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Short communication

The oldest Silvanid beetles from the Upper Cretaceous Burmese amber (Coleoptera, Silvanidae, Brontinae)

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ABSTRACT

The first Cretaceous taxa of Brontini, *Cretoliota cornutus* gen. et sp. nov. and *Protoliota antennatus* gen. et sp. nov. are described from the Burmese amber, representing the oldest fossil records of the family Silvanidae. *Pleuroceratos burmiticus* Poinar and Kirejtshuk, 2008 originally placed in Silvanidae is removed from this family to Cucujoidea, family uncertain. The discovery of a diverse fauna of Brontini in the Upper Cretaceous sheds a new light on the early evolution of Silvanidae and superfamily Cucujoidea.

1. Introduction

The family Silvanidae is a small cosmopolitan family of Cucujoid beetles, comprising approximately 61 genera and 500 valid species (Thomas and Leschen, 2010; Thomas, 2011; Karner et al., 2015; Yoshida et al., 2017). For a long time, it has been classified as subfamily within broadly defined Cucujidae until it was elevated to the family level by Crowson (1973). Based on the form of male genitalia, Thomas (1984) proposed division of Silvanidae into two subfamilies, Silvaninae with the aedeagus oriented dorso-ventrally and Uleiotinae with the aedeagus inverted. He postulated that an inverted aedeagus in Uleiotinae was a derived feature facilitating back to back copulating position in these beetles occurring mostly under bark. Uleiotinae was further divided by Thomas (1984) into tribe Uleiotini with externally open procoxal cavities and Telephanini with procoxal cavities externally closed. Considering the priority of the publications, Lawrence and Newton (1995) replaced Uleiotinae Gistel, 1848 with Brontinae Erichson, 1845 which has been followed by subsequent authors. The subfamilies of Silvanidae and the composition of subfamily Silvaninae are well established, however, the tribal classification within the Brontinae remains unclear. The rather sharp original morphological gap between relatively large, flat and sparsely setose Brontini (Thomas, 2004), and the smaller, convex Telephanini with possessing lobed tarsomeres has been gradually obliterated by discoveries in the following years, especially by a new Australian genus *Notophanus* Thomas, 2011, which externally resembles the members of Telephanini but has externally opened procoxal cavities (Thomas and Nearns, 2008). According to a preliminary phylogeny of Silvanidae the Silvaninae and Brontinae are monophyletic but Brontini is paraphyletic with Telephanini derived within this clade (Thomas and Nearns, 2008). Further research is needed to establish phylogenetic relationships within Brontini as their principal distinguishing character, the externally open procoxal cavities should be plesiomorphic and cannot be used to delimit monophyletic groups.

The fossil record of Silvanidae is sparse, and so far, a single specimen from Burmese amber (~99 Ma) attributed to Silvanidae (Poinar et al., 2008) constitutes the oldest known species of the family (but see discussion below). Further fossil Silvanidae have been found in much younger deposits, e.g., 55.8–48.6 Ma of Oise (Kirejtshuk and Nel, 2013) or 37.2–33.9 Ma of Baltic amber

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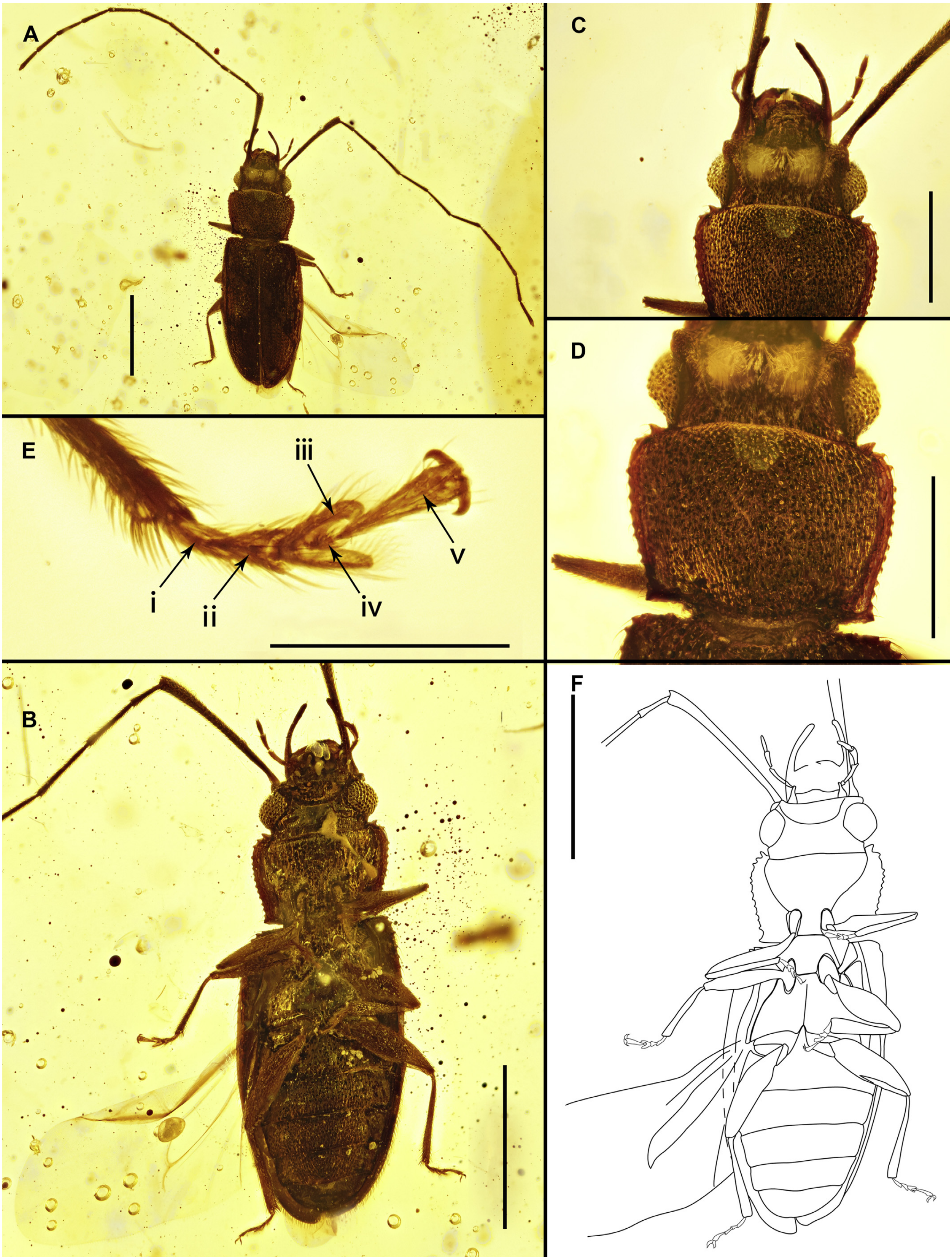
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(Kirejtshuk, 2011; Alekseev and Bukejs, 2016), but no older Jurassic fossils of Silvanidae have been described. Kirejtshuk (2011) described the first species of Brontinae from the Baltic amber. Recently, we found several well-preserved specimens from the Burmese amber (ca. 99 Ma) which clearly belong to subfamily Brontinae and the tribe Brontini, establishing the oldest occurrence of this family.

2. Material and methods

This study is based on four specimens of Silvanidae embedded in the Burmese amber originating from the Hukawng Valley of northern Myanmar (Cruickshank and Ko, 2003; Dong et al., 2015: fig. 1), which is renowned for yielding rich and exquisitely preserved insect groups (Grimaldi et al., 2002; Grimaldi and Engel, 2005; Ross et al., 2010). The age of the amber deposits is generally considered to be the earliest Cenomanian (Grimaldi et al., 2002) or possibly latest Albian (Ross et al., 2010). The recently conducted UePb zircon dating restricted its age at 98.79 ± 0.62MY, which is equivalent to the Late Cretaceous (Shi et al., 2012). The amber specimens included in this study are deposited in the Nanjing Institute of Geology and Palaeontology, CAS, Nanjing, China (NIGP) and Capital Normal University, China (CNU). All extant specimens included in the study for comparison are deposited in Australian National Insect Collection (ANIC).

The material was prepared using a razor table, polished with emery papers with different grain sizes and finally lustrated with polishing powder. Images were taken using a BK Lab Plus system http://www.duninc.com/bk-plus-lab-system.html, then aligned and stacked in Zerene Stacker, a Leica DFC500 camera mounted on a Leica M205C microscope with the software program Leica Application Suite (LAS) V4.9 were also used for the images of *Pleuroceratos burmicus* Poinar and Kirejtshuk; images were then edited in Photoshop CS6. Line drawings were primarily made under a Leica M205C stereomicroscope with a drawing attachment, then processed in Adobe Illustrator CS6. Measurements were taken as follows: length from anterior margin of clypeus to apices of elytra; head width (HW) across the maximum width (including eyes); pronotal length (PL) along mid line from anterior to posterior margin; pronotal width (PW) across the maximum width; elytra length (EL) along suture, including scutellum; elytral width (EW) across the maximum width of paired elytra. The morphological terminology of Silvanidae employed here is largely based on that of Thomas and Leschen (2010).

3. Systematic palaeontology

Order Coleoptera Linnaeus, 1758
Family Silvanidae Kirby, 1837
Subfamily Brontinae Erichson, 1845
Tribe Brontini Erichson, 1845

Cretoliota gen. nov.
Type species: *Cretoliota cornutus* sp. nov.

Etymology. The generic name is an arbitrary combination of letters but referring to the Cretaceous age of the fossil beetle. Gender, masculine.
Diagnosis. *Cretoliota* closely resembles the extant genera of Brontini in a general body shape, long antennae and externally opened procoxal cavities. Among known Brontini it is most similar to *Uleiota* in sharing the presence of unique mandibular horn in the male, and the paired setose depressions on frons are similar to some *Parahyliota*. However, it can be easily distinguished from them by its much smaller size and the pseudotetramerous tarsi with bilobed tarsomere 3, and very short tarsomere 4 (Fig. 1e). Also, *Cretoliota* has elongate maxillary palpomeres, pronotum with anterolateral tooth small and mandibular horn in males long and weakly curved.
Description. Male (female unknown), based on the mandibular horn as in males of *Uleiota* and setose depressions on frons similar to some male *Parahyliota*. Length 2.9 mm. Body strongly flattened, finely pubescent, without distinct incrustations. Head transverse. Eyes moderately large, coarsely facetted and slightly protuberant, distinctly extending on ventral side. Frontoclypeal suture not observed. Clypeus protruding, rounded apically; labrum invisible dorsally. Mandible broad, apex bidentate; dorsal tubercle and cavity (mycangium) not observed; mandibular horn (Fig. 1c) long and slightly arcuate, blunt apically. Antenna extremely long, covered with dense short setae; scape weakly expanded apically, distinctly longer than pronotum. Maxillary palp four segmented with segment 1 short, remaining three palpomeres elongate, palpomere 2 longest. Frons with pair of slightly curved longitudinal carinae along eyes and large densely setose depressions between eyes (Fig. 1d). Temple and postocular constriction absent. Ventral side with a pair of depressions around eyes and curved depression between eyes; gular sutures not observed.

Prothorax trapezoidal, transverse, widest anteriorly with basal area slightly constricted, narrower than elytra at base. Pronotal surface uniformly and deeply granulose, covered with dense short setae; lateral margins denticulate with stronger triangular tooth on anterior margin near angles. Procoxal cavities externally open; prosternal process slightly broader that coxal cavity, expanding apically. Notosternal suture complete. Mesoventrite flat. Mesocoxal cavities laterally open to mesepimeron. Meso-metaventral junction in straight line. Scutellum small and transverse.

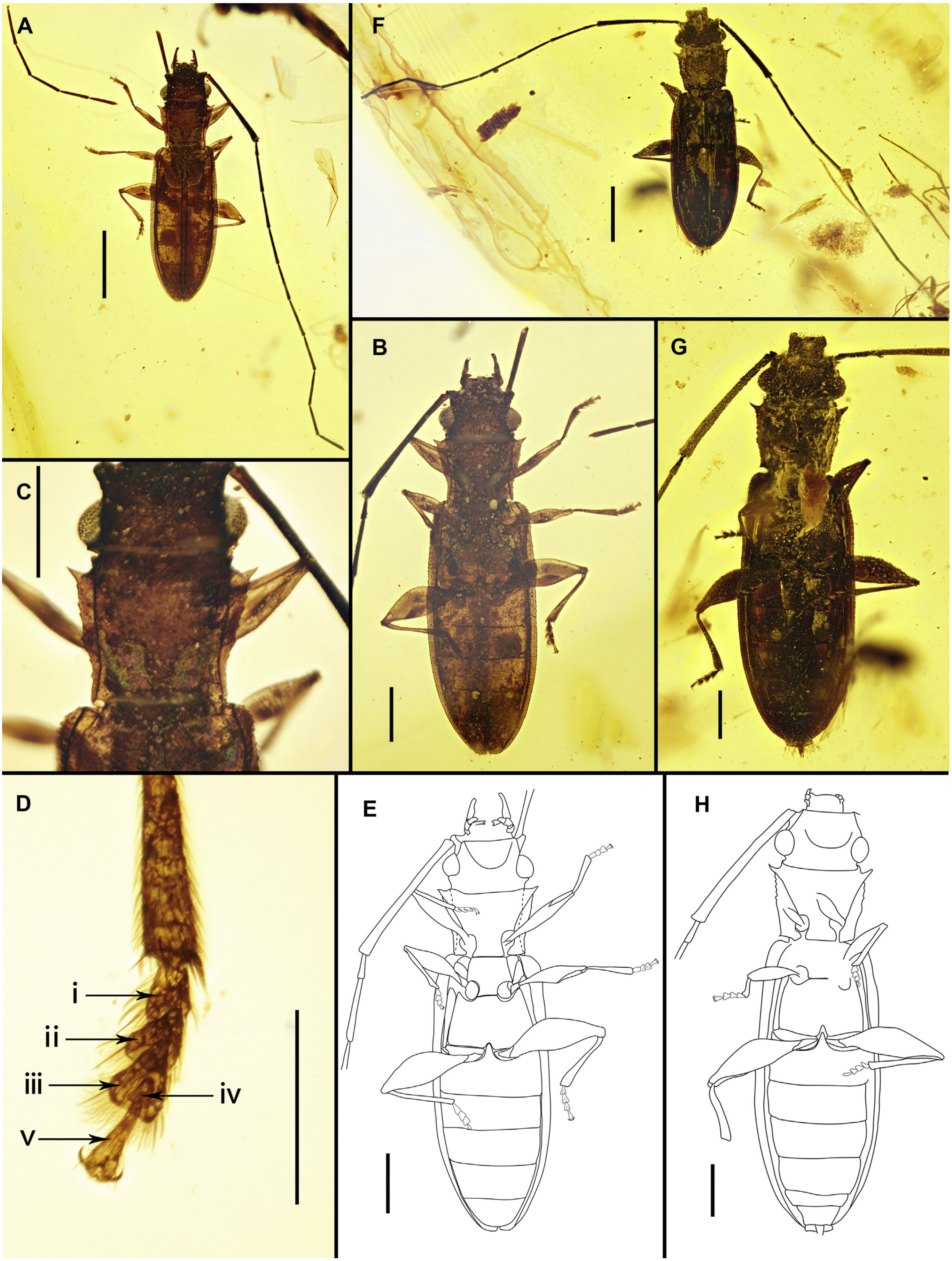
Elytra somewhat convex, widest at about middle, lateral margins weakly curved without distinct humeral carina; lateral margins narrowly explanate. Disc with punctures forming 6 weakly defined longitudinal striae; scutellary striole present, intervals flat. Epipleura moderately broad at base, gradually narrowed posteriorly and absent before apex. Legs with femora slightly dilated, tibiae slender slightly expanded apically; tarsi five segmented; tarsomeres 1 and 2 slightly lobed, tarsomere 3 deeply bilobed and tarsomere 4 very short (Fig. 1e); pretarsal claws simple. Abdomen with five subequal ventrites; intercoxal process very narrow and apicallyte, covered with dense short setae.

Cretoliota cornutus sp. nov.
Fig. 1

Etymology. The specific epithet is based on the Latin noun *cornu,* horn, referring to the mandibular horns in male of this species.
Holotype. No. NIGP169599, lowermost Cenomanian, Hukawng Valley, northern Myanmar (NIPG).
Diagnosis. As for the genus.
Description. Measurements: Length 2.9 mm, HW 0.73 mm, PW 0.83 mm, PL 0.60 mm, EW 1.1 mm, EL 1.8.

Body brown, flattened but dorsum very slightly convex; dorsum and venter both finely punctured; vestiture of dense

Fig. 1. *Cretoliota cornutus* gen et sp. nov., Holotype, NIGP169599; A. habitus, dorsal; B. habitus, ventral; C. head, dorsal; D. pronotum, dorsal; E, mesotarsi, dorsal; F. interpretative illustration, ventral. Scale bars: 1 mm in a-b and f; 0.5 mm in c-d; 0.2 mm in e.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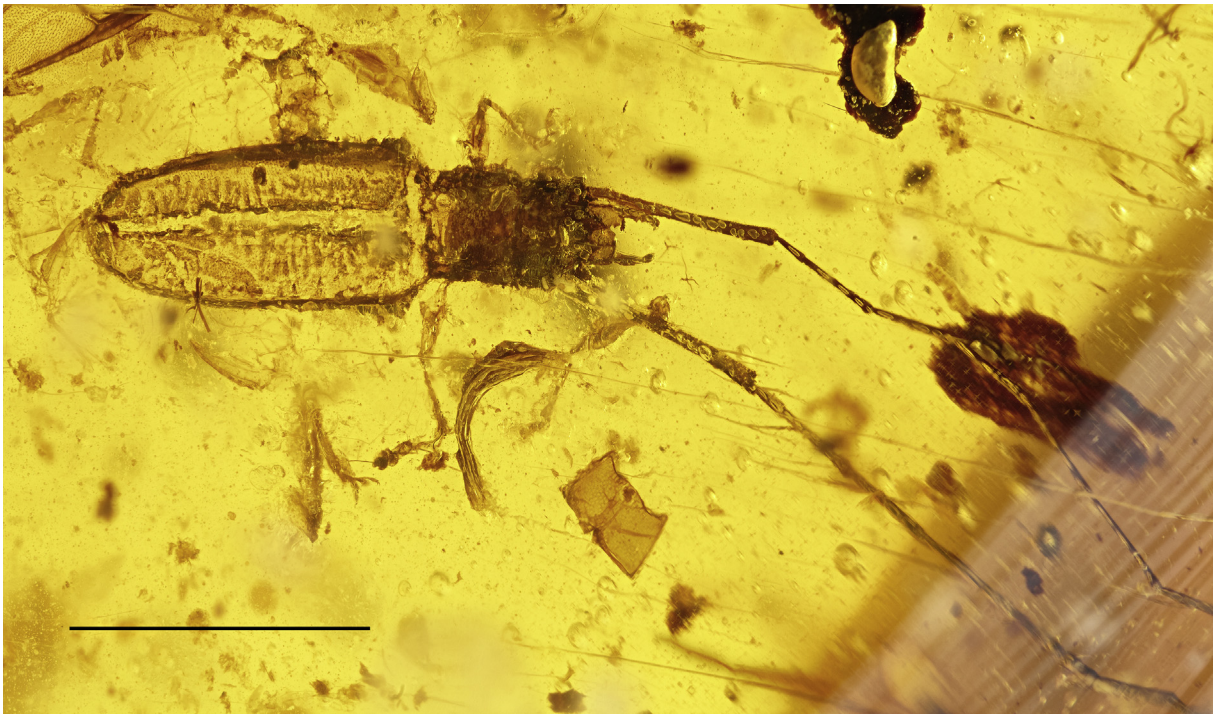

Fig. 3. *Protoliota* sp., CNU-COL-MA-2018101, habitus, dorsal. Scale bars: 1 mm.

short hairs. Head with distinct depressions on vertex, bearing dense and long whitish hairs; mandible with long and slightly curved lateral horn, length of mandible with horn 0.47 times as long as scape. Antennae extremely long, about 4.2 mm; ratio of antennomeres 1–11 as follows: 4.6: 1.0: 1.7: 2.0: 2.0: 1.9: 1.9: 1.9: 1.0: 1.4: 1.7. Pronotum 0.72 times as long as wide; lateral margins denticulate with anterolateral tooth only slightly bigger than lateral denticles; posterior angles sharp. Elytra about 1.6 times as long as wide, sides slightly curved, slightly dentate at humeral area.

Protoliota gen. nov.
Type species: *Protoliota antennatus* sp. nov.

Etymology. Protoliota is an arbitrary combination of letters. Gender musculine.

Diagnosis. Protoliota is similar to *Cretoliota* and *Uleiota* sharing long antennae and well developed mandibular horns in male. It can be distinguished from *Uleiota* by the presence of straight mandibular horns, weakly dentate lateral margins and distinctly 5-segmented tarsi with lobed tarsomeres. *Protoliota* and *Cretoliota* share unique pseudotetramerous tarsi but *Protoliota* has the pronotum with a pair of sublateral carinae, strongly projecting anterior angles and more flattened dorsum, the tarsomeres 2 and 3 distinctly lobed below.

Description. Male. Body dorsally flattened, densely punctate, covered with extremely short adpressed setae. Head prognathous, transverse covered with moderately dense short setae; frontal area with a pair of slightly curved longitudinal carinae beside eyes. Eyes moderately large, coarse and prominent. Vertex weakly depressed between eyes; gena long, about two thirds of eye length, temple behind eyes short and somewhat acute; gula depressed. Antenna extremely long, much longer than body with scape extending beyond humeral angles of elytra; antennomeres covered with dense and very short setae. Clypeus protruding, sub-triangular, labrum invisible. Mandibles bidentate apically with rather short and almost straight lateral mandibular horns (Fig. 1a, 1b). Maxillary palp 4-segmented with the first segment small, second and third palpomeres longer and broader with apical segment narrower with sharp apex.

Prothorax trapezoidal and weakly transverse. Pronotum (Fig. 1c) with complete lateral carina along lateral margin; pronotal disc finely punctate with dense short setae. Lateral margins almost straight and micro dentate; anterior angle with prominent triangular tooth. Prosternum and pterothorax not distinctly punctured, pubescent. Pro- and mesocoxal cavities both ovate and moderately separated, metacoxal cavities transverse and more narrowly separated. Procoxal cavities narrowly externally open; mesocoxal cavities laterally open to mesepimeron. Scutellum transverse, somewhat pentagonal.

Elytra very long; lateral margins nearly parallel to apical third and then gradually narrowed apically; epipleuron only 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; scutellary striole absent; impressed sutural stria complete; surface with regular but very small punctures bearing short setae; spare black bristles visible along lateral carinae and on the disc. Fore and mid legs with femora slightly dilated, hind femora strongly dilated; tibiae slender with apex slightly expanded. Tarsi five segmented with the tarsomere 1 weakly dilated, tarsomeres 2 and 3 distinctly lobed, tarsomere 4 small and more or less concealed (Fig. 1d). Abdomen five segmented with all ventrites almost the same length, not distinctly punctured with moderately dense short setae.

Fig. 2. *Protoliota antennatus* gen. et sp. nov.; A-E. Holotype male, NIGP169600; F-H. paratype female, NIGP169601; A, F. habitus, dorsal; B, G. habitus, ventral; C. pronotum, dorsal; D. tarsi, dorsal; E, H. interpretative illustration, ventral. Scale bars: 1 mm in A and F; 0.5 mm in B-C, E and G-H, 0.2 mm in D.

Female (Fig. 1f, 1g, 1h) resembles the male in body shape and vestiture, but differs in having mandibles without lateral horn, hind femora less strongly dilated.

Protoliota antennatus sp. nov.
Fig. 2

Etymology. The specific epithet refers to the extremely long antennae of this species.
Types. Holotype, NIGP169600, male, lowermost Cenomanian, Hukawng Valley, northern Myanmar (NIPG); paratype, NIGP169601, female, lowermost Cenomanian, Hukawng Valley, northern Myanmar (NIPG).

Diagnosis. As for the genus.
Description. Measurements: male length 3.6 mm, HW 0.7 mm, PW 0.87 mm, PL 0.7 mm, EW 1.0 mm, EL 2.3 mm; female length 4.3 mm, HW 0.95 mm, PW 1.1 mm, PL 0.79 mm, EW 1.3 mm, EL 2.8 mm.

Body brown, distinctly flattened; dorsum and venter both with fine setiferous punctures. Head with gena elongate, 0.67 times as long as length of eyes, apex distinctly protruding anterolaterally; male mandible with moderately long lateral horn, about 0.32 times as long as scape; antenna extremely long, ratio of antennomeres as following: 6.2: 1.0: 2.7: 2.7: 2.8: 2.8: 2.9: 2.7: 2.6: 2.3: 2.8. Pronotum about 0.8 times as long as wide, sides slightly dentate with distinct flanges and elongate anterolateral tooth. Elytra 2.2–2.3 times as

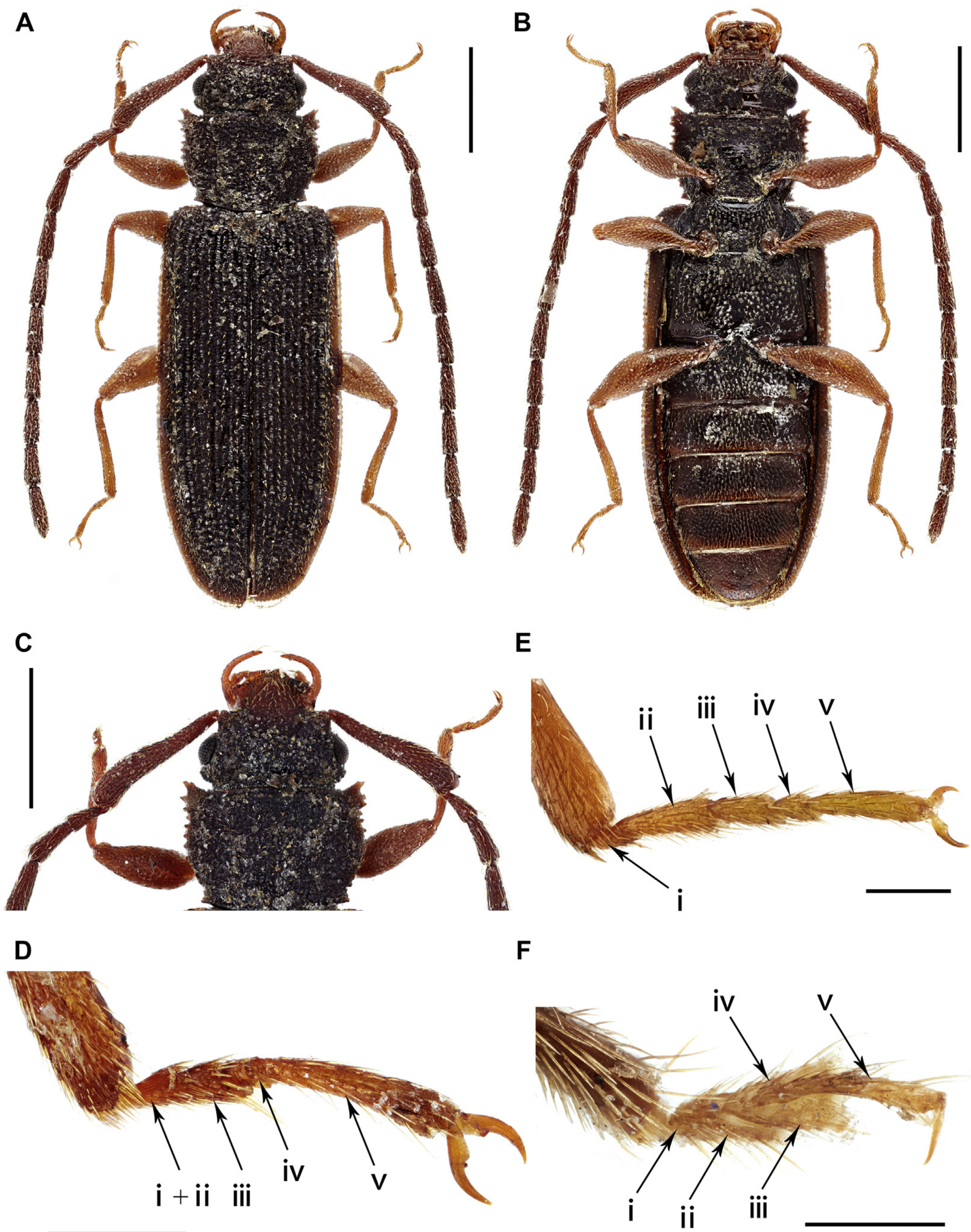

Fig. 4. A-D. *Uleiota planatus* (Linnaeus, 1761), male, ANIC; A. dorsal view; B. ventral view; C. mandible; D. tarsus; E. tarsus of *Dendrophagus* sp., ANIC; F, tarsus of *Telephanus* sp., ANIC. Scale bars: 1 mm in A-C, 0.2 mm in D-F.

long as wide, sides slightly dentate and almost parallel to apical third, with distinct flanges.

Remarks. A highly transparent specimen (Fig. 3) with similar mandibular horns was also found to at least belong to this genus or even the same species, but we do not include it in the type series because of the poor preservation.

4. Discussion

The placement of *Cretoliota* and *Protoliota* in Brontini is firmly established based on their overall body form, long filiform antennae with long scape and without club, 5-5-5 tarsi and narrowly open procoxal cavities. The distinct mandibular horns further suggest a close relationship with *Uleiota* (Fig. 4a-c), which is the only extant genus with strongly prominent mandibular horns (Thomas, 2004). However, species of the extant *Uleiota* are much bigger than those two fossil taxa, have the mandibular horns strongly arcuate, the antennal scape distinctly clavate, and the simple tarsi with the tarsomeres 1 and 2 fused (Fig. 4d). Also, t*Cretoliota* differs from all the extant Silvanidae in having nearly smooth elytra without striate punctations.

Distinctly lobed tarsomeres found in both Cretaceous genera are unknown in the extant Brontini (Thomas, 2004). Most genera of Brontini, including the Eocene *Dendrobrontes* Kirejtshuk, 2011, have simple tarsi with elongate tarsomere 2 (Fig. 4e). Tarsi with lobed tarsomere 3 are present in most of Telephanini (Fig. 4f), with *Cryptamorpha* Wollaston and *Megapsammoecus* Karner having tarsomere 3 bilobed (Thomas and Nearns, 2008). This intermediate character development of the Cretaceous genera between the recent Telephanini and Brontini adds arguments to the already expressed opinions that the tribes of the subfamily Brontinae are paraphyletic assemblages (McElrath et al., 2015; Robertson et al., 2015).

Pleuroceratos burmiticus Poinar and Kirejtshuk (Poinar et al., 2008), from the Burmese amber was placed in Silvanidae and the subfamily Silvaninae based on the superficial similarities to *Oryzaephilus* Ganglbauer (Fig. 5a-b). We were able to examine three well preserved specimens of that species and have established that the procoxae of that species are transversely oval with partially exposed trochantin, the procoxal cavities are externally open (Fig. 5d) and the mesocoxal cavities are closed or very narrowly open to mesepimeron (Fig. 5c). Based on these discoveries, especially in having the oblique procoxa with exposed protrochantin, *Pleuroceratos* is excluded from Silvanidae and placed in Cucujoidea as a family uncertain pending further research.

With *Pleuroceratos* excluded from Silvanidae, the genera described above are the only brontine silvanids known from the Cretaceous period so far. *Antiphloeus* Kirejtshuk and Nel, from the Oise amber represents the oldest Telephanini, and the oldest Silvaninae (37.2–33.9 Ma) are known only from the Eocene Baltic amber (Alekseev and Bukejs, 2016). Thus, the origin of Silvanidae should probably be sought during the Early Cretaceous or even

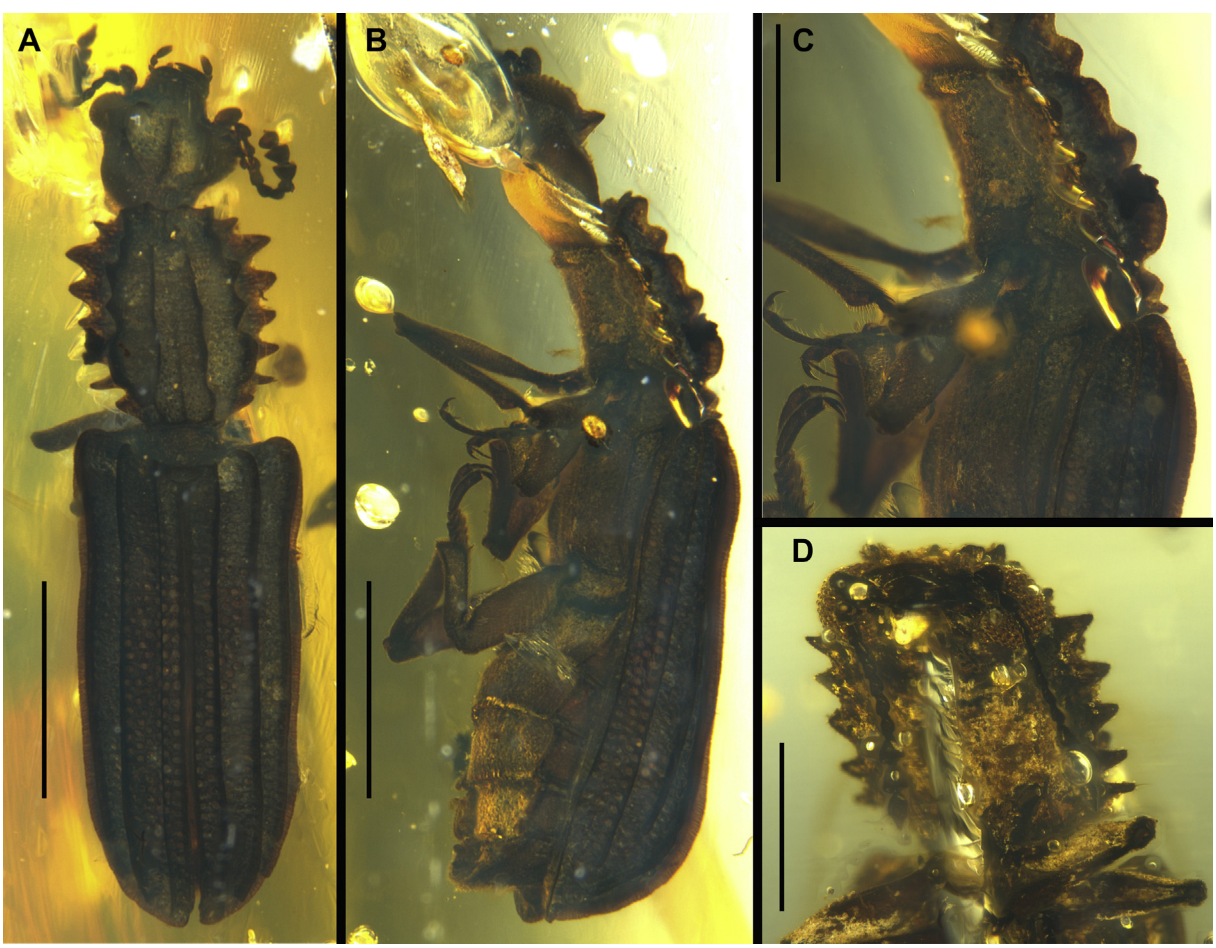

Fig. 5. A-F. *Pleuroceratos burmiticus* Poinar and Kirejtshuk, A-C. NIGP169603, D. NIGP169602; A. dorsal view; B. lateral view; C. thorax, lateral view; D. head and prothorax, ventral view. Scale bars: 1 mm in A and B, 0.5 mm in C and D.

older, in contrast to the result of Toussaint et al. (2017) placing the origin of Cucujoidea around the mid-Triassic (244.79 Ma).

5. Concluding remarks

We described two new genera and two new species of Brontinae from the Upper Cretaceous, which represent the earliest records of the family Silvanidae. The plesiomorphic features of the earliest Brontinae and their flattened bodies with long filiform antennae suggest that the earliest lineages of Silvanidae were probably arboreal and living under bark beetles. Their strong morphological similarities with the extant members of Brontini suggest that they also shared similar fungivorous diet. The compact, more heavily sclerotised bodies of Silvaninae with shorter and clubbed antennae have evolved much latter but allowed exploration of more diverse habitats and leading to great diversification of phylogenetic lineage (McElrath et al., 2015).

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