

New minute clubbed beetles (Coleoptera, Monotomidae, Lenacini) from mid-Cretaceous amber of Northern Myanmar

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ABSTRACT

Three fossil species classified in the family Monotomidae are described from mid-Cretaceous Burmese amber. They are attributed to the recent tribe Lenacini Crowson, known so far from a single extant endemic species, *Lenax mirandus* Sharp, from New Zealand. *Lenax karenae* Liu, Tihelka, McElrath and Yamamoto sp. nov., *Cretolenax carinatus* Liu, Tihelka, McElrath and Yamamoto gen. et sp. nov., and *Cretolenax diabolus* Tihelka, Liu, McElrath and Yamamoto gen. et sp. nov. reveal high diversity and a much broader distribution of Lenacini during the Cretaceous. The discovery of the Burmese amber taxa closely related to the New Zealand endemic supports growing evidence about the Gondwanan origin of the West Burma Block.

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1. Introduction

Monotomidae Laporte, 1840, also known as the minute-clubbed beetles, is a relatively small family with 257 extant and extinct species placed in 36 genera (Bousquet, 2010; McElrath, unpublished data). Though with poorly documented feeding habits, monotomids are thought to be mycophagous or predatory (the commonly used "root eating beetles" is inaccurate), and are found in all zoo-geographical regions of the World (Sen Gupta, 1988; Bousquet, 2010). The family was formerly known as Rhizophagidae until Pakaluk et al. (1994) recognized the priority of Monotomidae. Members of monotomids were once included in

Nitidulidae and Cucujidae (see Bousquet, 2010) until Crowson (1952, 1955) recognized them as a distinct family. Monotomidae is currently considered one of the early diverging groups of Cucujoidea (Crowson, 1955; Lawrence and Newton, 1995; Leschen et al., 2005). Recent molecular analyses of beetles on a larger scale (e.g., Bocak et al., 2014; McKenna et al., 2015; Robertson et al., 2015; Zhang et al., 2018) recovered Monotomidae with good support as a sister group to a clade comprising Nitidulidae, Cybocephalidae and Kateretidae, which agrees with the original placement suggested by Crowson (1952, 1955).

Crowson (1952) proposed a four subfamily system: Rhizophaginae Redtenbacher, 1845 (including only *Rhizophagus* Herbst, 1793, restricted to the Northern Hemisphere); Lenacinae Crowson, 1952 (including only *Lenax* Sharp, 1877, restricted to New Zealand); Thioninae Crowson, 1952 (including two genera of highly modified cylindrical beetles distributed in tropical regions of the Western

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and Eastern hemispheres); and finally Monotominae Laporte, 1840 (including the majority of the genera and distributed worldwide). Sen Gupta (1988) reviewed the genera of the world and suggested a two subfamily system, Rhizophaginae as in Crowson, 1952, and Monotominae including all the other genera. Monotominae was further divided into four tribes: Monotomini Laporte, 1840 for *Monotoma* Herbst, 1793, Lenacini and Thionini [with the same genera as the subfamilies of Crowson (1952)] and Europini Sen Gupta, 1988 for the remaining genera. Although numerous errors in this review were mentioned by Pakaluk and Slipiński (1993), the taxonomy of tribes and subfamilies of Sen Gupta (1988) was still followed by subsequent authors (Lawrence and Newton, 1995; Bousquet, 2010; Bouchard et al., 2011). This system, however, is not supported by any phylogenetic analysis and is likely artificial, but will be followed herein.

The monotypic genus *Lenax* contains the species *Lenax mirandus* Sharp, 1877 (Figs. 1–2), endemic to both islands of New Zealand. It can be easily distinguished from other monotomid genera by possessing deep subantennal grooves extending behind the eyes, a pair of large depressions on the vertex next to the eyes, and a number of other distinctive features (Fig. 2). While it has been suggested that these cavities and grooves may serve as mycangia (Grebennikov and Leschen, 2010), that has yet to be empirically demonstrated. The biology of *Lenax* is poorly studied, although Klimaszewski and Watt (1997) mentioned that adults had been collected from under bark of dead trees of *Nothofagus fuscus* and *N. menziesii*, and in *Platypus* tunnels in dead heketara [*Olearia rani* (A.Cunn.) Druce]. Milligan (1979) noted the common association with *Platypus* Herbst, 1793 galleries, which has recently been confirmed in the field (McElrath, unpublished data). However, fungal spores found in their guts suggest that it is doubtful that *L. mirandus* feeds on *Platypus* beetles directly, but on fungus either in their galleries or under bark (McElrath, unpublished data).

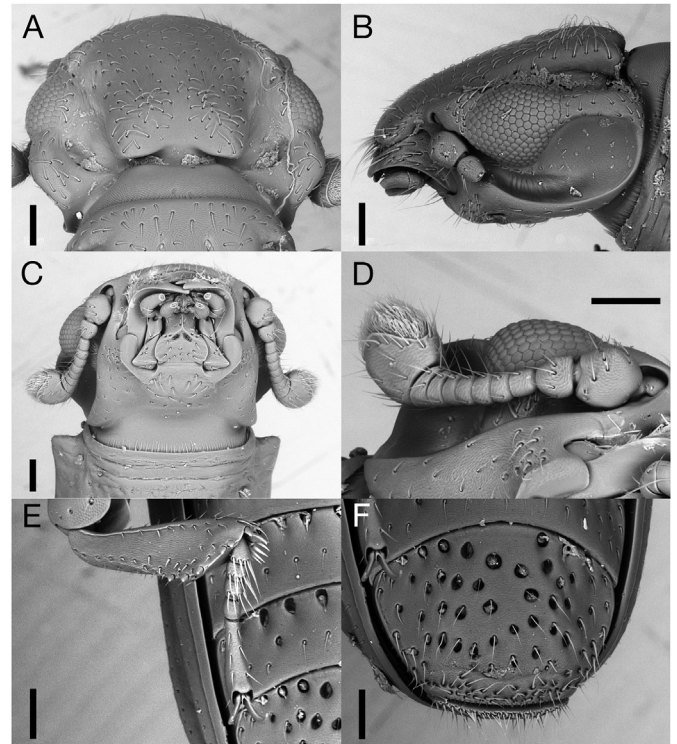


Fig. 2. *Lenax mirandus* Sharp, 1877, female, SEM micrographs captured using a Leica 1450 EP Environmental Scanning Electron Microscope at Georgia Electron Microscopy (Barrow Hall, University of Georgia). (A) Dorsal head, showing posterolateral cavities and groove, as well as microdebris accumulated in groove; (B) Lateral head with antenna removed, showing ventral groove and cavity where antenna may be retracted alongside head capsule; (C) Ventral head, showing mouthparts and antennae partially retracted under head; (D) Right antennae close up; (E) Right metatibia and metatarsus; (F) Abdominal ventrite 5 and downturned pygidium.

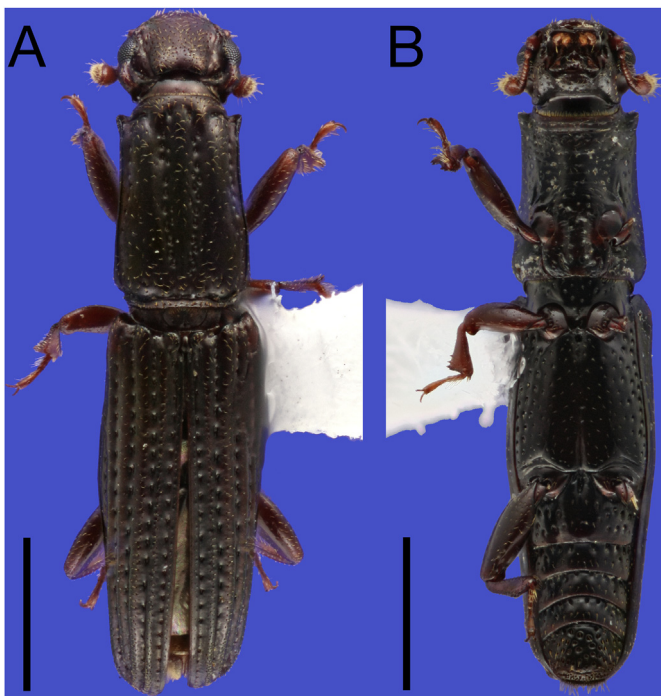


Fig. 1. *Lenax mirandus* Sharp, 1877, female (Scale = 1.0 mm), (A) dorsal and (B) ventral habitus photomicrographs. Specimen (NZAC) collected under bark by Rich Leschen in Mt. Pirongia SF, New Zealand.

Fossil Monotomidae are rare and have mostly been found in Eocene Baltic amber (Peris and Delclòs, 2015), though only *Europs interburgensis* Alekseev and *Aneurops daugpilensis* Bukejs and Alekseev were described recently (Alekseev, 2014; Bukejs and Alekseev, 2015). Kirejtshuk et al. (2009) described the first Mesozoic monotomids, *Rhizophptoma elateroides* Kirejtshuk and Azar from Lower Cretaceous Lebanese amber and established a new subfamily, Rhizophptominae Kirejtshuk and Azar, to contain it. Two more *Rhizophptoma* species from the same locality were described later (Kirejtshuk and Azar, 2013). Peris and Delclòs (2015) described another species of *Rhizophptoma* and a new genus, *Cretakarenni* Peris and Delclòs, with two species within the same subfamily from Lower Cretaceous Spanish amber. Currently, the oldest known monotomid is from the Middle Jurassic Daohugou Formation in northeastern China (Cai et al., 2015), suggesting an older origin of Monotomidae. Recently, several specimens of Monotomidae that resemble the genus *Lenax* have been found in Burmese amber. These specimens represent the first representatives of Monotomidae from mid-Cretaceous Burmese amber, the oldest record of Lenacini, and also the first Lenacini not known to be restricted to the New Zealand landmass.

2. Material and methods

Specimens were found from amber deposits in Kachin (Hukawng Valley) of Northern Myanmar, approximately 100 km southeast of the Village of Tanai (26°20' N, 96°36' E) (Dong et al., 2015: fig. 1). The age of the amber deposits may be earliest

Cenomanian, Late Cretaceous (98.79 ± 0.62 Ma) by U–Pb zircon dating (Shi et al., 2012) or alternatively, a slightly older age of late Albian (at the Albian–Cenomanian boundary, 100.5 ± 0.9 Ma) (Cruickshank and Ko, 2003; Mao et al., 2018; Yu et al., 2019). Botanical and spectroscopic studies indicate that the fossilized resin probably originated from Araucariaceae trees (Poinar et al., 2007), but Grimaldi and Ross (2017) suggested the dawn redwood genus *Metasequoia* Miki (Cupressaceae) as an alternate botanical origin. The tropical palaeoenvironment of the Burmese amber producing forests has been suggested (Grimaldi et al., 2002).

Specimens are referenced from or deposited in the following institutions:

- BRSMG: Geological Collections, Bristol Museum and Art Gallery; Bristol, UK (Deborah Hutchinson, debbie.hutchinson@bristol.gov.uk)
- CNU: Key Laboratory of Insect Evolution and Environmental Changes, Capital Normal University; Beijing, China (Dong Ren, 4989@cnu.edu.cn)
- FMNH: Field Museum of Natural History; Chicago, IL, USA (Julia Snyder, jsnyder@fieldmuseum.org)
- NIGP: Nanjing Institute of Geology and Palaeontology, CAS, Nanjing, China (Bo Wang, bowang@nigpas.ac.cn)
- NZAC: New Zealand Arthropod Collection; Auckland, NZ (Richard A.B. Leschen, leschenr@landcareresearch.co.nz)
- SYSBM: Sun Yat-sen University; Guangzhou, Guangdong, China (Hong Pang, lssh pang@mail.sysu.edu.cn)
- QUST: Qingdao University of Science and Technology; Qingdao, Shandong, China (Shuo Wang, shuowang@qust.edu.cn)

Amber was prepared using a razor table, polished with emery papers of different grain sizes, and finally lustrated with polishing powder.

Specimens were examined and photographed using one of the following microscopy regimes:

1. Leica M205C stereomicroscopes and Dun Ink BK PLUS Lab System (<http://www.duninc.com/bk-plus-lab-system.html>; accessed 11 Mar 2019) (ZL)
2. Bresser Advance ICD Zoom 63 stereomicroscope fitted with a Bresser Mikrocam PRO HDMI (Bresser GmbH, Germany) (ET)
3. Olympus SZX12 stereomicroscope and a Zeiss SteREO Discovery V.20 stereomicroscope with a Plan-Apochromat S 0.63x objective, a Plan-Apochromat S 1.5x objective, and an AxioCam HRC Rev. 3 digital camera (TCM)

SEM images were captured using a Leica 1450 EP Environmental Scanning Electron Microscope at Georgia Electron Microscopy (Barrow Hall, University of Georgia) by TCM. Line drawings were made using a camera lucida attachment to microscopy regime three (above), then scanned and digitally illustrated in Adobe Illustrator CS6 on a Wacom Intuos 5 Touch drawing tablet by TCM.

Source images were aligned and stacked in Zerene Stacker or Helicon Focus 6 and edited in Adobe Photoshop. Measurements were taken as follows: total length from anterior margin of clypeus to apex of elytra (TL); head width across the maximum width (including eyes) (HW); pronotal length (PL) along mid line from anterior to posterior margin; pronotal width (PW) across the maximum width; elytral length (EL) along suture, including scutellum; elytral width (EW) across the maximum width of elytra.

New taxonomic acts introduced herein have been registered in ZooBank with the electronic publication LSID: urn:lsid:zoo-bank.org:pub:71060BB7-81C2-47E9-A803-7964125FD8BB and new nomenclatural act LSIDs are listed under each new name.

3. Systematic paleontology

Order: Coleoptera Linnaeus, 1758
 Superfamily: Cucujoidea Latreille, 1802
 Family: Monotomidae Laporte, 1840
 Subfamily: Monotominae Laporte, 1840

Tribe Lenacini Crowson, 1952.

Type genus: *Lenax* Sharp, 1877:269.

Figs. 1–7.

Diagnosis. Lenacini can be diagnosed by the large impressions or grooves on the posterior portion of the head behind the eyes, moderately-widely separated procoxal cavities (~ 1 – 1.25 × length of procoxal cavities), moderately-broadly rounded abdominal process, and elytra with four raised ridges with puncture rows between.

Remarks. Previous diagnoses of Lenacini were based on misinterpretations of the tarsal formula. Initially, Crowson (1952) diagnosed Lenacinae based on the 5-5-5 tarsi in both sexes as opposed to 5-5-4 in males in Rhizophaginae, Europini, and Monotomini. However, males of extant *Lenax mirandus* are very rare in collections, at around a 75:1 female:male ratio (male secondary sexual characters and genitalia have never been described) (TCM, personal observation). However, a male found by TCM (NZAC) possesses 5-5-4 tarsi, and thus the tarsal formula cannot be used for diagnosis as it shares the same tarsal formula as all other described Monotomidae.

Genus *Lenax* Sharp, 1877.

Type species: *Lenax mirandus* Sharp, 1877:269 by monotypy.

Figs. 1–4

Diagnosis. *Lenax* can be separated from *Cretolenax* (see next section) by the possession of a 10-segmented antenna (truly 11-segmented with the 11th antennomere withdrawn partially into and fused with 10th) with a 1-segmented club (Figs. 2D, 3E) (2-segmented in *Cretolenax*).

Lenax karenae Liu, Tihelka, McElrath, and Yamamoto sp. nov.

LSID Zoobank: urn:lsid:zoo-bank.org:act:87462FC2-C89A-4FCA-8A8D-AAB4FED00F6C.

Figs. 3–4

Derivation of name. This species name is a feminine Latinized honorific for the corresponding author's wife, Karen McElrath, in appreciation of her devoted partnership. The specific epithet is a noun in the genitive case.

Type material. Holotype. FMNHINS-3966011 (FMNH). Paratypes. (CNU) No. CNU-COL-MA-0193, No. CNU-COL-MA-0387 (male), No. CNU-COL-MA-0401, No. CNU-COL-MA-446, No. CNU-COL-MA-0489, (BRSMG) CE9818-05.

Locality and horizon. Upper Albian–lower Cenomanian, Hukawng Valley, Kachin, Northern Myanmar

Diagnosis. This species resembles *Lenax mirandus* in body shape, punctuation, and modified head structures. But it can be easily recognized by much smaller size (less than 3 mm compared to 4–5 mm in *L. mirandus*), proportionally shorter prothorax and elytra, and dense and erect setae on temples.

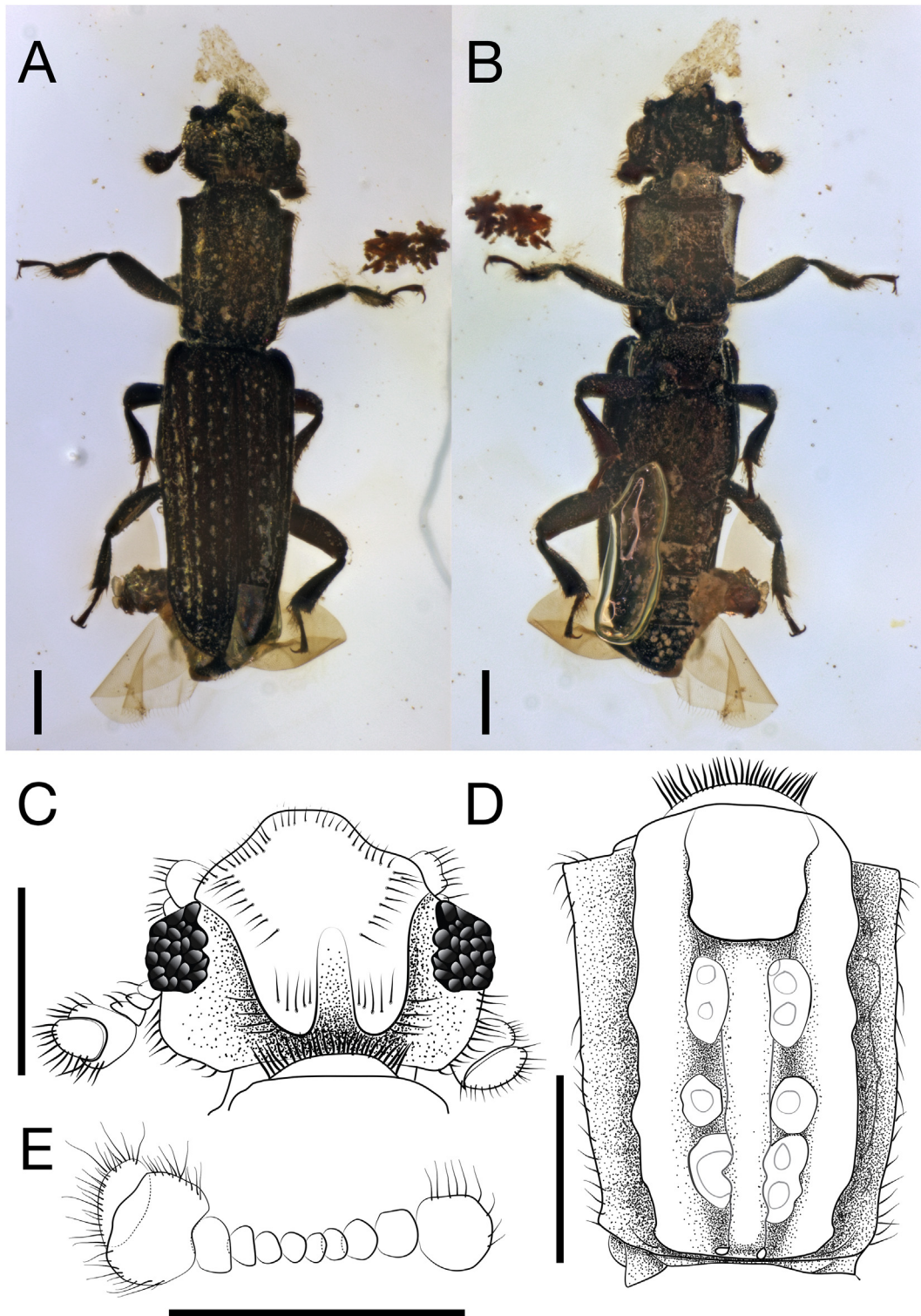


Fig. 3. *Lenax karenae* new species, female, holotype specimen FMNHINS-3966011 (Scale = 200 μ m) (A) Dorsal habitus photomicrograph; (B) Ventral habitus photomicrograph; (C) Dorsal head digital illustration; (D) Dorsal prothorax digital illustration; (E) Ventral antenna digital illustration.

Description.

Length 1.63–2.60 mm, width 0.42–0.52 mm, 3.7–4.0 times as long as wide. Body elongate-cylindrical, nearly parallel-sided.

Head weakly transverse, almost as broad as prothorax; dorsal surface covered with sparse short setae. Eyes relatively small, only

slightly protuberant and partially exposed from above. Frontoclypeal suture absent. Clypeus broadly rounded apically, labrum not visible dorsally. Mandibles short, concealed by clypeus. Antennae widely separated, closely inserted in front of eyes, insertions concealed from above. Antennae short, reaching posterior

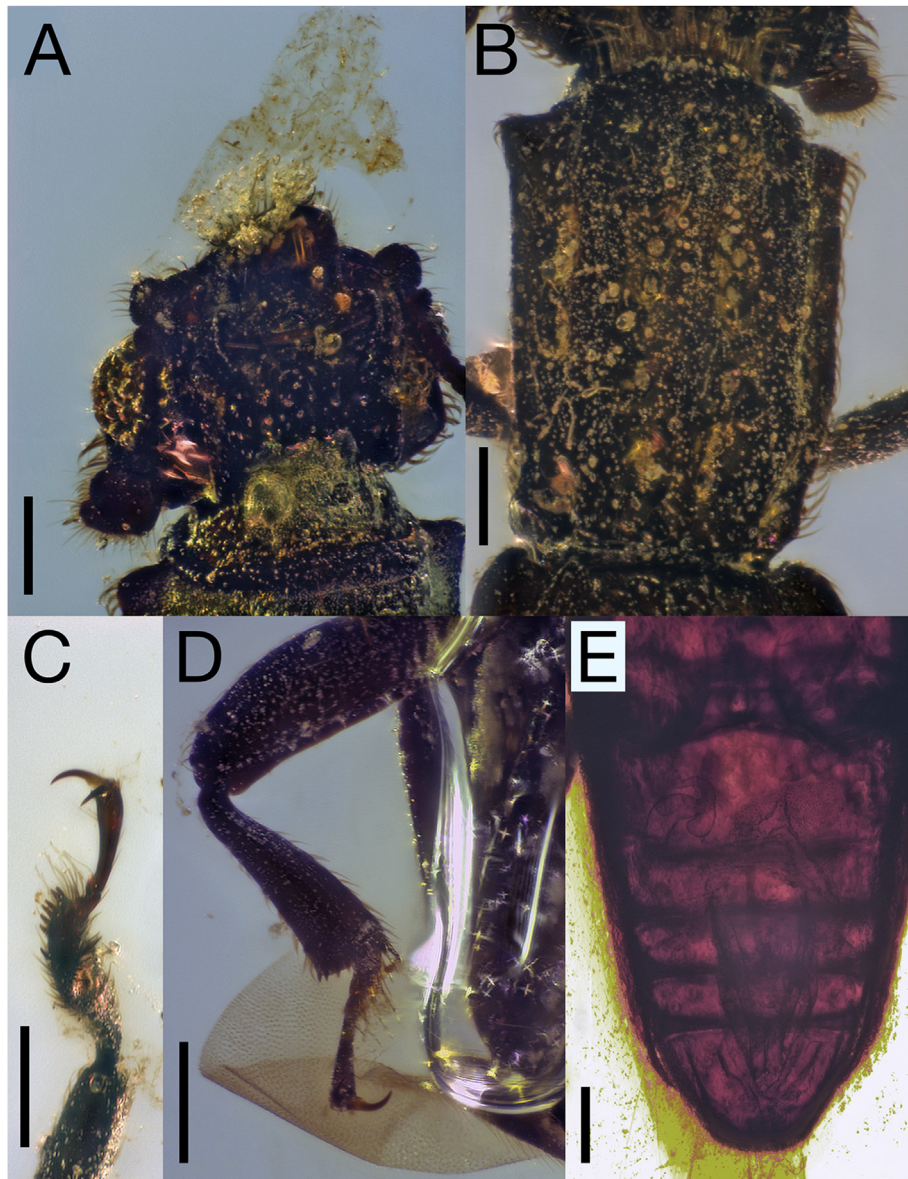


Fig. 4. *Lenax karenae* new species, female, details (Scale = 100 μ m). A–D) Holotype specimen FMNHINS-3966011; E) Paratype CNU-COL-MA-0193: (A) Ventral head close-up; (B) Dorsal pronotum; (C) Protibia and protarsus; (D) Metafemur, metatibia, and metatarsus; (E) Backlit abdomen showing spermatheca (visible under abdominal ventrite 1).

portion of head when extended backwards; appearing 10-segmented (truly 11-segmented) with abrupt, distinct apparently 1-segmented club (actually 2-segmented, with apical antennomere withdrawn into preapical), covered with dense short setae; scape enlarged, pedicel slightly enlarged, antennomeres 3–8 small, short, subequal, approximately half length and width of pedicel, gradually increasing in width, until antennomere 9–1.5x width of 3. Vertex with a pair of deep concavities next to eyes extending most of the length of the head, area between eyes distinctly elevated and with longitudinal depression at middle and deep transverse groove behind the elevation, so the middle of the head has two paramedian protuberances. Temples distinct, about 0.9 times as long as eyes, covered with dense and erect setae. Posterior edge of head with dense, elongate setation filling median area. Maxillary palps short, with 3 visible segments; first two palpomeres stout, the terminal palpomere slightly elongate and fusiform. Mentum possibly with pair of small ovoid

cavities. Ventral side with distinct and deep subantennal grooves along eyes, extending to the ventral side of temples. Pregular area trapezoidal, wider than long, sparsely setose and with sparse punctation.

Prothorax slightly elongate, about 1.1–1.3 times as long as wide, sub-rectangular, widest anteriorly, as wide as elytra at base; lateral margins carinate, nearly straight, very weakly narrowed posteriorly, with single row of elongate setae on edge. Anterior angles sub-acute and slightly produced laterally, but not anteriorly, posterior angles broadly obtusely angulate. Pronotal disc with a pair of elevated sublateral ridges, distinctly more elevated anteriorly, forming elevated median pronotal disc area, covered with short setae; medial disc between ridges with pair of series of deep punctures forming obscure, interrupted grooves, diverging anteriorly, forming slightly more elevated anterior protuberance. Prosternum and pronotum fused together, nototernal suture absent. Prosternum in front of coxae distinctly

longer than prosternal process. Prosternal process between coxae distinctly broader than procoxal cavities (approx. 1.7x as wide as coxal length), slightly depressed at middle, slightly expanded apically with apical margin nearly truncate. Procoxae circular with trochantins concealed, procoxal cavities externally closed.

Mesoventrite elongate and slightly convex; mesoventral process broad with apical margin truncate, slightly narrower than width of mesocoxal cavity. Mesocoxae rounded (approx. 1.5x longer than wide); mesocoxal cavities moderately separated (approx. 0.8x the coxal length), laterally closed. Metaventrite with short discrimen, sparse small punctures, evenly covered in fine erect setae, transverse suture present but curved in front of metacoxae. Metacoxae weakly transverse; metacoxal cavities widely separated, laterally open to elytra. Scutellum small, triangular with rounded, sub-acute apex, 1.7x longer than wide.

Elytra nearly parallel-sided, 2.0–2.2 times as long as wide, slightly expanded at about anterior third. Dorsal surface deeply punctured with five punctate striae visible on each elytron, three on elytral disc, two on inflexed portion of elytral epipleuron; interval areas slightly elevated, distance between about equal to puncture diameter; scutellary striole absent. Epipleura narrow, absent before apex. Short, sparse pubescence present at apical margin.

Pygidium with median longitudinal groove, apex extremely downturned, ventrally visible as thin strip of cuticle.

Legs with femora slightly dilated, larger and more dilated in pro- and meta-femora, tibiae distinctly expanded apically with several short spines along outer edges anteriorly; tarsi 5-5-5 in female, tarsomeres 1–4 small and short with distinct setae beneath, tarsomere 5 longer than the first 4 segments combined; tarsi 5-5-4 in male. Claws simple.

Abdomen with five ventrites in female, six in male; fifth ventrite sub-trapezoidal, ratio of the length of each ventrite about 2.8:1.0:1.0:0.9:1.9 [0.5 (male ventrite 6)], ventrites with large, closely approximate punctures. Intercoxal process broadly rounded-truncate anteriorly, with deep and small median concavity between metacoxae.

Genus **Cretolenax** Liu, Tihelka, McElrath and Yamamoto gen. nov.
Type species: *Cretolenax carinatus* Liu, Tihelka, McElrath and Yamamoto sp. nov.

LSID Zoobank: urn:lsid:zoobank.org:act:C21C1FA2-3AE4-4863-BADB-878E0F49CE1A.

Figs. 5–7

Derivation of name. The name *Cretolenax* is derived partly from the Greek stem of the word Cretaceous, in reference to the age of the fossils, and the already described, relict, genus *Lenax*. The name *Lenax* does not seem to be derived from any obvious Greek or Latin words. Other Latin words with the ending “ax” are generally treated as neutral gender. However, when Sharp described *Lenax*, the type species by monotypy, *L. mirandus*, had a specific epithet that is demonstrably a masculine Latin participle meaning “to be wondered or marveled at”. Thus, because *Lenax* is not easily demonstrable as male or neutral, we assert that *Cretolenax* to be a singular masculine noun to continue the prevailing usage of the root-name *Lenax*.

Diagnosis. *Cretolenax* strongly resembles *Lenax* in general body features and in possessing a strongly transverse head, ventrally bearing large and deep subantennal grooves extending behind eyes, as well as deep impressions along the inner edge of the eyes on dorsal side. However, it can be distinguished from *Lenax* by the antennal club being composed of the withdrawn 11th, 10th, and enlarged 9th antennomeres in *Cretolenax* (Fig. 6E, G) (only the

withdrawn 11th and 10th form the antennal club in *Lenax*) so that *Cretolenax* appears to possess a “two-segmented” club (while *Lenax* appears to only have a “one-segmented” club); sharper, more distinct ridges on pronotum and the elytra (smoother in *Lenax*) (Fig. 6F); coarser punctation and sculpturing on the ventral side; and the more slender tibiae that are less expanded apically compared to *Lenax*.

Description.

General Body elongate, semi-cylindrical, vestiture of short and curved setae. Length 2.25–2.40 mm, width 0.50–0.54 mm. Widest at basal half of elytra.

Head weakly transverse, slightly wider than prothorax. Eyes, small, not protuberant, slightly exposed from above, coarsely faceted. Antennae widely separated, closely inserted in front of eyes, insertions concealed. Frontoclypeal suture absent; clypeus with apical margin rounded; labrum invisible from above; mandibles short with apex bidentate, concealed by clypeus. Maxillary palp 4-segmented with basal three segments short, terminal palpomere more or less elongate and fusiform; labial palp 3-segmented, short; mentum with a pair of small ovate concavities. Antennae short, reaching to about posterior portion of head when posteriorly extended, appearing 10-segmented (truly 11-segmented) with distinct apparently 2-segmented club (truly 3-segmented), covered with dense short setae; scape enlarged, globular; pedicel slightly enlarged globular; antennomeres 3–7 small, short, subequal, approximately half length and width of pedicel, gradually increasing in width, until antennomere 8 is 1.25x width of antennomere 3, antennomere 9 as wide as 10. Head dorsally with deep impressions along inner edge of eyes on dorsal side. Temples distinct, longer than eyes from above, covered with dense and erect setae; vertex/frons slightly elevated at middle between eyes. Tempora pronounced. Head dorsal surface covered with sparse short setae. Ventral side with large, deep subantennal grooves below, extending behind eyes.

Prothorax longer than wide (PL/PW = 1.1–1.5), sub-rectangular with sides almost parallel, constricted for anterior 1/8th and posterior 1/8th, narrower than elytra basally. Pronotal disc with a pair of well-developed sub-lateral carinae and a narrow central carina, sub-lateral carinae bifurcated anteriorly, forming 2 small antero-lateral cells, central carina interrupted anteriorly in apical fourth, forming small central cavity; surface with scattered sparse short setae, lateral margins carinate, nearly straight, with short sparse pubescence on lateral margin. Pronotal hypomeron fused with prosternum, notosternal suture incomplete. Prosternum in front of procoxae distinctly longer than prosternal process. Prosternal process across procoxae much wider than procoxal cavities, apex broad with truncate apical margin. Procoxae rounded, procoxal cavities externally closed.

Meso- and metaventrites both finely and coarsely punctured, meso-metaventral junction simple (forming a straight line where they intersect). Mesoventral process along mesocoxae almost same width as mesocoxal cavities, apical margin truncate. Mesocoxae rounded, mesocoxal cavities laterally closed. Metaventrite with discrimen present, distinctly depressed along discrimen, transverse suture absent. Metacoxae slightly transverse; metacoxal cavities widely separated, laterally open to elytra. Scutellum small and sub-triangular.

Elytra elongate, widest basally, sides gradually narrowed posteriorly with apex sub-acute. Humeri sharp, tooth-like, oriented medially. Distance between punctures smaller than puncture diameter. Elytral disc deeply and coarsely punctate, forming three rows of striae punctures on dorsal side; four interstriae with longitudinal ridges bearing short, depressed setae. Epipleuron narrow and absent before the apex.

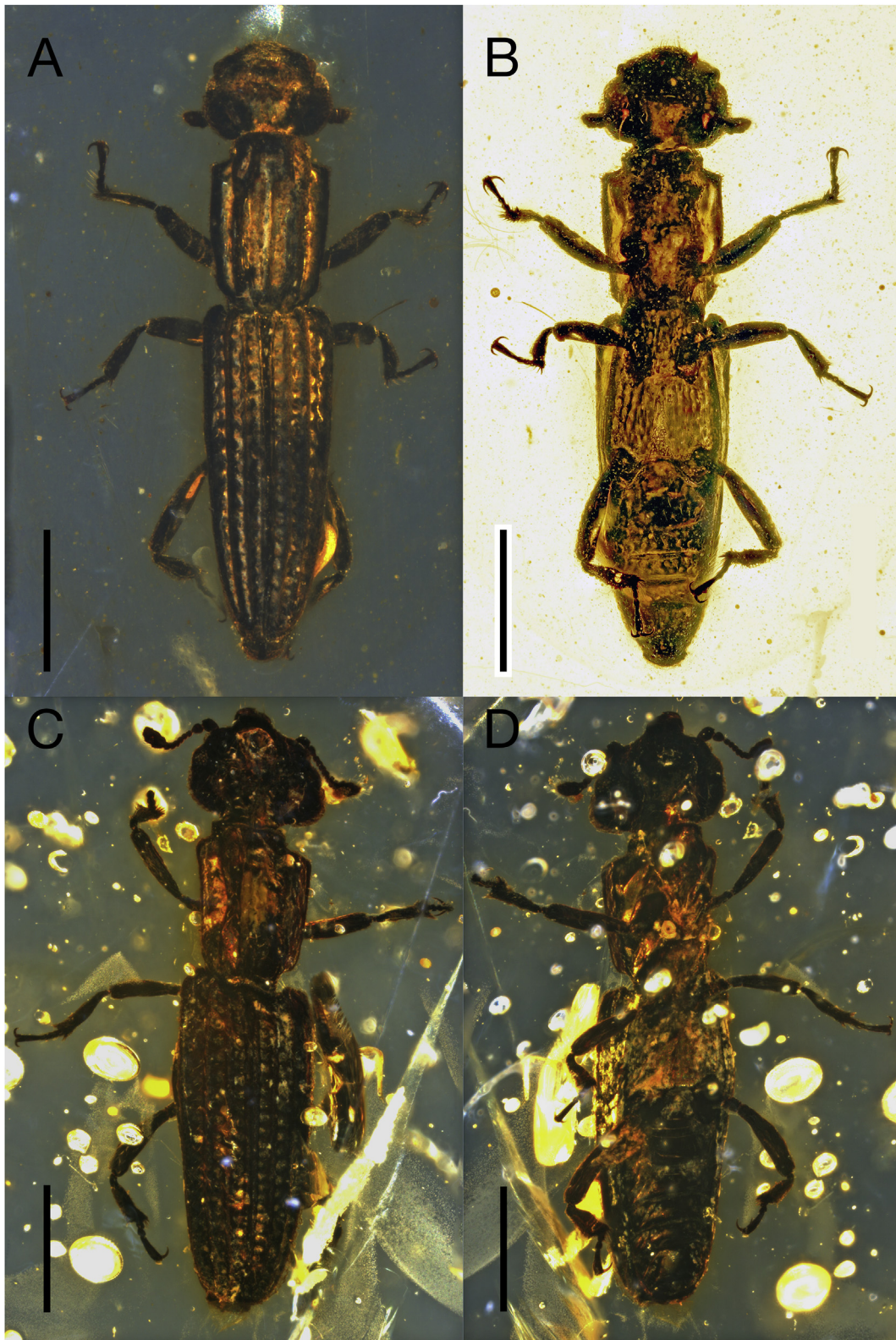


Fig. 5. *Cretolenax carinatus* new species. Female holotype NIGP171018 (Scale = 0.5 mm) (A) Dorsal and (B) Ventral habitus. Male paratype CNU-COL-MA-0447 (Scale = 0.5 mm), (C) Dorsal and (D) Ventral habitus.

Abdomen with five ventrites in female, six in male, coarsely punctured, narrowed posteriorly. Ventrite 1 elongate, as long as the next three ventrites combined, intercoxal process depressed at middle between metacoxae, broadly rounded apically;

ventrites 2–4 short, nearly equal in length, ratio of ventrites about 3.0:1:1:1:2.0 (0.75 male ventrite 6); ventrite 5 elongate, sub-trapezoidal. In male, ventrite 6 small, about half as wide as fifth.

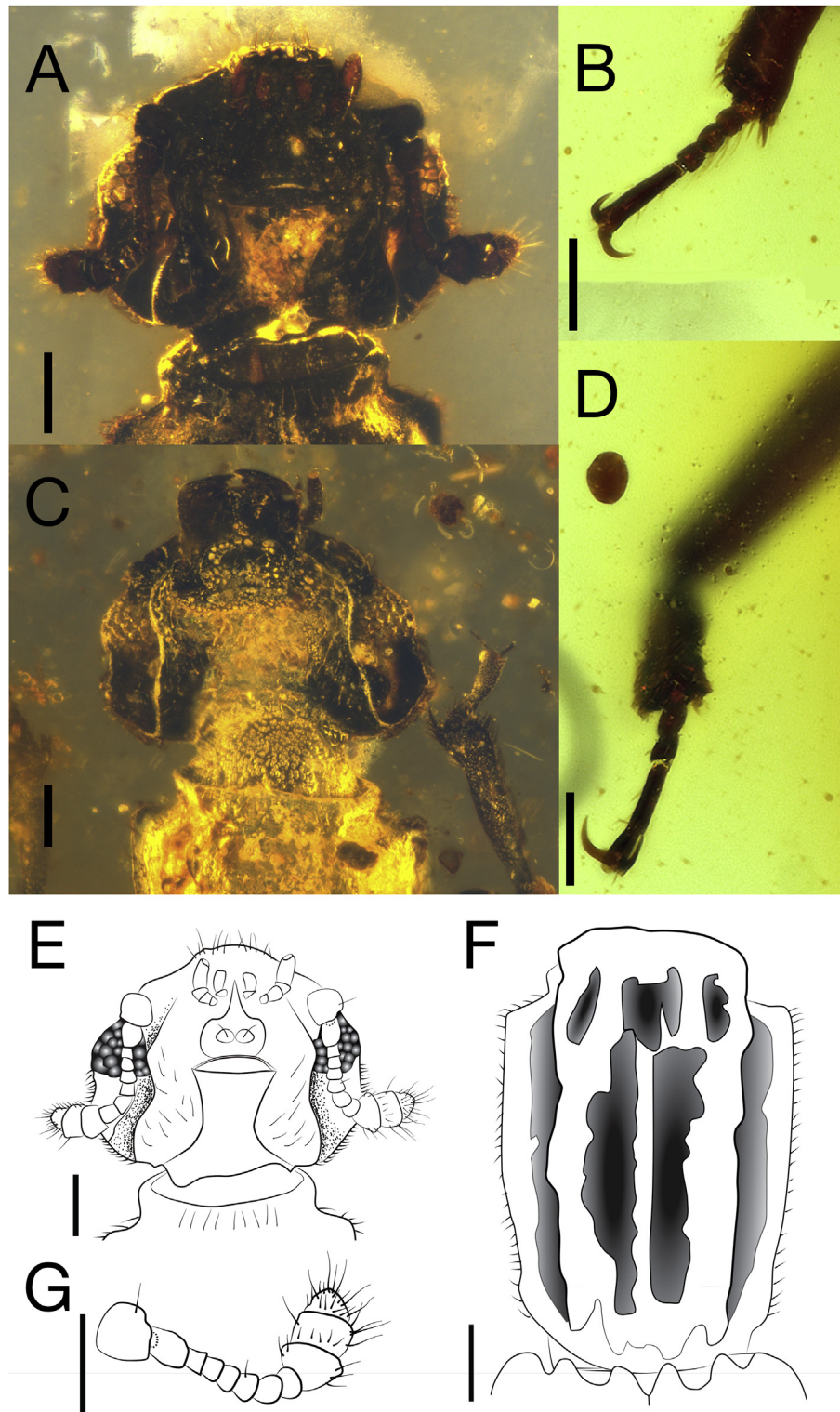


Fig. 6. *Cretolenax carinatus* new species (Scale = 100 μm) (A) Female ventral head close-up photomicrograph showing partially withdrawn antennae, holotype specimen NIGP171018; (B) Male mesotarsus, 5-segmented, specimen FMNH-3966015; (C) Female ventral head, antennae fully withdrawn into antennal cavity; specimen SYS-ENAM0008; (D) Male metatarsus, 4-segmented, specimen FMNH-3966015; (E) Female ventral head digital illustration, holotype specimen NIGP171018; (F) Dorsal pronotum digital illustration, holotype specimen NIGP171018; (G) Ventral antenna digital illustration, holotype specimen NIGP171018.

Legs with femora slightly dilated, pro- or mesofemur subequal in length and slightly shorter than metafemur; tibiae a little shorter and slightly expanded apically, mostly lacking short spines along outer edges, tibial apex with more elongate, clustered setae, with

pair of asymmetrical spurs; tarsi 5-5-5 in female and 5-5-4 in male, tarsomeres 1-4 (or 1-3 in male) short, subequal, equally pubescent. Terminal tarsomere longer than remaining tarsomeres combined. Claws simple.

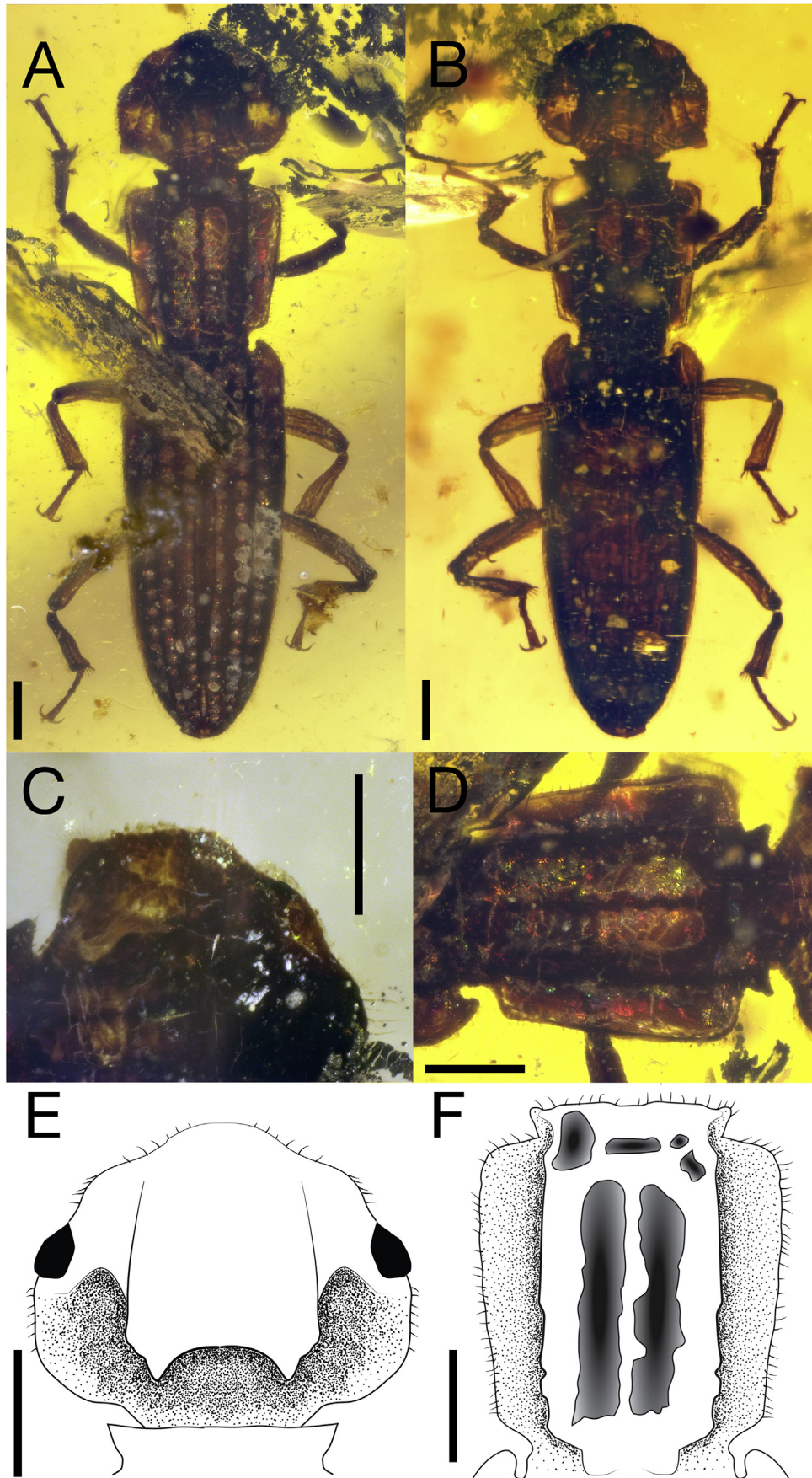


Fig. 7. *Cretolenax diabolus* new species female holotype (BRSMG) CE9818-07 (Scale = 200 μ m) (A) Dorsal habitus photomicrograph; (B) Ventral habitus photomicrograph; (C) Dorsal head close-up photomicrograph, showing antennae visible underneath through translucent cavity; (D) Dorsal pronotum close-up photomicrograph, showing characteristic "horns" and pronotal shape; (E) Dorsal head digital illustration; (F) Dorsal pronotum digital illustration.

Cretolenax carinatus Liu, Tihelka, McElrath, and Yamamoto sp. nov. LSID Zoobank: urn:lsid:zoobank.org:act:2ABA2A71-8D06-48B1-A94D-CBD7476A6F2E.

Figs. 5–6

Derivation of name. Name derived from the nominative singular masculine Latin adjective form of “carina”, referring to the numerous ridges and carinae on the pronotum and elytra of this species.

Type material. Holotype. (NIGP) NIGP171018. Paratypes. (FMNH) FMNHINS-3966012, (FMNH) FMNHINS-3966013, (FMNH) FMNHINS-3966014, (FMNH) FMNHINS-3966015 (male), (SYSBM) SYS-ENAM0008, (QUST) QUAT-INSECT-0004, (CNU) No. CNU-COL-MA-0403, No. CNU-COL-MA-0447.

Locality and horizon. Upper Albian–lower Cenomanian, Hukawng Valley, Kachin, Northern Myanmar.

Diagnosis. This species is very similar to *C. diabolus* except that it has a much longer pronotum relative to the pronotal width, and lacks the pointed pronotal angles of *C. diabolus*.

Description.

General. Length 2.27–2.32 mm, width 0.50–0.54 mm, 4.3–4.5 times as long as wide.

Head ~1.1 times as wide as widest point of pronotum. Temples ~1.7 times as long as eyes from above. Gena with two transverse sutures.

Prothorax ~1.5 times as long as wide, anteriorly narrowed section of pronotum ~0.7 times less wide at broadest point than maximal pronotum width, forming a 70° angle with pronotal lateral margin, with rounded, obtuse angles; posteriorly narrowed section portion of pronotum ~0.6 times wider than maximum pronotum width, forming an angle of 130° with pronotal lateral margin.

Meso- and metaventrites Metacoxal cavities wider than long, broadly rounded, ~1.5x times wider than long, distance between them ~1.0x times coxal width. Metaventrite with ellipsoidal, nearly contiguous punctures with associated longer setae forming wavy weak grooves except for median area crowded with more dense, smaller punctures extending just over half of posterior portion.

Elytra ~2.1–2.5 times as long as wide. Anterior lateral elytral humeri with obtuse, rounded angles that only project slightly from anterior elytral margin.

Abdomen with deep punctures on ventrites. Ventrite 1 with coarse punctures.

Legs short, femur widest medially, tibiae with two spurs, apical comb of setae absent. Protarsal segments 1–3 normal, short, equal, sparsely pubescent.

Cretolenax diabolus Tihelka, Liu, McElrath, and Yamamoto sp. nov. LSID Zoobank: urn:lsid:zoobank.org:act:86FCBDBC-AAFF-461E-B782-882F0779082F.

Fig. 7

Derivation of name. Nominative singular of the Latin “diabolus” (masculine), relating to or connoting with the devil, for the species’ characteristic horn-like pronotal neck angles and elytral humeri.

Type material. Holotype. (BRSMG) CE9818-07, female

Locality and horizon. Upper Albian–lower Cenomanian, Hukawng Valley, Kachin, Northern Myanmar.

Diagnosis. This species is very similar to *C. carinatus* except for the much shorter pronotum relative to the pronotum width, and the pointed, acute, horn-like pronotal neck angles.

Description.

General. Length 2.42 mm, width 0.55 mm, 4.4 times as long as wide.

Head ~1.1 times as wide as widest point of the pronotum, Temples ~1.8 times as long as eyes from above. Gena with two transverse sutures.

Prothorax ~1.1 times longer than wide; anteriorly narrowed section of pronotum ~0.6 times less wide at broadest point than

maximal pronotum width, forming a 70° angle with pronotal lateral margin, with projecting tooth or horn-like angles; posteriorly narrowed section portion of pronotum 0.5 times wider than maximum pronotum width, forming an angle of 101° with pronotal lateral margin. Procoxal cavities roughly elliptical, widest in their first third, distance between them ~1.7 times coxal length.

Meso- and metathorax Mesocoxal cavities difficult to observe in type specimen. Metacoxal cavities elliptical, rounded, ~1.6 times longer than wide, distance between them ~0.9 times coxal length.

Elytra ~2.4 times longer than wide. Anterior lateral elytral humeri with acute, rounded, horn or tooth-like projections, extending distinctly past anterior elytral margin.

Abdomen with deep punctures on ventrites. Ventrite 1 with three adjacent central pits.

Legs short, femur widest medially, tibiae with two spurs, apical comb of setae absent. Protarsal segments 1–3 apically emarginate, short, equal, sparsely pubescent.

Remarks. The deep pronotal grooves of the type specimen contain some particulate debris. This suggests that this fossil species also could potentially carry fungal spores like extant *Lenax* (see discussion below).

4. Discussion

4.1. Fossil Lenacini within the Monotomidae

The systematic placement of these Lenacini within Monotomidae is well supported by having a typical habitus, antennae appearing 10 segmented with a 1 or 2 segmented antennal club (with the true 11th-segment withdrawn into the true 10th), procoxal cavities broadly closed externally, one or two abdominal tergites exposed beyond the elytra, and possessing five abdominal ventrites (six in males) with the first and fifth ventrites each being longer than ventrites 2–4, which are subequal. Molecular data groups extant *Lenax* with other monotomids as well (Robertson et al., 2015).

These fossils of Lenacini also highlight morphological details of phylogenetic importance for Monotomidae as a whole. The clarification of the tarsal formula supports its status as a shared character for the entire family. Within the tribe, all Lenacini are now thought to possess two small cavities on the submentum, a presumed apomorphy. The presence of head cavities on both the dorsal and ventral sides is another presumed synapomorphy; other monotomids may possess antennal grooves, but none nearly as pronounced as Lenacini. The presence of deep pronotal grooves may not be an evolutionary novelty in Monotomidae, as they are also present in the genus *Crowsonius* (although the relationship between these genera is unclear). Both genera have members exhibiting a range of groove development, spanning from grooves that are more or less developed from loosely aligned punctures, all the way to deeply impressed grooves that nearly obliterate any smooth pronotal disc area. These grooves and united punctures may be used to commensally or symbiotically transfer microbiota (e.g. yeasts, other fungal spores) from microhabitat to microhabitat (see below). However, until a cladistic or molecular phylogenetic analysis is performed for this family, the closest relatives of Lenacini are only suppositions.

4.2. Palaeodiversity and Biogeography

The three monotomid fossil taxa described herein from mid-Cretaceous Burmese amber represent the oldest record of Austral-endemic Lenacini in the fossil record, showing the antiquity and long-term morphological stasis of this characteristic tribe. Together with *Cretakarenni birmanicus* Peris and Delclòs, 2015

(Monotominae: Cretakarenniini) from Burmese amber, these records indicate potentially high species and morphological diversity in a tropical forest in Myanmar during the mid-Cretaceous. These fossil records are also congruent with a hypothesis of the relatively older origin of Monotomidae among the cucujoid families, suggested by molecular data (Toussaint et al., 2017; Zhang et al., 2018), and by direct fossil evidence from the Middle Jurassic and Lower Cretaceous (Kirejtshuk et al., 2009; Kirejtshuk and Azar, 2013; Cai et al., 2015; Peris and Delclòs, 2015).

Though a few monotomids have been described from the Jurassic and Cretaceous fossil records, none of them were included in any extant genus. However, the *Lenax* and *Cretolenax* gen. nov. species described herein are quite similar to the extant *Lenax mirandus* in many characters, indicating the ancient origin of this now species-poor and narrowly distributed lineage. The occurrence of *Lenax* and a related genus in Burmese amber suggests an ancient connection between the amber producing West Burma Block (Broly et al., 2015; Poinar, 2018) and New Zealand. Traditionally, New Zealand has been suggested to be part of Gondwana (Sanmartin and Ronquist, 2004), and Myanmar has been suggested to form a part of Laurasia (Mitchell, 1993; Sevastjanova et al., 2016), or separated from an older Gondwana (Heine and Müller, 2005; Seton et al., 2012; Metcalfe, 2013, 2017). Recently, however, it has been suggested by biologists and geologists (Hall, 2012; Metcalfe, 2005 (Poinar, 2018); that the flora and fauna in Burmese amber provide evidence of the Gondwanan origin of at least the West Burma Block, as there are several taxa that have been found there (e.g. Dilleniaceae; Poinar and Chambers, 2018; Arachaeidae; Wood et al., 2013; Crocinae; Lu et al., 2019) that are otherwise restricted to Gondwanan areas. There are even several beetle examples known: e.g., the Neotropical *Lepicerus* (Lepiceridae; Kirejtshuk and Poinar, 2006; Jajoszyński et al., 2017; Poinar, 2018) and *Acalyptomerus* and *Sphaerotherax* (Clambidae; Cai et al., 2019). The recent discovery of another beetle endemic to New Zealand, *Cyclaxyra* (Cylaxyridae; Wu et al., 2018), in Burmese amber provides further evidence to this ancient association. Thus, both the discovery of the New Zealand endemic Cylaxyridae and Lenacini in Burmese amber provide more evidence to the Gondwanan origin of the West Burma Block. However, caution is warranted in postulating the Gondwanan origin of Burmese amber based on our results, because the general distributional patterns of organisms are frequently affected by later extinction and dispersal events. This means more evidence is required to assume the relictual Gondwanan distributions of extant Lenacini, as in discussed in Yamamoto et al. (2019). For example, the South American endemic Solieriinae rove beetles are now known from Lebanese, Spanish, and Burmese amber, each with a different geological background (Thayer et al., 2012; Peris et al., 2014). On the other hand, the fossil dragonfly genus *Araripegomphus*, which until recently was only known from the Lower Cretaceous Crato Formation in Brazil, was very recently discovered from Burmese amber (Zheng et al., 2018). Therefore, the recent separation of West Burma Block from Gondwana, possibly during the Lower Cretaceous (Poinar, 2018), has received increasing support in recent years.

4.3. Are the cuticular cavities of Lenacini mycangia?

Extant *Lenax mirandus* are saproxylic and found subcortically near or inside galleries made by pinhole borers or ambrosia beetles (Curculionidae: Platypodinae) (Milligan, 1979; Klimaszewski and Watt, 1997). The general morphology of fossil lenacines agrees well with extant *L. mirandus*, suggesting a presumably subcortical and possibly parasitic or commensal nature of Lenacini for nearly 100 million years. In *Cretolenax diabolus*, *C. carinatus*, and *L. mirandus*, the postocular cavities are so deep that when a

specimen of any of these species is viewed dorsally under high illumination, an outline of the antennae folded under the head is evident (Fig. 7C). *Cretolenax diabolus* also possesses three deep cavities on ventrite one. The same is true of the recent *L. mirandus*, albeit in this case only one cavity on ventrite one is present. Sen Gupta (1988) interpreted this cavity as a gland opening. However, Grebennikov and Leschen (2010) note both cavities of *L. mirandus* are often packed with debris and included these structures in their review of beetle mycangial structures; however, they concluded there was not enough evidence to claim this was a true mycangium. Spores of indeterminate fungi have been found in these cavities when viewed under ESEM (Fig. 2A). Fungal spores and hyphae of indeterminate Ascomycetes have been found in the guts of multiple *L. mirandus* females (McElrath, personal observation).

Taken together, these data suggest that lenacine lifecycles are intricately tied to fungi. However, this does not necessarily mean that the head, pronotal, and ventral pits and grooves are mycangia. Using the criteria of Grebennikov and Leschen (2010), the following points can be made regarding Lenacini: 1) they are associated with fungi in the adult stage (feed on fungus directly); 2) fungal spores have been observed in cuticular pits; 3) the pits have been investigated by scanning electron microscopy (SEM); 4) other reports of fungal transmission are known for monotomid beetles (albeit not directly linked to a mycangial structure) (Hinds, 1972); 5) direct biological observation and testing of these cavities has not been performed; and 6) the role of these structures as mycangia have been questioned, but not dismissed. Thus, Lenacini satisfy 3 or 4 of the criteria for possessing a true mycangium, rating either as “likely” or “not likely” on the Grebennikov and Leschen (2010) scale (depending on how strictly their criteria are interpreted). Structurally, the head cavities may simply serve as antennal grooves or receptacles when the beetles are navigating subcortically. However, this does not rule out the evolutionary “co-option” of these cavities as potential mycangial structures. Further investigations into the mycangial nature of the structures on extinct and extant lenacine monotomids, using tools like micro-CT or next-gen sequencing, could lead to novel evolutionary insights regarding monotomid evolution. The economic nature of *Lenax* fungal associations are as yet unknown, and may be important to the New Zealand timber industry.

5. Concluding remarks

Herein, one new genus and three new species of Monotomidae, *Lenax karenae*, *Cretolenax carinatus*, and *C. diabolus*, are described from mid-Cretaceous Burmese amber. These fossils are well-supported as members of the Lenacini within the Monotomidae, and provide essential information about the evolution of the extant members of the family. The only extant member of the genus *Lenax* is endemic to New Zealand, but the present fossils highlight that the Lenacini diversified by at least the mid-Cretaceous period. These fossils provide more evidence to the Gondwanan origin of the West Burma Block. Both fossil and extinct taxa may possess fungal transporting structures. When and if more amber specimens of this tribe are found in the future, they could shed more light on the evolution of insect-fungi associations.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2019.104255>.