Article

Sexual dimorphism in mid-Cretaceous silvanid beetles from northern Myanmar (Coleoptera, Silvanidae, Brontinae)

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Abstract

Silvanidae is a small group of cucujoid beetles, and their fossil record is poorly documented. The two recently described genera from Burmese amber, *Cretoliota* Liu *et al.* and *Protoliota* Liu *et al.*, are distinctive among all known Silvanidae, displaying markedly long antennae and mandibular horns in males, as found in the extant *Uleiota* Latreille. Due to the limited sampling of fossil specimens, the morphological variations of male mandibular horns remain a mystery. Here we report six well-preserved specimens of *Protoliota* with both male and female genitalia exposed from mid-Cretaceous Burmese amber. Our discovery confirms the presence of remarkable sexual dimorphism in *Protoliota*. Males of *Protoliota antennatus* Liu *et al.* display short to very long mandibular horns and much longer antennae. Interesting morphological convergence of the beetles (Silvanidae and Staphylinidae) living under the bark of dead trees is briefly discussed. Our discovery represents the first definitive sexual dimorphism in beetles from Burmese amber.

Keywords: sexual dimorphism, convergence, Cucujoidea, Burmese amber, Silvanidae

Introduction

With approximately 500 described extant species and 61 genera, the cucujoid beetle family Silvanidae is a small widespread group of polyphagan beetles (Thomas & Leschen, 2010; Karner *et al.*, 2015; Yoshida *et al.,* 2017; Liu *et al.*, 2019). Silvanidae is currently divided into two extant subfamilies, Brontinae and Silvaninae, with the former composed of two tribes, Brontini and Telephanini (Thomas, 1984; Bouchard *et al.,* 2011). Recent molecular-based phylogenies have yielded incongruent results about the monophyly of Silvanidae, *i.e.*, Silvanidae is not monophyletic based on eight genes in both Bayesian and maximum likelihood analyses (McKenna *et al*., 2005), whereas it is monophyletic based on a larger scale of sampling of genes (95 protein-coding genes) (Zhang *et al.*, 2018). In morphology, Silvanidae can be defined based on several characters in combination: galea at least 2.5 times as wide as lacinea, procoxal cavity internally closed, scutellary strioles absent, metacoxae widely separated, three or fewer wing veins in the medial field, abdominal process broad, larval pretarsus unisetose, and abdominal tergum IX simple (Leschen *et al.,* 2005; Thomas & Leschen, 2010). The systematic position of Silvanidae within Cucujoidea remain elusive. Leschen *et al.* (2005) has suggested a close relationship between Silvanidae (the genera *Ahasverus des Gozis* and *Cryptamorpha Wollaston* are used as exemplars) and Cucujidae based on both adult and larval morphological characters, but this result is not supported by recent molecular-based phylogenies (McKenna *et al.*, 2005; Zhang *et al*., 2018). According to Zhang *et al*. (2018), the monophyletic Silvanidae is a sister group to Cryptophagidae, and the subfamily Silvaninae is polyphyletic. Thomas & Nearns (2008) presented a preliminary phylogeny of Silvanidae based on sixteen characters and both Silvaninae and Brontinae are monophyletic. Therefore, further detailed studies are required to establish a robust phylogeny of the family.

The biology and life cycles of most species of Silvanidae are largely unknown, but many of them seem to be fungivorous, and share the character of a large pit for fungal transport called the "mycangium" on each mandible (Thomas, 2002). The mycangial functions, however, cannot be verified experimentally in Silvanidae (Grebennikov & Leschen, 2010). In particular, extant members of the tribe Brontini (Brontinae) are collected primarily under bark, where both adults and larvae

probably feed on fungi (Crowson & Ellis, 1969; Thomas & Leschen, 2010).

Fossil silvanids are rare. Liu *et al.* (2019) have summarized the published fossil record of Silvanidae. The earliest representatives of Silvanidae are confined to the mid-Cretaceous Burmese amber, some 99 million years old (Shi *et al.*, 2012). To date, two monotypic silvanid genera (*Cretoliota* Liu, Ślipiński, Wang & Pang, and *Protoliota* Liu, Ślipiński, Wang & Pang) are known from the Mesozoic era. The first described putative silvanid fossil from Burmese amber, *Pleuroceratos burmiticus* Poinar & Kirejtshuk (Poinar *et al.*, 2008), has been recently been removed from Silvanidae, and transferred to the superfamily Cucujoidea with an uncertain familial placement (Liu *et al.* 2019). Younger fossils of Silvanidae have been documented from the Eocene Baltic and Oise ambers (Kirejtshuk, 2011; Kirejtshuk & Nel, 2013; Alekseev & Bukejs, 2016). Compression fossils of Silvanidae remain unknown.

The two recently described genera *Cretoliota* and *Protoliota* are distinctive among all known Silvanidae. They display markedly long antennae and well-developed mandibular horns in males, as found in the sole extant genus *Uleiota* Latreille. Due to the limited sampling of fossil specimens of these extinct genera, the morphological variations of male mandibular horns and the characterization of genitalic structures of both sexes remain a mystery. Here we reported a series of well-preserved specimens of *Protoliota* with both male and female genitalia exposed, from the same amber deposit as the type specimens of *Protoliota antennatus* Liu, Ślipiński, Wang & Pang (Brontinae: Brontini).

Material and Methods

The fossil material studied here (six specimens, three males and three females) is preserved in mid-Cretaceous Burmese amber. These fossil specimens are derived from the same amber locality as the type specimens of *Protoliota antennatus* Liu, Ślipiński, Wang & Pang. To date, a diversity of bioinclusions have been described from this amber source, including birds (feathers and skeletons), dinosaurs (represented by a tail), fungi (including mushrooms), cycads (as pollen), conifers, angiosperms, nematodes, onychophorans, spiders, ticks, and especially insects (e.g., Grimaldi *et al.*, 2002; Cai *et al.*, 2017; Cai *et al.*, 2018; Ross, 2019). The typical fossil locality has been mapped in Cruickshank & Ko (2003) and Yin *et al.* (2018). Shi *et al.* (2012) have provided a radiometric date of at least 98.8 million years, or earliest Cenomanian for this deposit. A recent study based on various amberground marine animals associated with

Burmese amber has implied a slighter older age for the amber inclusions, and a mid-Cretaceous age is adopted here (Mao *et al.*, 2018).

The type specimen was prepared by cutting with a hand-held saw and polishing with sandpapers of various grain sizes and with polishing powder. The specimens were studied using a Zeiss Discovery V20 stereo microscope, measured with an ocular micrometer attached to the same microscope. Photomicrographs in Fig. 2C, F & G were taken using a Zeiss Axio Imager 2 compound microscope under normal reflected light. Photomicrographs with green and red backgrounds (Figs 2B, E, 3) were taken using a fluorescent light source attached to a Zeiss Axio Imager 2 microscope.

Measurements were taken as follows: length from anterior margin of the clypeus to the apices of the elytra; head width across the maximum width (including eyes); pronotal length along mid line from anterior to posterior margin; pronotal width across the maximum width; elytra length along the suture, including the scutellum; elytral width across the maximum width of the elytra. The morphological terminology of Silvanidae applied here follows that of Thomas & Leschen (2010) and Liu *et al.* (2019).

Systematic Palaeontology

Order Coleoptera Linnaeus, 1758
Family Silvanidae Kirby, 1837
Subfamily Brontinae Erichson, 1845
Tribe Brontini Erichson, 1845
Genus *Protoliota* Liu, Ślipiński, Wang & Pang, 2019

***Protoliota antennatus* Liu, Ślipiński, Wang & Pang, 2019**
(Figs. 1–3)

Material. Males: NIGP170226, NIGP170228 and NIGP170229. Females: NIGP170227, NIGP170230 and NIGP170231 (not photographed).

Locality and horizon. Mid-Cretaceous ambers from the Hukawng Valley, northern Myanmar.

Description. Body elongate, 3.60–4.61 mm long; strongly flattened, covered with short, dense and fine setae. Body dark brown, with antennae and sublateral carinae on head, pronotum and elytra darkened.

Head large, subtriangular in shape, covered with pale, dense and short setae; frontal area with a pair of nearly straight longitudinal carinae along internal margins of eyes. Eyes large, coarse and protruding laterally. Vertex weakly depressed between eyes. Temples behind eyes very short. Antennal insertions completely concealed under
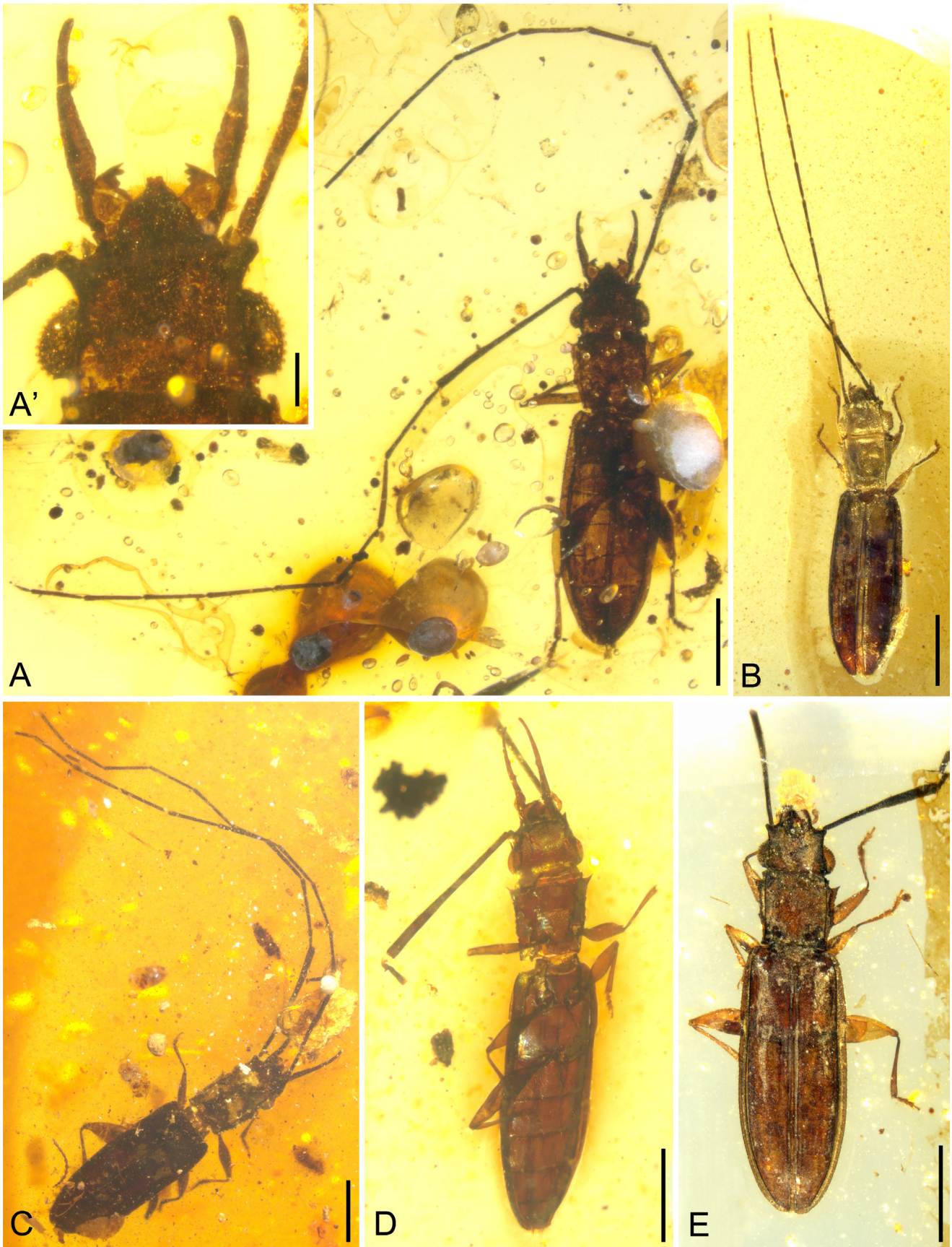
FIGURE 1. *Protoliota antennatus* Liu, Ślipiński, Wang and Pang from mid-Cretaceous Burmese amber. **A**, Dorsal view, male, NIGP170226. **A'**, Enlargement of **A**, showing head and mandibles. **B**, Dorsal view, female, NIGP170227. **C**, Dorsal view, male, NIGP170228. **D**, Ventral view, male, NIGP170229. **E**, Dorsal view, female, NIGP170230. Scale bars: 200 μm in **A'**, 1 mm in others.
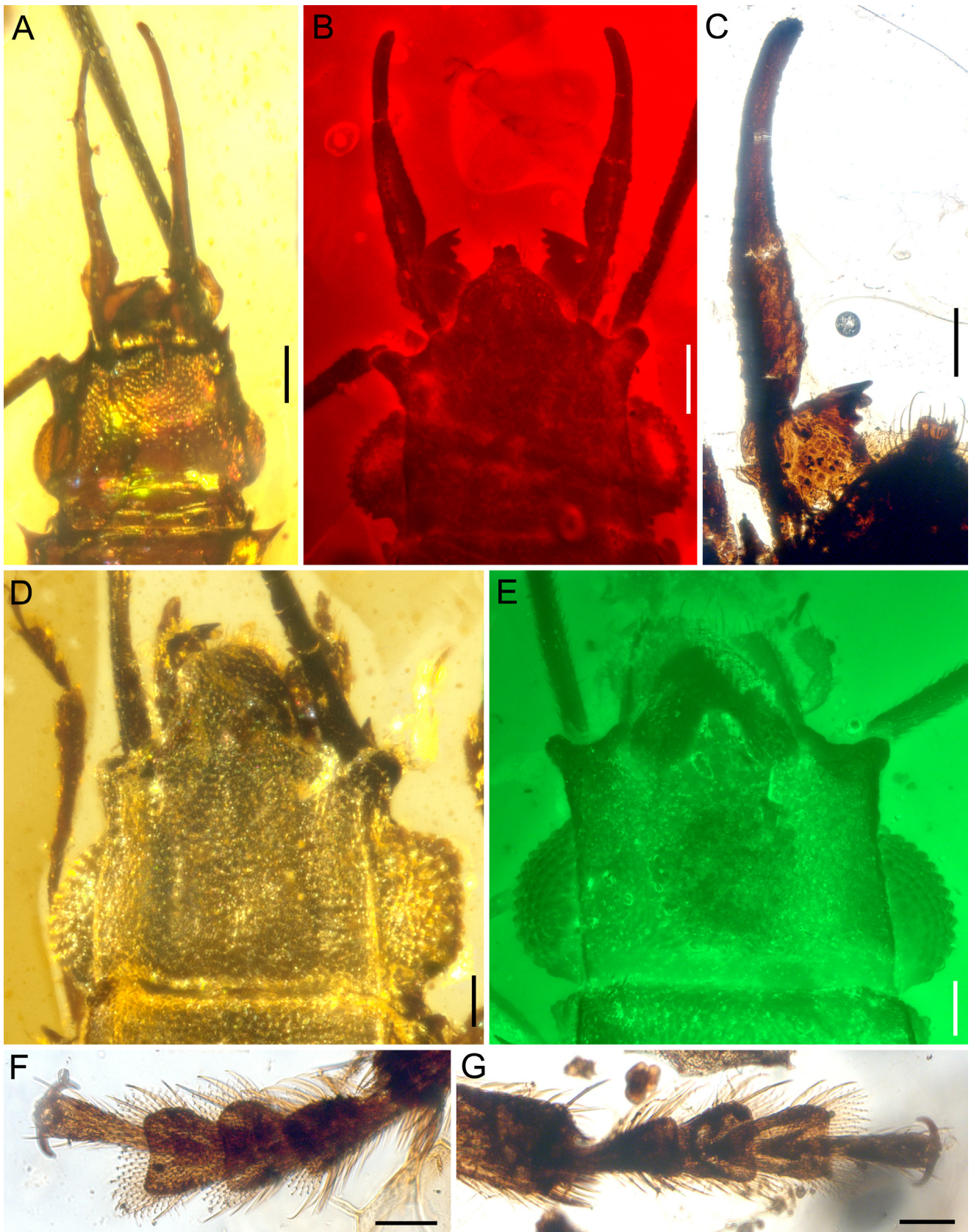
FIGURE 2. Details of *Protoliota antennatus* Liu, Ślipiński, Wang & Pang from mid-Cretaceous Burmese amber. **A**, Head of NIGP170229 (male), ventral view. **B**, Head of NIGP170226 (male), dorsal view. **C**, Enlargement of **B**, right mandible. **D**, Head of NIGP170227 (female). **E**, Head of NIGP170230 (female). **F** and **G**, Metatarsi of NIGP170226. Scale bars: 200 μm in **A** and **B**, 100 μm in **C**–**E**, 50 μm in **F** and **G**.
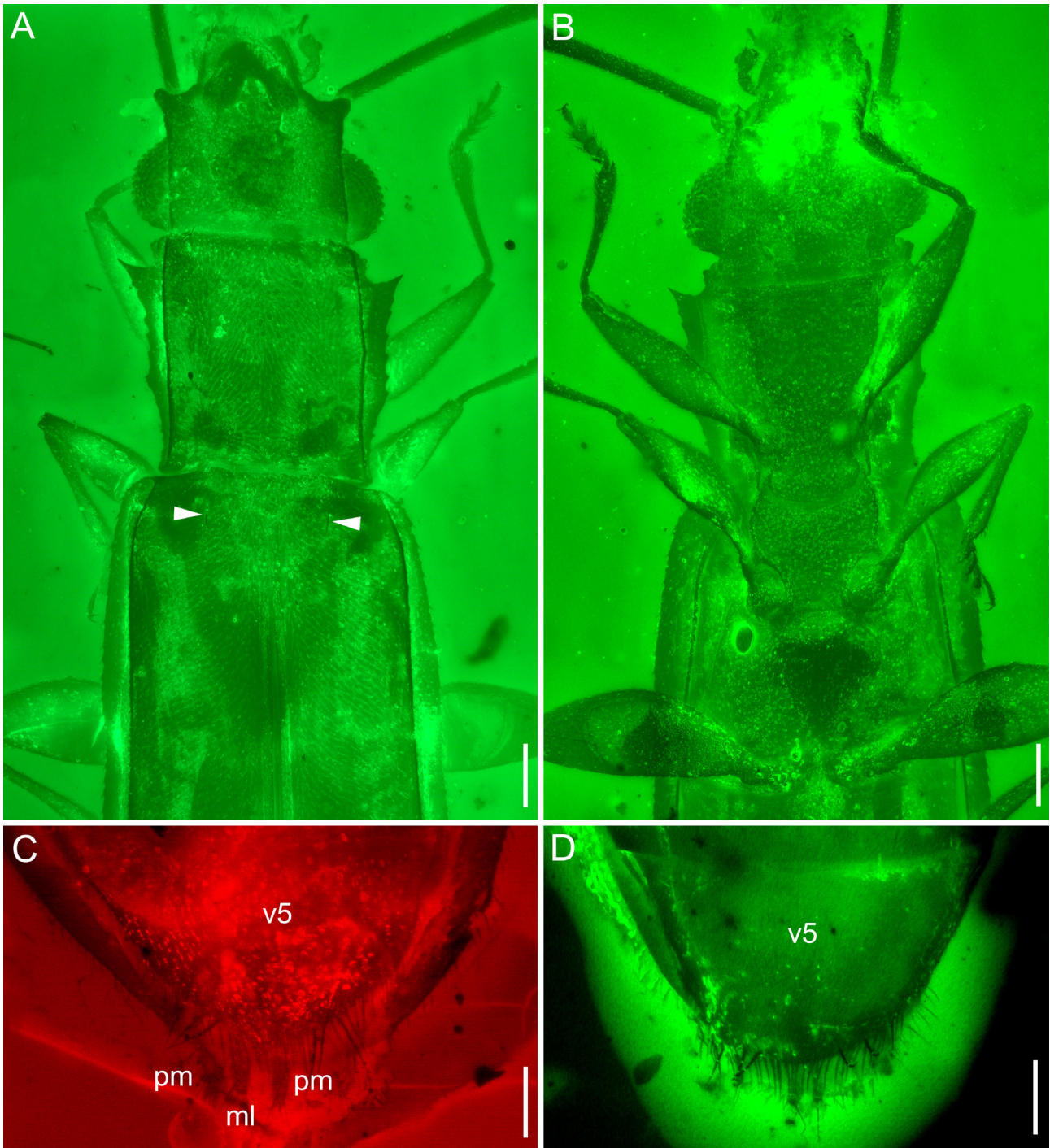
FIGURE 3. Details of *Protoliota antennatus* Liu, Ślipiński, Wang & Pang from mid-Cretaceous Burmese amber. **A**, Dorsal view of forebody, NIGP170230, with two long strong setae indicated. **B**, Same as **A**, ventral view. **C**, Male genitalia of NIGP170226. **D**, Female genitalia of NIGP170227. Abbreviations: ml, median lobe; pm, paramere; v5, ventrite 5. Scale bars: 200 μm in **A** and **B**, 100 μm in **C** and **D**.

sharp and well-developed anterolateral corners. Antennae densely setose, extremely long, distinctly longer than body; scape (antennomere 1) longest, at least extending beyond humeral angles of elytra, 5.1–7.2 times as long as antennomere 2; antennomere 2 elongate, much shorter and narrower than antennomere 1; antennomere 3 about more than 3 times as long as antennomere 2; antennomeres 4–7 elongate, almost in same shape and size; antennomere 8–10 successively shortened, each shorter than antennomere 7. Clypeus protruding, subtriangular, apex with a small notch in the middle. Labrum not visible. Mandibles robust, curved, bidentate apically, inner margin with one preapical tooth. Maxillary palpi short, palpomere 1 small; palpomere 2 slightly curved, long; palpomere 3 wider than

palpomere 2, gradually broadened apically; palpomere 4 narrower than shorter than palpomere 3, with sharp apex. Prothorax trapezoidal, gradually narrowed posteriorly (Fig. 3A). Pronotal disc with a pair of complete sublateral carinae near lateral margin; pronotal disc with dense short setae (Fig. 3A). Lateral margins with a few micro-dentations; anterolateral angle with prominent and sharp tooth (Fig. 3A). Prosternum and pterothorax finely and densely punctate, finely pubescent. Prosternal process broad, dilated at apex; apex broadly curved (Fig. 3B). Procoxal cavities round, widely separated, narrowly externally open (Fig. 3B). Mesocoxal cavities ovate moderately separated, laterally open to mesepimeron. Metacoxal cavities strongly transverse, narrowly separated (Fig. 3B). Metaventrite with almost complete discrimen. Scutellum transverse, with exposed portion pentagonal.

Elytra long, wider than head and pronotum; lateral margins slightly curved. Elytral epipleura slightly narrowed posteriorly and almost reaching the apex. Disc with sharp humeral carina extending from humeral angle to apex but not reaching the apical margin; elytral surface with short and fine setae; spare, black and longer setae present along lateral carinae and on the disc. Pro- and mesofemora slightly dilated; metafemora strongly dilated, much longer than mesofemora. Tibiae slender, gradually broadened toward apex. Tarsi short, 5–segmented; tarsomere 1 elongate, subtriangular dilated, tarsomeres 2 and 3 distinctly lobed, ventral side with dense and fine adhesive setae; tarsomere 4 reduced, concealed; tarsomere 5 elongate (Fig. 2F, G).

Abdomen with five visible ventrites; intercoxal process acute; ventrite 1 slightly longer than ventrite 2; ventrites 3–5 almost in the same length; ventrite 5 distinctly shorter than ventrite 4.

Male. Mandibular horns present (Figs 1A, 2A–C), short to very long, slightly curved near apex. Antennae much longer than those of female, about 1.9 times as long as body length; scapes much longer than those of female, about 2.4 times as long as head. Aedeagus with median lobe broadly elongated, parameres well-developed and slender (Fig. 3C).

Female. Mandibular horns absent (Fig. 2D, E). Antennae long, but shorter than those of male, about 1.4 times as long as body length; scapes much shorter than those of male, about 1.4 times as long as head. Apex of stylus with a single long seta (Fig. 3D).

Discussion

Liu *et al.* (2019) described two extinct genera (*Cretoliota* and *Protoliota*) of Silvanidae from Burmese amber. Both genera display remarkably long antennae and mandibular horns in the males, making them readily recognizable from other genera of Silvanidae. Based on their general body form, long filiform antennae, 5-segmented tarsi and narrowly open procoxal cavities, these genera can be firmly placed in the extant tribe Brontini (subfamily Brontinae). *Cretoliota* and *Protoliota* also lack scutellary strioles, a character present in most Brontini but not in *Parahyliota* Thomas, *Brontopriscus* Sharp or *Uleiota* (*e.g.*, Thomas, 2004), suggesting a close relationship to the latter three extant genera. Males of some species of extant brontine genera bear more or less distinct erect dorsal mandibular horns, although their exact function is unknown (Thomas, 2004). To our knowledge, the present of mandibular horns in male silvanids is confined only to three extant genera: *Macrohyliota*, *Parahyliota* and *Uleiota*. In males of *Macrohyliota* and *Parahyliota*, the mandibular horns are comparatively small and inconspicuous in dorsal view (Fig. 7 in Thomas, 2004; Fig. 3 in Háva, 2018). In contrast, such horns are conspicuous in the males of *Uleiota* (Fig. 1 in Thomas, 2004). The mandibular horns in males of *Cretoliota* are more curved than those of *Protoliota*, closely resembling those of *Uleiota*. In males of *Protoliota*, the mandibular horns are short to very long, and are slightly curved (not straight, as mentioned in Liu *et al.*, 2019). As such, among all extant silvanids, *Cretoliota* and *Protoliota* have a close affinity to the genus *Uleiota* (Liu *et al.,* 2019). However, the former two can be easily separated from the latter by a considerably smaller body size, the smooth elytra without striae or punctation, and the 5-segmeted tarsi (tarsal formula 4-4-4 in *Uleiota*).

Little is known about the morphological variations of mandibular horns in the extant male *Uleiota*, but our discovery of a series of well-preserved male specimens of *Protoliota antennatus* sheds new light on the intraspecific variation of such a peculiar character. Based on our observation of three new male specimens and the holotype of *P. antennatus*, we have found that the length of the mandibular horns and the body size may vary within a species. The length of the mandibular horns generally corresponds to the body size of the specimen: the larger the body size is, the comparatively longer mandibular horns. In the holotype (NIGP169600), the body size is 3.6 mm long, and the mandibular horns are about 0.7 times as long as head length. By contrast, in NIGP170229, the largest specimen of *P. antennatus*, the body size is 4.6 mm long, and the mandibular horns are about 1.3 times as long as head length. Such peculiar variations in the male mandibular horns, to our knowledge, have never been documented among all beetles, but analogous variations are well known in the mandibles (rather than mandibular horns) of some male stag beetles, such as *Lamprima* Latreille (Lucanidae: Lampriminae) (Reid *et al.*, 2018).

In addition to the mandibular horns, the antennal

lengths and proportions of the scapes are different between males and females of *P. antennatus*. Males generally have distinctly longer antennae than females, and the scapes in males are comparatively longer than those of the females. Such a sexually dimorphic character in beetles is not uncommon (e.g., Cerophytidae and Rhinorhipidae; Lawrence, 1988; Costa *et al.*, 2003), although this has not been confirmed in extant Silvanidae.

The external morphology, including the flat body with long filiform antennae, suggests that the mid-Cretaceous silvanids were probably living under the bark of dead trees. Their strong morphological similarities with some extant Brontini suggest a similar fungivorous diet (Liu *et al.*, 2019). It is quite interesting that some rove beetles such as species of *Siagonium Kirby & Spence* (Staphylinidae: Piestinae) from the same habits also have a superficially similar body form as found in the extant *Uleiota* and the extinct *Cretoliota* and *Protoliota*. More importantly, these piestine species also display similar sexual dimorphism in both head and antennal characters (Newton *et al.*, 2000). Males of *Siagonium* have longer antennae than females, and they have a pair of cephalic horns, which are somewhat analogous to the mandibular horns in some male silvanids. Additionally, like brontine genera, *Siagonium* has a flat, elongate and subparallel body and short tarsi.

Conclusion

Our discovery of six well-preserved specimens of *Protoliota* with both male and female genitalia exposed from mid-Cretaceous Burmese amber confirms the presence of remarkable sexual dimorphism in the extinct genus *Protoliota* from the Mesozoic. Males of *Protoliota antennatus* display short to very long mandibular horns and much longer antennae and give evidence of morphological convergence of the beetles living under the bark of dead trees. The unrelated species of the polyphagan beetle families Silvanidae and Staphylinidae share not only similar external morphology and life habits, but also remarkable sexual dimorphism in antennae and modifications of the head and mandibles. Our discovery represents the first definitive sexual dimorphism in beetles from Burmese amber.

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