Derinilipia, a new genus of Ripidiini from mid-Cretaceous amber of northern Myanmar (Coleoptera: Ripiphoridae)

Yan-Da Li, Di-Ying Huang & Chen-Yang Cai

A new fossil of Ripiphoridae, *Derinilipia alekseevi* gen. et sp. nov., is reported from mid-Cretaceous Kachin amber of northern Myanmar. *Derinilipia* is distinctive within the tribe Ripidiini, as it has unfused 4-segmented maxillary palps, contiguous elytra, tibial spurs present on all legs, and pectinate pretarsal claws. The new genus is suggested as a stem-group member of Ripidiini based on a cladistic analysis. • Key words: Ripidiinae, Kachin amber, Cretaceous, fossil, phylogeny.

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Ripiphoridae is a distinctive beetle family of Tenebrionoidea with parasitic life stages (Lawrence *et al.* 2010). Recent phylogenomic studies have confirmed that Ripiphoridae is not a monophyletic group, with Mordellidae *sensu stricto* nested within it (Zhang *et al*. 2018, McKenna *et al.* 2019, Cai *et al*. 2022). Ripiphoridae currently includes five extant subfamilies: Ptilophorinae, Pelecotominae, Hemirhipidiinae, Ripidiinae and Ripiphorinae. Although several studies have attempted to resolve the phylogeny of Ripiphoridae using morphological or molecular data (Falin 2003, Batelka *et al.* 2016, Batelka & Prokop 2023), a reliable phylogenetic framework regarding the relationships of the subfamilies has not yet been established.

Ripidiinae is notable among the subfamilies of Ripiphoridae, due to its larviform females (state unknown in Eorhipidiini) and reduced mouthparts (*e.g.* Riek 1955, Besuchet 1956, Batelka *et al*. 2021). The subfamily includes two tribes, Eorhipidiini and Ripidiini (Iablokoff-Khnzorian 1986). Compared to the more plesiomorphic Eorhipidiini, Ripidiini possesses many specialized characters, such as eyes forming a continuous ring around head, antennae flabellate, mandibles absent, maxillary palps at most 3-segmented and sometimes fused, prothorax with contiguous coxal cavities, elytra widely separated, and abdominal sternite II visible externally.

Several fossils of Ripidiini have been discovered in mid-Cretaceous Kachin amber from Myanmar. Some of them exhibit morphological features that are unknown or rarely present in their modern relatives. For example, *Protoripidius* Cai *et al.*, 2018 has filiform antennae (uniflabellate in all other male Ripidiini) (Cai *et al.* 2018), *Amberocula* Batelka *et al*., 2018 has compound eyes divided into upper and lower lobes (known otherwise only in *Neopauroripidius* Falin & Engel, 2014) (Batelka *et al.* 2018), and *Ripidinelia* Batelka & Prokop, 2019 has a spur on all tibiae (absent in all other Ripidiini) and pectinate pretarsal claws (rare in Ripidiini, though possible present in *Riekella* Selander, 1957) (Batelka & Prokop 2019, Li *et al.* 2024). In the present study, we report a new genus of Ripidiini from Kachin amber, which again shows an unusual combination of morphological characters unknown in extant ripiphorids.

Material and methods

The Kachin (Burmese) amber specimen studied herein (Figs 1–4) originated from amber mines near Noije Bum (26° 20′ N, 96° 36′ E), Hukawng Valley, Kachin State, northern Myanmar. The amber specimen is deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China. The amber piece was trimmed with a saw mounted on a handheld rotary tool, ground with emery paper of different grit sizes, and finally polished with polishing powder.

Figure 1. General habitus of *Derinilipia alekseevi* gen. et sp. nov., holotype, NIGP205468, under incident light. A – dorsal view. B – ventral view. Scale bars: 1 mm.

Photographs under incident light were taken with a Zeiss Discovery V20 stereo microscope. Widefield fluorescence images were captured with a Zeiss Axio Imager 2 light microscope combined with a fluorescence imaging system. Confocal images were obtained with a Zeiss LSM710 confocal laser scanning microscope, using the 488 nm (Argon) laser excitation line (Fu *et al.* 2021). Images were stacked with Helicon Focus 7.0.2, Zerene Stacker 1.04 and Adobe Photoshop CC, and were further processed in Adobe Photoshop CC to adjust brightness and contrast.

To evaluate the systematic placement of *Derinilipia* gen. nov., we conducted a morphology-based phylogenetic analysis. The data matrix was modified based on Batelka & Prokop (2023), and the character list was identical to that in Batelka & Prokop (2023). Characters 18 and 23 of *Ripidinelia* were recoded according to the new specimens reported by Li *et al.* (2024). In Batelka & Prokop (2023), several female or larval characters (14, 29 and 30) were coded for genera of which no female or larvae are known, based solely on assumed systematic affinity. This in fact artificially increased the weight of other characters that were used to determine the systematic affinity, which we believe is inappropriate. Therefore, we recoded the aforementioned characters as "?" for genera of which females or larvae are unknown.

The parsimony analysis was performed under implied weights, using R 4.1.0 (R Core Team, 2021) and the R package TreeSearch 1.3.1 (Smith 2023). The concavity constant was set to 12, following the suggestion by Goloboff *et al*. (2018) and Smith (2019). A majority-rule consensus was calculated. Clade supports were generated based on 1,000 jackknife pseudoreplicates. To examine whether the dramatic topological difference between our new result (Fig. 5B) and Batelka & Prokop (2023) was caused by the inclusion of *Derinilipia* (rather than different searching parameters or recoding of characters of other taxa), we reanalyzed our data matrix using the same procedure described above, except that *Derinilipia* was excluded (Fig. 5A).

The resulting trees were visualized with the online tool iTOL 6.6 (Letunic & Bork 2024) and graphically edited with Adobe Illustrator CC 2017. Pelecotominae (or *Pelecotoma* Fischer, 1809) was artificially designated at the base of the trees, according to Batelka *et al*. (2016) and Cai *et al*. (2024). However, as the true basalmost taxon of Ripiphoridae is not completely certain, and unequivocal tenebrionoid outgroups were not used in the analyses, the

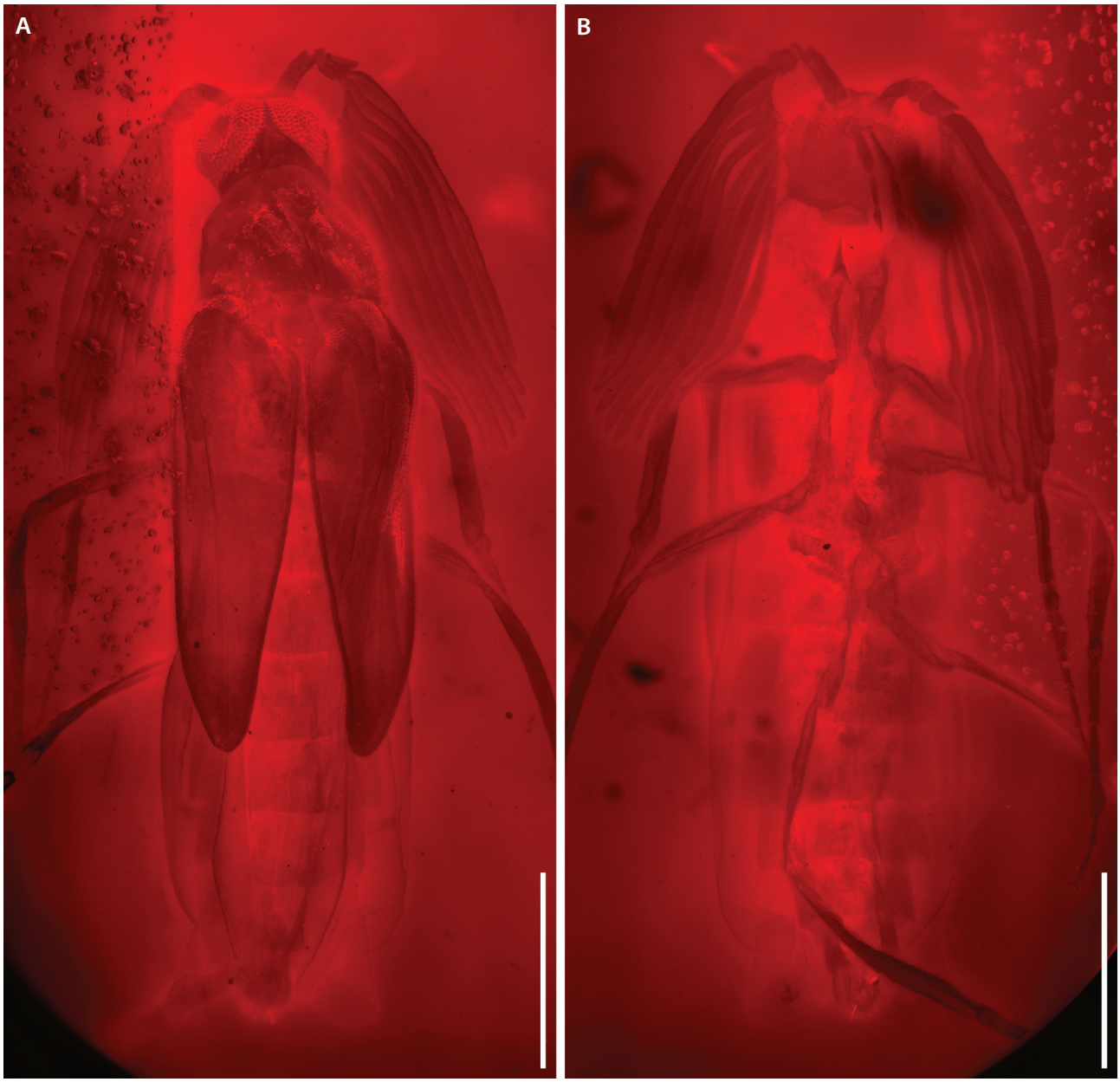

Figure 2. General habitus of *Derinilipia alekseevi* gen. et sp. nov., holotype, NIGP205468, under widefield fluorescence. A – dorsal view. B – ventral view. Scale bars: 1 mm.

trees shown in the present results should be viewed as unrooted, rather than rooted.

Systematic palaeontology

Order Coleoptera Linnaeus, 1758
Superfamily Tenebrionoidea Latreille, 1802
Family Ripiphoridae Laporte, 1840 (see Bousquet & Bouchard 2018, ICZN 2020)
Subfamily Ripidiinae Gerstaecker, 1855
Tribe Ripidiini Gerstaecker, 1855

Genus *Derinilipia* gen. nov.

LSID. – urn:lsid:zoobank.org:act:D8189552-7EA7-402A-9C9A-A0456E634BD1

Type species. – *Derinilipia alekseevi* sp. nov.

Etymology. – The generic name is an anagram of *Ripidinelia* and is feminine in gender. The new genus shares with *Ripidinelia* the presence of a single spur on all tibiae and the pectinate tarsal claws, which are otherwise at least extremely rare in Ripidiinae (Li *et al.* 2024).

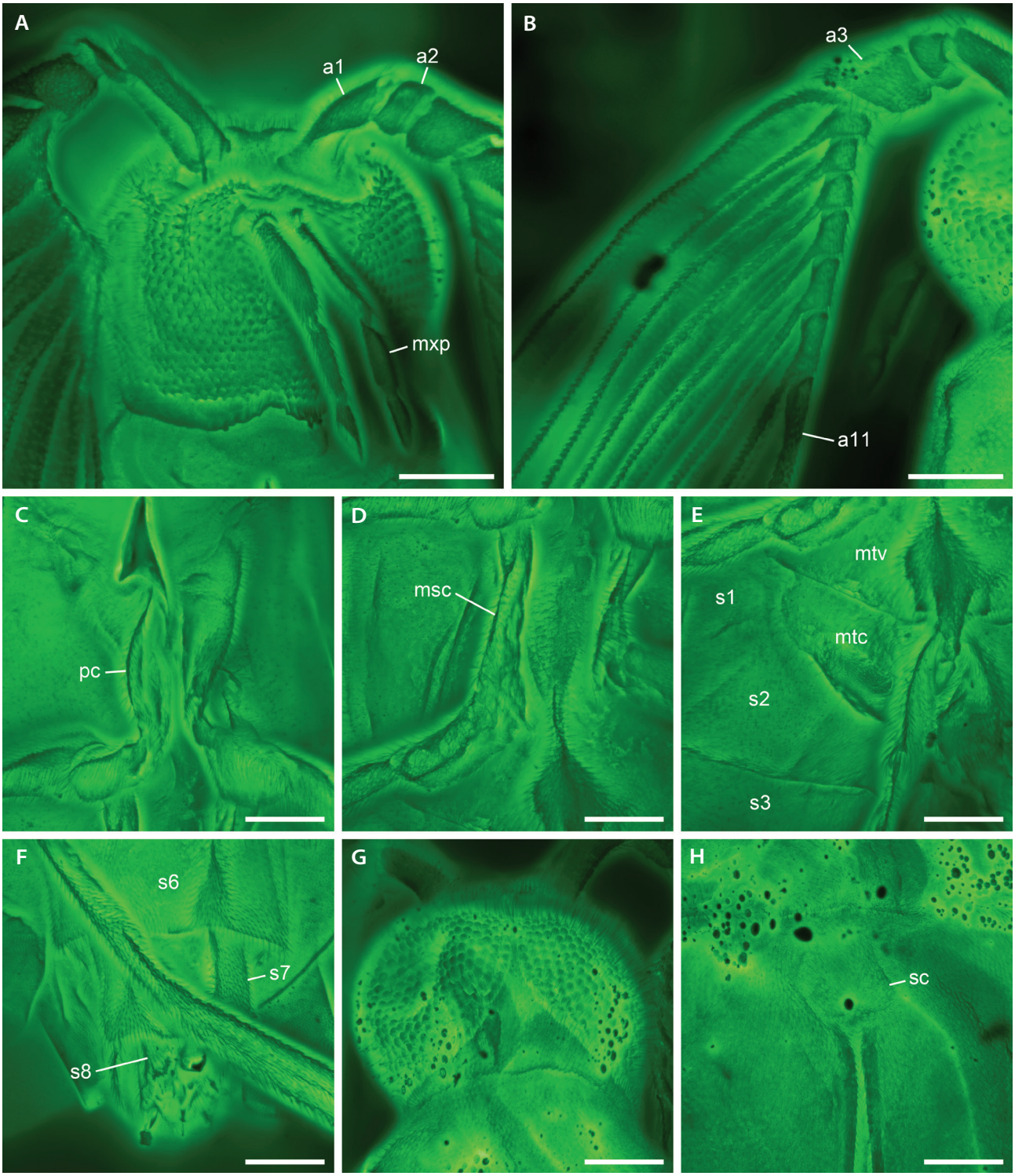

Figure 3. Details of *Derinilipia alekseevi* gen. et sp. nov., holotype, NIGP205468, under confocal microscopy. A – head, ventral view. B – antenna. C – procoxae. D – mesocoxae. E – abdominal base, ventral view. F – abdominal apex, ventral view. G – head, dorsal view. H – elytral base, dorsal view. Abbreviations: a1–11 – antennomeres 1–11; msc – mesocoxa; mtc – metacoxa; mtv – metaventrite; mxp – maxillary palp; pc – procoxa; s1–8 – abdominal sternites I–VIII; sc – scutellum. Scale bars: 200 µm.

Diagnosis. – Eyes forming unbroken ring around head (Fig. 3A, G). Antennae 11-segmented, uniflabellate from antennomere 4 (Fig. 3B). Maxillary palps unfused, 4-segmented (Fig. 3A). Procoxae contiguous (Fig. 3C). Elytra not fully covering abdomen, contiguous behind scutellum (Fig. 3H). Tibial spurs single on all legs (Fig.

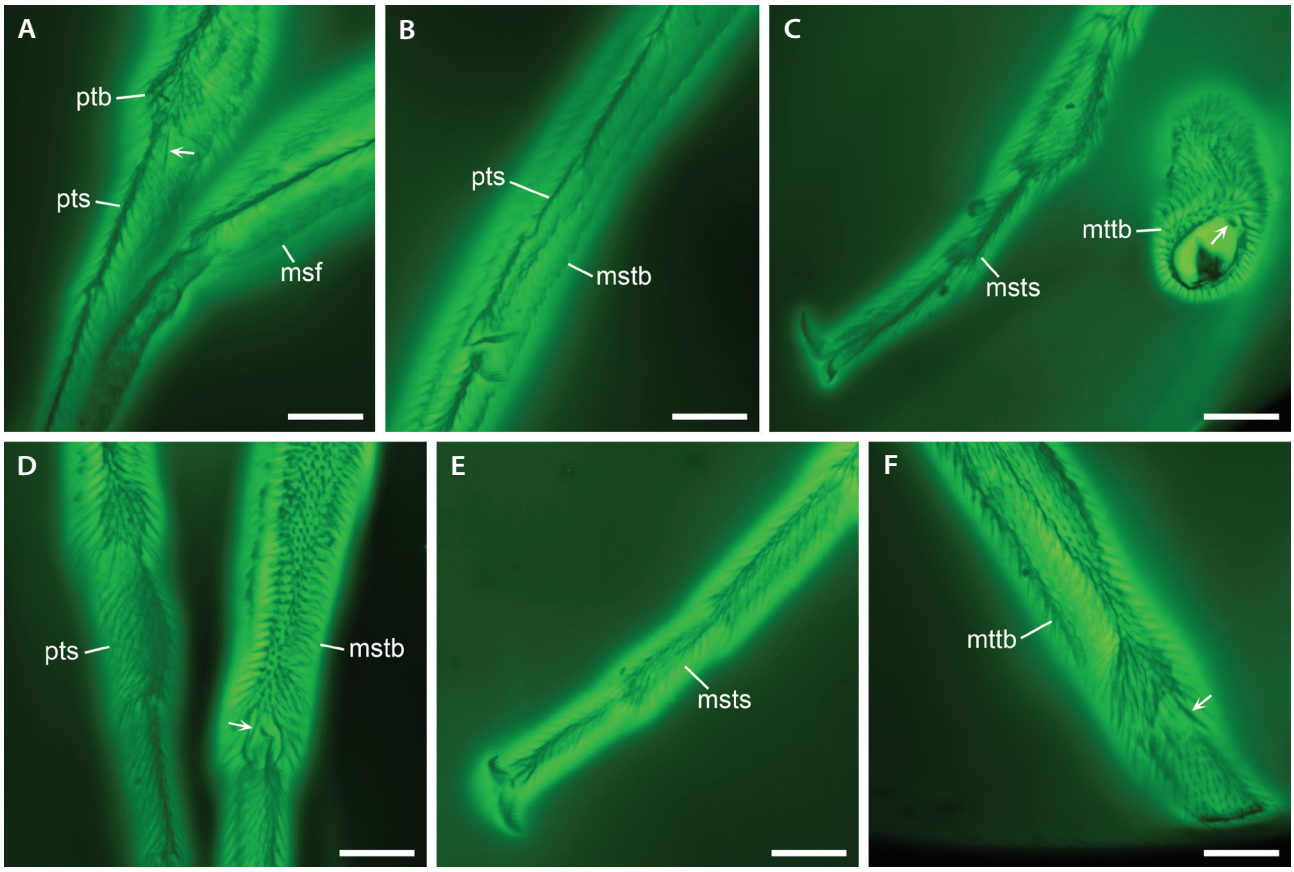

Figure 4. Tibial spurs (arrows) and pretarsal claws of *Derinilipia alekseevi* gen. et sp. nov., holotype, NIGP205468, under confocal microscopy. Abbreviations: ptb – protibia; pts – protarsus; msf – mesofemur; mstb – mesotibia; msts – mesotarsus; mttb – metatibia. Scale bars: 100 μm.

4A, C, D, F). Pretarsal claws pectinate (Fig. 4B, C, E). Abdominal sternites I–VIII externally visible (Fig. 3E, F).

***Derinilipia alekseevi* sp. nov.**
Figures 1–4

LSID. – urn:lsid:zoobank.org:act:110D1B1B-BD92-45E8-839D-7EAA4BC45E4A

Type horizon and locality. – Unnamed horizon, mid-Cretaceous, Upper Albian to Lower Cenomanian. Amber mine located near Noije Bum Village, Tanai Township, Myitkyina District, Kachin State, Myanmar.

Material. – Holotype, NIGP205468, male.

Etymology. – The species is named after the coleopterist Dr. Vitalii I. Alekseev.

Diagnosis. – As for the genus.

Description. – Body elongate, about 4.7 mm long, 1.2 mm wide, apparently weakly sclerotized; surface with dense fine short hairs.

Head with mouthparts strongly reduced. Compound eyes large, dorsally contiguous anteriad, ventrally entirely contiguous, with moderately long interfacetal setae. Antennae 11-segmented, uniflabellate; antennomere 1 elongate; antennomeres 2 and 3 submoniliform, moderately wide; antennomeres 4–10 each with one long ramus; body of antennomeres 4–10 narrower than antennomeres 2 and 3, progressively becoming narrower and longer; antennomere 11 long, expanded, similar in shape to rami of previous antennomeres. Mouthparts completely reduced except for maxillary palps. Maxillary palps 4-segmented, basally unfused; palpomere 1 short; palpomeres 2 and 3 elongate; palpomere 4 moderately elongate, somewhat cultriform.

Pronotum campaniform. Procoxae contiguous, projecting. Scutellum relatively long, wider in posterior half. Elytra contiguous behind scutellum, each with apex narrowly rounded, moderately long, reaching base of abdominal segment IV. Mesocoxae projecting, separated. Metacoxae contiguous.

Legs moderately long and slender. Trochanterofemoral joints strongly oblique, though with femora well separated from coxae. Tibiae with one unequivocal apical spur on all legs. Tarsi 5-5-4 (metatarsi not preserved, deduced

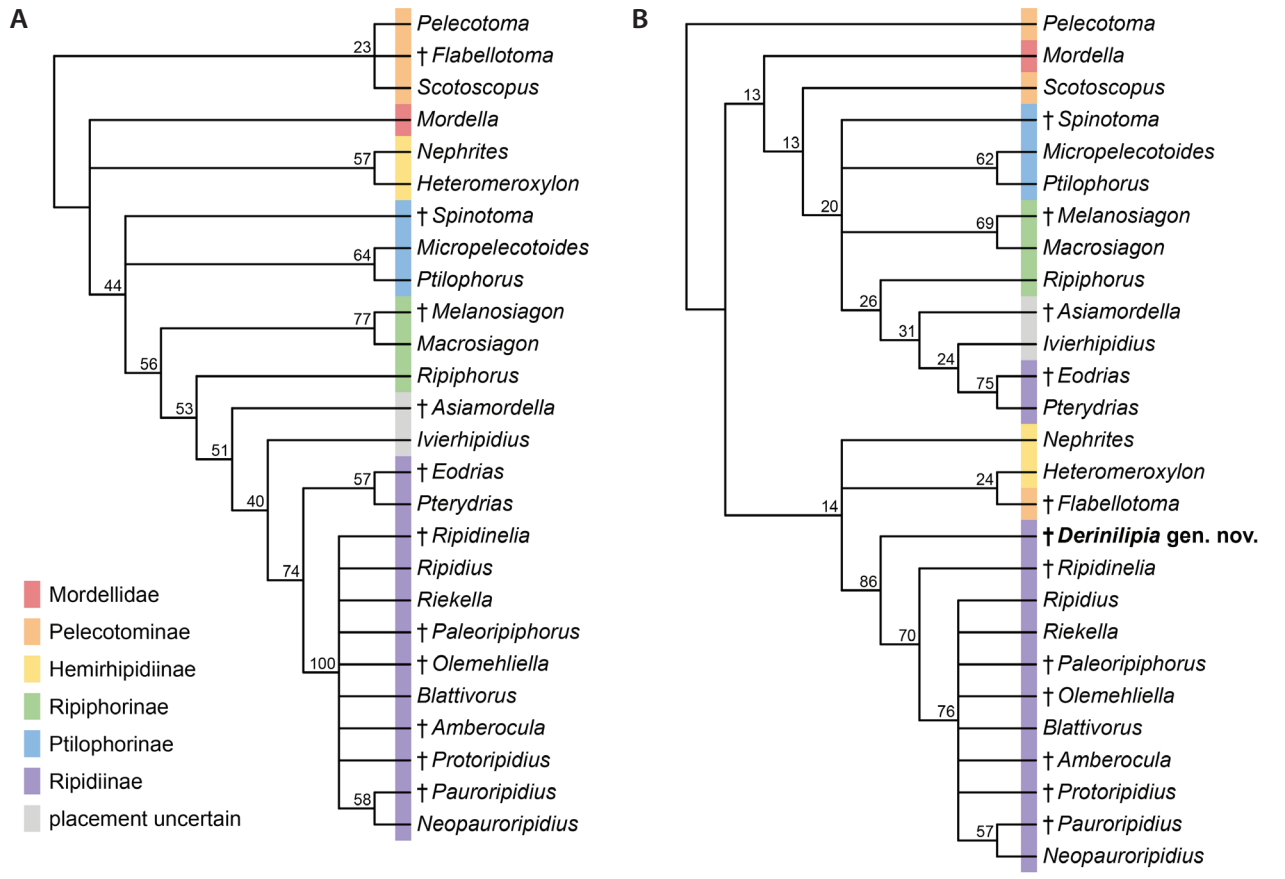

Figure 5. Morphology-based phylogenies of Ripiphoridae, based on parsimony analyses under implied weights. The fossil genera are indicated by a dagger symbol. A – *Derinilipia* gen. nov. not included. B – *Derinilipia* gen. nov. included.

based on the ground plan of tenebrionoids); tarsomeres simple. Pretarsal claws pectinate.

Abdomen with sternites I–VIII externally visible.

Discussion

Morphology-based phylogeny of Ripiphoridae

When *Derinilipia* gen. nov. is not sampled, the phylogenetic result (Fig. 5A) is fully compatible with Batelka & Prokop (2023). Eorhipidiini is resolved as closely related to Ripidiini, although whether *Pterydrias* Reitter, 1895 and *Eodrias* Batelka & Prokop, 2023 form a monophyletic group is unclear. However, when *Derinilipia* is included, the topology changes dramatically (Fig. 5B). In particular, Eorhipidiini is located in a group together with *Ripiphorus* Bosc, 1791, *Asiamordella* Hong, 2002 and *Ivierhipidius* Barclay, 2015 and far away from Ripidiini. In fact, in Batelka *et al*. (2016), the only molecular study with Eorhipidiini sampled, Eorhipidiini was variably resolved as sister to Ripidiini or Ripiphorinae, or even outside Ripiphoridae + Mordellidae. Interestingly, in our analysis including *Derinilipia*, Ripiphorinae appears to be closer to Mordellidae, rather than Ripidiini, which is accordant with the molecular analyses by Batelka *et al.* (2016). It should be nevertheless noted that Batelka *et al*. (2016) used only four gene fragments. Further studies with denser sampling of taxa and genes would be helpful to clarify the internal relationships of Ripiphoridae + Mordellidae. Our results align with a recent simulation study evaluating the performance of inference methods across varying levels of fossil sampling and missing data (Mongiardino Koch *et al*. 2021). It is evident that the integration of fossils improves the phylogenetic analysis of morphological datasets.

Morphology and systematic placement of *Derinilipia*

Derinilipia can be confidently placed in Ripidiinae based on the coarsely facetted eyes, reduced mouthparts (with maxillary palps present only) and shortened elytra (not fully covering abdomen) (Viana 1971; Iablokov-

Khnzorian 1975, 1986). *Derinilipia* appears to be close to Ripidiini, as it has eyes forming an unbroken ring around head, antennae uniflabellate from antennomere 4, mouthparts with only maxillary palps present, contiguous procoxal cavities and externally visible abdominal sternite II. However, it also has a few Eorhipidiini-like plesiomorphic characters. In *Derinilipia*, the maxillary palps are 4-segmented and unfused, and the elytra are contiguous behind scutellum, both of which are plesiomorphic and unknown in the crown-group Ripidiini. Our analysis resolves *Derinilipia* as a stem-group member of Ripidiini, which is accordant with the above discussion.

Data availability. – The data matrix for the phylogenetic analysis is available in the Electronic supplement. The original confocal data are available in the Zenodo repository (*https://doi.org/10.5281/zenodo.14586549*).

Electronic supplement. – Morphological dataset used for the phylogenetic analysis, derived from Batelka & Prokop (2023).

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