

## Short communication

## The first fossil record of the rove beetle subfamily Protopselaphinae (Coleoptera: Staphylinidae) from mid-Cretaceous Burmese amber

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## ABSTRACT

Protopselaphinae is a small rove beetle subfamily endemic to southeast Asia with only eight extant species placed into a single genus. Here we describe and illustrate the first fossil representative of Protopselaphinae, *Protopselaphus thayerae* sp. nov., from mid-Cretaceous Burmese amber (Albian-Cenomanian). The new species is distinguished from all extant taxa of *Protopselaphus* by having tarsomeres 1 and 2 not subequal in length and mentum with a shallow emargination. The new fossils provide evidence of an ancient origin of Protopselaphinae, a 'missing link' between the megadiverse Pselaphinae and other subfamilies in the Omaliine group. *Protopselaphus thayerae* sp. nov. is a testament to an extreme morphological and probably also ecological stasis in Protopselaphinae over the last 99 million years.

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## 1. Introduction

Staphylinidae, also known as rove beetles, is the most species-rich beetle family and also the largest family in the animal kingdom (Grebennikov and Newton, 2009). Over 63,650 species in 33 subfamilies (including one extinct subfamily) have been described to date, with many more awaiting discovery (Grebennikov and Newton, 2009; Herman, 2001; Yamamoto and Takahashi, 2019). Perhaps the single most significant factor responsible for the tremendous evolutionary success of rove beetles has been the shortening of their elytra and the associated development of complex asymmetrical wing folding mechanisms

(Saito et al., 2014). This provides rove beetles with a much greater range of movement of the abdomen, enabling them to inhabit very small cavities and spaces, while keeping their delicate hindwings well protected (Parker, 2017). Additional morphological innovations, such as the emergence of novel feeding strategies, have sparked further diversification in some rove beetle lineages (Žyła et al., 2017; Cai et al., 2019b). Since the Mesozoic, staphylinids have colonized diverse ecological niches (Cai et al., 2016, 2017a,b; Yamamoto et al., 2017); the family includes predators of diverse invertebrates, omnivores, specialized algivores, mycophages, detritivores, ectoparasites, and even social insect symbionts (Caterino et al., 2005).

Protopselaphinae is one of the smallest staphylinid subfamilies. It has been erected relatively recently to accommodate the genus *Protopselaphus* known to date only from south east Asia (Fig. 1; Newton and Thayer, 1995). Since its inception, the subfamily has been considered to represent a 'missing link' uniting the diverse Pselaphinae with over 10,000 described species (Yin et al., 2018c) and the subfamilies of the Omaliine group characterized by having

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**Fig. 1.** Extant species of Protopselaphinae, male *Protopselaphus watrousi*, from Pahang, Malaysia. Scale bar = 500  $\mu$ m.

3-segmented tarsi (Dasycerinae and Neophoninae). Notably, protopselaphines share the presence of defensive glands on the eight sternite with Pselaphinae (Thayer, 1987; Newton and Thayer, 1995).

Here we describe the first fossil species of *Protopselaphus* from Burmese amber as the first protopselaphine rove beetle in the geological record.

## 2. Material and methods

The eight fossil specimens preserved in Burmese amber studied by us originated from mines at the Noiye Bum hill (26°20'N 96°36'E) in the Hukawng Valley, Kachin State, northern Myanmar (Cruickshank and Ko, 2003). Zircon dating of the amber-bearing horizon has established  $98.8 \pm 0.6$  Ma as the minimum age of the amber deposit (Shi et al., 2012; Mao et al., 2018). The fossil resin was most likely secreted by dawn redwood trees in a tropical forest standing at the seashore (Grimaldi and Ross, 2017).

The specimens were prepared by polishing the amber pieces with sandpapers of gradually finer grits and finally with diatomite powder. A Zeiss Discovery V20 stereomicroscope was used for observation and photography. Green fluorescence microphotographs were taken using the Zeiss Axio Imager 2 light microscope under the eGFP mode. The type specimens are deposited in the amber collection of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

## 3. Systematic palaeontology

Order Coleoptera Linnaeus, 1758

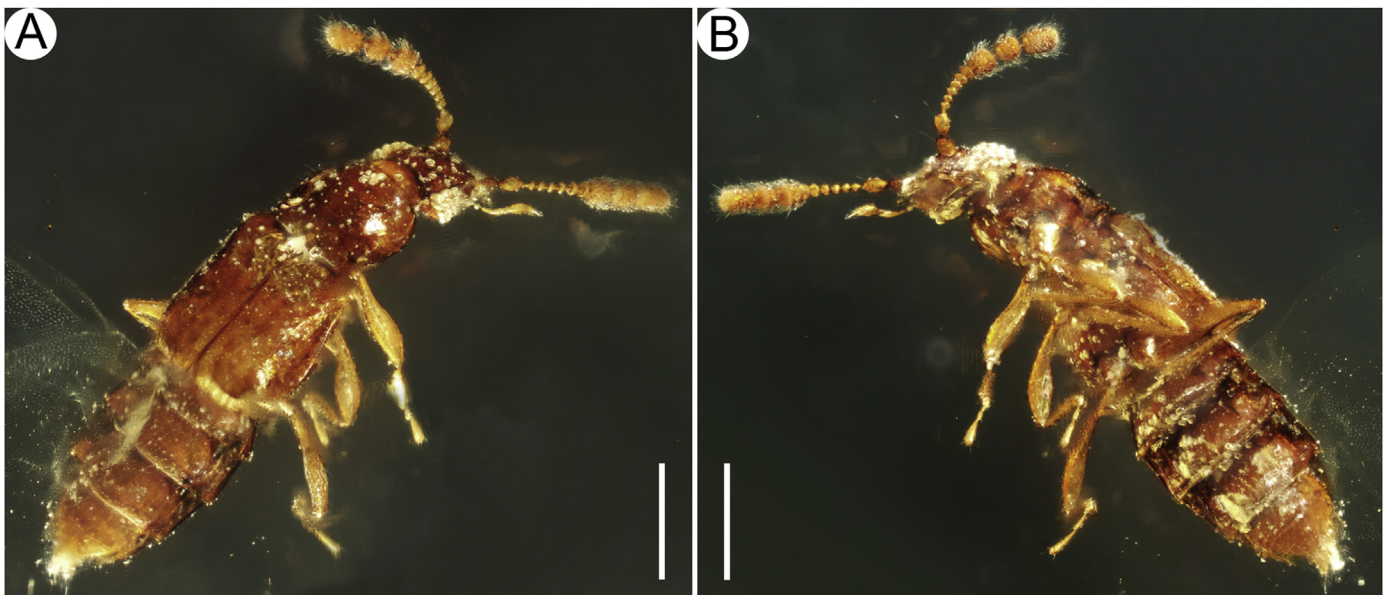
Family Staphylinidae Latreille, 1802

Subfamily Protopselaphinae Newton and Thayer, 1995

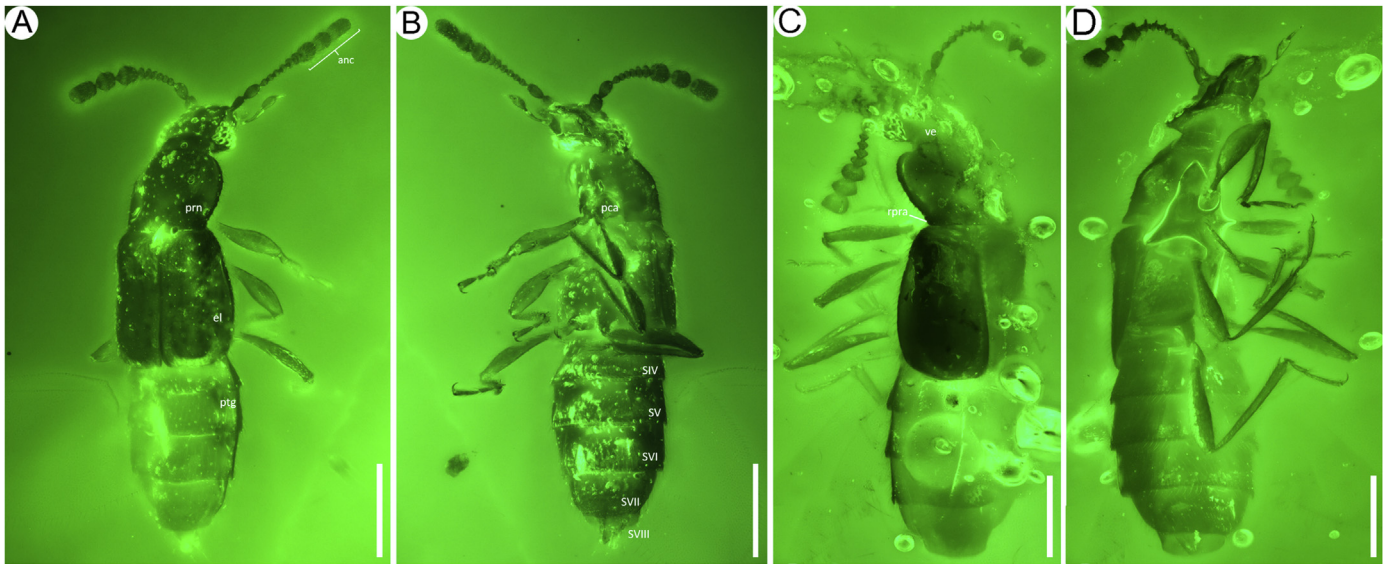
Genus *Protopselaphus* Newton and Thayer, 1995

***Protopselaphus thayerae*** sp. nov. Liu, Tihelka and Cai  
Figs. 2–6

**Etymology.** The specific epithet is a patronym formed from the surname of Dr. Margaret K. Thayer (Field Museum of Natural



**Fig. 2.** *Protopselaphus thayerae* sp. nov. (holotype, NIGP171356) under normal reflected light; A, dorsal and B, ventral view. Scale bars = 200  $\mu$ m.



**Fig. 3.** *Protopselaphus thayerae* sp. nov. under green fluorescence. A and B, holotype (NIGP171356). C and D, paratype (NIGP171357). A, dorsal and B, ventral view; C, dorsal and D, ventral view. Scale bars = 500  $\mu$ m. Abbreviations: el, elytra; pca, procoxa; pr, pronotum; ptg, paratergite; rpra, rounded pronotal angle; SIV–VIII, sternites IV–VIII; ve, vertex. Scale bars = 200  $\mu$ m. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

History) in recognition of her exceptional contribution to the study of staphylinid diversity.

**Locality and horizon.** Noije Bum hill amber mine, Hukawng Valley, Kachin state, northern Myanmar; upper Albian to lower Cenomanian (mid-Cretaceous).

**Type material.** Eight specimens. Holotype, NIGP171356, sex indeterminate. Paratypes, NIGP171357–NIGP171363. NIGP171358 slightly distorted during fossilization.

**Diagnosis.** Eyes multifaceted (Fig. 2, 3). Vertex smoothly rounded, not elevated (Fig. 4A). Antennae long, reaching to elytral base, with a distinct 3-segmented club, lacking bifurcate or trifurcate sensilla (Fig. 5A). Anterior notch on mentum broadly U-shaped, but no deeper than one eighth of mentum length. Pronotum broadest antemedially with disc smooth, lacking deep furrows or carinae. Posterior pronotal angles rounded, not elongate. Elytra longer than wide, broadest medially, their length not exceeding their combined width. Hind wings present (Fig. 5D). Tarsomere 1 distinctly shorter than tarsomere 2.

**Description.** Body elongate and parallel-sided, moderately flattened. Body length 0.99–1.30 mm from clypeus to abdominal apex, body width 0.24–0.36 mm across elytra at broadest point. Body setose, lacking foveae, dark brown. Winged and with large eyes.

Head strongly prognathous, 0.13 mm long and 0.15 mm wide (in holotype), broadest at eyes, with pronounced temples and a broad posterior neck region. Mandibles robust, lacking contiguous molar lobes and preapical teeth. Maxillary palps 4-segmented, palpomere 2 1.1 times the length of the apical palpomere; palpomere 3 broadest and longest, 1.1 times palpomere 4 length; apical palpomere subulate. Mentum with a shallow U-shaped apical emargination incised no deeper than one eighth of mentum length (Fig. 4B). Coarsely faceted compound eyes present, ocelli apparently absent. Antennal insertions located anterior to eyes, visible dorsally. Antennae 11-segmented, setose, forming a distinct apical club composed of three anteriorly lengthening segments, lacking bifurcate or trifurcate sensilla, reaching to the base of the elytra. Antennomere 1 barrel-shaped, equally wide throughout, 0.7 times as long as the following segment; antennomere 2 broadest

medially, 2.4 times longer than the following segment; antennomeres 3–8 markedly narrower and shorter than preceding segments but gradually shortening and widening apically, with antennomere 3 1.3 times longer than the following segment and antennomere 8 0.4 times the length of the following segment; antennomeres 9–11 distinctly wider and longer than the preceding segments and cylindrical in shape with antennomere 9 as long as the following segment; antennomere 10 0.7 times the length of the following segment; antennomere 11 broadly rounded apically (Fig. 4C). Gular sutures indistinct. Vertex smoothly rounded, without raised carinae (Fig. 4A). Temples straight.

Pronotum 0.19 mm long and 0.21 mm wide, longest medially and broadest antemedially, lacking distinct lateral carinae. Pronotal disc without raised carinae or furrows, mostly glabrous. Anterior and posterior pronotal angles broadly rounded. Pronotal margin setose.

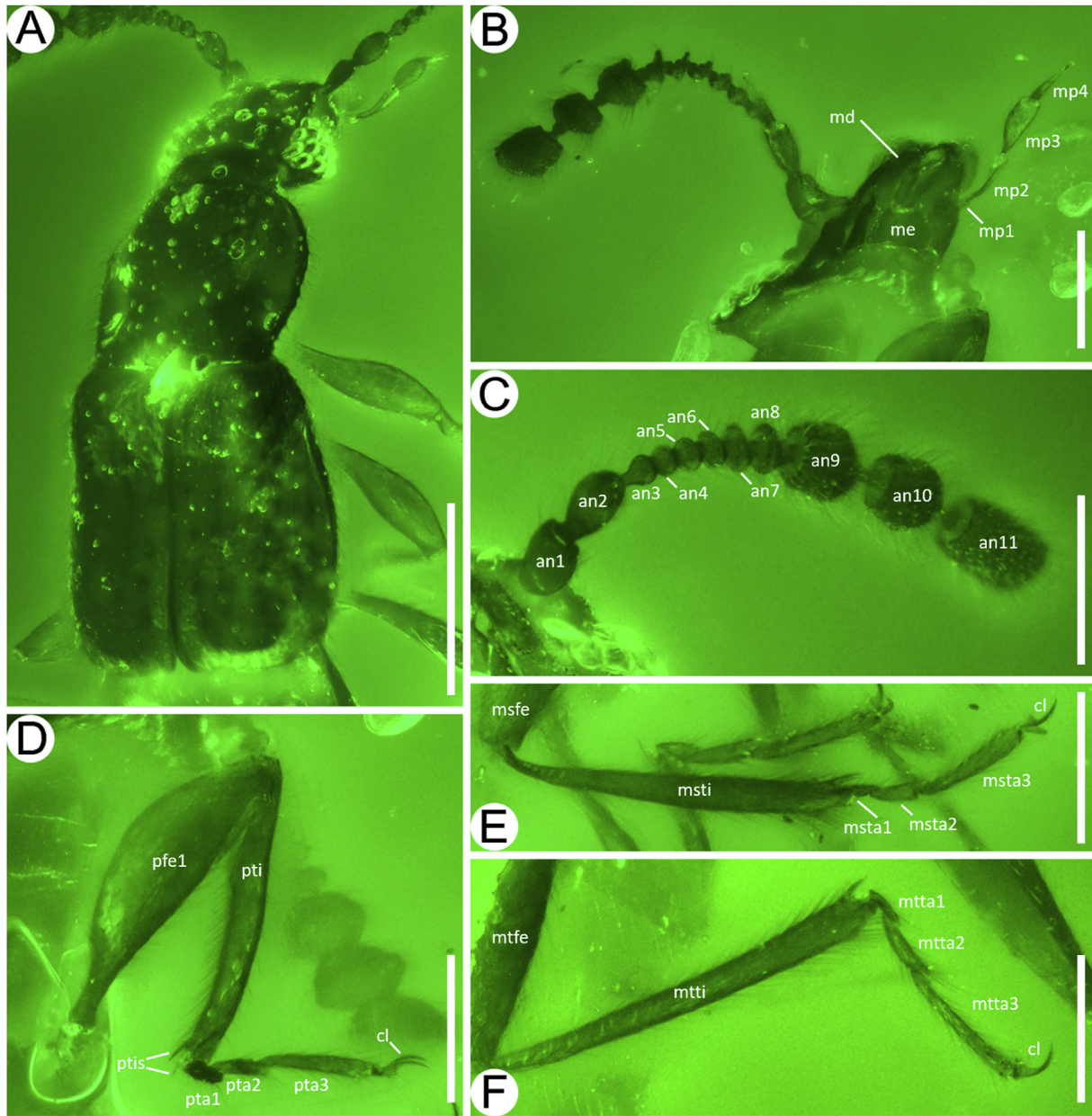
Elytra truncate and short, exposing five sternites, combined elytral width 0.9 times elytral length. Elytra lacking striae or punctate rows, sparsely setate. Sutural keels absent. Epipleural margin with an indistinct keel terminating in the apical third of the elytra. Hindwings present.

Abdomen elongate, broadest medially and nearly glabrous. Abdominal segments 3–7 each with a pair of laterosclerites. Sternites 5–7 subequal in length.

Legs slender. Procoxae adjacent, protrochantin concealed. Coxae clavate, without keel. Tibia lacking strong external spines, terminating with two straight spurs. Tarsal formula 3-3-3. Tarsomere 1 less than half of tarsomere 2 length, tarsomere 3 2.2 times longer than the preceding segment. Claws simple, with two long empodial setae.

#### 4. Discussion

The new staphylinid fossils can be placed into the Omaliine group of subfamilies (although not monophyletic, McKenna et al.,

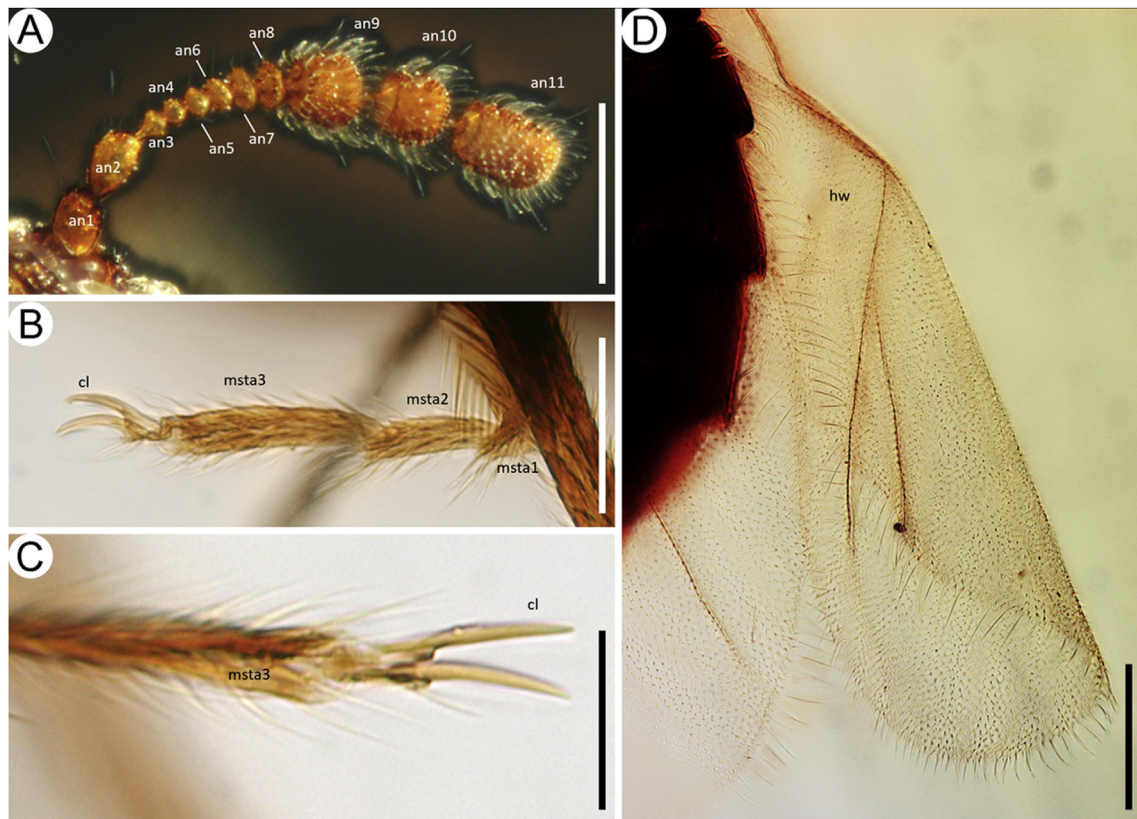


**Fig. 4.** Morphological details of *Protopselaphus thayerae* sp. nov. under green fluorescence. A, head, pronotum and elytra in dorsal view; B, head in ventral view; C, antenna; D, prothoracic leg; E, mesothoracic leg; F, metathoracic leg. Abbreviations: Holotype NIGP171356 (A, C), paratype NIGP171357 (B, D–F). Abbreviations: an1–11, antennomeres 1–11; cl, pretarsal claws; md, mandible; mp1–4, maxillary palpomeres 1–4; me, mentum; msfe, mesofemur; msta1–3, mesotarsomeres 1–3; msti, mesotibia; mtfe, metafemur; mtta1–3, metatarsomeres 1–3; mtti, metatibia; pfe, profemur; pta1–3, protarsomeres 1–3; pti, protibia; ptis, protibial spurs. Scale bars = 200  $\mu$ m (A), 100  $\mu$ m (B–E). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2015) on the basis of having a somewhat ovoid body shape, relatively long elytra, contiguous and broad metacoxae, and possessing one pair of paratergites on abdominal segments 4–6 (Newton and Thayer, 1995; Cai and Huang, 2013). It can be distinguished from most members of the Omaliine group by the closure of the procoxal fissure and concealed protrochantins, although it notably shares these two characters with Pselaphinae. Placement into the subfamily Protopselaphinae is supported by the absence of a small 5th segment of the maxillary palp (Fig. 4B), anteriorly incised mentum (Fig. 4B), absence of metasternal carinae delimiting mesocoxal cavities (Fig. 3), mesocoxae separated by a mesosternal process (Fig. 6B) and the presence of two long empodial setae (Fig. 5C). The nature of the amber inclusions precludes observation of the

diagnostically important epipharynx, mandibular base, and genitalia, but the combination of the characters cited above is unique among staphylinids and unambiguously support the placement of the fossils in the subfamily Protopselaphinae and the extant genus *Protopselaphus*, following the diagnosis provided by Newton and Thayer (1995).

Eight extant species of this genus are known from south east Asia. *Protopselaphus watrousi* (Fig. 1) and *P. grandis* occur in Peninsular Malaysia, *P. burckhardti*, *P. crowsoni*, *P. loebli*, and *P. poringensis* occur in Sabah in Malaysia, while *P. frogneri* and *P. taylori* were recorded from Sarawak in Malaysia (Newton and Thayer, 1995). *Protopselaphus* was furthermore reported from Yunnan, southwest China (Nomura, 2000) and from Thailand



**Fig. 5.** Morphological details of *Protopselaphus thayerae* sp. nov. under normal reflected light. A, antenna (holotype, NIGP171356); B, mesotarsus (paratype, NIGP171357); C, pretarsal claws (paratype, NIGP171357); D, partly exposed wings (paratype, NIGP171358). Abbreviations: an1–11, antennomeres 1–11; eps, empodial setae; cl, pretarsal claws; hw, hindwing; msta1–3, mesotarsomeres 1–3. Scale bars = 100  $\mu$ m (A, D), 50  $\mu$ m (B), 25  $\mu$ m (C).

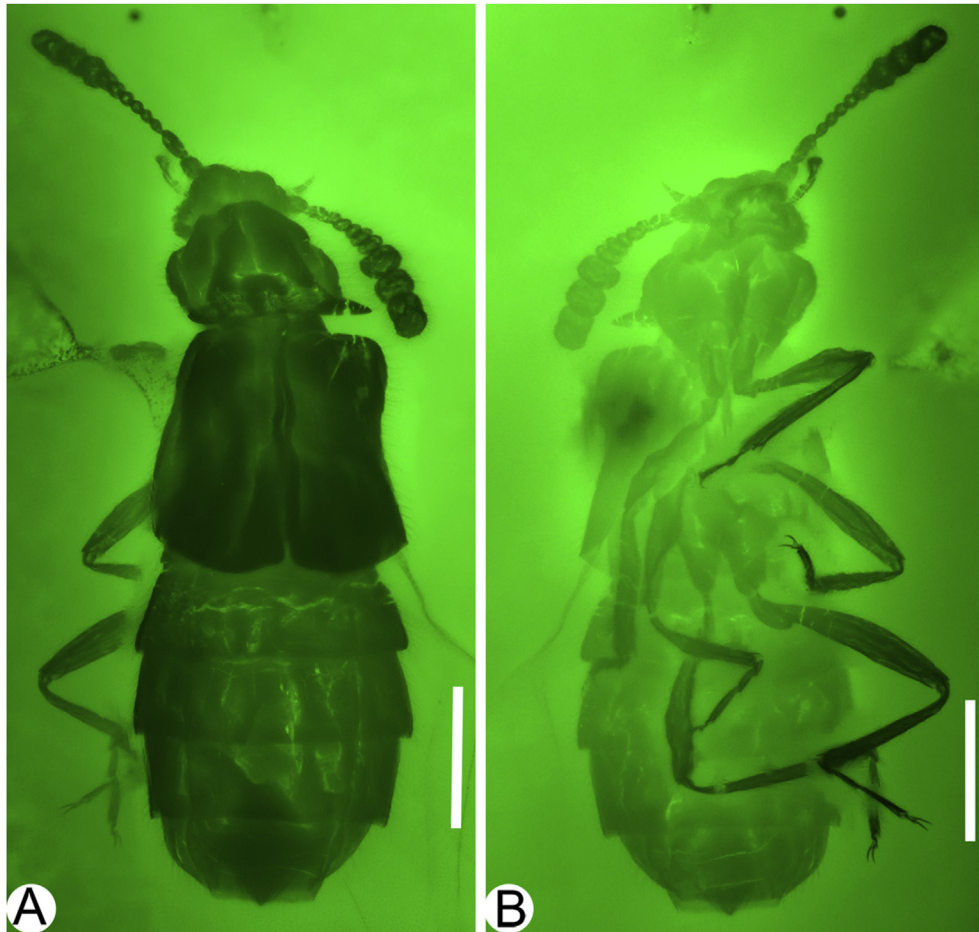
(Nomura et al., 2008). It is however very likely that additional species of this overlooked subfamily still await discovery. The new fossil species differ from all extant representatives of the genus in having tarsomere 1 distinctly shorter than tarsomere two, while in all recent species both basal tarsomeres are subequal (Newton and Thayer, 1995). While all extant species of *Protopselaphus* are characterized by a deeply notched mentum, the notch is very shallow in *P. thayerae* sp. nov. (Newton and Thayer, 1995).

Winged and wingless specimens of the extant species of *Protopselaphus* are known. Newton and Thayer (1995) reported that all winged *Protopselaphus* specimens studied by them were males, but not all males had wings. At least three of the specimens studied by us appear to possess wings (Fig. 5D), suggesting that they may be male. Aside from the presence of wings, members of the genus *Protopselaphus* apparently lack obvious external sexually dimorphic characters.

Tectonic evidence suggests that the West Burmese Block (or the Burma Terrane) rifted from north-western Australia and drifted north to its current position between the late Triassic and late Cretaceous (Metcalf, 1998; Westerweel et al., 2019). This scenario is further supported by recent palaeontological findings which show that many of the plant and animal taxa recorded from Burmese amber are restricted to Australasia and South America today (Cai and Huang, 2017; Poinar, 2018; Cai et al., 2019a) and beetles are no exception to this pattern. Some, such as the monotomid tribe Lenacini or the family Cyclaxyridae, among many others, have an exclusively Gondwanan distribution today (Jajoszyński et al., 2017; Wu et al., 2018; Liu et al., 2019; Cai et al., 2019a). The discovery of a member of the extant genus *Protopselaphus* in Burmese amber adds another endemic Gondwanan

species to the list of Burmese amber taxa and provides further evidence of the Gondwanan origin of the West Burma block. Given their current distribution and the east Gondwanan origin of a part of modern Malaysia, south China, and Thailand (Metcalf, 1998, 2009), Protopselaphinae may have had a wider distribution throughout the Gondwanan landmass in the mid-Cretaceous than today.

Seven genera and nine species belonging to Pselaphinae have already been reported from Burmese amber (Yin et al., 2018c, 2019a, b), but no fossils belonging to the subfamily Protopselaphinae have been known to date (Chatzimanolis, 2018). As such, *P. thayerae* sp. nov. from Burmese amber represents the earliest fossil record of this genus and subfamily. Our discovery of the earliest *Protopselaphus* fossils confirms that the subfamily Protopselaphinae originated by at least the mid-Cretaceous and that the last common ancestor of Protopselaphinae and Pselaphinae lived during the Early Cretaceous at the latest. The remarkable similarity between *P. thayerae* sp. nov. and extant members of the genus points towards a prolonged morphological stasis since at least the Mesozoic. Highly conserved morphologies have already been observed in many beetles (e.g. Clarke and Chatzimanolis, 2009; Cognato and Grimaldi, 2009; Yamamoto & Solodovnikov, 2016; Cai et al., 2017b, 2018, 2019a; Yin and Cai, 2019) and other insect lineages (Yin et al., 2018a,b) recorded from Burmese amber, suggesting that protopselaphines occupied a similar ecological niche over the past 99 million years. Little is known about the life of extant members of the genus *Protopselaphus*; they have a narrow distribution range and are easy to overlook due to their minute size. Most specimens in entomological collections were collected from leaf litter in tropical montane and lowland



**Fig. 6.** Habitus photographs of *Protopselaphus thayerae* sp. nov. (paratype, NIGP171358) under green fluorescence; A, dorsal and B, ventral view. Scale bars = 200  $\mu$ m. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

rainforests (Newton and Thayer, 1995). Cretaceous protopselaphines likely inhabited similar microhabitats in the Burmese amber rainforest.

## 5. Conclusions

A new minute rove beetle species, *Protopselaphus thayerae* sp. nov., is described from mid-Cretaceous Burmese amber. As the first fossil representative of the subfamily Protopselaphinae, *P. thayerae* sp. nov. fills a gap in the fossil record of rove beetles (Chatzimanolis, 2018) and will be important for dating the staphylinid tree of life. The remarkable morphological similarity between both Cretaceous species and extant members of the genus provides evidence of prolonged morphological and probably also ecological stasis in this group of rove beetles. *Protopselaphus* represents yet another endemic Gondwanan taxon from Burmese amber (Jałoszyński et al., 2017; Wu et al., 2018; Liu et al., 2019; Cai et al., 2019a) and suggests a possibly more widespread distribution of Protopselaphinae in the Mesozoic.

## CRedit authorship contribution statement

**Yuchu Liu:** Writing - original draft, Writing - review & editing. **Erik Tihelka:** Writing - original draft, Writing - review & editing. **Shūhei Yamamoto:** Data curation, Investigation. **Ziwei Yin:** Data curation, Methodology. **Diying Huang:** Methodology, Writing - review & editing. **Li Tian:** Writing - original draft, Writing - review & editing. **Chenyang Cai:** Methodology, Writing - review & editing.

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