



Oncelytris esquamatus gen. et sp. nov. from mid-Cretaceous amber of northern Myanmar (Coleoptera: Lucanidae)

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Lucanidae, or stag beetles, represents a spectacular group of scarabaeoid beetles, with mandibles often remarkably enlarged in males (Mizunuma & Nagai 1994). The earliest fossil of Lucanidae was documented from the Middle-Late Jurassic Daohugou biota (Nikolajev *et al.* 2011). Recently three fossil genera have also been reported from the mid-Cretaceous Burmese amber (Cai *et al.* 2017; Qiu *et al.* 2017; Wu *et al.* 2022). Here we describe a new lucanid fossil, *Oncelytris esquamatus* Li & Cai **gen. et sp. nov.**, from Burmese amber, which shares a similar protibial morphology with the extant tribe Ceratognathini. The tuberculate elytra of *Oncelytris* are unique within the family.

Material and methods

The Burmese amber specimen studied herein (Figs 1–3) originated from amber mines near Noije Bum (26°20' N, 96°36' E), Hukawng Valley, Kachin State, northern Myanmar. The 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 small table saw, ground with emery paper of different grit sizes, and finally polished with polishing powder.

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) or 561 nm (DPSS 561-10) laser excitation line (Fu *et al.* 2021; Li *et al.* 2023). Images under incident light and widefield fluorescence were stacked in Helicon Focus 7.0.2 or Zerene Stacker 1.04. Confocal images were semi-manually stacked with Helicon Focus 7.0.2 and Adobe Photoshop CC. Images were further processed in Adobe Photoshop CC to adjust brightness and contrast.

The subfamilial classification system of Lucanidae follows Howden & Lawrence (1974), where Nicaginae was treated as an independent subfamily. Although some researchers (*e.g.*, Holloway 1969, 2007) treated nicagines as a part of Aesalinae, the molecular phylogeny by Kim & Farrell (2015) has revealed a paraphyletic Aesalinae with nicagines included. Nicaginae could be reasonably separated from Aesalinae both morphologically (Howden & Lawrence 1974) and molecularly (Paulsen 2013).

Systematic palaeontology

Order Coleoptera Linnaeus, 1758**Family Lucanidae Latreille, 1804****Subfamily Nicaginae LeConte, 1861****Tribe Ceratognathini Sharp, 1899****Genus *Oncelytris* Li & Cai gen. nov.****Type species.** *Oncelytris esquamatus* Li & Cai sp. nov.

Etymology. The generic name is a combination of the Greek “*onkos*” and “*elytron*”, referring to its exceptionally tuberculate elytra. The name is masculine in gender.

Diagnosis. Dorsal surface without scales (Fig. 2A). Vertex with a pair of not well-separated protuberances (Fig. 3H). Antennae non-geniculate, with 3-segmented, moderately lamellate club (Fig. 3E). Mandibles small (Fig. 3A). Prosternal process strongly narrowed; procoxae subcontiguous (Fig. 3B). Outer protibial edge with one large apical spine, one large postmedial spine, one moderately enlarged premedial spine, and numerous equal-sized small spines (Fig. 3F). Elytra tuberculate in posterior half (Fig. 3I).

Remarks. *Oncelytris* generally has many characters plesiomorphic in Lucanidae, such as the entire eyes not divided by canthus, non-geniculate antennae, small mandibles, and the strongly narrowed prosternal process and subcontiguous procoxae (Kim & Farrell 2015). Among the five subfamilies, *Oncelytris* could be confidently ruled out from Aesalinae and Lucaninae, as the latter two have a well-developed prosternal process and well separated procoxae (Howden & Lawrence 1974; Kim & Farrell 2015: fig. 3). Compared with *Oncelytris*, members of Lampriminae generally have much more developed mandibles and fewer but larger spines on protibiae.

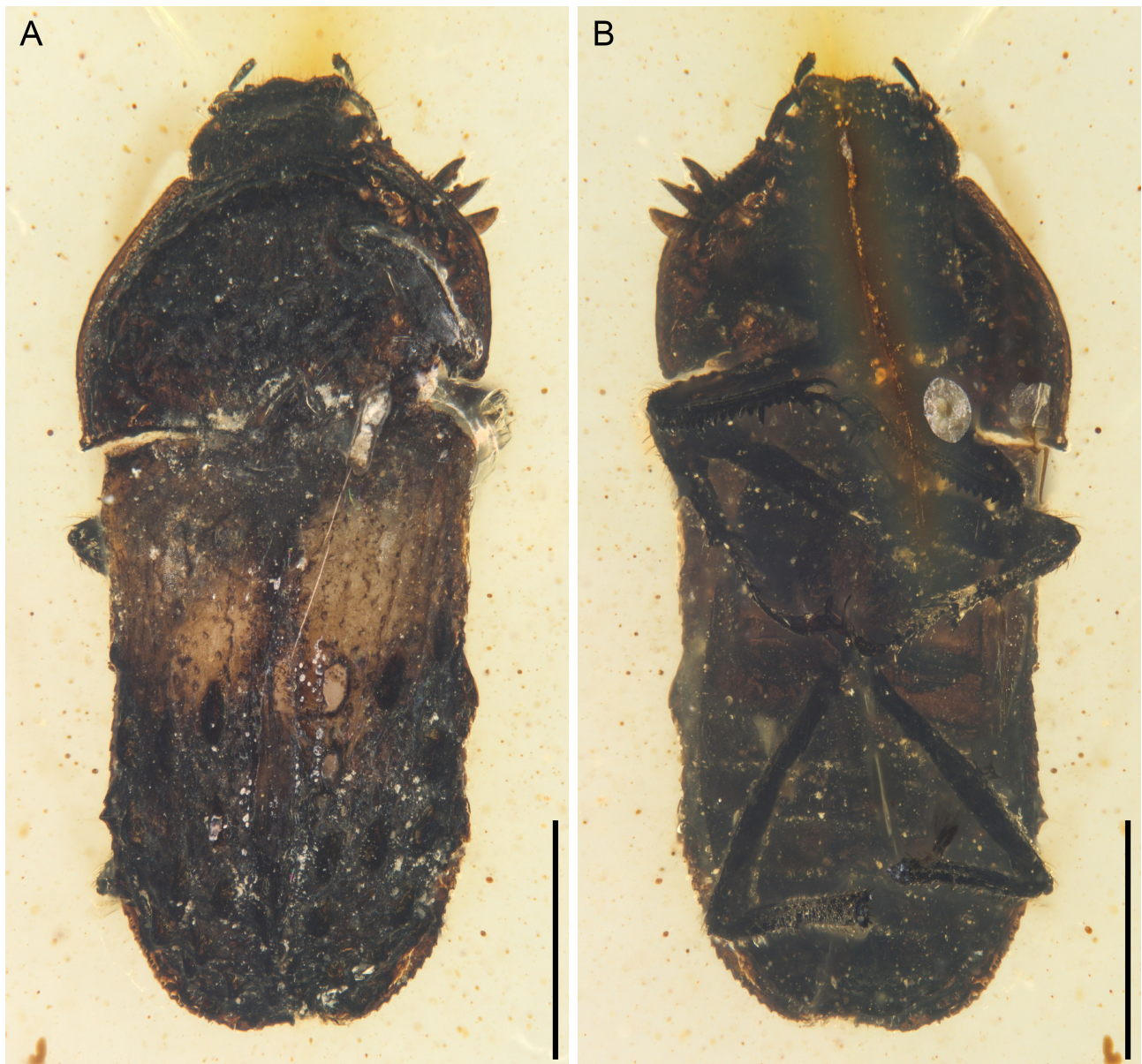


FIGURE 1. General habitus of *Oncelytris esquamatus* Li & Cai **gen. et sp. nov.**, holotype, NIGP200820, under incident light. **A**, Dorsal view. **B**, Ventral view. Scale bars: 1 mm.

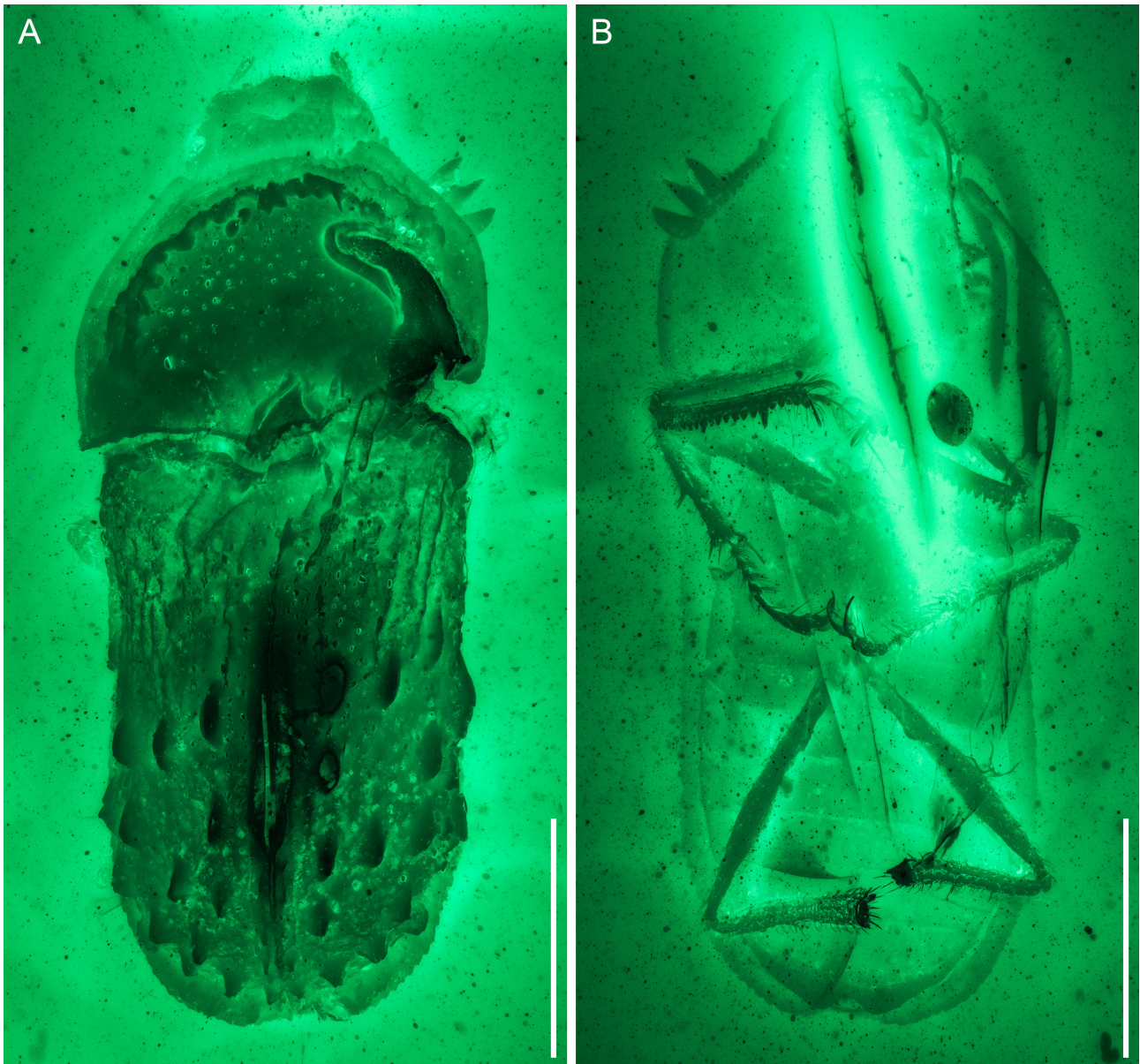


FIGURE 2. General habitus of *Oncelytris esquamatus* Li & Cai **gen. et sp. nov.**, holotype, NIGP200820, under widefield fluorescence. **A**, Dorsal view. **B**, Ventral view. Scale bars: 1 mm.

It would be more difficult to confidently rule out *Oncelytris* from Syndesinae. The differentiation of subfamilies relies heavily on the male genitalic structure, and other important characters such as mandibles or antennal clubs are often sexually dimorphic (Holloway 1960). Here we are unable to confidently determine the sex of the single specimen with genital organ unexposed. Syndesinae includes three tribes: Syndesini, Ceruchini and Sinodendrini (Holloway 1968; Huang *et al.* 2011; Huang & Chen 2017a), although the monophyly of the subfamily is contentious (Huang & Chen 2013; Kim & Farrell 2015). Nevertheless, *Oncelytris* could be separately differentiated from all these syndesine tribes: from Syndesini in having a 3-segmented antennal club, from Sinodendrini in frons without median tubercle or horn, and from Ceruchini in having smaller mandibles.

In general, *Oncelytris* is most similar to the tribe Ceratognathini of Nicaginae (Fig. 4). The only other tribe in Nicaginae, Nicagini, differs from *Oncelytris* in having shorter antennomere 1 and protibia without numerous small spines (Paulsen & Smith 2005). Ceratognathini includes four extant genera: *Ceratognathus* Westwood, 1838, *Mitophyllus* Parry, 1843, *Hilophyllus* Paulsen & Mondaca, 2006 and *Holloceratognathus* Nikolaev, 1998 (Paulsen 2013). The outer protibial edge of all ceratognathin genera shares a large apical spine and a large postmedial spine, but the morphology of other smaller spines varies among genera (Holloway 1998; Paulsen & Mondaca 2006). The small spines are variably-

sized in *Holloceratognathus*, while in the remaining genera the small spines are more or less equal-sized. *Mitophyllus* and *Hilophyllus* do not have moderately enlarged spines on the proximal half of protibiae. *Ceratognathus* has two or three moderately enlarged spines on the proximal half of protibiae. The protibia of *Oncelytris* is somewhat similar to that of *Ceratognathus*, but with only a single moderately enlarged spine on the proximal half. *Oncelytris* also shares with *Ceratognathus* the somewhat paired protuberances on the dorsal side of head, which are absent in other genera of Ceratognathini (Holloway 1998).

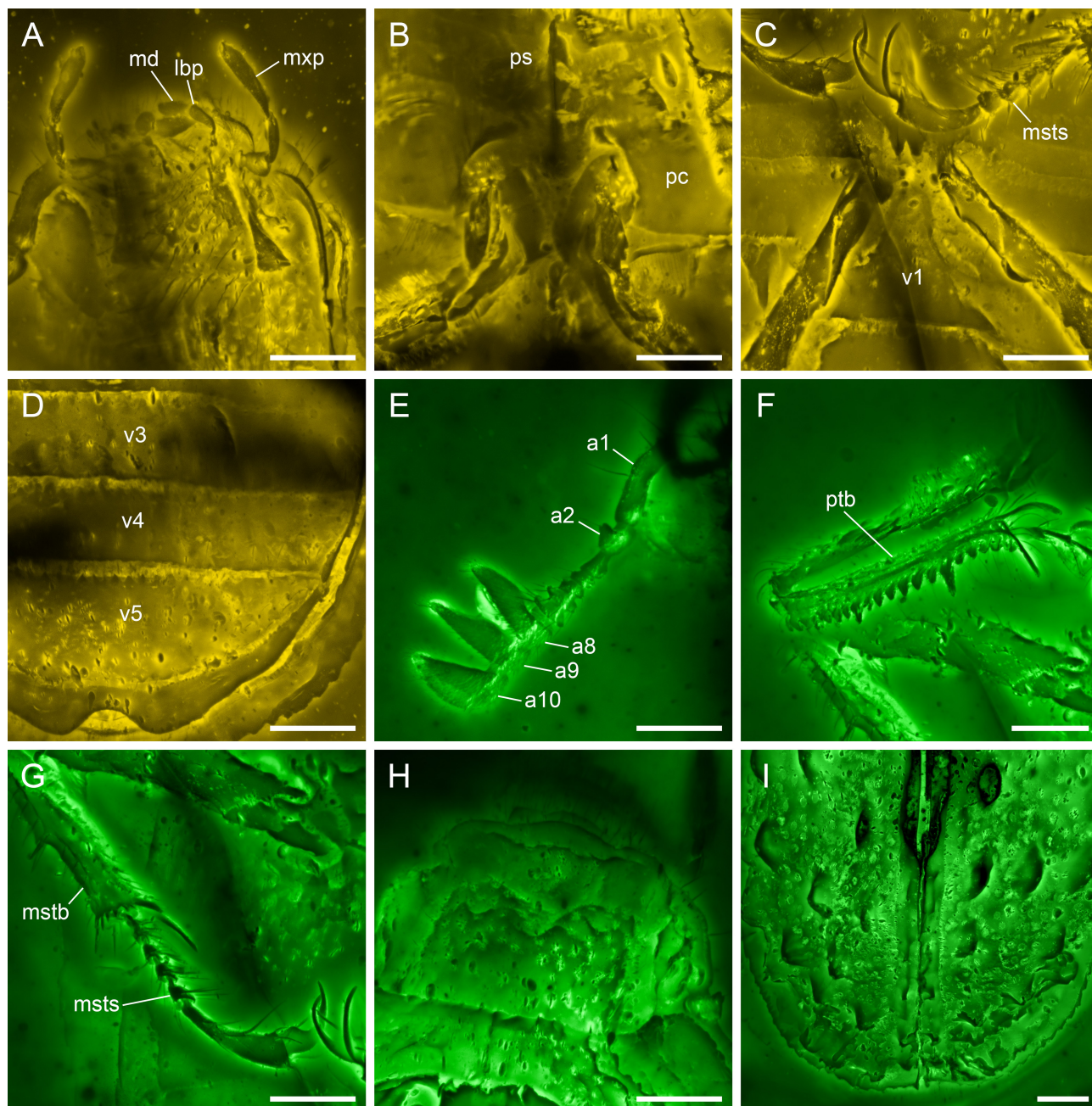


FIGURE 3. Details of *Oncelytris esquamatus* Li & Cai **gen. et sp. nov.**, holotype, NIGP200820, under confocal microscopy. **A**, Mouthparts, ventral view. **B**, Prothorax, ventral view. **C**, Abdominal base, ventral view. **D**, Abdominal apex, ventral view. **E**, Antenna, ventral view. **F**, Protibia. **G**, Mid leg. **H**, Head, dorsal view. **I**, Elytral apex, dorsal view. Abbreviations: a1–10, antennomeres 1–10; lbp, labial palp; md, mandible; mstb, mesotibia; msts, mesotarsus; mxp, maxillary palp; pc, procoxa; ps, prosternum; ptb, protibia; v1–5, ventrites 1–5. Scale bars: 200 μ m.

The distinctly tuberculate elytra of *Oncelytris* are quite exceptional, which are unknown in any other member of Nicaginae (and even Lucanidae). Such tuberculate elytra are reminiscent of some members of the closely related family Trogidae (Strümpher *et al.* 2015; Tihelka *et al.* 2021; Cai *et al.* 2022). It is worth mentioning that the elytra of some

Aesalini have a superficially similar tuberculate appearance, which, however, are due to the presence of clustered scales (e.g., Huang *et al.*, 2015; Huang & Chen 2016, 2017b; Paulsen 2018). *Oncelytris* additionally differs from most Nicaginae in the absence of well-developed scales on elytra, although in the New Zealand *H. passaliformis* (Holloway, 1962) the elytral scales are also reduced (Fig. 4A; Holloway 1997).

***Oncelytris esquamatus* Li & Cai sp. nov.**

(Figs 1–3)

Type material. Holotype, NIGP200820, possibly male (as the emarginate abdominal ventrite 5 is present in only some of the males of the presumably closely-related *Holloceratognathus* and *Mitophyllus*; Holloway 1998).

Etymology. The specific name refers to the absence of scales on its dorsal surface.

Locality and horizon. Amber mine located near Noiye Bum Village, Tanai Township, Myitkyina District, Kachin State, Myanmar; unnamed horizon, mid-Cretaceous, Upper Albian to Lower Cenomanian.

Diagnosis. As for the genus.

Description. Body moderately elongate, about 4.0 mm long, 1.7 mm wide; surface without scales.

Head small, shorter than half pronotal length and narrower than half pronotal width; vertex with a pair of not well-separated protuberances. Eyes moderately protuberant; ocular canthus probably absent. Anteocular process moderately developed, weakly pointed laterally (rather than anteriorly). Antennae 10-segmented, with 3-segmented club; antennomere 1 more than three times as long as wide, curved, with almost constant width; antennomeres 4–7 short, each wider than length, successively widened; antennomeres 8–10 moderately lamellate. Mandibles short, not extending beyond labial palps. Maxillary palp 4-segmented; apical palpomere elongate.

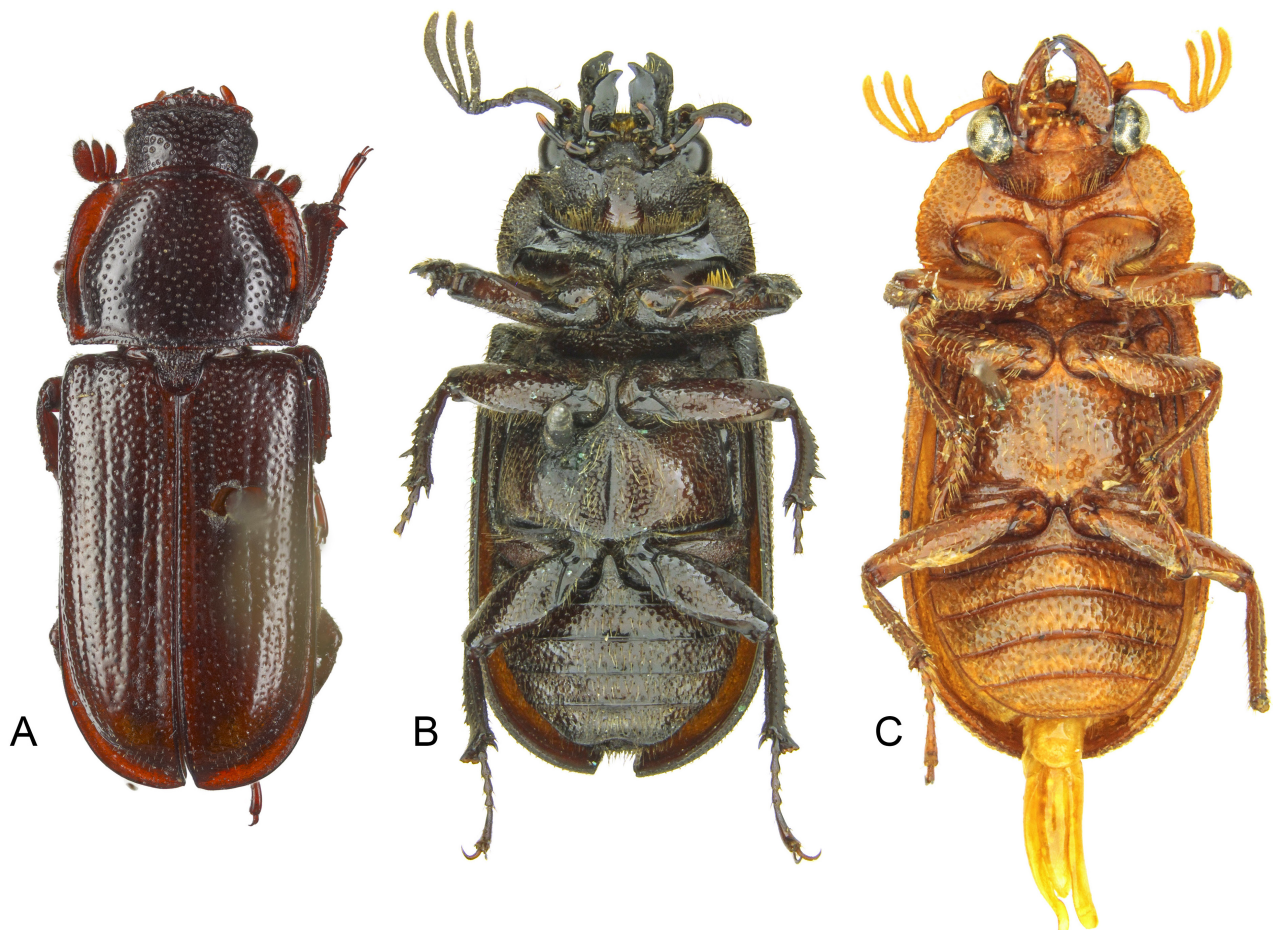


FIGURE 4. Extant representatives of Ceratognathini. **A**, *Holloceratognathus passaliformis* (Holloway, 1962) (male), dorsal view. © Museum of New Zealand Te Papa Tongarewa, registration number AI.000059, licensed under CC BY 4.0. **B**, *Holloceratognathus helotoides* (Thomson, 1862) (male), ventral view. **C**, *Ceratognathus ocellaris* Carter, 1925 (male), ventral view.

Pronotal disc widest basally, slightly wider than elytra combined; surface simple; lateral sides smooth, subparallel in posterior half and converging anteriorly in anterior half; anterior angles slightly produced; posterior angles right-angled. Prosternum with median longitudinal carina; prosternal process narrow, with procoxae subcontiguous.

Elytra 1.6 times as long as combined width, nearly parallel-sided in anterior three-fifths; lateral sides serrulate (at least in posterior half); punctures on surface likely not forming distinct rows; distinct tubercles present in posterior half of elytral surface. Mesocoxal cavities likely narrowly separated. Posterior intercoxal process of metaventricle apically with two acute points. Metacoxae transverse, subcontiguous.

Protibia with one large apical spur; outer protibial edge with one large apical spine, one large postmedial spine, one moderately enlarged premedial spine, and numerous equal-sized small tooth-like spines. Mesotibia with paired apical spurs. Tarsi 5-segmented. Pretarsal claws simple; empodium well developed and bisetose.

Abdomen with five ventrites; ventrite 5 apically emarginate.

Data availability

The original confocal data are available in Zenodo repository (<https://doi.org/10.5281/zenodo.7627293>).

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