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Specialized variegated mud-loving beetles from mid-Cretaceous Burmese amber (Coleoptera: Heteroceridae)

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Abstract

Variegated mud-loving beetles, or Heteroceridae, are a small family belonging to the polyphagan superfamily Byrrhoidea. To date, only two poorly preserved compression fossils have been known from the Early Cretaceous of Eurasia. Here we describe the first heterocerid beetles in mid-Cretaceous amber from northern Myanmar, *Excavotarsus lini* **gen. et sp. nov.** and *Ex. minor* **sp. nov.** The two new fossil species are distinguished from all extant heterocerids by their elongate body shape, apical 8–9 antennomeres forming a loose serrate club, pronotum longer than wide, protibia lacking robust spines, and two-segmented protarsi. This peculiar combination of plesiomorphic and derived characters suggests that *Excavotarsus* represents an early-diverging lineage of Heteroceridae and indicates that the family originated and diversified before the mid-Cretaceous.

Keywords: Heteroceridae, *Excavotarsus*, Mesozoic, palaeoecology, Burmese amber

Introduction

Heteroceridae, or variegated mud-loving beetles, is a group of widespread and relatively common beetles belonging to the polyphagan superfamily Byrrhoidea, occurring on every continent except Antarctica (Vanin *et al.*, 2016). Variegated mud-loving beetles are represented in the Recent fauna by approximately 300 described species (Vanin *et al.*, 2016), but their biodiversity is still not fully documented (*e.g.*, Skalický, 2017; Sazhnev, 2018). Heterocerids inhabit riparian habitats adjacent to freshwater, brackish, and saltwater bodies (Mascagni, 2015). As their name suggests, the beetles excavate tunnels in mud and occasionally wet sand using their robust mandibles and anterior legs armed with prominent

spines (Kaufmann & Stansly, 1979). The beetles are able to survive flooding of their tunnels since their water-repellent setae are able to maintain a ‘cushion’ of air to facilitate respiration (Messner, 1973). Larvae and pupae co-inhabit the burrows with adults, which feed predominantly on algae, plankton, and humid vegetational matter in the mud (Kaufmann & Stansly, 1979). Egg guarding has been reported in one species (Folkerts, 1989).

Extant heterocerids are characterized by their densely pubescent body, large head with prominent mandibles and labrum, peculiar 9–11 segmented antennae with the distal half forming a loosely serrated club, a series of spines at the outer edges of the tibiae, 4-segmented tarsi, short mesosternum, and presence of stridulate ridges on the first abdominal segment (Clarke, 1973; Vanin *et al.*, 2016). Many heterocerid species are almost indistinguishable without examining the morphology of the male genitalia. Their rather uniform morphology possibly represents an optimal adaptation to their environment (Charpentier, 1968; Clarke, 1973).

The placement of Heteroceridae in the superfamily Byrrhoidea is supported by their wing-holding pattern and the shortened anterior process of the metendosternite (Vanin *et al.*, 2016), but the precise phylogenetic position of the family is not yet settled. Beutel (1995) recovered Limnichidae as the sister group to Heteroceridae based on larval morphological characters, while the morphological phylogeny of Costa *et al.* (1999) placed Heteroceridae in a clade with Dryopidae + paraphyletic Limnichidae. Molecular studies have likewise yielded inconsistent results. Kundrata *et al.* (2017) found Heteroceridae in a clade with Chelonariidae and paraphyletic Limnichidae after analyzing a dataset of four DNA fragments, while Zhang *et al.* (2018) and McKenna *et al.* (2019) recovered Heteroceridae nested within a paraphyletic

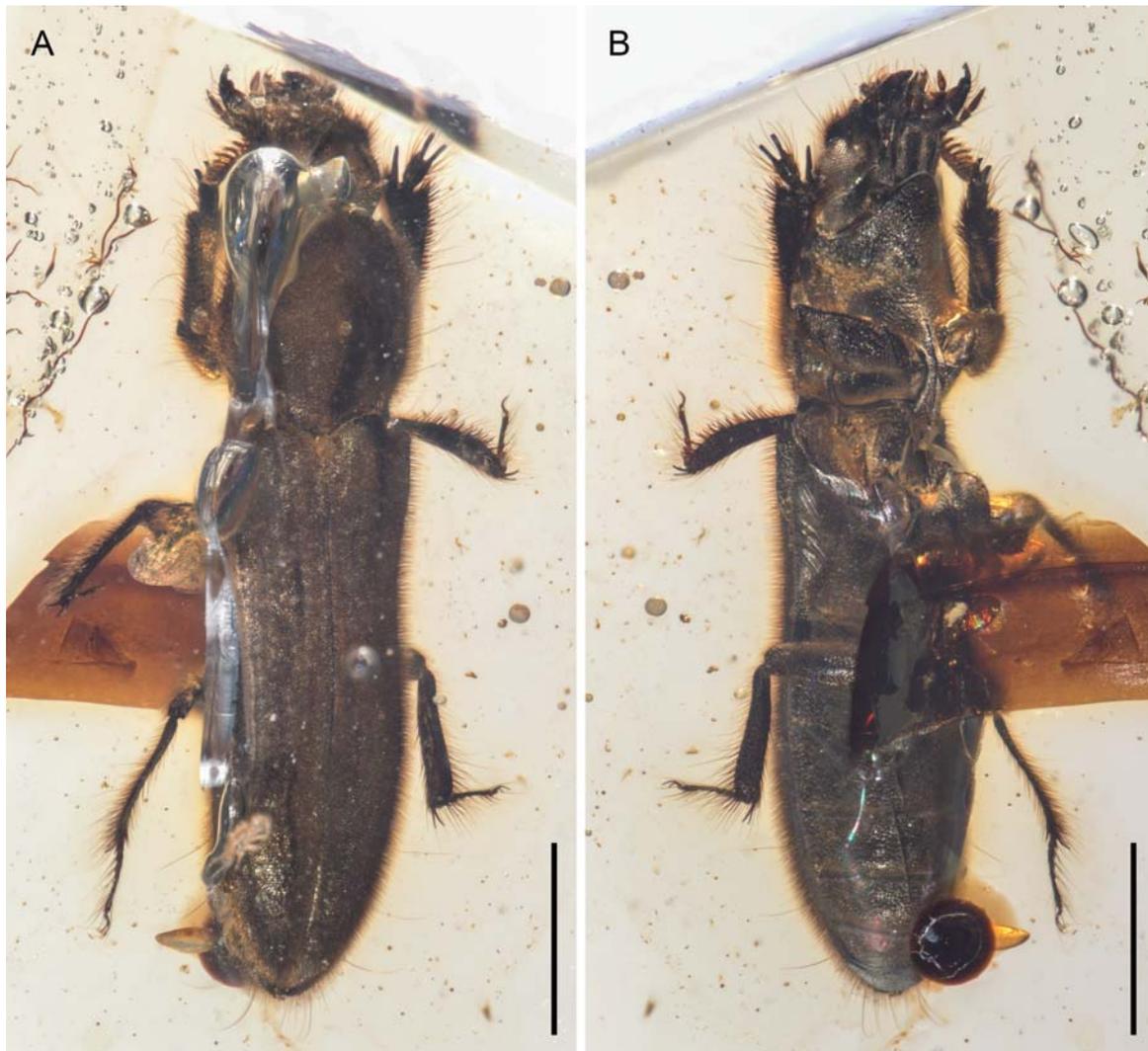


FIGURE 1. General habitus of *Excavotarsus lini* **gen. et sp. nov.**, holotype, NIGP171737. **A**, Dorsal view. **B**, Ventrolateral view. Scale bars: 1 mm.

Limnichidae based on analyses of 95 genes and 89 genes, respectively.

Although Pacheco (1964) split heterocerids into 19 genera, a recent molecular phylogenetic analysis revealed that many of these proposed genera were polyphyletic (King *et al.*, 2011). Therefore, King *et al.* (2011) suggested that it is most appropriate to divide Heteroceridae into two subfamilies and five genera: *Augyles* Schiödte, *Heterocerus* Fabricius, *Micilus* Mulsant & Rey, 1872 and *Tropicus* Pacheco, 1964 belonging to the cosmopolitan subfamily Heterocerinae, and the monospecific Australian genus *Elythomerus* Waterhouse in the subfamily Elythomerinae.

The fossil record of Heteroceridae is very sparse, with only two pre-Quaternary fossil heterocerid species. Both were placed into the formal genus *Heterocerites* Ponomarenko that accommodates putative Mesozoic heterocerid compression fossils of an unclear phylogenetic position. The first Mesozoic heterocerid, *H. kobdoensis*

Ponomarenko, was described from the Lower Cretaceous Gurvan-Eren Formation at the Myangad locality in western Mongolia (Ponomarenko, 1986). However, the type specimen is poorly preserved, lacking the diagnostically important antennae and tarsi and leaving open the possibility that the species does not belong to Heteroceridae at all, as it cannot be excluded from Bostrichidae. The second, and more convincing Mesozoic species, *H. magnus* Prokin & Ren is known from the Lower Cretaceous Yixian Formation at Huangbanjigou, Beipiao City, northeastern China (Prokin & Ren, 2011). It preserves a part of the serrate antennae and remnants of characteristic spots on the elytra similar to those found in extant heterocerids.

Here, we report a new genus and two new species of Heteroceridae from mid-Cretaceous Burmese amber, *Excavotarsus lini* **gen. et sp. nov.** and *Ex. minor* **sp. nov.** The discovery of two species of variegated mud-loving



FIGURE 2. General habitus of *Excavotarsus lini* **gen. et sp. nov.**, paratype, NIGP171738. **A**, Dorsal view. **B**, Ventral view. Scale bars: 1 mm.

beetles in the Mesozoic is important for setting a timescale for the evolution of Byrrhoidea and understanding the historical biogeography of the family.

Material and methods

The Burmese amber specimens originated from amber mines near Noiye Bum Village (26°20' N, 96°36' E), Hukawng Valley, Kachin State, northern Myanmar. Burmese amber is probably the richest source of exceptionally preserved Cretaceous insects (Ross, 2019). The precise dating of amber from the Hukawng Valley has long represented a contentious issue. Recent zircon analyses of the amber-bearing horizon have proposed a Cenomanian age of 98.8 ± 0.6 Ma (Shi *et al.*, 2012), while a possibility of a Late Albian age cannot be ruled out (Mao *et al.*, 2018). The resin was most likely secreted in a humid tropical rainforest by araucarioid trees (Poinar *et al.*, 2007; but see Dutta *et al.*, 2011), probably in the proximity of the sea (Yu *et al.*, 2019).

The type specimens are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGP), Nanjing, China. The amber pieces were cut with a small handheld cutter, polished with emery papers of different grain sizes and finished with polishing powder. Photographs were taken under incident light with a Zeiss Discovery V20 stereo microscope. Epifluorescence images were captured with the Zeiss Axio Imager 2 light microscope combined with a fluorescence imaging system. Images were stacked in Helicon Focus 7.0.2 or Zerene Stacker 1.04 to increase the depth of field, and further processed in Adobe Photoshop CC to enhance contrast.

Systematic palaeontology

Order Coleoptera Linnaeus, 1758
Suborder Polyphaga Emery, 1886
Superfamily Byrrhoidea Latreille, 1804
Family Heteroceridae MacLeay, 1825

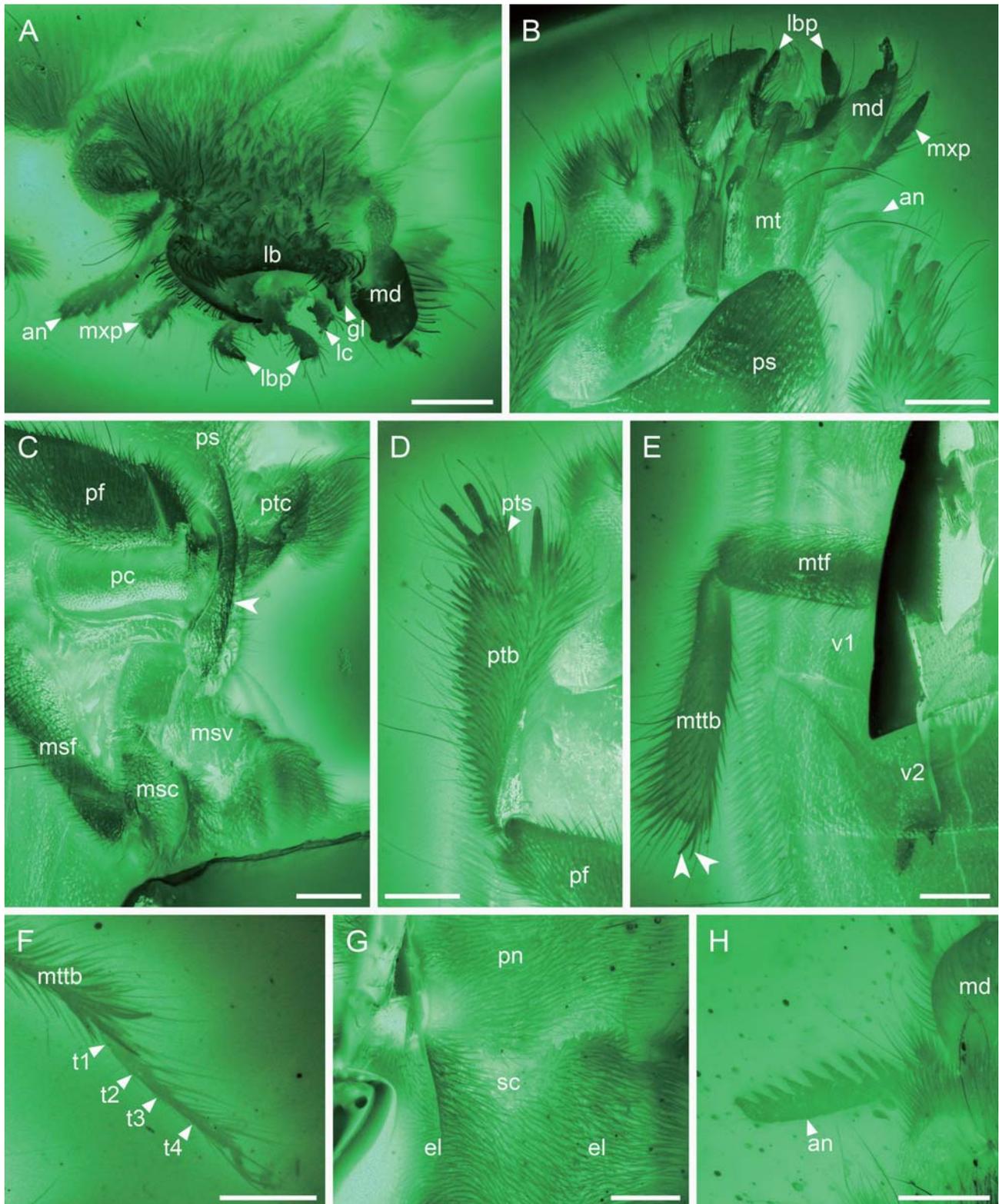


FIGURE 3. Details of *Excavotarsus lini* **gen. et sp. nov.**, under epifluorescence. **A–G**, Holotype, NIGP171737; **H**, paratype, NIGP171738. **A**, Head, anterior view. **B**, Head, ventrolateral view. **C**, Ventrolateral view, showing the medial carina on the prosternal process (arrowhead). **D**, Protibia and protarsus, ventrolateral view. **E**, Ventrolateral view, showing the two metatibia spurs (arrowheads) and no stridulatory file on the first ventrite. **F**, Metatarsus. **G**, Dorsal view, showing the small and not distinctly elevated scutellum. **H**, Antenna, dorsal view. Abbreviations: an, antenna; el, elytron; gl, galea; lb, labrum; lbp, labial palp; lc, lacinia; md, mandible; msc, mesocoxa; msf, mesofemur; msv, mesoventrite; mt, mentum; mtf, metafemur; mttb, metatibia; mxp, maxillary palp; pc, procoxa; pf, profemur; pn, pronotum; ps, prosternum; ptc, protrochanter; pts, protarsus; sc, scutellum; t1–4, metatarsomeres 1–4; v1,2, ventrites 1,2. Scale bars: 200 μ m.

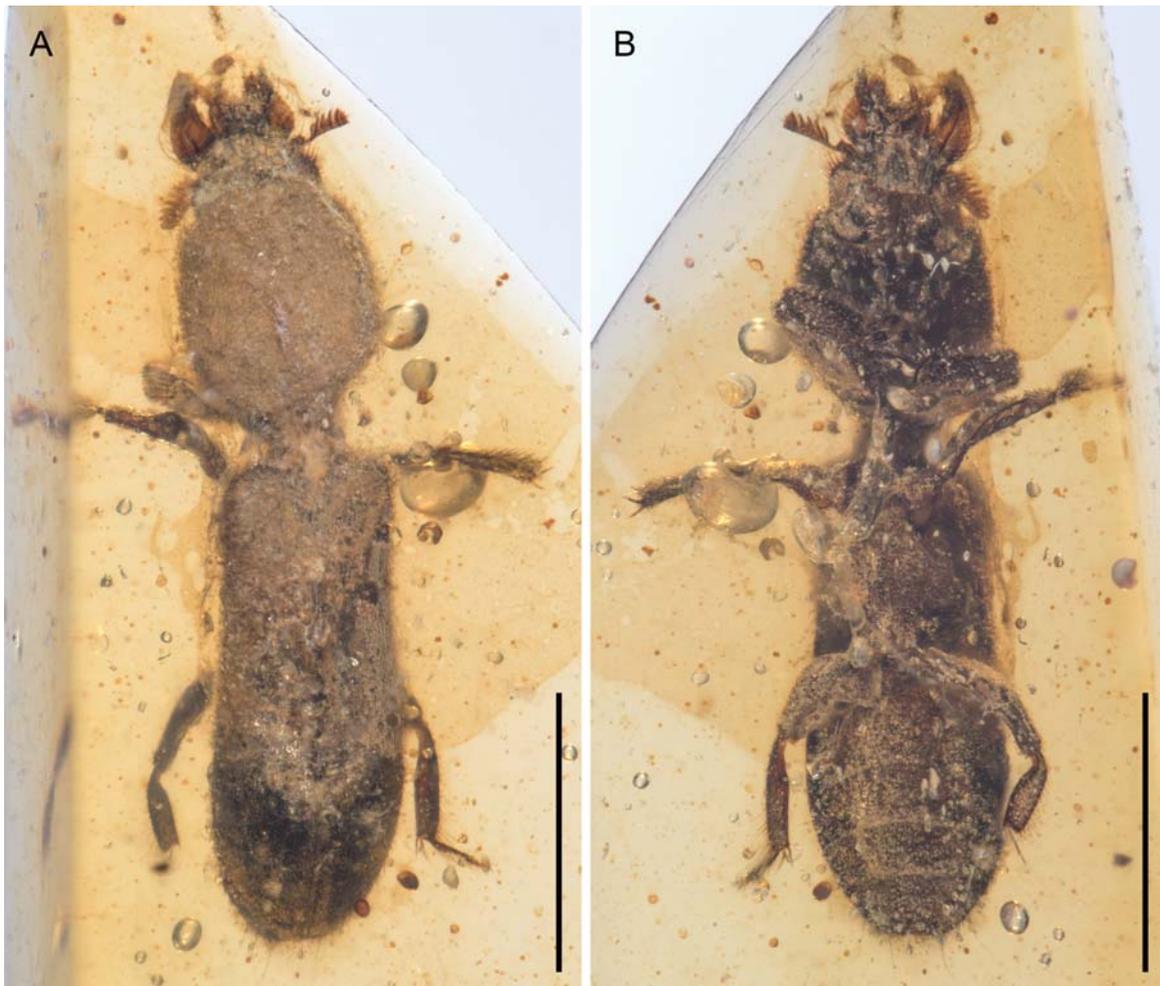


FIGURE 4. General habitus of *Excavotarsus minor* sp. nov., holotype, NIGP171739. **A**, Dorsal view. **B**, Ventral view. Scale bars: 1 mm.

Subfamily incertae sedis

***Excavotarsus* gen. nov.**

Type species. *Excavotarsus lini* sp. nov.

Etymology. The generic name is a combination of the Latin ‘excavo’ and ‘tarsus’, referring to the short protarsi presumably specialized for digging. The gender of the name is masculine.

Diagnosis. Body distinctly elongate. Mandibles without teeth on the outer edge. Antennae with basal two segments with long setae; distal 8–9 antennomeres forming a loose serrate club. Prosternal process visible between procoxae, somewhat acute apically. Mesocoxae widely separated. External margin of protibia without a row of stout spines, but with densely-spaced thin spines or thickened setae. Protibia with a single straight apical spur longer than the tarsus (excluding claws). Protarsi short, 2-segmented. Stridulatory file absent.

Remarks. The genus *Excavotarsus* exhibits remarkable differences from extant species in

Heteroceridae. Still, it shares many diagnostic features with extant relatives, including the densely pubescent body, prognathous head with prominent mandibles, and club-forming antennae. More importantly, the 4-segmented tarsi have been suggested as an autapomorphy of Heteroceridae (Costa *et al.*, 1999). Though the protarsi of *Excavotarsus* are specialized and only consist of two segments, the meso- and metatarsi are clearly 4-segmented. Therefore, this new genus can be confidently placed in the family Heteroceridae.

***Excavotarsus lini* sp. nov.**

(Figs 1–3)

Material. Holotype, NIGP171737. Paratype, NIGP171738.

Etymology. The specific epithet is a patronym formed from the surname of Prof. Qi-Bin Lin, a pioneering Chinese palaeoentomologist.

Locality and horizon. Amber mine located near Noiye Bum Village, Tanai Township, Myitkyina District,

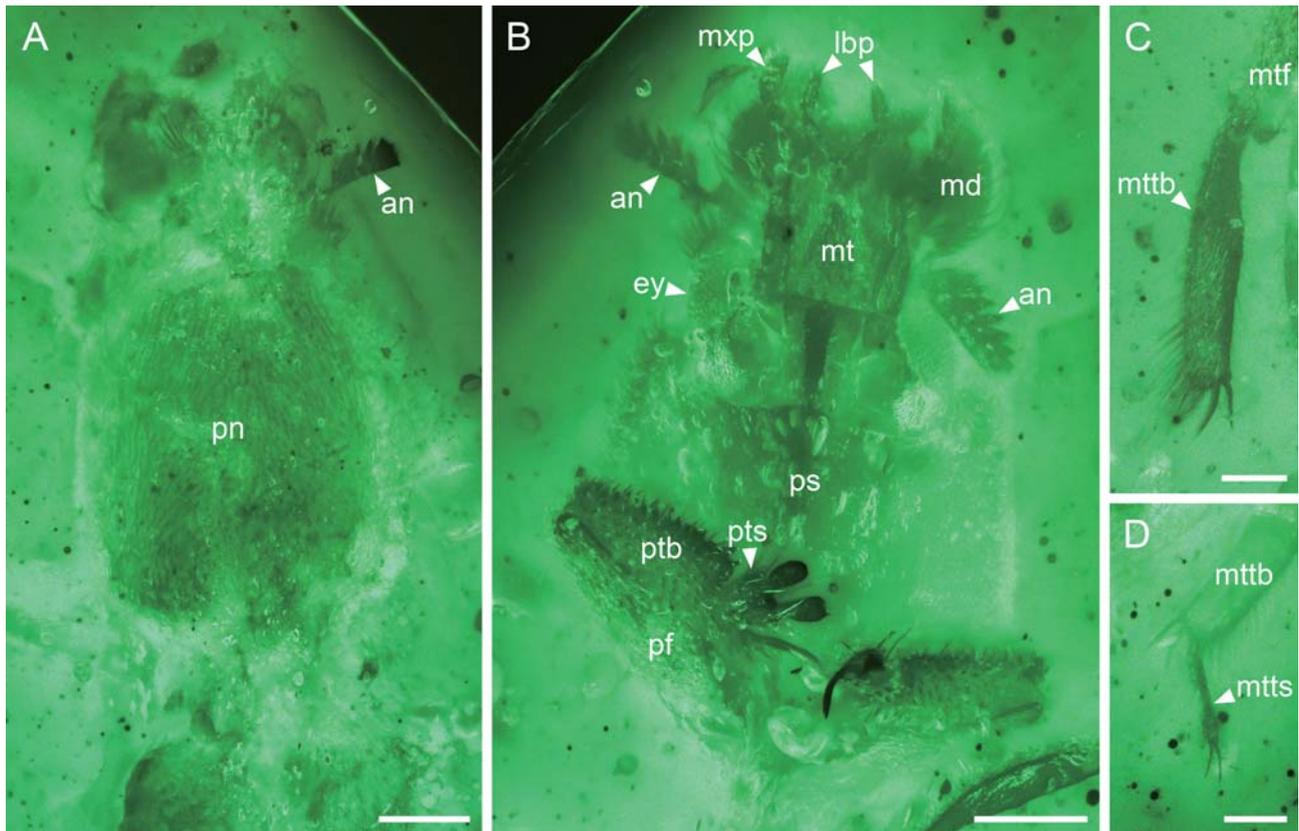


FIGURE 5. Details of *Excavotarsus minor* sp. nov., holotype, NIGP171739, under epifluorescence. **A**, Forebody, dorsal view. **B**, Forebody, ventral view. **C**, Metatibia. **D**, Metatarsus. Abbreviations: an, antenna; ey, compound eye; lbp, labial palp; md, mandible; mt, mentum; mtf, metafemur; mttb, metatibia; mtts, metatarsus; mxp, maxillary palp; pf, profemur; pn, pronotum; ps, prosternum; ptb, protibia; pts, protarsus. Scale bars: 200 μ m in **A** and **B**, 100 μ m in **C** and **D**.

Kachin State, Myanmar; unknown horizon, upper Albian or lower Cenomanian (mid-Cretaceous).

Diagnosis. As for the genus with additional characters: prosternum forming an elongate chin piece medially overlapping mentum with lateral sides of prosternum extended anteriorly and reaching approximately to half of chin piece length, thus giving the anterior margin of prosternum a distinct W-shaped appearance; apical nine antennomeres serrate.

Description. Body elongate, parallel-sided, somewhat flattened. Body length 4.8–4.9 mm, body width 1.0 mm across broadest point of pronotum. Body densely setose, lacking any distinct spots or markings.

Head (Fig. 3A, B) prognathous, broadest in ocular region, inserted deeply into the prothorax, 0.6–0.7 mm wide; the portion exposed in dorsal view 0.6–0.7 mm long (including mandibles). Labrum large. Mandibles robust, elongate, and flattened; biting edge bearing subapical teeth; outer edge without teeth and bearing stout setae. Maxillary palpi 4-segmented; palpomere 3 approximately half the length of palpomeres 2; palpomere 4 fusiform. Labial palpi 3-segmented; palpomere 2 subtriangular; palpomere 3 fusiform and rounded apically. Mentum

subrectangular and apically emarginate. Compound eyes convex, slightly protruding, finely faceted, lacking interfacetal setae. Antennae (Fig. 3B, H) short, with apical nine antennomeres serrate.

Pronotum oblong and rounded, 1.1 mm long and 1.0 mm wide, slightly wider than base of elytra, without furrows or raised keels, setose and with isolated elongate hairs; lateral pronotal carinae absent. Prosternum (Fig. 3B) forming an elongate chin piece medially with lateral sides of prosternum extended anteriorly and reaching approximately to half of chin piece length, thus giving the anterior margin of prosternum a distinct W-shaped appearance. Prosternal process (Fig. 3C) visible between procoxae, curved dorsally behind procoxae, slightly expanded apically, with a distinctly raised medial carina originating slightly above procoxae continuing to the apex. Mesoventrite fitting with prosternal process anteriorly; mesoventral process reaching to the mid of mesocoxae, pointed apically.

Procoxae (Fig. 3C) broad, distinctly wider than long. Tibiae (Fig. 3D, E) without a row of prominent spines along outer edge, but protibiae with densely-spaced minor spines or enlarged setae; protibiae with a single stout

apical spur; meso- and metatibiae with paired thin spurs. Tarsal formula 2-4-4 (Fig. 3D, F); protarsi short, expanded distad; protarsomere 1 less than quarter the length of protarsomere 2. Pretarsal claws of foreleg stout.

Scutellum (Fig. 3G) small, subtriangular, not distinctly elevated. Elytra elongate, 3.1 times as long as their combined width, subparallel, gradually tapering in the apical quarter. Elytral surface with dense, short setae. Sutural margin without a raised keel.

Abdomen with five ventrites. Stridulatory file absent (Fig. 3E). Ventrites 3–5 with several elongate hairs.

***Excavotarsus minor* sp. nov.**

(Figs 4, 5)

Etymology. The specific epithet refers to the smaller body size of the new species.

Material. Holotype, NIGP171739.

Locality and horizon. Amber mine located near Noiye Bum Village, Tanai Township, Myitkyina District, Kachin State, Myanmar; unknown horizon, upper Albian or lower Cenomanian (mid-Cretaceous).

Diagnosis. As for the genus with additional characters: prosternum not forming an elongate chin piece medially and therefore not overlapping mentum; apical eight antennomeres serrate.

Description. Body elongate, parallel-sided, somewhat flattened. Body length 3.1 mm, body width 0.7 mm across broadest point of pronotum. Body densely setose, lacking any distinct spots or markings.

Head (Fig. 5A, B) prognathous, broadest in ocular region, inserted deeply into the prothorax, 0.5 mm wide; the portion exposed in dorsal view 0.4 mm long (including mandibles). Labrum large. Mandibles robust, elongate, and flattened; biting edge bearing subapical teeth; outer edge without teeth and bearing stout setae. Mentum subrectangular. Compound eyes convex, slightly protruding, finely faceted, lacking interfacetal setae. Antennae short, with apical eight antennomeres serrate.

Pronotum (Fig. 5A) oblong and rounded, 0.9 mm long and 0.7 mm wide, slightly wider than base of elytra, without furrows or raised keels, setate and with isolated elongate hairs; lateral pronotal carinae absent. Prosternum (Fig. 5B) slightly protruding medially, not overlapping mentum; lateral sides of prosternum extended anteriorly, giving the anterior margin of prosternum an approximately U-shaped appearance.

Protarsi (Fig. 5B) possibly 2-segmented, short, expanded distad. Pretarsal claws of foreleg stout.

Elytra elongate, 2.3 times as long as their combined width, subparallel, gradually tapering in the apical quarter. Elytral surface with dense, short setae. Sutural margin without a raised keel.

Abdomen with five ventrites. Stridulatory file absent. Abdominal ventrite 5 with several elongate hairs.

Discussion

Until recently, only two Mesozoic species of Heteroceridae have been known, *Heterocerites kobdoensis* and *H. magnus*. Although the preservation state of these fossils doesn't allow an accurate comparison with extant genera (Ponomarenko, 1986; Prokin & Ren, 2011), the body shape, broadly separated mesocoxae, and large spines on tibia of the better-preserved *H. magnus* clearly indicate a kinship with Heterocerinae. The new genus described herein, *Excavotarsus* **gen. nov.**, however, shows critical differences from both extant heterocerid subfamilies Elythomerinae and Heterocerinae. Despite superficially resembling *Elythomerus* by its elongate body, *Excavotarsus* differs from it in many important characters. While *El. elongatulus*, the sole constituent of Elythomerinae, has antennae with a non-serrate compact club, and species in Heterocerinae have antennae with the last 6–7 segments forming a serrate club, the antennae of *Excavotarsus* have a serrate club formed by the last 8–9 segments. *Elythomerus elongatulus* and many Heterocerinae species possess a subtrapezoidal mentum, with the anterior margin narrower than the base, while the mentum in *Excavotarsus* is subrectangular, with the widths similar at the anterior margin and the base. The pronotum in extant heterocerid species is usually 0.5–0.6 times as long as wide (Lawrence & Ślipiński, 2013). However, the length of pronotum in *Excavotarsus* is slightly larger than the width. The prosternal process is less significant in *Elythomerus*, and only slightly overlaps mesoventrite (Lawrence *et al.*, 2000–2018). By contrast, in *Excavotarsus* the prosternal process is clearly visible between procoxae, and overlaps mesoventrite moderately, which is consistent with Heterocerinae. While in *Elythomerus* the mesocoxae are narrowly separated (Waterhouse, 1874), in *Excavotarsus* as well as in Heterocerinae the mesocoxae are widely separated (Lawrence & Ślipiński, 2013). The shape of prosternum in *Ex. lini* **sp. nov.** is different from the other known congener, *Ex. minor* **sp. nov.**, and is also unique among Heteroceridae, therefore it might be an automorphy of that species. Given these peculiarities, further phylogenetic studies will be necessary to determine the precise systematic position of *Excavotarsus* **gen. nov.**

The most unusual character of *Excavotarsus* is the morphology of the legs, especially the forelegs. Extant heterocerids live in mud and sand along the waterside, or in brackish mud flats, digging in the sediment. The tibiae

of all known heterocerids are equipped with a row of stout spines, which enable the beetles to borrowing effectively (Clarke, 1973). The tibial spines of *Excavotarsus* are not as robust as seen in extant heterocerids but are much more closely spaced and more slender. *Excavotarsus* is the only heterocerid genus to possess two-segmented protarsi, which probably represented an adaptation for its specialized mode of life in littoral sediment. Together with its densely setose body, this suggests that Burmese amber heterocerids may have shared a similar lifestyle with extant variegated mud-loving beetles, providing evidence of behavioral stasis in Heteroceridae over at least the past ~100 Ma.

Recent discoveries of aquatic species in Burmese amber, including ammonites (Yu *et al.*, 2019), marine ostracods (Xing *et al.*, 2018), marine mollusks (Smith & Ross, 2018), along with various aquatic and semi-aquatic beetles (Fikáček *et al.*, 2017; Yamamoto *et al.*, 2017; Cai & Huang *et al.*, 2018; Yang *et al.*, 2019; Zhao *et al.*, 2019; Liang *et al.*, 2020) suggest that the Burmese amber forest was located at the coast or at the mouth of a river. The present discovery of heterocerid beetles provides further evidence for the palaeoenvironment in which Burmese amber was produced.

Conclusion

Our discovery of two species of *Excavotarsus* **gen. nov.** in the mid-Cretaceous amber from northern Myanmar greatly extends the morphological diversity of the family. *Excavotarsus* differs from both extant subfamilies of Heteroceridae, especially by the lack of stout spines on tibiae and the shortened protarsi. Considering that Heterocerinae-like fossils have already been recorded from the Early Cretaceous, this unique genus likely represents an early diverging branch of Heteroceridae. Further palaeontological studies are necessary for a precise determination of the phylogenetic position of this enigmatic genus. The fossils document a behavioral stasis in Heteroceridae since the mid-Cretaceous and provide further evidence that the Burmese amber forest stood close to the sea or possibly near a river mouth.

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