Zootaxa 5082 (3): 223–244
https://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5082.3.2
http://zoobank.org/urn:lsid:zoobank.org:pub:EFB0E4A5-6B60-4B39-A651-1C6470FD7222

On the Nosodendridae from mid-Cretaceous amber of northern Myanmar (Coleoptera: Nosodendroidea)

YAN-DA LI[1,4], ERIK TIHELKA[1,2,5], LOÏC DAHAN[3,6], DI-YING HUANG[1,7] & CHEN-YANG CAI[1,2,8]*

[1]*State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, and Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, Nanjing 210008, China*
[2]*School of Earth Sciences, University of Bristol, Life Sciences Building, Tyndall Avenue, Bristol BS8 1TQ, UK*
[3]*O. D. Taxonomy and Phylogeny – Entomology, Royal Belgian Institute of Natural Sciences, Vautierstreet 29, B-1000 Brussels, Belgium*
[4] *ydli@pku.edu.cn; https://orcid.org/0000-0002-9439-202X*
[5] *wn20250@bristol.ac.uk; https://orcid.org/0000-0002-5048-5355*
[6] *loicdahan@hotmail.com; https://orcid.org/0000-0001-5680-0304*
[7] *dyhuang@nigpas.ac.cn; https://orcid.org/0000-0002-5637-4867*
[8] *cycai@nigpas.ac.cn; https://orcid.org/0000-0002-9283-8323*
**Corresponding author*

Abstract

Nosodendridae is a small polyphagan beetle family with a sparse fossil record. Herein, the fossil Nosodendridae from mid-Cretaceous Burmese amber (ca. 99 Ma) are systematically reviewed. *Nosodendron cretaceum* Deng *et al.* is transferred into *Archaenosodendron* Li & Cai **gen. nov.**, as *A. cretaceum* (Deng *et al.*) **comb. nov.**, primarily based on the morphology of prosternum. Three new species of *Archaenosodendron* from Burmese amber, *A. explanatum* Li & Cai **sp. nov.**, *A. remotidens* Li & Cai **sp. nov.**, and *A. angulare* Li & Cai **sp. nov.**, are also described and illustrated. A key to nosodendrid genera and species from Burmese amber is provided.

Key words: palaeodiversity, *Nosodendron*, fossil, Burmese amber, disparity

Introduction

Nosodendridae is a small beetle family with a high degree of morphological uniformity, represented by two genera and about 100 species in the extant fauna (e.g., Reichardt 1976; Háva 2003, 2019, 2021; Hisamatsu *et al.* 2011; Yoshitomi 2013a, 2013b; Yoshitomi *et al.* 2015). Recent molecular analyses have revealed that Nosodendridae occupies a relatively isolated position within the suborder Polyphaga, and represent the sole member of the recently recognized superfamily Nosodendroidea (Zhang *et al.* 2018; McKenna *et al.* 2019; Cai *et al.* 2021). Nosodendrid adults generally share a highly conserved morphology (Fig. 1), which has been well illustrated by Nomura & Kamezawa (2014) and Nomura (2015). Both adults and larvae are often found submerged in the sap exudations of wounded trees (Osborne & Kulhavy 1975; Kulhavy 1980), where they may feed on fungi by filtering (Yoshitomi 2015; Yoshitomi *et al.* 2015; but also see Hirota *et al.* 2020).

The fossil record of Nosodendridae is quite sparse. To date only three species have been described from the mid-Cretaceous Burmese amber, which show a strikingly higher morphological diversity compared to their extant relatives (Deng *et al.* 2019; Tihelka *et al.* 2021a 2021b). The current study aims to synthesize the taxonomy of fossil Nosodendridae by re-examining all published nosodendrid species from Burmese amber with confocal microscopy. As a result, the fossil *Nosodendron cretaceum* Deng *et al.* is transferred into a new genus, *Archaenosodendron* **gen. nov.** Three new species of *Archaenosodendron* from Burmese amber are also reported.

Accepted by Z.-W. Yin: 3 Dec. 2021; published: 17 Dec. 2021

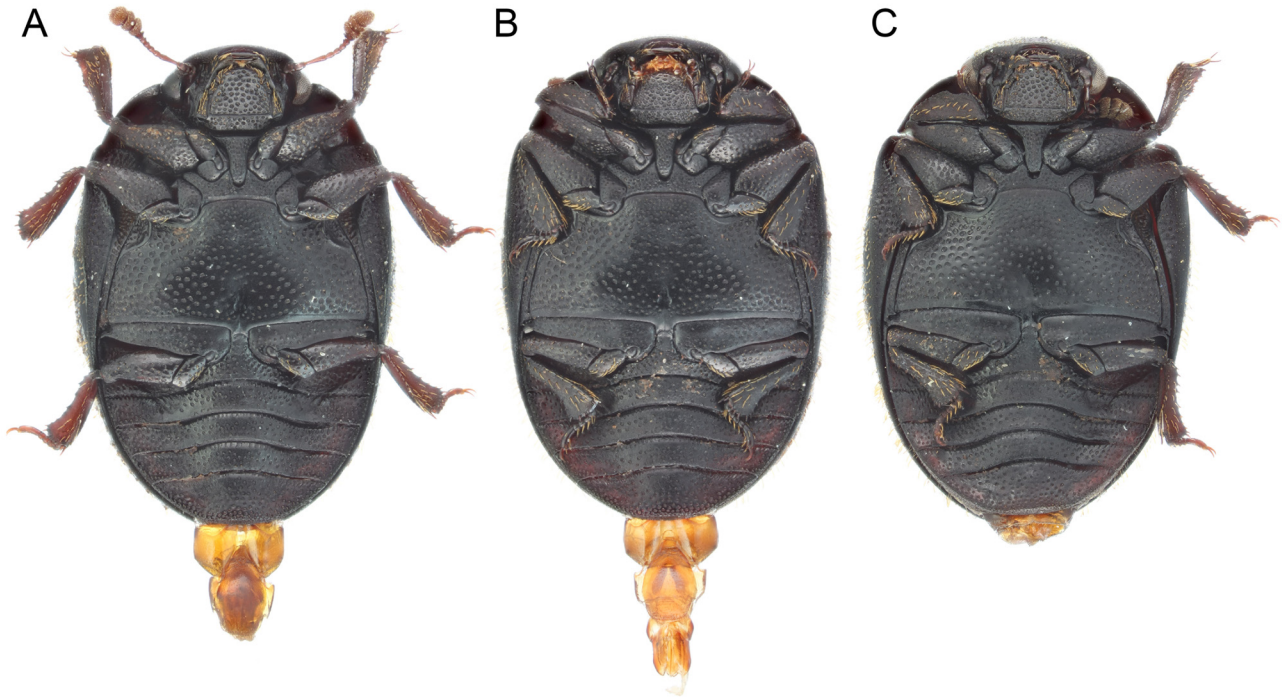

FIGURE 1. General habitus of extant *Nosodendron fasciculare* (Olivier), ventral view.

Materials and methods

The Burmese amber specimens studied herein (Figs 2–19) originated from amber mines near Noije Bum (26°20' N, 96°36' E), Hukawng Valley, Kachin State, northern Myanmar. The holotype of *Archaenosodendron cretaceum* (CNU-COL-MA-0321) is deposited in the Capital Normal University, Beijing, China. All other fossil specimens are deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China. The amber pieces were trimmed with a small table saw, ground with emery papers of different grit sizes, and finally polished with polishing powder.

The specimens of the extant *Nosodendron fasciculare* (Olivier) (Fig. 1) were collected by L.D. in Bois de Fa, Grez-Doiceau, Walloon Brabant, Belgium on 15 May 2020, using traps baited with red vinegar.

Photographs under incident light were mainly taken with a Zeiss Discovery V20 stereo microscope. Confocal images were obtained with a Zeiss LSM710 confocal laser scanning microscope, using the 488 nm Argon laser excitation line (Fu *et al.* 2021). 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 in Helicon Focus 7.0.2 and Adobe Photoshop CC. The holotype of *A. explanatum* was also imaged using high-resolution X-ray microtomography (Zeiss Xradia 520 Versa) at the micro-CT laboratory of NIGP. Scanning parameters were as follows: isotropic voxel size, 4.4634 μm; power, 3 W; acceleration voltage, 40 kV; exposure time, 4 s; projections, 2501. The tomographic data were analyzed using VGStudio MAX 3.0. Images were further processed in Adobe Photoshop CC to enhance contrast.

The morphological terminology follows Lawrence and Ślipiński (2013). The measurements of body length were taken as the apparent distance from mandibular apex to elytral apex in dorsal view. These measurements are affected by the conformation of the beetle body (whether curved or fully stretched), and therefore should only be regarded as rough approximations (Yoshitomi 2016).

Systematic paleontology

Order Coleoptera Linnaeus, 1758
Suborder Polyphaga Emery, 1886

Superfamily Nosodendroidea Erichson, 1846

Family Nosodendridae Erichson, 1846

Key to extant and extinct genera of family Nosodendridae (modified from Tihelka *et al.* 2021a)

1. Prosternum in front coxae extremely shortened, shorter than the half length of prosternal process; lateral portions of prosternum separated from the medial portion by a complete boundary, distinctly lowered for the reception of protrochanters and -femora (Fig. 1) **2**

- Prosternum in front coxae not extremely shortened, longer than the half length of prosternal process; lateral and medial portions of prosternum never separated by a complete boundary (Figs 4C, 8D, 11D, 12D, 18D) **3**

2. Loose antennal club consisting of three segments. Body length 4.0–10.0 mm . . . . . ***Nosodendron* Latreille**

- Compact antennal club consisting of two segments, with the basalmost antennomere strongly transverse. Body length typically 2.3–2.8 mm . . . . . ***Nosoglobulus* Háva**

3. Tarsomeres 2–4 wide, distinctly lobed ventrally (Fig. 18G–I). . . . . ***Mesonosa* Tihelka *et al.***

- Tarsomeres 2–4 slender, not distinctly lobed ventrally (Figs 4G–K, 8I, 11H–I, 14G–I, 16F) **4**

4. Body large, longer than 10 mm. Antennal grooves on prosternum complete (figs 1B, 4A in Tihelka *et al.* 2021a) . . . . . ***Basinosa* Tihelka *et al.***

- Body smaller, shorter than 5 mm. Antennal grooves on prosternum incomplete (Figs 8D, 11D) . . . . . ***Archaenosodendron* Li & Cai gen. nov.**

Genus *Archaenosodendron* Li & Cai gen. nov.

Type species. *Nosodendron cretaceum* Deng, Zhou, Ślipiński, Ren & Pang, 2018

Etymology. The generic name is composed of "*Archae-*", ancient, and "*Nosodendron*". The name is neuter in gender.

Diagnosis. Body elongated oval, generally less than 5 mm long. Eyes not strongly protuberant. Prosternum in front coxae not extremely shortened, longer than half length of prosternal process, with incomplete antennal grooves. Protibia expanded apically; outer edge of protibia with one row of distinct denticles. Tarsomeres slender, not distinctly lobed.

Remarks. Deng *et al.* (2019) originally placed *N. cretaceum* in the extant genus *Nosodendron*, since the species differs from the only other extant genus, *Nosoglobulus*, in having a larger body and relatively loosely articulated antennal club. They additionally noted that *N. cretaceum* differs from both of the extant subgenera in *Nosodendron* in the combination of several characters. Recently, we discovered several additional species related to *N. cretaceum* from Burmese amber. Based on the examination of the new materials, as well as the holotype of *N. cretaceum*, we suggest that the difference between this fossil group and extant *Nosodendron* is large enough to justify a new genus, which is herein designated as *Archaenosodendron*.

In extant *Nosodendron* (and *Nosoglobulus*), the prosternum in front of coxae is extremely shortened, while in *Archaenosodendron* the prosternum is relatively long. More importantly, in extant *Nosodendron*, the lateral portions of prosternum are clearly delimited and are distinctly lower compared to the medial portion (raised mesal shelf; fig. 4B in Nomura & Kamezawa 2014), so that when in repose the fore legs can fold compactly and the protrochanters and profemora could lay exactly on the lowered lateral portions of prosternum. In *Archaenosodendron*, although the lateral portions of prosternum might be somewhat lowered, there is no clear and complete boundary between the lateral and medial portions, and the protrochanters and profemora are unlikely to be able to lay compactly against the prosternum.

Key to species of *Archaenosodendron*

1. Mentum with somewhat longitudinally arranged larger punctures along the lateral margins and smaller punctures in the medial (anteromedial) region (Fig. 8B) . . . . . ***A. explanatum* Li & Cai sp. nov.**

- Punctures on the mentum not forming the pattern above. **2**

2. Outer edge of protibia with about 14–16 relatively sparsely arranged denticles/stout setae, with the apical two distinctly stouter and more closely situated (Fig. 11G). Medial and lateral portions of prosternum not clearly separated (Fig. 11D). . . . . ***A. remotidens* Li & Cai sp. nov.**

- Outer edge of protibia with more denticles/stout setae; the apical two not forming the pattern above. Medial and lateral portions of prosternum separated by an incomplete ridge (Figs 4C, 14D). **3**

3. Outer edge of protibia with about 30 densely arranged denticles (Fig. 4G–J). Mentum with anterior angles not obviously produced (Fig. 4A). . . . . ***A. cretaceum* (Deng *et al.*)**

- Outer edge of protibia with about 20 denticles/stout setae (Fig. 14F–H). Mentum with anterior angles pointed anterolaterally (Fig. 14B) . . . . . ***A. angulare* Li & Cai sp. nov.**

Archaenosodendron cretaceum (Deng, Zhou, Ślipiński, Ren & Pang, 2018) comb. nov.

(Figs 2–4)

Nosodendron cretaceum Deng, Zhou, Ślipiński, Ren & Pang 2018: 212

Material examined. Holotype, CNU-COL-MA-0321.

Diagnosis. Medial antennomeres about as long as wide (Fig. 4B). Lateral regions of mentum without longitudinally arranged larger punctures (Fig. 4A). Anterior angles of mentum not obviously produced (Fig. 4A). Antennal grooves on prosternum about as long as half-length of prosternum in front of coxae. Outer edge of protibia with about 30 densely arranged denticles (Fig. 4G–J). Medial and lateral portions of prosternum separated by an incomplete ridge (Fig. 4C).

Remarks. Extant nosodendrids exhibit a high degree of morphological uniformity. Differences between different congeners are often very minute (e.g., Háva 2019). As we show below, some *Archaenosodendron* species are also very similar to each other, which makes it difficult to determine the differences under a normal stereo microscope. As we did not have a chance to check the paratype of *A. cretaceum* (deposited in a private collection) personally, we are not sure if the holotype and the paratype represent the same species or not.

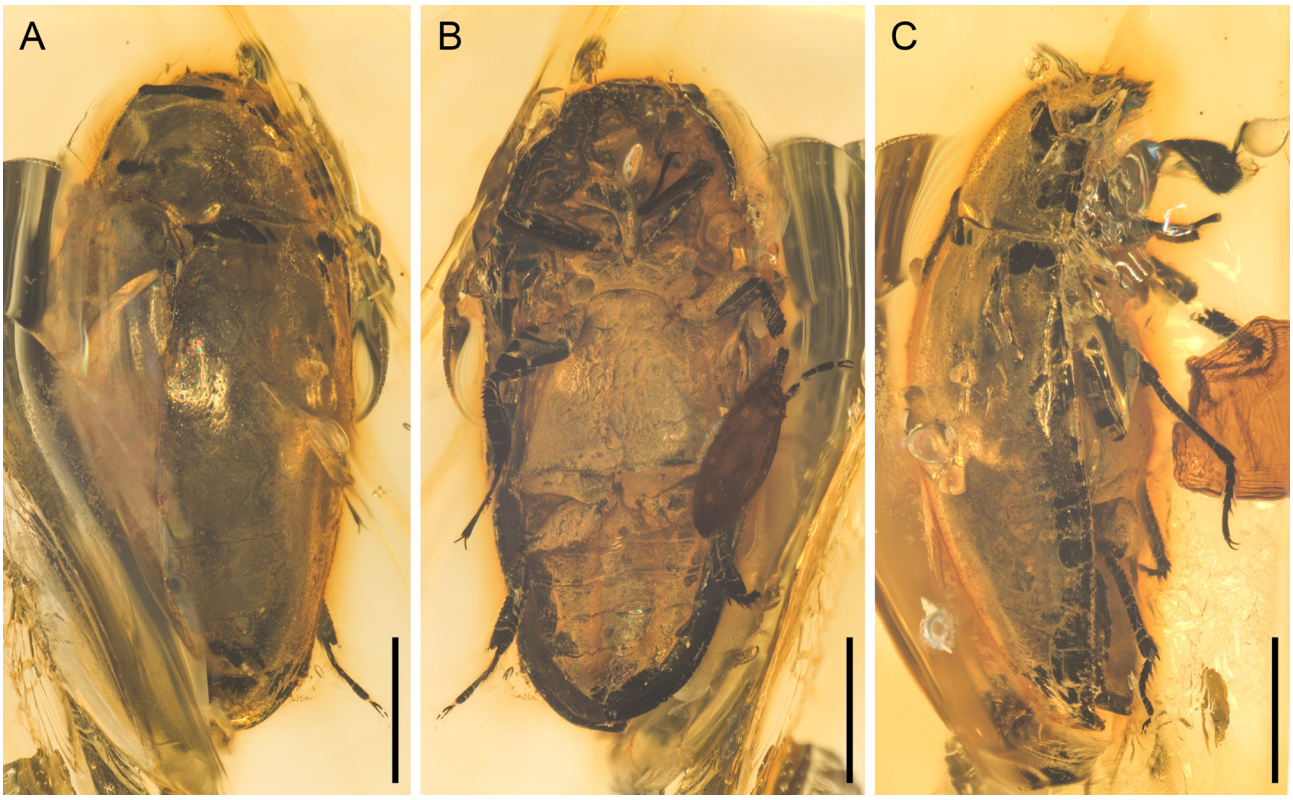

FIGURE 2. General habitus of *Archaenosodendron cretaceum* (Deng *et al.*, 2018) **comb. nov.**, holotype, CNU-COL-MA-0321, under incident light. **A**, Dorsal view. **B**, Ventral view. **C**, Lateral view. Scale bars: 1 mm.

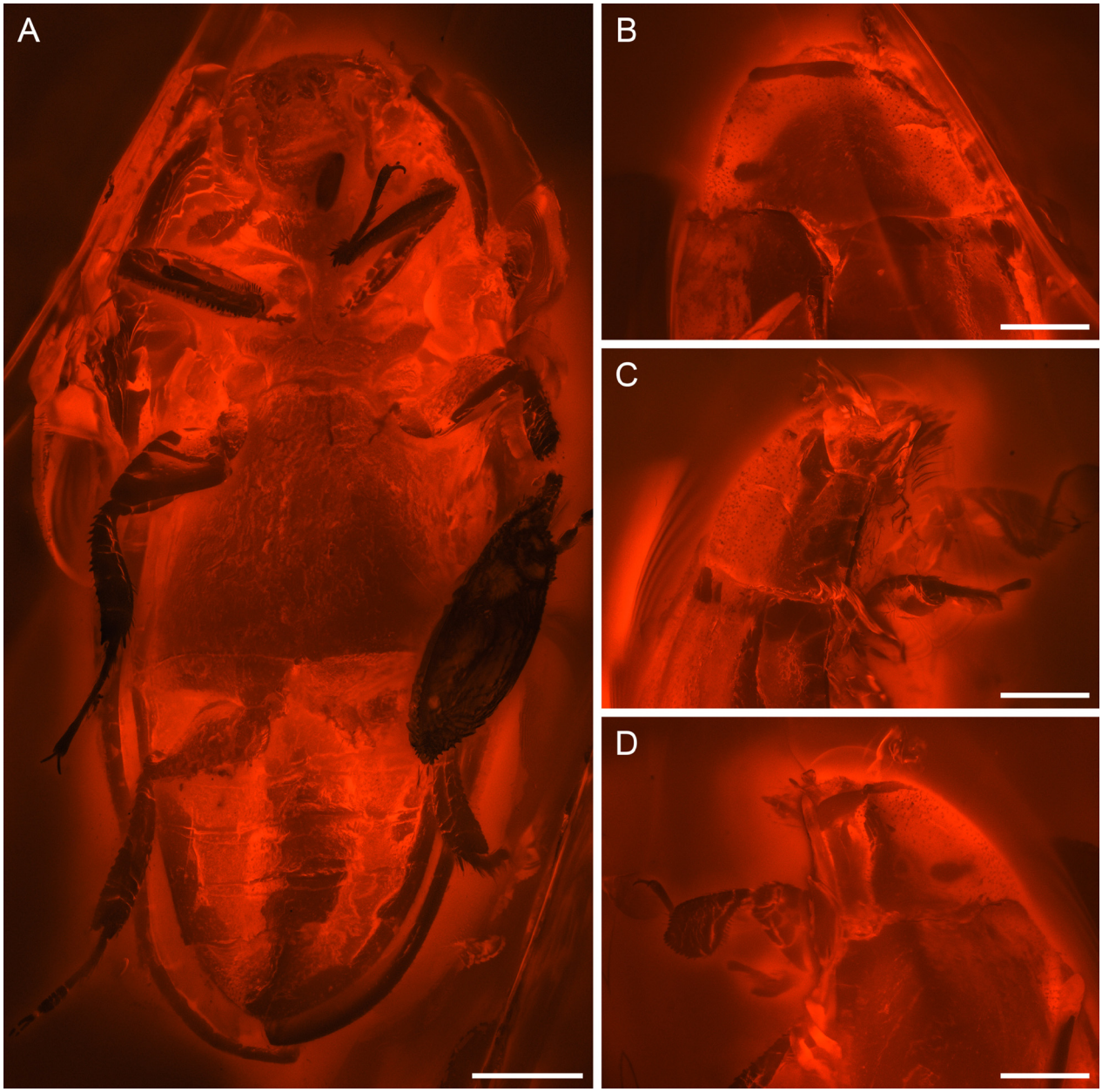

FIGURE 3. *Archaenosodendron cretaceum* (Deng *et al.*, 2018) **comb. nov.**, holotype, CNU-COL-MA-0321, under widefield fluorescence. **A**, Ventral view. **B**, Prothorax, dorsal view. **C**, **D**, Prothorax, lateral view. Scale bars: 500 μm.

Archaenosodendron explanatum Li & Cai sp. nov.

(Figs 5–8)

Material. Holotype, NIGP177613. The specimen seems to have been damaged before entrapment in amber, with many appendages (mouthparts, antennae, and tarsi) detached and head outstretched.

Etymology. The specific name refers to its flattened body.

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

Diagnosis. Body flattened and relatively elongate (Fig. 7). Lateral regions of mentum with somewhat longitudinally arranged larger punctures (Fig. 8B). Anterior angles of mentum produced anteriorly (Fig. 8B). Antennal grooves on prosternum longer than half-length of prosternum in front of coxae (Fig. 8D). Outer edge of protibia with about 21–23 denticles/stout setae (Fig. 8E–G). Medial and lateral portions of prosternum not separated by a ridge (Fig. 8D).

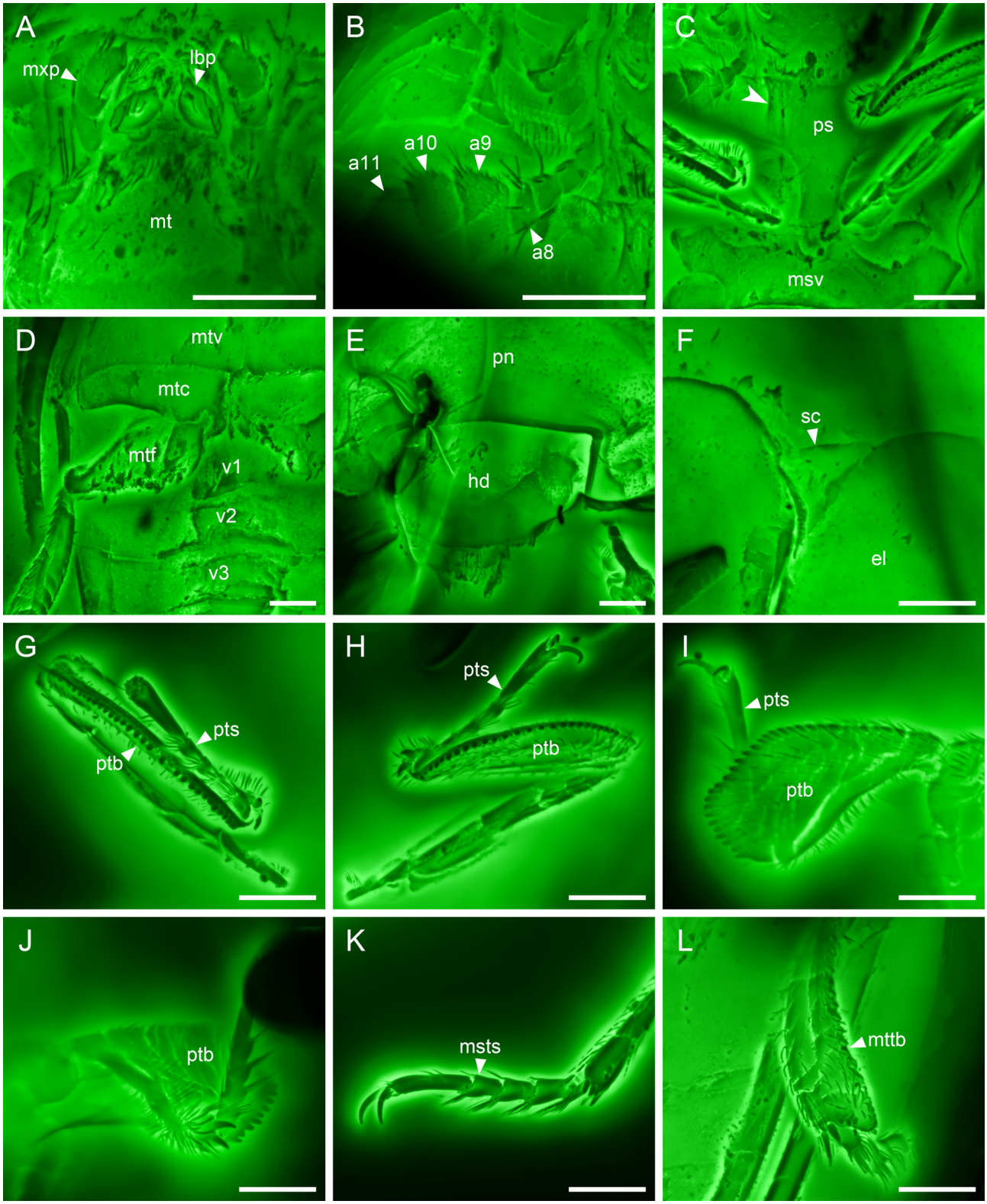

FIGURE 4. Details of *Archaenosodendron cretaceum* (Deng *et al.*, 2018) **comb. nov.**, holotype, CNU-COL-MA-0321, under confocal microscopy. **A**, Mouthparts, ventral view. **B**, Antenna, ventral view. **C**, Prothorax, ventral view, showing the incomplete boundary between the lateral medial portions of prosternum (arrowhead). **D**, Abdominal base, ventral view. **E**, Head, anterodorsal view. **F**, Scutellar shield, dorsal view. **G–J**, Fore legs. **K**, Mesotarsus. **L**, Metatibia. Abbreviations: an8–11, antennomeres 8–11; el, elytron; hd, head; lbp, labial palp; msts, mesotarsus; msv, mesoventrite; mt, mentum; mtc, metacoxa; mtf, metafemur; mttb, metatibia; mtv, metaventrite; mxp, maxillary palp; pn, pronotum; ps, prosternum; ptb, protibia; pts, protarsus; sc, scutellum; v1–3, ventrites 1–3. Scale bars: 200 μm.

FIGURE 5. General habitus of *Archaenosodendron explanatum* Li & Cai **sp. nov.**, holotype, NIGP177613, under incident light. **A**, Dorsal view. **B**, Ventral view. Scale bars: 1 mm.

Description. Body flattened and relatively elongate, about 3.67 mm long, 1.4 mm wide.

Head prognathous. Eyes not strongly protuberant. Antennal insertions widely separated and concealed from above. Antennal grooves on head well developed. Frontoclypeal suture absent. Mandibles broad, unidentate. Maxillae with setose lacinia (galea and palp detached). Mentum subtrapezoidal, widest at base; lateral regions with somewhat longitudinally arranged larger punctures; anterior angles produced anteriorly.

Pronotal disc subtrapezoidal, widest at base; anterior margin with very shallow emarginations laterally, slightly protruding medially. Prosternum in front coxae transverse, not extremely shortened; medial and lateral portions of prosternum not separated by a ridge; antennal grooves on prosternum longer than half-length of prosternum in front of coxae; prosternal process relatively slender. Procoxae strongly transverse, well separated. Procoxal cavities broadly open posteriorly.

Scutellar shield triangular, posteriorly acute. Elytra elongate, subparallel in the anterior half, tapering apically; anterior corners almost right. Mesoventrite short, anteriorly with well-developed mesoventral cavity and procoxal

rests. Mesocoxal cavities widely separated. Metaventrite transverse, flattened; anterolateral portion with curved line delimiting the impression. Metacoxae narrowly separated.

Femora with groove for receiving tibia. Tibiae expanded distally, with two apical spurs; outer edge of protibia with about 21–23 denticles/stout setae.

Abdomen with five ventrites. Ventrites 1 and 2 with a pair of impressions for receiving hind legs. Anterior margin of ventrites smooth, without notches.

FIGURE 6. General habitus of *Archaenosodendron explanatum* Li & Cai **sp. nov.**, holotype, NIGP177613, under widefield fluorescence. **A**, Dorsal view. **B**, Ventral view. Scale bars: 1 mm.

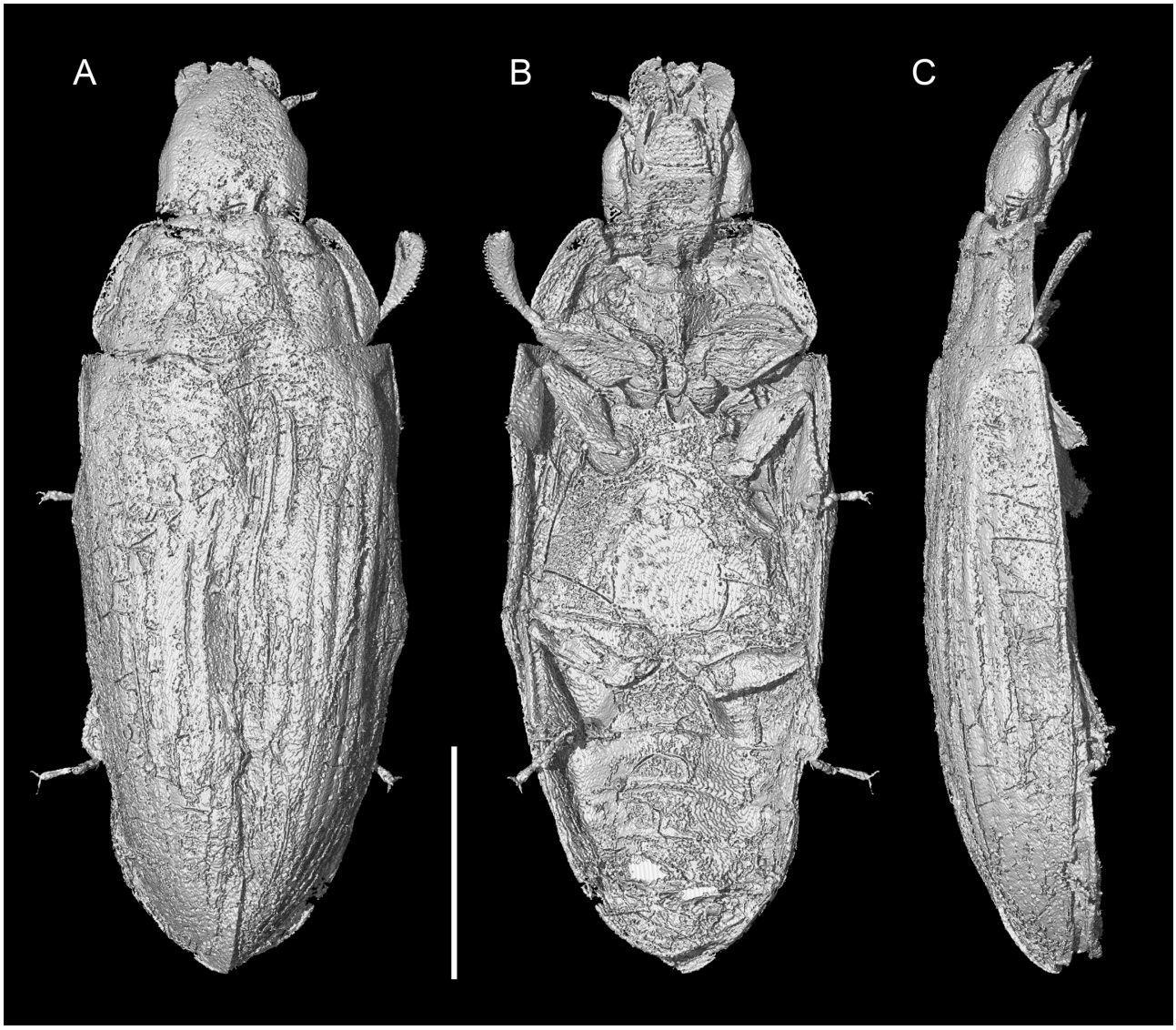

FIGURE 7. X-ray microtomographic reconstruction of *Archaenosodendron explanatum* Li & Cai **sp. nov.**, holotype, NIGP177613. **A**, Dorsal view. **B**, Ventral view. **C**, Lateral view. Scale bar: 1 mm.

Archaenosodendron remotidens Li & Cai sp. nov.

(Figs 9–11)

Material. Holotype, NIGP177614.

Etymology. The specific name refers to the relatively sparsely arranged denticles/stout setae on the outer edge of its protibia.

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

Diagnosis. Medial antennomeres longer than wide (Fig. 11C). Lateral regions of mentum without longitudinally arranged larger punctures (Fig. 11B). Anterior angles of mentum not obviously produced (Fig. 11B). Antennal grooves on prosternum shorter than half-length of prosternum in front of coxae (Fig. 11D). Outer edge of protibia with about 14–16 relatively sparsely arranged denticles/stout setae, with the apical two distinctly stouter and more closely situated (Fig. 11G). Medial and lateral portions of prosternum not separated by a ridge (Fig. 11D).

Description. Body elongated oval, about 3.6 mm long, 1.8 mm wide.

Head prognathous. Eyes not strongly protuberant. Antennal insertions widely separated and concealed from above. Antennal grooves on head well developed. Frontoclypeal suture absent. Antennae 11-segmented; antenno-

mere 2 about twice as long as wide; antennomere 3 about as long as but slender than 2; antennomeres 3–8 progressively shorter and wider; antennomeres 9–11 enlarged, forming a relatively loose club. Mandibles broad, unidentate. Maxilla with setose galea and lacinia; maxillary palps 4-segmented; palpomeres 1 and 4 longer than 2 and 3. Mentum with lateral edges subparallel in the basal half, then converging anteriorly; surface without clearly visible punctures; anterior angles not produced. Apical labial palpomere seemingly enlarged.

Pronotal disc subtrapezoidal, widest at base; anterior margin with shallow emarginations laterally, slightly protruding medially. Prosternum in front coxae transverse, not extremely shortened; medial and lateral portions of prosternum not separated by a ridge; antennal grooves on prosternum shorter than half-length of prosternum in front of coxae; prosternal process relatively slender. Procoxae strongly transverse, well separated. Procoxal cavities broadly open posteriorly.

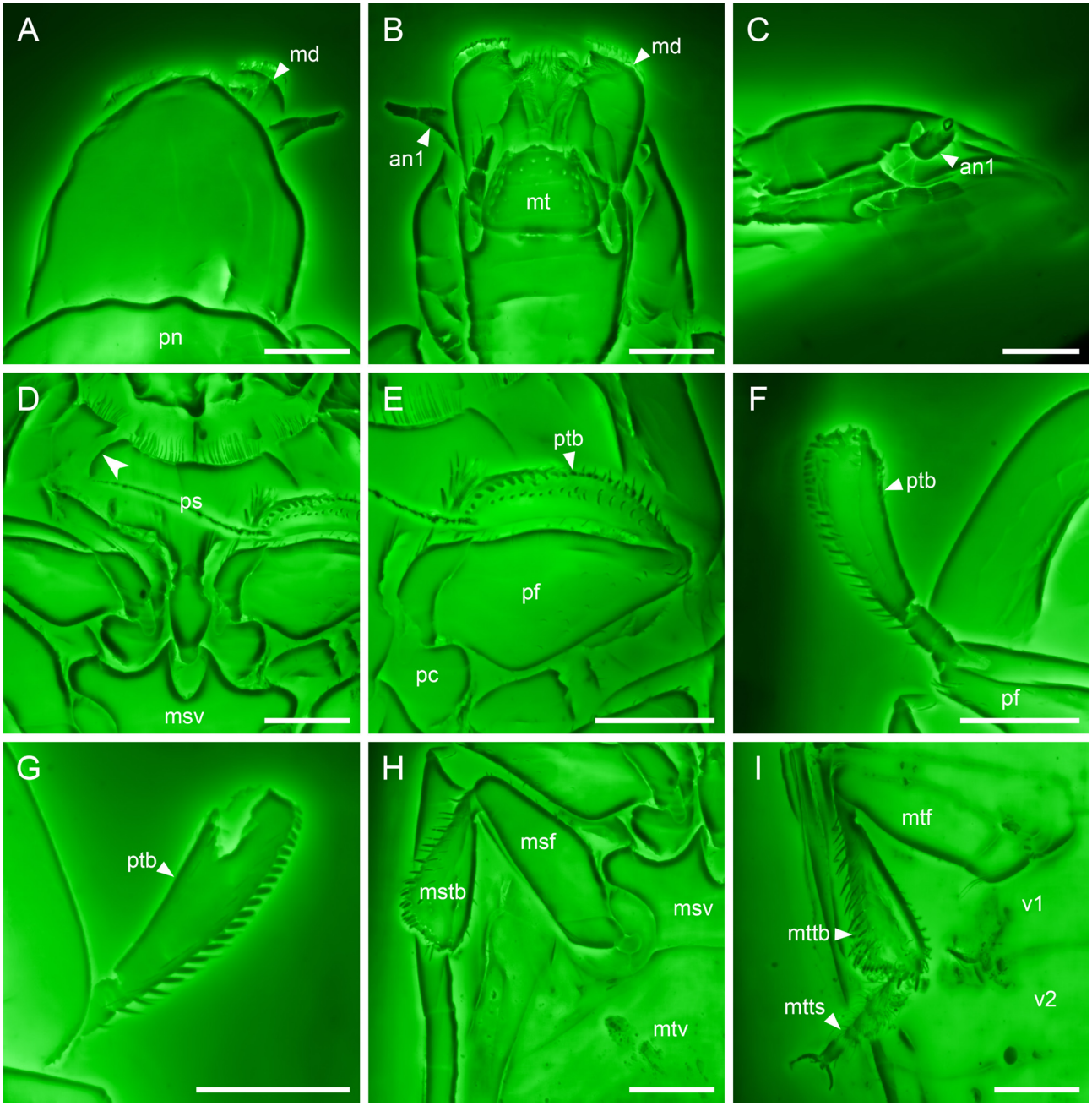

FIGURE 8. Details of *Archaenosodendron explanatum* Li & Cai **sp. nov.**, holotype, NIGP177613, under confocal microscopy. **A**, Head, dorsal view. **B**, Head, ventral view. **C**, Head, lateral view. **D**, Prothorax, ventral view, showing the incomplete antennal groove on prosternum. **E**–**G**, Fore legs. **H**, Mid leg. **I**, Hind leg. Abbreviations: an1, antennomere 1; md, mandible; msv, mesoventrite; mt, mentum; mtf, metafemur; mttb, metatibia; mtts, metatarsus; mtv, metaventrite; pc, procoxa; pf, profemur; pn, pronotum; ps, prosternum; ptb, protibia; v1,2, ventrites 1,2. Scale bars: 200 μm.

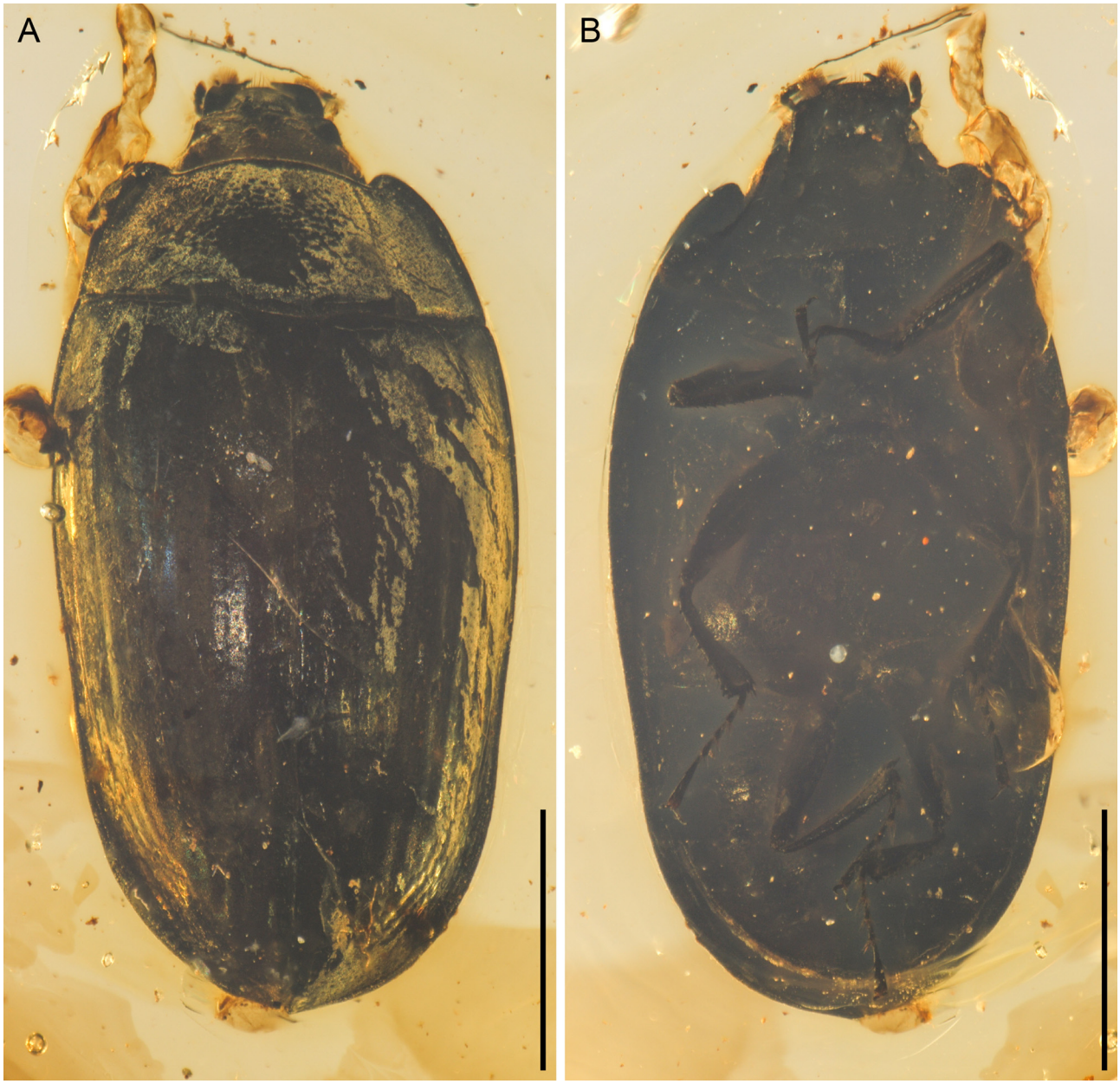

FIGURE 9. General habitus of *Archaenosodendron remotidens* Li & Cai **sp. nov.**, holotype, NIGP177614, under incident light. **A**, Dorsal view. **B**, Ventral view. Scale bars: 1 mm.

Scutellar shield triangular, posteriorly acute. Elytra widest at anterior third; anterior corners weakly obtuse. Mesoventrite short, anteriorly with well-developed mesoventral cavity and procoxal rests. Mesocoxal cavities widely separated. Metaventrite transverse, flattened. Metacoxae narrowly separated.

Femora with groove for receiving tibia. Tibiae expanded distally, with two apical spurs; outer edge of protibia with relatively sparsely arranged denticles/stout setae, with the apical two distinctly stouter and more closely situated. Tarsi 5-5-5; tarsomeres slender, not distinctly lobed; tarsomeres 1–4 ventrally with a cluster of long hairs at apex. Pretarsal claws simple.

Abdomen with five ventrites. Ventrites 1 and 2 with a pair of impressions for receiving hind legs. Anterior margin of ventrites smooth, without notches.

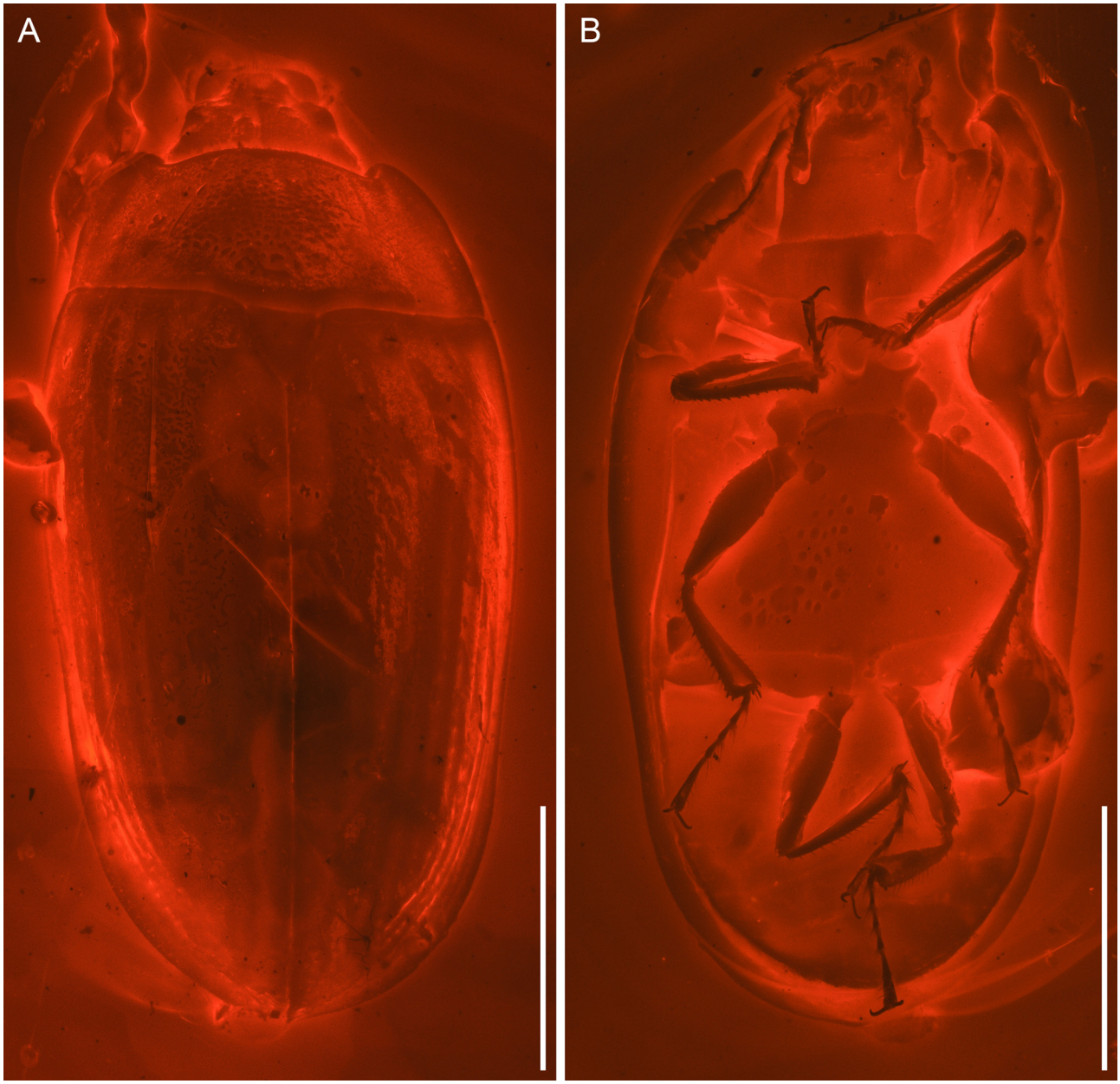

FIGURE 10. General habitus of *Archaenosodendron remotidens* Li & Cai **sp. nov.**, holotype, NIGP177614, under widefield fluorescence. **A**, Dorsal view. **B**, Ventral view. Scale bars: 1 mm.

Archaenosodendron angulare Li & Cai sp. nov.

(Figs 12–14)

Material. Holotype, NIGP177615.

Etymology. The specific name refers to anterolaterally produced anterior angles of mentum.

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

Diagnosis. Medial antennomeres slightly longer than wide (Fig. 14C). Lateral regions of mentum without longitudinally arranged larger punctures (Fig. 14B). Anterior angles of mentum produced anterolaterally (Fig. 14B). Outer edge of protibia with about 20 denticles/stout setae (Fig. 14F–H). Medial and lateral portions of prosternum separated by an incomplete ridge (Fig. 14D).

Description. Body elongated oval, about 3.1 mm long, 1.4 mm wide.

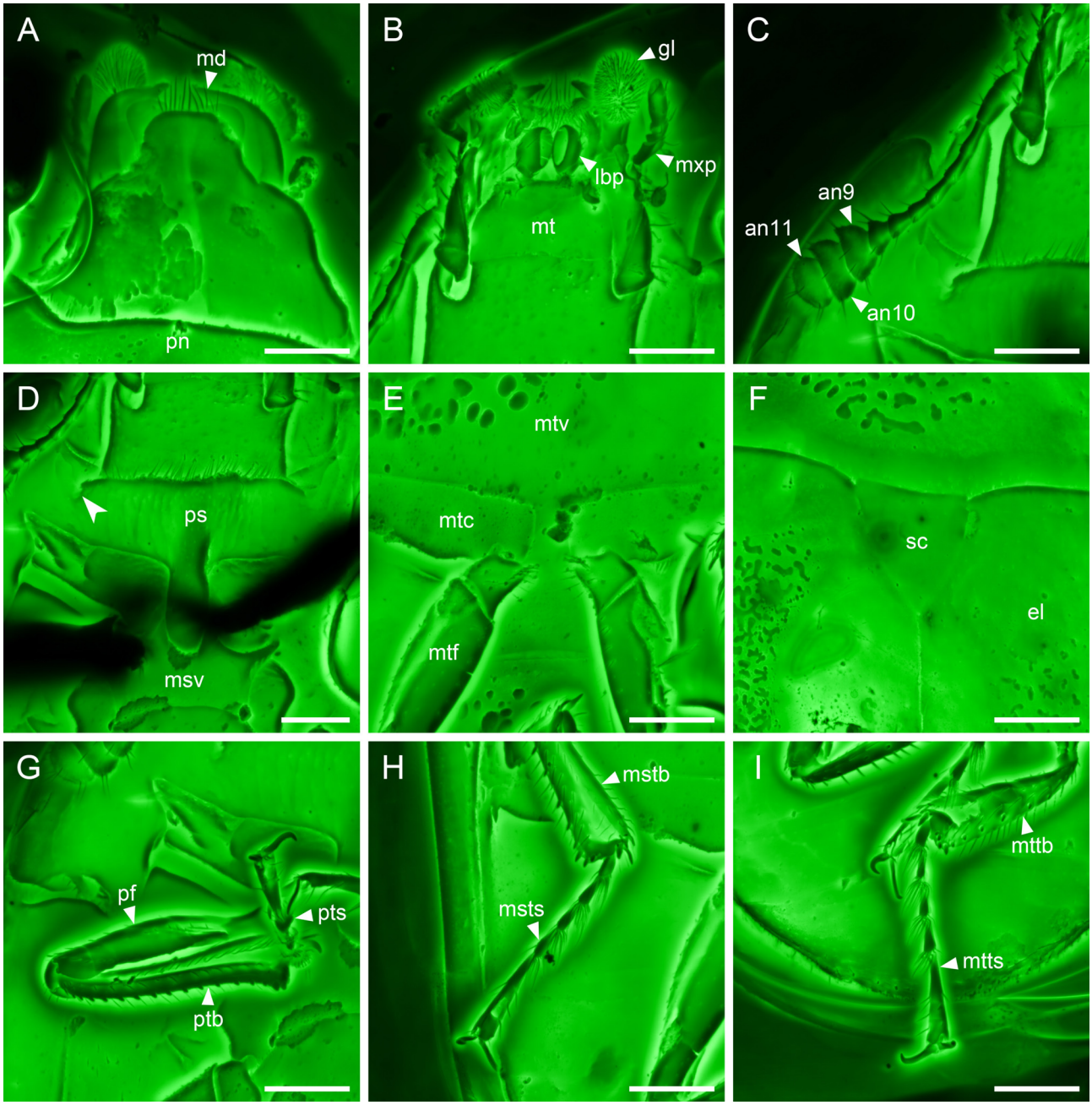

FIGURE 11. Details of *Archaenosodendron remotidens* Li & Cai **sp. nov.**, holotype, NIGP177614, under confocal microscopy. **A**, Head, dorsal view. **B**, Mouthparts, ventral view. **C**, Antenna, ventral view. **D**, Prothorax, ventral view, showing the incomplete antennal groove on prosternum (arrowhead). **E**, Abdominal base, ventral view. **F**, Scutellar shield, dorsal view. **G**, Fore leg. **H**, Mesotibia and -tarsus. **I**, Metatibia and -tarsus. Abbreviations: an9–11, antennomeres 9–11; el, elytron; gl, galea; lbp, labial palp; md, mandible; mstb, mesotibia; msts, mesotarsus; msv, mesoventrite; mt, mentum; mtc, metacoxa; mtf, metafemur; mttb, metatibia; mtts, metatarsus; mtv, metaventrite; mxp, maxillary palp; pf, profemur; pn, pronotum; ps, prosternum; ptb, protibia; pts, protarsus; sc, scutellum. Scale bars: 200 μm.

Head prognathous. Eyes not strongly protuberant. Antennal insertions widely separated and concealed from above. Antennal grooves on head well developed. Frontoclypeal suture absent. Antennae 11-segmented; antennomeres 3–8 progressively shorter and wider; antennomeres 9–11 enlarged, forming a relatively loose club. Mandibles unidentate. Maxillary palps 4-segmented; palpomere 4 longer than others. Mentum with lateral edges subparallel in the basal third, then converging anteriorly; surface with similar-sized punctures in lateral and anterior portions; anterior angles produced anterolaterally. Ligula bilobed. Apical labial palpomere seemingly enlarged.

FIGURE 12. General habitus of *Archaenosodendron angulare* Li & Cai **sp. nov.**, holotype, NIGP177615, under incident light. **A**, Dorsal view. **B**, Ventral view. Scale bars: 1 mm.

Pronotal disc subtrapezoidal, widest at base; anterior margin with shallow emarginations laterally, slightly protruding medially. Prosternum in front coxae transverse, not extremely shortened; medial and lateral portions of prosternum separated by an incomplete ridge; prosternal process relatively slender. Procoxae strongly transverse, well separated. Procoxal cavities broadly open posteriorly.

Scutellar shield triangular, posteriorly acute. Elytra widest at anterior third; anterior corners weakly obtuse. Mesoventrite short, anteriorly with well-developed mesoventral cavity and procoxal rests. Mesocoxal cavities widely separated. Metaventrite transverse, flattened; anterolateral portion with curved line delimiting the impression. Metacoxae narrowly separated.

Femora with groove for receiving tibia. Tibiae expanded distally, with two apical spurs; outer edge of protibia with about 20 denticles/stout setae. Tarsi 5-5-5; tarsomeres slender, not distinctly lobed; tarsomeres 1–4 ventrally with a cluster of long hairs at apex. Pretarsal claws simple.

Genus *Basinosa* Tihelka, Huang & Cai, 2020

(Figs 15, 16)

Type species. *Basinosa pengweii* Tihelka, Huang & Cai, 2020.

Material examined. Holotype of *B. pengweii*, NIGP173119.

Remarks. The amber piece containing the holotype of *B. pengweii* is somewhat nontransparent, making it difficult to determine many of the characters using normal optical methods. Partly due to tomographic artefacts, some

characters were not clearly visualized in previous micro-CT reconstructions. For example, one of the key diagnostic characters for Nosodendridae, the 11-segmented antenna with 3-segmented club, could not be observed in Tihelka *et al.* (2021a), although other diagnostic characters could be confirmed.

Here we reexamine the original CT data for the holotype of *B. pengweii*. It turns out that the majority of the beetle body has high absorption (white), while the antennae (especially the left one) appear to have lower absorption (black) (Fig. 16A). Therefore, the antennae were not properly reconstructed in the simple reconstruction, where only regions with a density higher than a selected threshold were extracted. Confocal microscopy confirms the 3-segmented club of *B. pengweii* (Fig. 16C). Since the strong laser could penetrate the somewhat opaque amber matrix better, and out-of-focus light is blocked, the confocal microscope could image this material much better than widefield ones (Fu *et al.* 2021). The medial antennomeres of *B. pengweii* appears to be relative elongate (Fig. 16B), while in extant *Nosodendron* the medial antennomeres are almost as long as wide. Confocal microscopy additionally reveals that the prosternal process (Fig. 16E) is not as slender as shown in the CT reconstruction by Tihelka *et al.* (2021a), which was subsequently adopted as one of the characters differentiating *Basinosa* from *Mesonosa* (Tihelka *et al.* 2020b). Detecting the boundaries of structures under CT is a challenging task (Coleman & Colbert 2007); the boundaries between the beetle and the amber matrix are not clearly defined, but are instead represented by a continuum of transitional values. Thus, a different selection of the threshold value for extraction could sometimes greatly affect the visual appearance.

The 3-segmented antennal club, together with the previously shown subantennal groove, wide metaventrite, clearly delimited anterolateral depression of metaventrite for the reception of mesotibial apex and basal mesotarsomeres, and narrowly separated metacoxae (all present in extant Nosodendridae and fossil Nosodendridae from the Burmese amber; fig. 23C in Ge *et al.* 2007), further confirm the placement of *Basinosa* in Nosodendridae. *Basinosa* is unique in Nosodendridae in having a relatively large body and complete antennal grooves on prosternum.

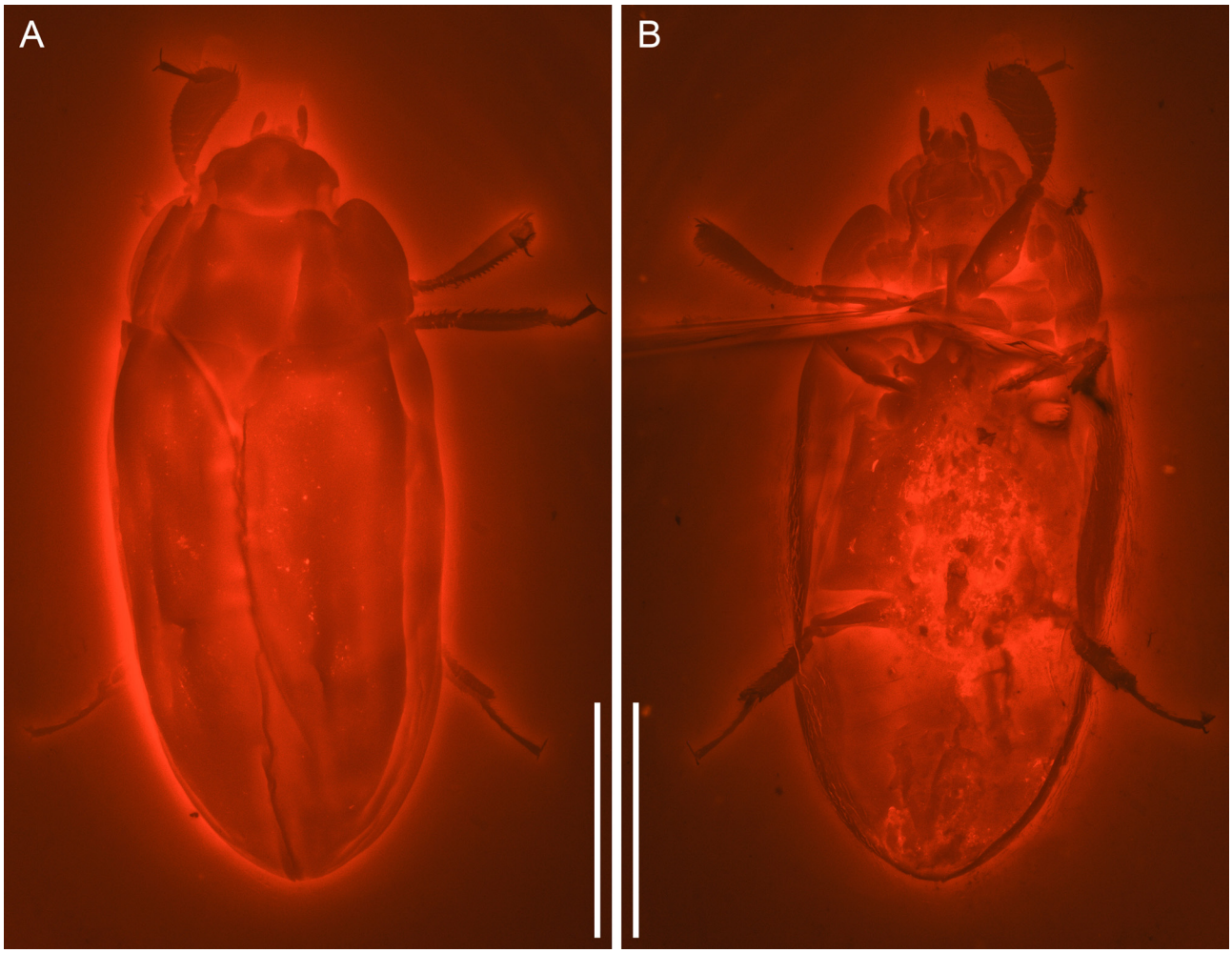

FIGURE 13. General habitus of *Archaenosodendron angulare* Li & Cai **sp. nov.**, holotype, NIGP177615, under widefield fluorescence. **A**, Dorsal view. **B**, Ventral view. Scale bars: 1 mm.

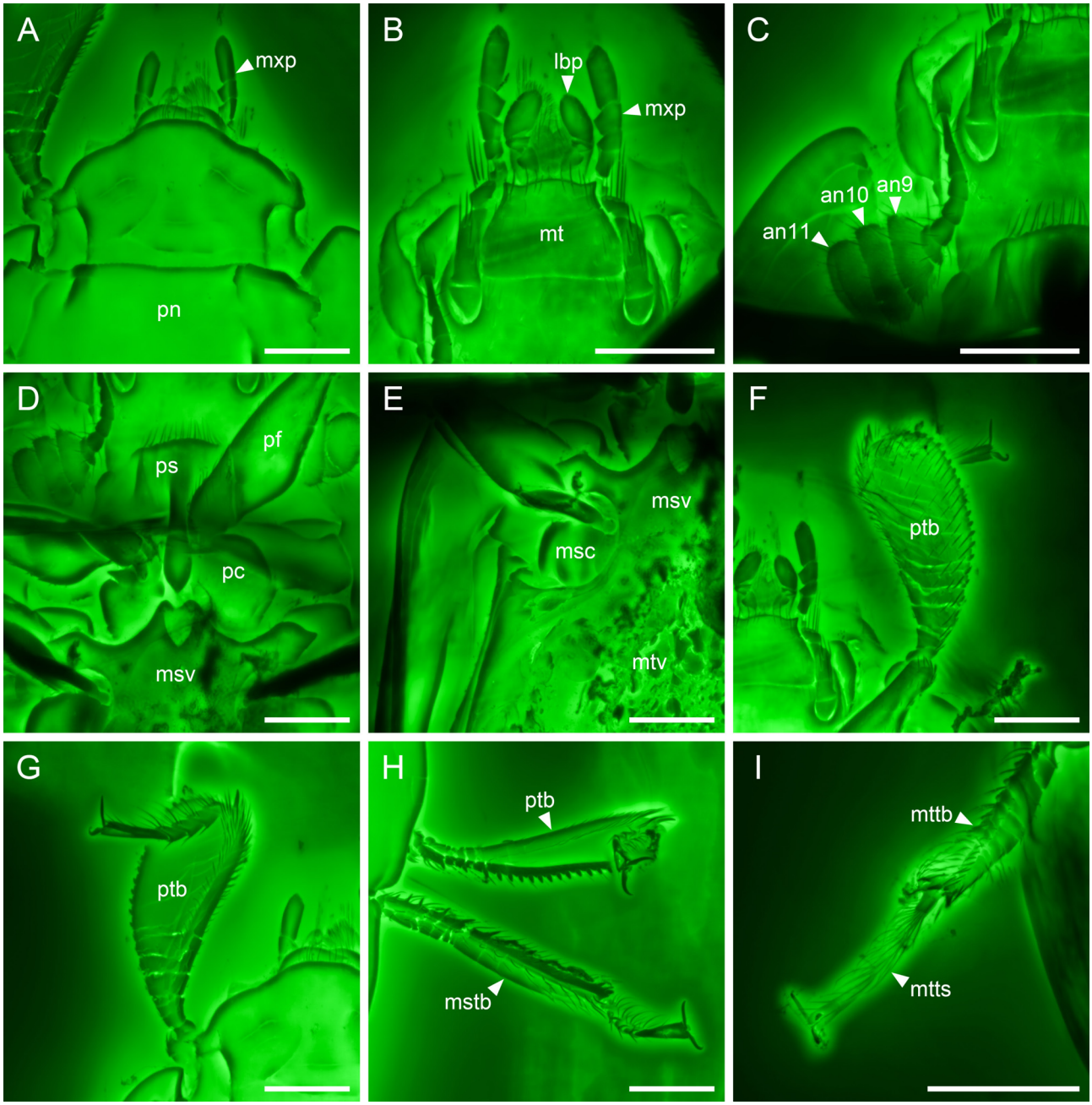

FIGURE 14. Details of *Archaenosodendron angulare* Li & Cai **sp. nov.**, holotype, NIGP177615, under confocal microscopy. **A**, Head, dorsal view. **B**, Mouthparts, ventral view. **C**, Antenna, ventral view. **D**, Prothorax, ventral view. **E**, Anterolateral depression of metaventrite, ventral view. **F**, **G**, Protibia and -tarsus. **H**, Fore and mid legs. **I**, Metatibia and -tarsus. Abbreviations: an9–11, antennomeres 9–11; lbp, labial palp; msc, mesocoxa; mstb, mesotibia; msv, mesoventrite; mt, mentum; mttb, metatibia; mtts, metatarsus; mtv, metaventrite; mxp, maxillary palp; pc, procoxa; pf, profemur; pn, pronotum; ps, prosternum; ptb, protibia. Scale bars: 200 μm.

Genus *Mesonosa* Tihelka, Li, Huang & Cai, 2020

(Figs 17–19)

Type species. *Mesonosa scandens* Tihelka, Li, Huang & Cai, 2021.

Material examined. Holotype of *M. scandens*, NIGP173928.

Remarks. The maxillary and labial palpi of the holotype of *M. scandens* appears to be enlarged in both the

widefield photos and the micro-CT reconstruction by Tihelka *et al.* (2021b). As noted by Tihelka *et al.* (2021b), this enlargement is merely an artefact. In the confocal photomicrographs it is clear that the maxillary and labial palpi *M. scandens* are slender (Fig. 18B). The apparent enlargement is caused by gas bubbles enclosing the palpi. The holotype of *M. scandens* was cited as sex indeterminate in Tihelka *et al.* (2021b). Our reexamination of the CT data reveals the genitalia inside the body of *M. scandens*, which are likely to be female (Fig. 19).

Mesonosa is unique within Nosodendridae in having ventrally lobed tarsomeres 2–4 (Fig. 18G–I; Tihelka *et al.*, 2021b). *Mesonosa* additionally differs from other fossil nosodendrids in having a prosternum without antennal grooves (figs 2D, 4C in Tihelka *et al.*, 2021b) and antennomeres in the club very loosely connected (Fig. 18C).

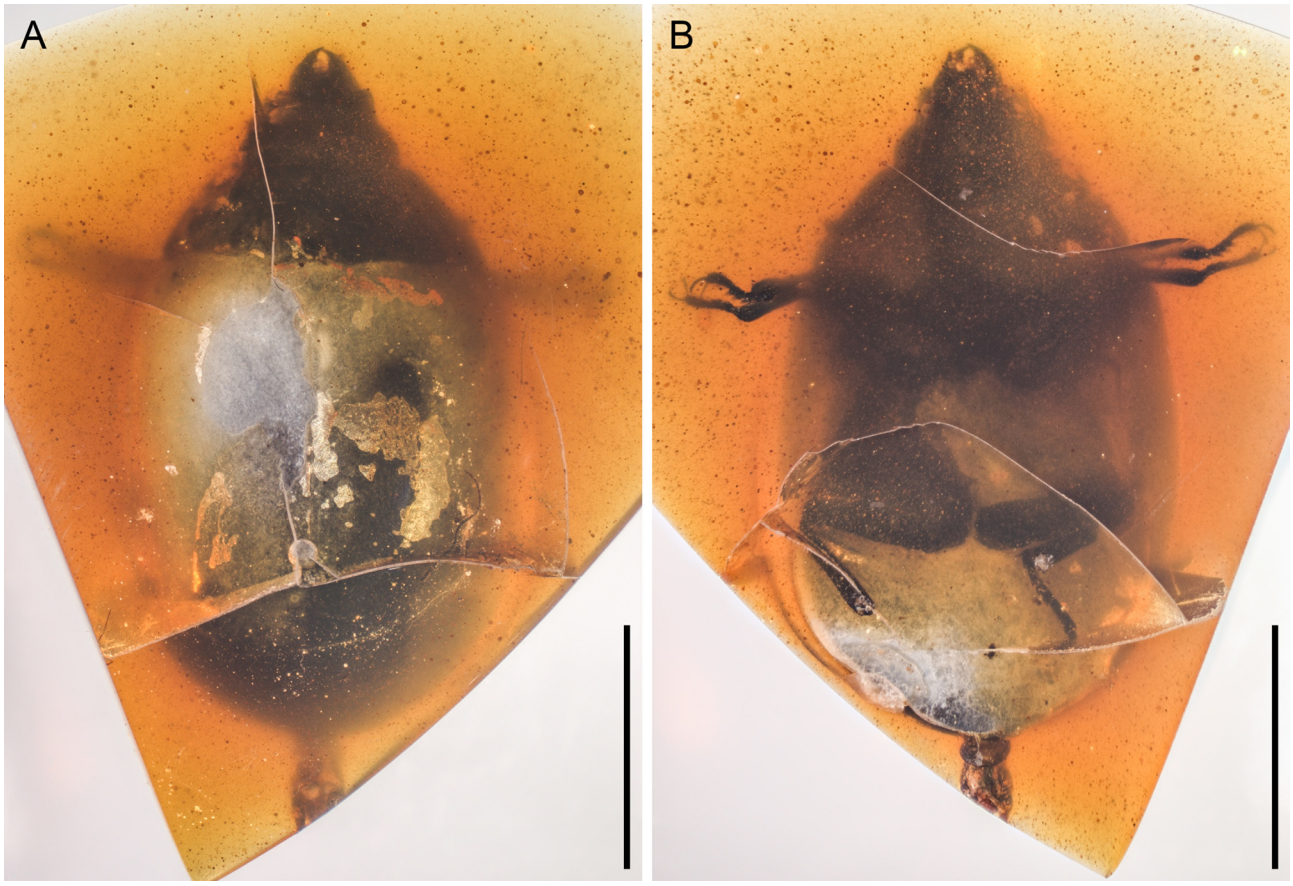

FIGURE 15. General habitus of *Basinosa pengweii* Tihelka *et al.*, holotype, NIGP173119, under incident light. **A**, Dorsal view. **B**, Ventral view. Scale bars: 5 mm.

Discussion

Both extant and extinct nosodendrids have a series of modifications for accommodating the appendages, including the antennal grooves on head, the depression on mesepimeron, elytral epipleuron and metaventrite for the reception of mid legs, and the depression on abdomen for the reception of hind legs. These protective modifications seem to be crucial for their cryptic lifestyle. Extant nosodendrids possess the further specialized prosternum for accommodating the fore legs, and are likely to have a more restricted ecological niche. Compared to their extant relatives, the mid-Cretaceous nosodendrids seem to have a much higher morphological disparity. The new species presented in the current study further support the family Nosodendridae as a relictual group, as noted by Tihelka *et al.* (2021b).

Data availability

The original confocal and micro-CT data are available in Zenodo repository: *Archaenosodendron* spp. (https://doi.org/10.5281/zenodo.5747307), *Basinosa pengweii* (https://doi.org/10.5281/zenodo.5677374), *Mesonosa scandens* (https://doi.org/10.5281/zenodo.5677418).

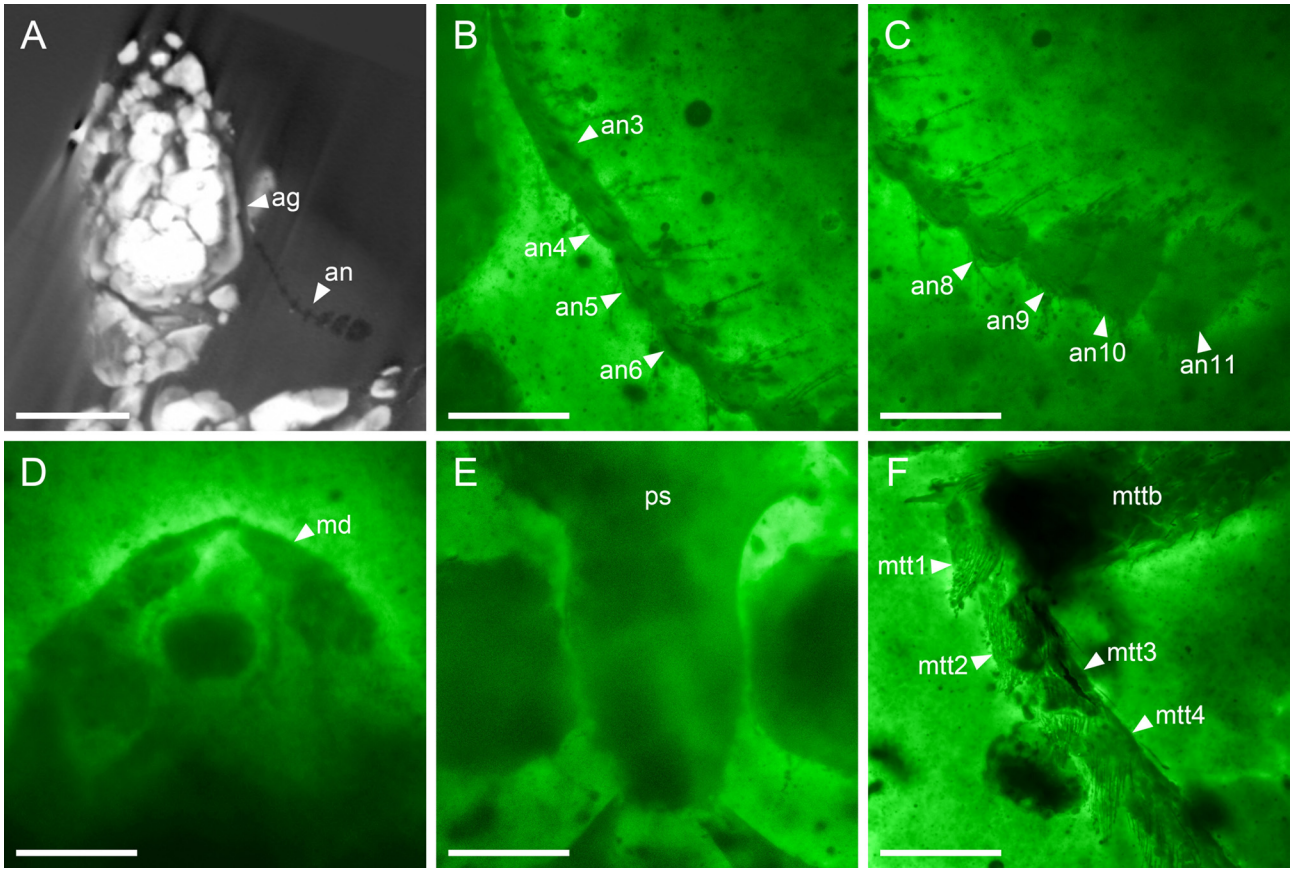

FIGURE 16. Details of *Basinosa pengweii* Tihelka *et al.*, holotype, NIGP173119. **A**, Weighted average stacking of micro-CT slices, showing the left antenna and antennal groove on head. **B**–**F**, confocal images. **B**, **C**, Antenna, ventral view. **D**, Mandibles, dorsal view. **E**, Prosternal process, ventral view. **F**, Metatarsus. Abbreviations: ag, antennal groove; an, antenna; an3–11, antennomeres 3–11; md, mandible; mtt1–4, metatarsomeres 1–4; mttb, metatibia; ps, prosternum. Scale bars: 1500 μm in **A**, 400 μm in **B**–**F**.

Acknowledgements

We are grateful to Su-Ping Wu for technical help with micro-CT reconstruction, Rong Huang for technical help with confocal imaging, Hong Pang and Dong Ren for help in arranging a loan of the holotype of *Archaenosodendron cretaceum*, and André Nel and Hiroyuki Yoshitomi for help with literature. Dany Azar and Jiří Háva provided helpful comments on the early version of this paper. Financial support was provided by the Second Tibetan Plateau Scientific Expedition and Research project (2019QZKK0706), the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000), and the National Natural Science Foundation of China (41688103).

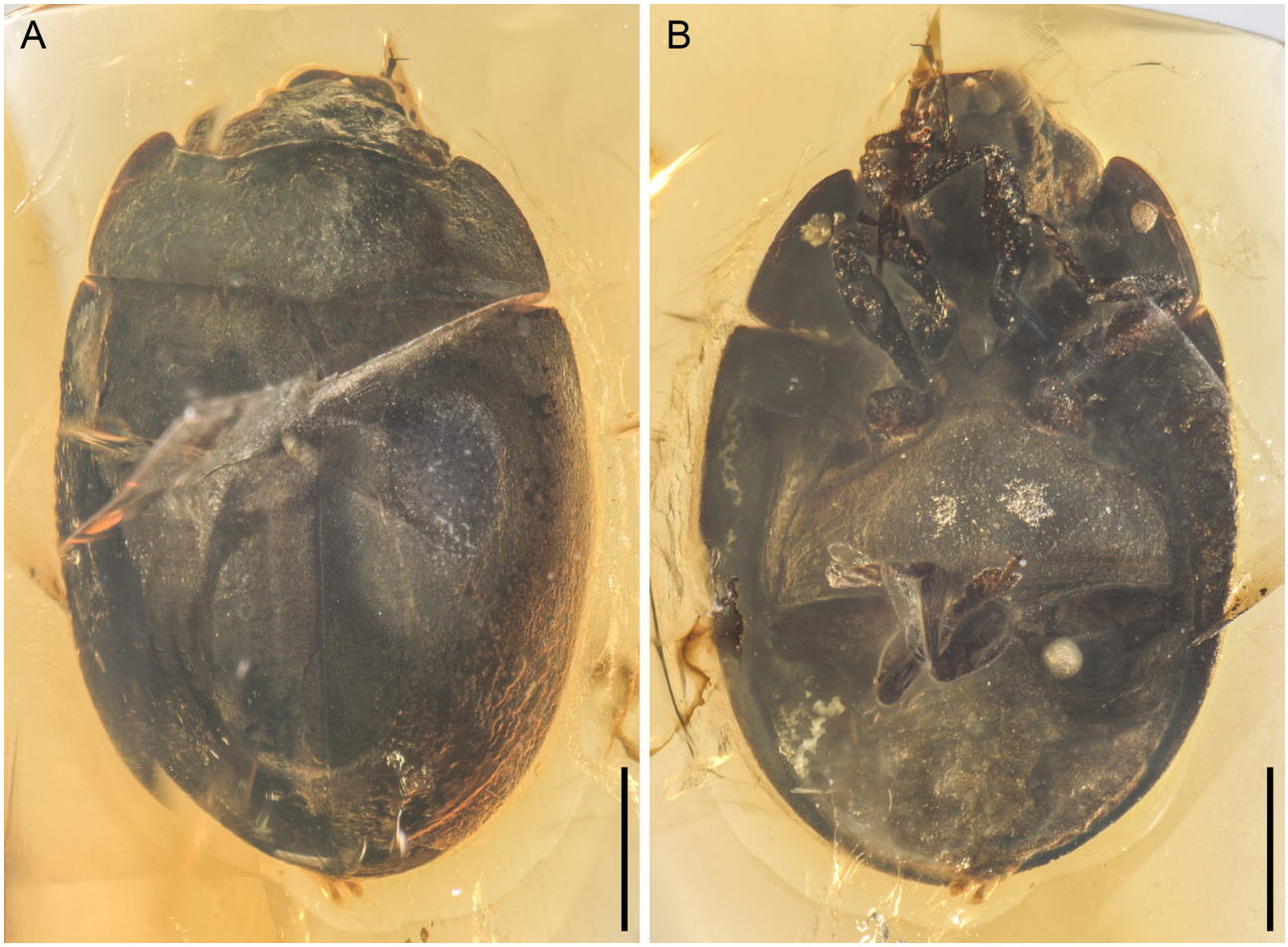

FIGURE 17. General habitus of *Mesonosa scandens* Tihelka *et al.*, holotype, NIGP173928, under incident light. **A**, Dorsal view. **B**, Ventral view. Scale bars: 1 mm.

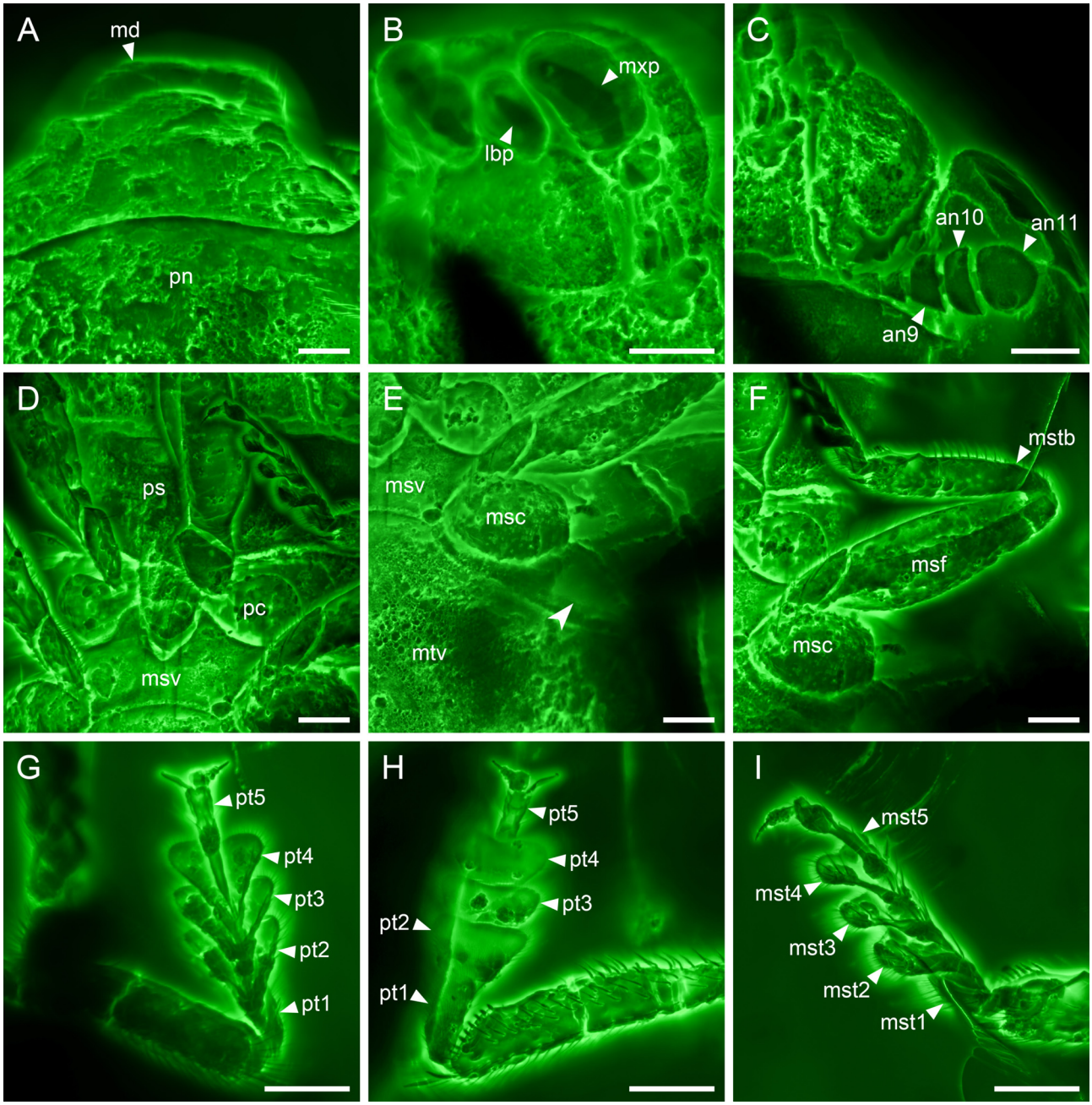

FIGURE 18. Details of *Mesonosa scandens* Tihelka *et al.*, holotype, NIGP173928, under confocal microscopy. **A**, Head, dorsal view. **B**, Mouthparts, ventral view. **C**, Antenna, ventral view. **D**, Prothorax, ventral view. **E**, Anterolateral depression of metaventrite (arrowhead), ventral view. **F**, Mid leg. **G**, **H**, Fore leg. **I**, Mesotarsus. Abbreviations: an9–11, antennomeres 9–11; lbp, labial palp; msc, mesocoxa; msf, mesofemur; mst1–5, mesotarsomeres 1–5; mstb, mesotibia; msv, mesoventrite; mtv, metaventrite; mxp, maxillary palp; pc, procoxa; pn, pronotum; ps, prosternum; pt1–5, protarsomeres 1–5. Scale bars: 200 μm.

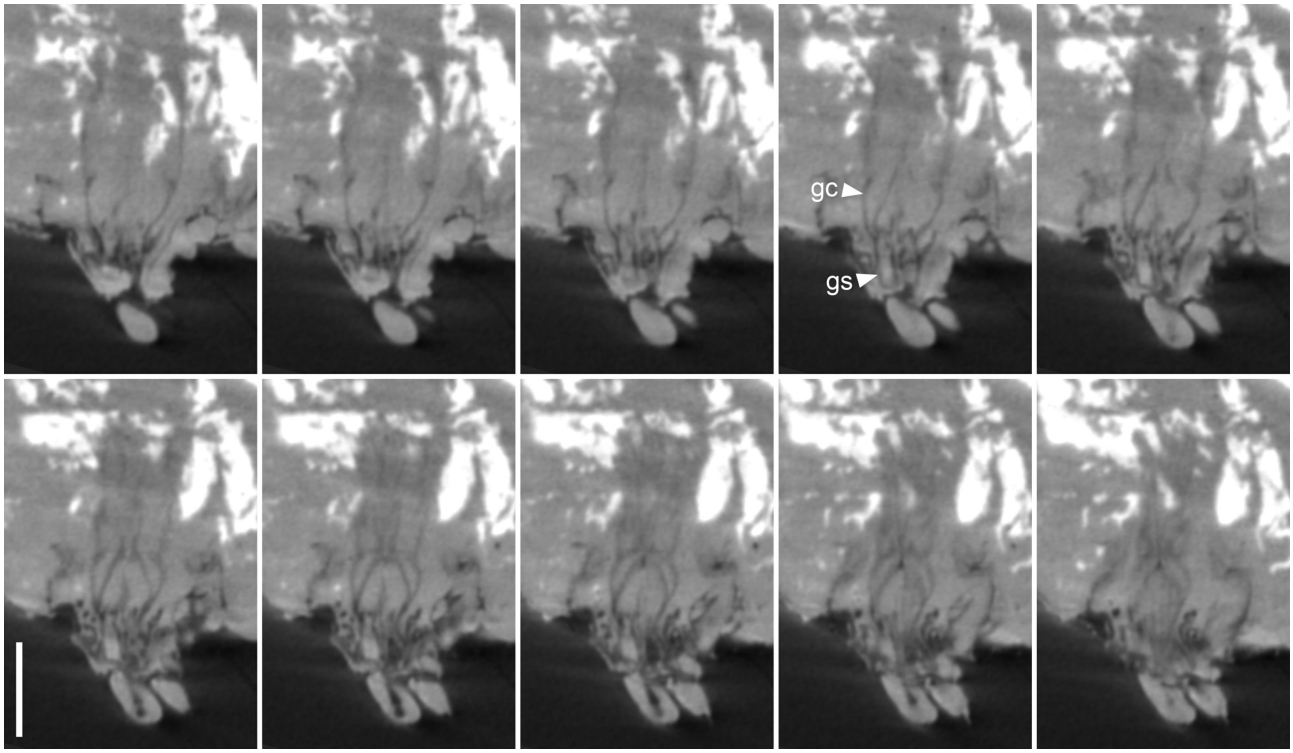

FIGURE 19. Female genitalia of *Mesonosa scandens* Tihelka *et al.*, holotype, NIGP173928, serial horizontal virtual sections based on X-ray microtomographic reconstruction. Abbreviations: gc, gonocoxite; gs, gonostylus. Scale bar: 350 μm.

References

Cai, C., Tihelka, E., Giacomelli, M., Lawrence, J.F., Slipinski, A., Kundrata, R., Yamamoto, S, Thayer, M.K., Newton, A.F., Leschen, R.A.B., Gimmel, M.L, Lü, L., Engel, M.S., Huang, D., Pisani, D. & Donoghue, P.C.J. (2021) Integrated phylogenomics and fossil data illuminate the evolution of beetles. *bioRxiv*. https://doi.org/10.1101/2021.09.22.461358

Coleman, M.N. & Colbert, M.W. (2007) CT thresholding protocols for taking measurements on three-dimensional models. *American Journal of Physical Anthropology*, 133, 723–725. https://doi.org/10.1002/ajpa.20583

Deng, C., Zhou, Y.-L., Ślipiński, A., Ren, D. & Pang, H. (2019) The first wounded-tree beetle (Coleoptera: Nosodendridae) from Cretaceous Burmese amber. *Cretaceous Research*, 93, 211–215. https://doi.org/10.1016/j.cretres.2018.09.019

Fu, Y.-Z., Li, Y.-D., Su, Y.-T., Cai, C.-Y. & Huang, D.-Y. (2021) Application of confocal laser scanning microscopy to the study of amber bioinclusions. *Palaeoentomology*, 4, 266–278. https://doi.org/10.11646/palaeoentomology.4.3.14

Háva, J. (2003) Distributional notes on some Nosodendridae (Insecta: Coleoptera)—III. Descriptions of a new subgenus and two new species from Nepal and China. *In*: Hartmann, M. & Baumbach, H. (Eds.), *Biodiversity and natural heritage in the Himalaya*. Verein der Freunde und Förderer des Naturkundemuseums Erfurt, Erfurt, pp. 247–249.

Háva, J. (2019) Distributional notes on some Nosodendridae (Coleoptera)—XX. Descriptions of a new species from the Philippines. *Euroasian Entomological Journal*, 18, 409–411. https://doi.org/10.15298/euroasentj.18.6.8

Háva, J. (2021) Distributional notes on some Nosodendridae (Coleoptera)—XXIII. Description of a new species, tenth from the Philippines. *Euroasian Entomological Journal*, 20, 288–289. https://doi.org/10.15298/euroasentj.18.6.08

Hirota, B., Meng, X.-Y. & Fukatsu, T. (2020) Bacteriome-associated endosymbiotic bacteria of *Nosodendron* tree sap beetles (Coleoptera: Nosodendridae). *Frontiers in Microbiology*, 11, 2556. https://doi.org/10.3389/fmicb.2020.588841

Hisamatsu, S., Yamasako, J. & Háva, J. (2011) A new species for the genus *Nosoglobulus* Háva, 2003 from Laos (Coleoptera, Nosodendridae). *Elytra, Tokyo,* New Series, 1, 89–92.

Kulhavy, D.L. (1980) Characterization of grand fir colonized by *Nosodendron californicum* Horn (Coleoptera: Nosodendridae). *The Coleopterists Bulletin*, 34, 171–173.

Lawrence, J.F. & Ślipiński, A. (2013) *Australian beetles. Vol. 1. Morphology, classification and keys*. CSIRO Publishing, Clayton, 576 pp.
https://doi.org/10.1071/9780643097292

McKenna, D.D., Shin, S., Ahrens, D., Balke, M., Beza-Beza, C., Clarke, D.J., Donath, A., Escalona, H.E., Friedrich, F., Letsch, H., Liu, S., Maddison, D., Mayer, C., Misof, B., Murin, P.J., Niehuis, O., Peters, R.S., Podsiadlowski, L., Pohl, H., Scully, E.D., Yan, E.V., Zhou, X., Ślipiński, A. & Beutel, R.G. (2019) The evolution and genomic basis of beetle diversity. *Proceedings of the National Academy of Sciences, USA*, 116, 24729–24737.
https://doi.org/10.1073/pnas.1909655116

Nomura, S. & Kamezawa, H. (2014) Records of *Nosodendron coenosum* (Wollaston, 1873) (Nosodendridae) from Shinagawa-ku, Tokyo, Japan and SEM observation of its morphological structures. *Sayabane*, (13), 21–25. [in Japanese]

Nomura, S. (2015) Opposite double binding patches of fore wing discovered in *Nosodendron coenosum* (Nosodendridae). *Sayabane*, (18), 26–29. [in Japanese]

Osborne, H.L. & Kulhavy, D.L. (1975) Notes on *Nosodendron californicum* Horn on slime fluxes of grand fir, *Abies grandis* (Douglas) Lindley, in northern Idaho (Coleoptera: Nosodendridae). *The Coleopterists Bulletin*, 29, 71–73.

Reichardt, H. (1976) Monograph of the New World Nosodendridae and notes on the Old World forms (Coleoptera). *Papéis Avulsos de Zoologia*, 29, 185–220.

Tihelka, E., Huang, D. & Cai, C. (2021a) A new genus of wounded-tree beetles from mid-Cretaceous northern Myanmar amber (Coleoptera: Nosodendridae). *Cretaceous Research*, 119, 104701.
https://doi.org/10.1016/j.cretres.2020.104701

Tihelka, E., Li, Y.-D., Huang, D.-Y. & Cai, C.-Y. (2021b) Are wounded-tree beetles living fossils? A new nosodendrid genus from Burmese amber with bilobed tarsi (Coleoptera: Nosodendridae). *Palaeoentomology*, 4, 50–56.
https://doi.org/10.11646/palaeoentomology.4.1.10

Yoshitomi, H. (2013a) A new species of *Nosodendron* Latreille (Coleoptera: Nosodendridae) from the Caroline Islands. *The Coleopterists Bulletin*, 67, 72–74.
https://doi.org/10.1649/0010-065X-67.2.72

Yoshitomi, H. (2013b) Nosodendridae (Coleoptera, Derodontoidea) of the Indochinese subregion. *Elytra, Tokyo*, New Series, 3, 213–224.

Yoshitomi, H. (2015) Nosodendridae of Japan. *Sayabane*, (18), 21–25. [in Japanese]

Yoshitomi, H. (2016) A consideration of measurement method for taxonomy. *Sayabane*, (21), 41–44. [in Japanese]

Yoshitomi, H., Kishimoto, T. & Lee C.F. (2015) The family Nosodendridae (Coleoptera: Derodontoidea) of Japan and Taiwan. *Japanese Journal of Systematic Entomology*, 21, 35–58.

Zhang, S.-Q., Che, L.-H., Li, Y., Liang, D., Pang, H., Ślipiński, A. & Zhang, P. (2018) Evolutionary history of Coleoptera revealed by extensive sampling of genes and species. *Nature Communications*, 9, 205.
https://doi.org/10.1038/s41467-017-02644-4