaldi, D., Engel, M.S., 2005. Evolution of the Insects. Cambridge University Press, Cambridge (xv + 755 pp.).

Grimaldi, D.A., Engel, M.S., Nascimbene, P.C., 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity and paleontological significance. Am. Mus. Nov. 3361, 1–72.

Grimaldi, D., Kathirithamby, J., Schawaroch, V., 2005. Strepsiptera and triungula in Cretaceous amber. Insect Syst. Evol. 36 (1), 1–20.

Hsiao, Y., Yu, Y., Deng, C., Pang, H., 2017. The first fossil wedge-shaped beetle (Coleoptera Ripiphoridae) from the middle Jurassic of China. Eur. J. Taxon. 277, 1–13.

Kaupp, A., Falin, Z., Nagel, P., 2001. An annotated catalogue of fossil Ripiphoridae, taxonomic notes, and the description of a new genus and species from Baltic amber (Coleoptera: Ripiphoridae: Ripidiinae), 85. Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg, pp. 165–195.

Lawrence, J.F., Falin, Z.H., Ślipiński, A., 2010. Ripiphoridae Gemminger and Harold, 1870 (Gerstaecker, 1855). In: Leschen, R.A.B., Beutel, R.G., Lawrence, J.F. (Eds.), Coleoptera, Beetles, 2. Walter de Gruyter, Berlin, pp. 538–548 (Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). In: Kristensen, N.P., Beutel, R.G. (Eds.), Handbook of Zoology, Arthropoda: Insecta.).

Linnaeus, C., 1758. Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, 10th revised ed., 1. Laurentius Salvius, Holmiae, Stockholm (iv + 824 pp.).

McKenna, D.D., Farrell, B.D., Caterino, M.S., Farnum, C.W., Hawks, D.C., Maddison, D.R., Seago, A.E., Short, A.E., Newton, A.F., Thayer, M.K., 2015. Phylogeny and evolution of Staphyliniformia and Scarabaeiformia: forest litter as a stepping stone for diversification of nonphytophagous beetles. Syst. Entomol. 40 (1), 35–60.

Perrichot, V., Nel, A., Néraudeau, D., 2004. Two new wedge-shaped beetles in Albo-Cenomanian ambers of France (Coleoptera: Ripiphoridae: Ripiphorinae). Eur. J. Entomol. 101 (4), 577–581.

Riek, E.F., 1955. The Australian rhipidiine parasites of cockroaches (Coleoptera: Rhipiphoridae). Aust. J. Zool. 3, 71–94 (pls 1-4).

Ross, A.J., Mellish, C., York, P., Crighton, B., 2010. Burmese amber. In: Penney, D. (Ed.), Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, pp. 208–235.

Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q., Li, X., 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Res. 37, 155–163.

Šmídová, L., Lei, X., 2017. The earliest amber-recorded type cockroach family was aposematic (Blattaria: Blattidae). Cretaceous Res. 72, 189–199.

Zaragoza Caballero, S., 1991. Nuevos Rhipidiinae de México (Coleoptera: Rhipiphoridae). An. Inst. Biol. 62, 481–495 (Universidad Nacional Autonoma de Mexico, Serie Zoologia).