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New species of *Notocupes* (Coleoptera: Archostemata) from the Middle Jurassic Daohugou beds, with discussion on the generic circumscription

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Abstract

Exquisitely preserved fossils from the Middle Jurassic Haifanggou Formation (the Daohugou beds; ~165 Ma) and mid-Cretaceous Burmese amber (~99 Ma) are studied to clarify the external morphology of *Notocupes*. Three new species from Daohugou are described as *N. spinosus* **sp. nov.**, *N. robustus* **sp. nov.**, and *N. daohugouensis* **sp. nov.** Our examination of specimens from Burmese amber does not support the division of *Notocupes* into *Notocupes s.s.* and *Echinocups*. Therefore we treat *Echinocups* **syn. nov.** as a junior synonym of *Notocupes*, and *N. ohmkuhnlei* **comb. rev.**, *N. neli* **comb. rev.** and *N. denticollis* **comb. rev.** are returned to *Notocupes* from *Echinocups*.

Keywords: *Notocupes*, *Echinocups*, adpression fossils, Burmese amber, new species, synonymy, new combinations

Introduction

Notocupes Ponomarenko is perhaps the most abundant genus of archostematans in Mesozoic deposits across Eurasia. The first fossil possibly related to *Notocupes*, represented by an isolated elytron, was reported from the United Kingdom by Giebel (1856). Further isolated elytra and body fossils have been known from Spain, Germany, Russia, Kazakhstan, Kyrgyzstan, Tajikistan, Mongolia, China, Korea, Myanmar, and even Australia (see Kirejtshuk, 2020). Despite its wide distribution, the morphology of *Notocupes* was insufficiently known until recently. As most *Notocupes* specimens were discovered as adpression (compression–impression) fossils from Mesozoic strata, many of the morphological characters were difficult to interpret or simply not preserved at all. The genus has been historically placed into the family Ommatidae (or Ommatinae in Cupedidae *s.l.*), and further into the tribe Notocupedini erected by Ponomarenko (1966). However, a recent cladistic analysis suggested that *Notocupes* is actually sister to Cupedidae *s.s.* (Li *et al.*, 2023).

The Jurassic Daohugou beds is well-known for the exceptionally preserved insects as adpression fossils. (Lian *et al.*, 2021; Li *et al.*, 2022). However, only a single *Notocupes* specimen has been described from there (Ponomarenko & Ren, 2010). Three *Notocupes* species have been reported from mid-Cretaceous Burmese amber (Tihelka *et al.*, 2019; Jarzembowski *et al.*, 2020; Jiang *et al.*, 2020), which, however, were later transferred to a separate genus, *Echinocups* Kirejtshuk & Jarzembowski (in Kirejtshuk, 2020). The morphology of all three species in Burmese amber remains insufficiently described (especially the ventral side), which hinders a detailed comparison with previously reported *Notocupes* preserved as adpressions.

Here we provide description for four exquisitely preserved *Notocupes* fossils from Middle–Late Jurassic Daohugou Biota and mid-Cretaceous Burmese amber. In addition, the type specimen of *N. denticollis* Jiang *et al.* from Burmese amber is re-examined. Our contribution is intended to improve the taxonomy of the group by clarifying its external morphology with the aid of various imaging techniques.

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Material and methods

The adpression fossils studied herein (Figs 1–9) originated from Daohugou Village, Ningcheng County, Inner Mongolia, China (~165 Ma). The Burmese amber specimens (Figs 10–14) originated from amber mines near Noije Bum (26°20′ N, 96°36′ E), Hukawng Valley, Kachin State, northern Myanmar (~99 Ma). The specimen STJ311 (holotype of *Notocupes denticollis*) is currently deposited in the Paleo-diary Museum of Natural History, Beijing, China (rather than Shenzhen Baoan Century Amber Museum as noted in Jiang *et al.,* 2020). The specimen BA202101 (*Notocupes* sp.) is deposited in the Lingpoge Amber Museum, Shanghai, China. All other specimens are deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China.

Photographs under incident light were taken with a Zeiss Discovery V20 stereo microscope. Where necessary, adpression fossils were moistened with 70% ethanol to improve contrast of morphological characters. Widefield fluorescence images were captured with a Zeiss Axio Imager 2 light microscope or a Zeiss Lumar V12 stereo microscope combined with a fluorescence imaging system. 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 stacked with colour coding for depth in ZEN 2.3 (Blue Edition), or manually stacked in Adobe Photoshop CC. Scanning electron microscopic (SEM) images were obtained with a Hitachi SU 3500 scanning electron microscope, operating with an accelerating voltage of 18 kV and a pressure of 60 Pa. Energy dispersive X-ray spectroscopy (EDS) analyses were conducted with a TESCAN MAIA3 field emission scanning electron microscope. Microtomographic data were obtained with a Zeiss Xradia 520 Versa 3D X-ray microscope at the micro-CT laboratory of NIGP, and analysed in VGStudio MAX 3.0. Scanning parameters were as follows: STJ311 [isotropic voxel size, 16.916 μm; power, 4 W; acceleration voltage, 50 kV; exposure time, 2 s; projections, 2001]; BA202101 [isotropic voxel size, 14.096 μm; power, 3 W; acceleration voltage, 40 kV; exposure time, 4 s; projections, 2001]. Images were further processed in Adobe Photoshop CC to adjust brightness and contrast.

Systematic palaeontology

Order Coleoptera Linnaeus, 1758

Suborder Archostemata Kolbe, 1908

Genus *Notocupes* Ponomarenko, 1964

Type species. *Notocupes picturatus* Ponomarenko, 1964.

Remarks. The three species from Burmese amber originally placed in *Notocupes* were transferred to *Echinocups* by Kirejtshuk & Jarzembowski (in Kirejtshuk, 2020). However, our examination reveals no valid difference between *Echinocups* and *Notocupes* (see Discussion), thus these species are transferred back to *Notocupes*, as *Notocupes ohmkuhnlei* Jarzembowski *et al*. **comb. rev.**, *Notocupes neli* Tihelka *et al.* **comb. rev.**, and *Notocupes denticollis* Jiang *et al*. **comb. rev.**

Notocupes spinosus Li & Cai sp. nov.

(Figs 1–3)

Material. Holotype, NIGP174673a (part) and NIGP174673b (counterpart), sex unknown.

Etymology. The specific name refers to the well-preserved spines on its elytra.

Diagnosis. *Notocupes spinosus* **sp. nov.** differs from *N. pingi* Ponomarenko & Ren, the sole species of *Notocupes* previously known from Daohugou, and *N. daohugouensis* **sp. nov.** in having two distinct posterior protuberances on head (Fig. 3A). *Notocupes spinosus* **sp. nov.** differs from *N. robustus* **sp. nov.** in having smooth pronotal edges and a single posterior protuberance on pronotum (Fig. 3B). *Notocupes spinosus* **sp. nov.** differs from *N. daohugouensis* **sp. nov.** additionally in having longer antennomeres 5–10 (Fig. 3C) and wider grooves on elytral epipleura for accommodating mesotibiae and -tarsi (Fig. 1D).

Locality and horizon. Daohugou Village, Ningcheng County, Inner Mongolia, China. Middle Jurassic, Haifanggou Formation.

Description. Body ovate, about 14.2 mm long, 7.4 mm wide, with scales at least on elytra.

Head (Fig. 3A) subquadrate, prognathous; dorsal surface with a pair of relatively laterally situated protuberances anteriorly and a pair of distinct median protuberances posteriorly. Compound eyes hemispherical and strongly protruding. Antennal insertions dorsolaterally situated. Antenna 11-segmented, serratiform (Fig. 3C).

Pronotal disc (Fig. 3B) approximately 2.1 times as wide as long; anterior angles strongly extending anteriorly; lateral edges not denticulate; dorsal surface with a pair of anterior protuberances and a single posterior protuberance, and a pair of shallow antennal grooves laterally. Prosternum in front of coxae subquadrate (Fig. 3G). Procoxae probably not contiguous (Fig. 3G). Propleura probably not reaching anterior prothoracic margin. Protarsal groove present along pleurosternal and notosternal sutures (Fig. 2E).

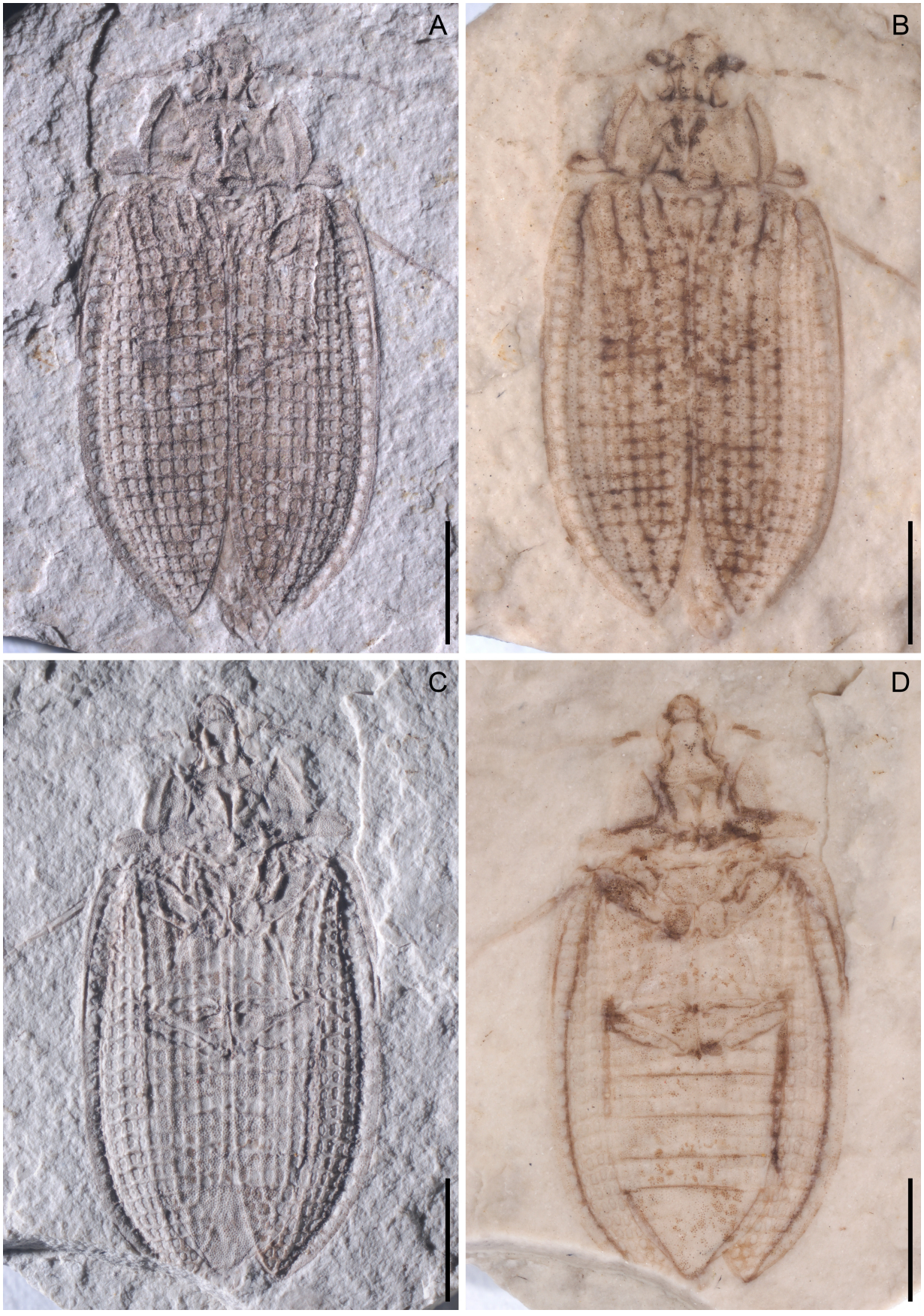

FIGURE 1. General habitus of *Notocupes spinosus* Li & Cai **sp. nov.**, holotype, NIGP174673, under incident light. **A**, NIGP174673a, dry. **B**, NIGP174673a, moistened with 70% ethanol. **C**, NIGP174673b, dry. **D**, NIGP174673b, moistened with 70% ethanol. Scale bars: 3 mm.

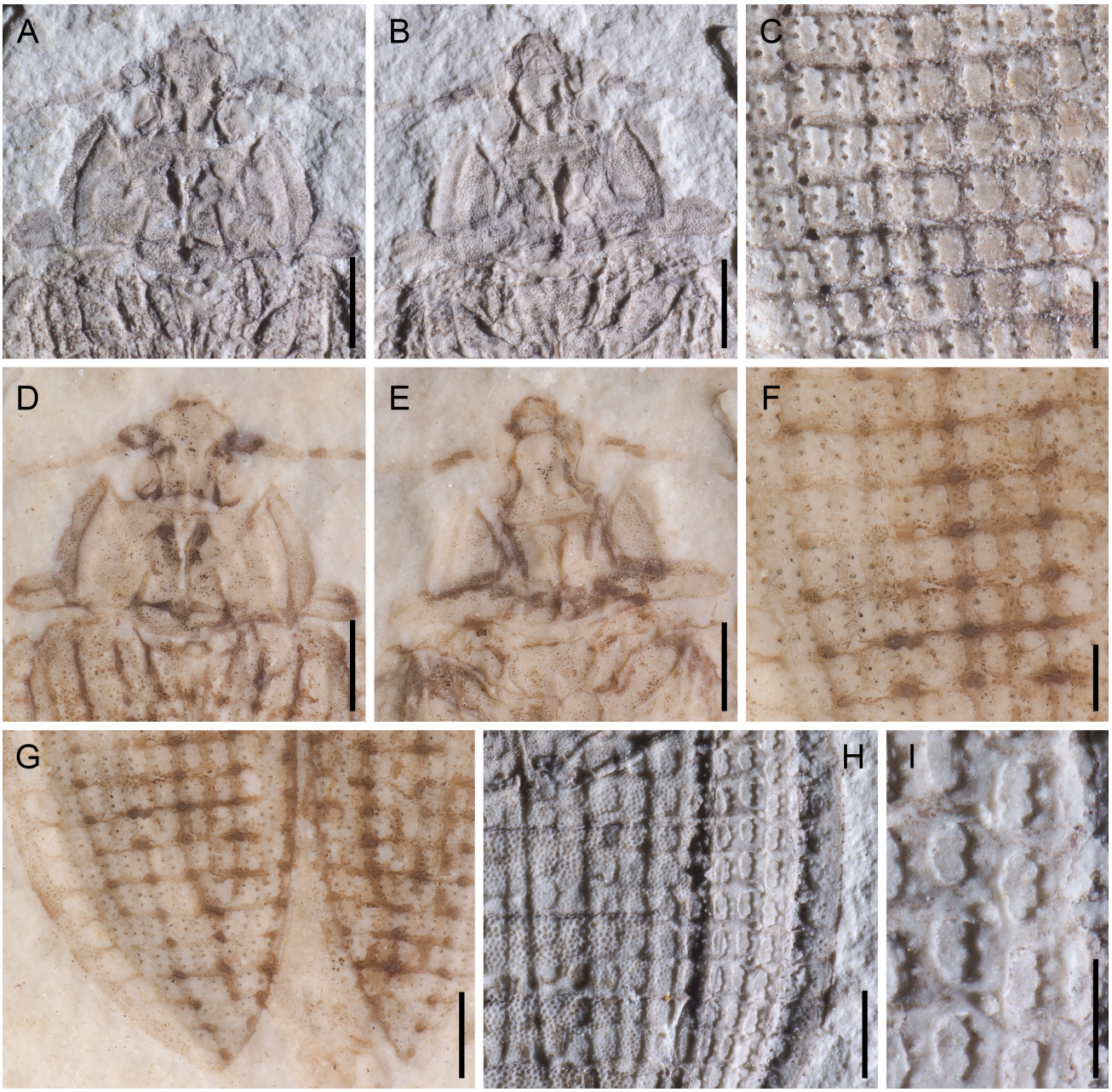

FIGURE 2. Details of *Notocupes spinosus* Li & Cai **sp. nov.**, holotype, NIGP174673, under incident light. **A**, **D**, NIGP174673a, head and prothorax. **B**, **E**, NIGP174673b, head and prothorax. **C**, **F**, **G**, NIGP174673a, elytra. **H**, NIGP174673b, abdomen and elytra. **I**, NIGP174673b, coniform protuberances (spines) on elytron. **A–C**, **H**, **I**, Dry. **D–G**, Moistened with 70% ethanol. Scale bars: 1.5 mm in **A–B**, **D–E**, 1 mm in **G–H**, 500 μm in **C**, **F**, **I**.

Elytra elongate, about 1.4 times as long as width combined; each elytron with ten longitudinal rows of window punctures on disc and one row of window punctures on explanate epipleuron (roughly 25 punctures per row) (Fig. 1A); every two rows separated by distinctly raised vein; veins with coniform protuberances (spines *sensu* Kirejtshuk, 2020) (Figs 2I, 3D); veins A1 and CuA fused before elytral apex (Fig. 2G); left elytra with posteriorly punctured sutural flange; anterior portion of explanate epipleura with relatively wide longitudinal groove (Fig. 1D). Mesoventrite with discrimen on posterior half (Fig. 3H). Mesocoxae contiguous (Fig. 3H). Metaventrite subtrapezoidal, with discrimen and katepisternal suture. Metacoxae transverse, contiguous.

Legs elongate. Femora stout. Tibiae thinner. Tarsomere 5 not distinctly narrower than penultimate one (Fig. 3E). Pretarsal claws simple.

Abdomen with five overlapping ventrites (Fig. 2H); ventrites 2–3 subequal in length; ventrite 4 about 0.7 times as long as ventrite 3; ventrite 5 subtriangular, about 2.2 times as long as ventrite 2.

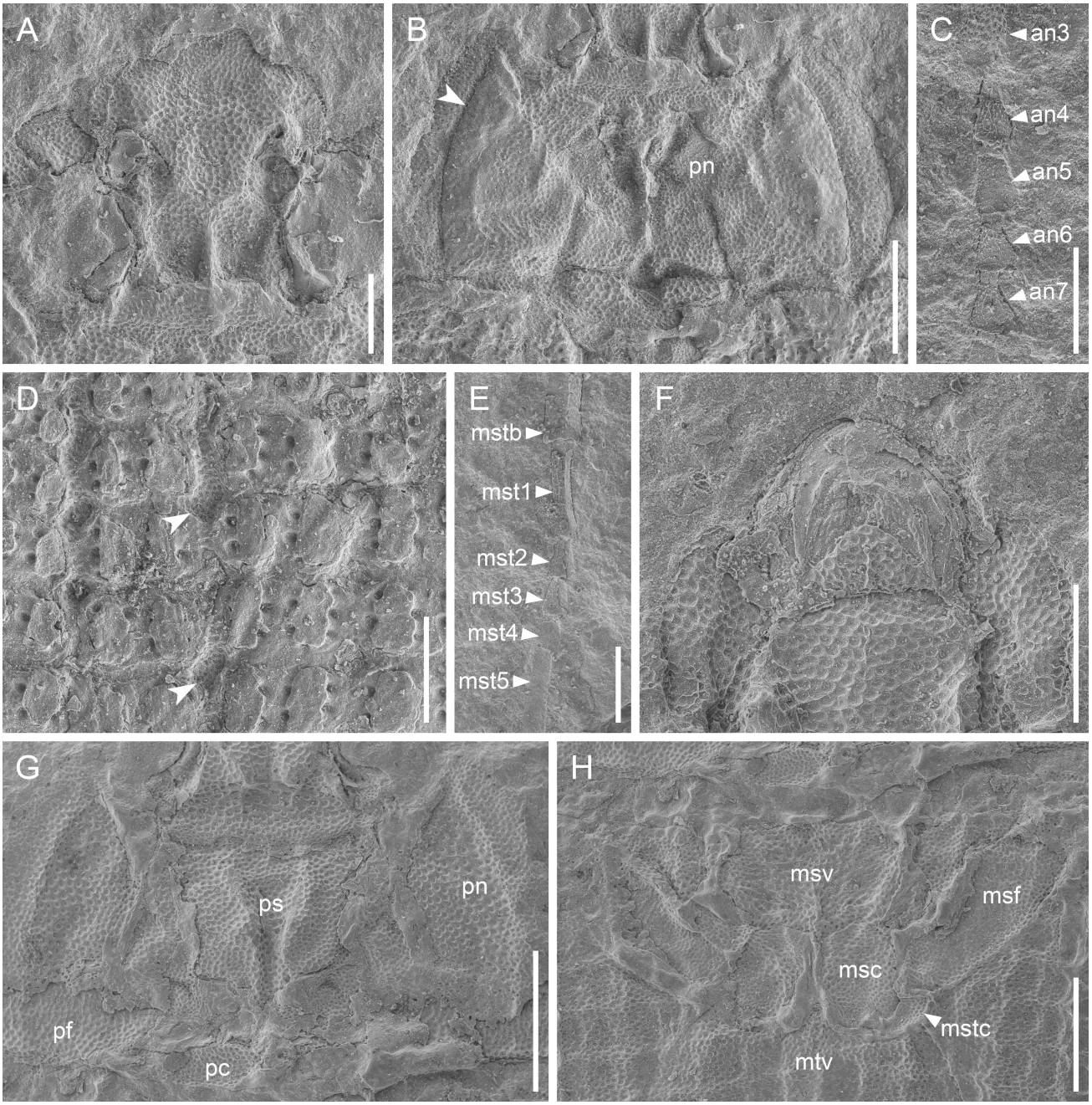

FIGURE 3. Details of *Notocupes spinosus* Li & Cai **sp. nov.**, holotype, NIGP174673, under scanning electron microscopy. **A–E**, NIGP174673a. **A**, Head. **B**, Prothorax, showing the prothoracic antennal groove (arrowhead). **C**, Antenna. **D**, Elytron, showing the coniform protuberances covered with scales (arrowheads). **E**, Mesotarsus. **F–H**, NIGP174673b. **F**, Mouthparts. **G**, Prothorax. **H**, Mesothorax. Abbreviations: an3–7, antennomeres 3–7; msc, mesocoxa; msf, mesofemur; mst1–4, mesotarsomeres 1–4; mstb, mesotibia; mstc, mesotrochanter; mtv, metaventrite; pc, procoxa; pf, profemur; pn, pronotum; ps, prosternum. Scale bars: 1 mm in **B**, **G–H**, 500 μm in **A**, **C–F**.

***Notocupes robustus* Li & Cai sp. nov.**
(Figs 4, 5)

Material. Holotype, NIGP174674, sex unknown.

Etymology. The specific name refers to its robust appearance.

Diagnosis. *Notocupes robustus* **sp. nov.** differs from other *Notocupes* species from Daohugou in being larger and having dentate pronotal edges (Fig. 4C). *Notocupes robustus* **sp. nov.** differs from *N. pingi* and *N. daohugouensis* **sp. nov.** in having two distinct posterior protuberances on head (Fig. 5A). The window cells on the outer and inner sides of CuA are well aligned in *N. pingi*, *N. spinosus* and *N. daohugouensis* **sp. nov.** (Figs 2E, 8B),

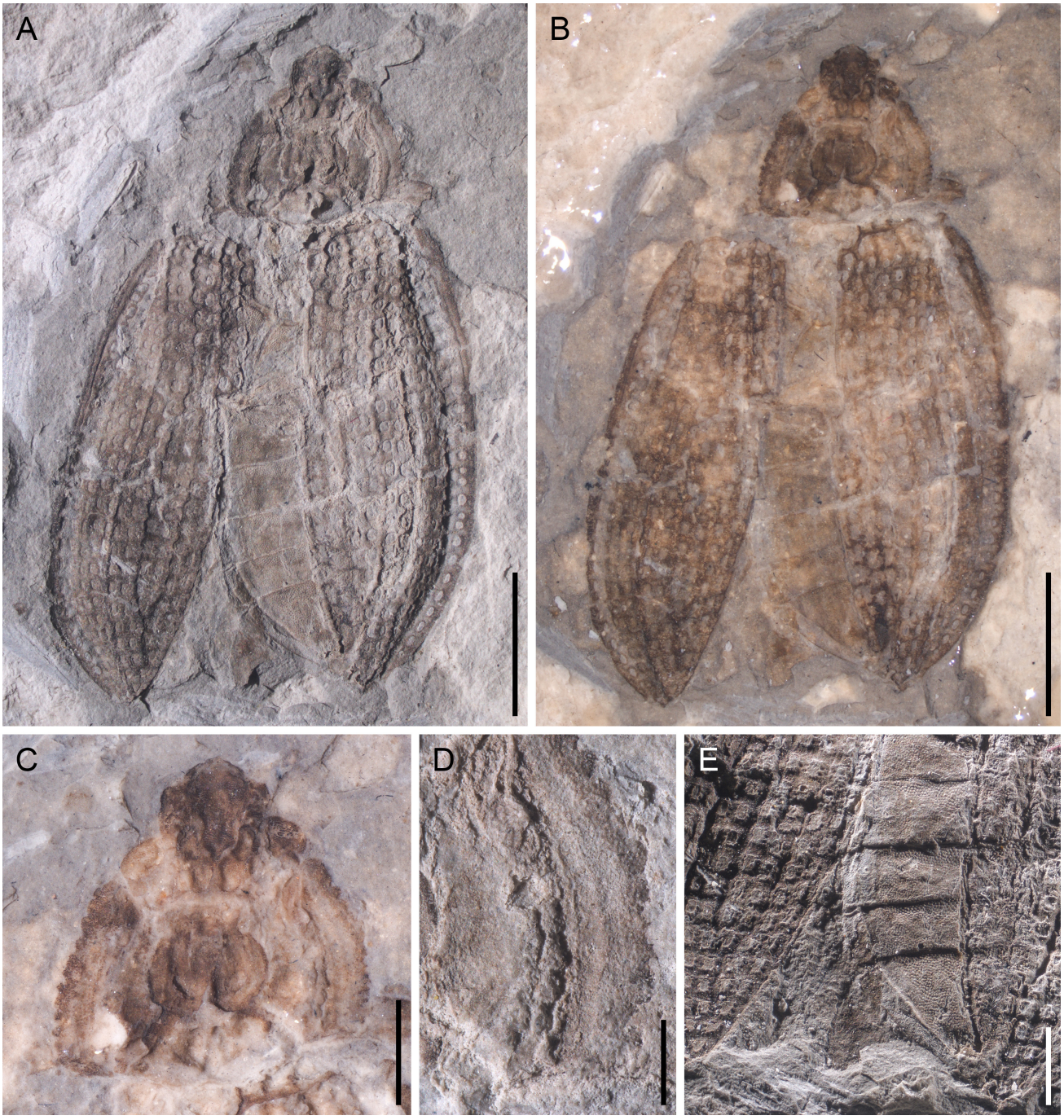

FIGURE 4. *Notocupes robustus* Li & Cai **sp. nov.**, holotype, NIGP174674, under incident light. **A**, General habitus, dry. **B**, General habitus, moistened with 70% ethanol. **C**, Head and prothorax, moistened with 70% ethanol. **D**, Antenna in the prothoracic antennal groove, dry. **E**, Abdomen and elytra, dry. Scale bars: 5 mm in **A**, **B**, 2 mm in **C**, **E**, 750 μm in **D**.

while they are misaligned by half a cell in *N. robustus* **sp. nov.** (Fig. 5E).

Locality and horizon. Daohugou Village, Ningcheng County, Inner Mongolia, China. Middle Jurassic, Haifanggou Formation.

Description. Body ovate, comparatively large, about 21.5 mm long, 11.3 mm wide.

Head subquadrate (Fig. 5A), prognathous; dorsal surface with a pair of relatively laterally situated protuberances anteriorly and a pair of distinct median protuberances posteriorly. Antennal insertions dorsolaterally situated. Antenna 11-segmented, serratiform (Figs 4D, 5C).

Pronotal disc (Fig. 5B) approximately 1.7 times as wide as long; anterior angles strongly extending anteriorly; lateral edges dentate; dorsal surface with a pair of anterior

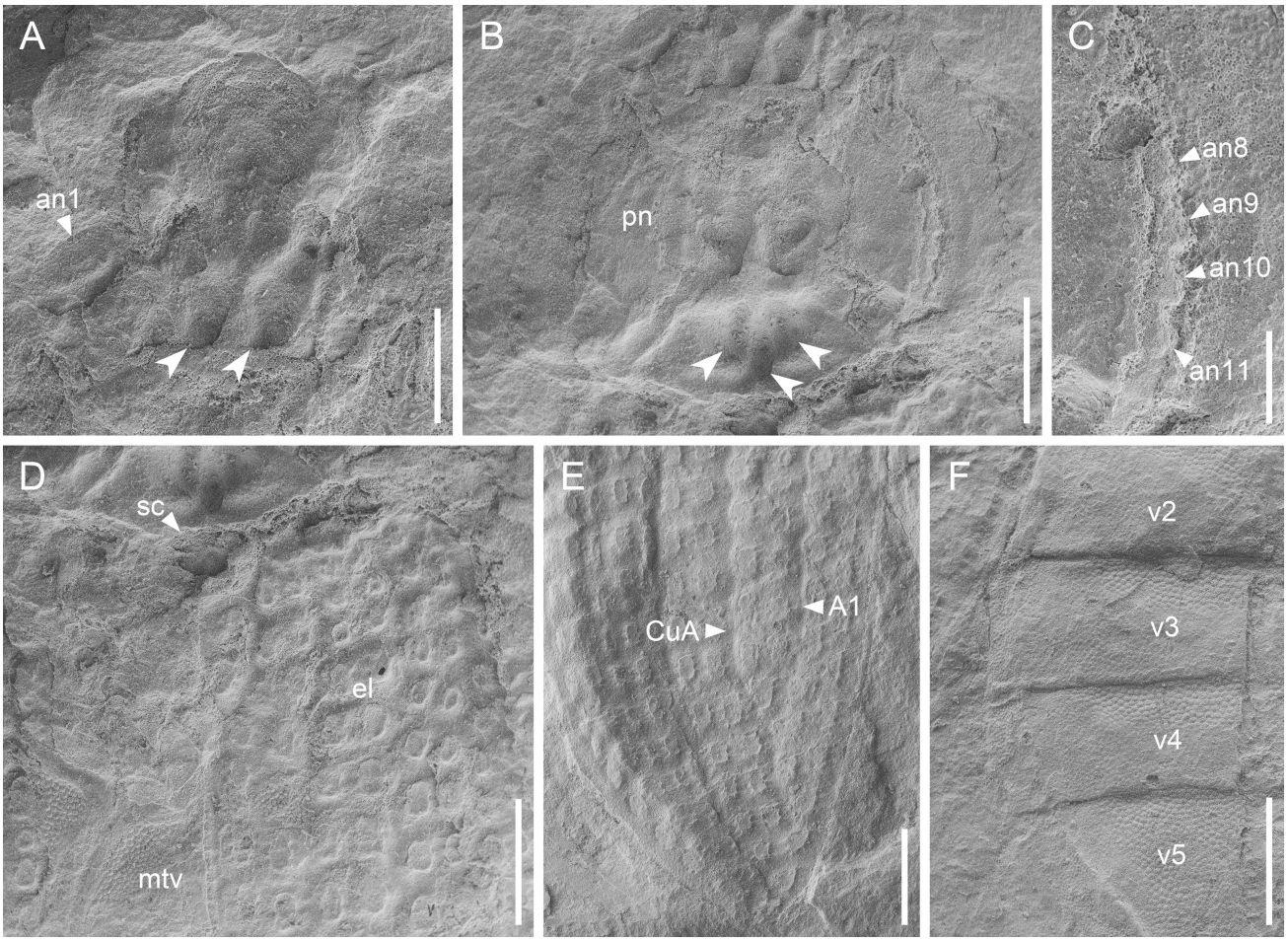

FIGURE 5. Details of *Notocupes robustus* Li & Cai **sp. nov.**, holotype, NIGP174674, under scanning electron microscopy. **A**, Head, showing the two posterior protuberances on head (arrowheads). **B**, Prothorax, showing the three posterior protuberances on pronotal disc (arrowheads). **C**, Antenna in the prothoracic antennal groove. **D**, Elytral base. **E**, Elytral apex. **F**, Abdomen. Abbreviations: an1–11, antennomeres 1–11; el, elytron; mtv, metaventrite; pn, pronotum; sc, scutellum; v2–5, ventrites 2–5. Scale bars: 1.5 mm in **B**, **D–F**, 1 mm in **A**, 500 μm in **C**.

protuberances and three posterior protuberances, and a pair of shallow antennal grooves laterally.

Elytra (Fig. 4A) elongate, about 1.4 times as long as width combined; each elytron with ten longitudinal rows of window punctures on disc and one row of window punctures on explanate epipleuron (roughly 23 punctures per row); every two rows separated by distinctly raised vein; veins A1 and CuA fused before elytral apex (Fig. 5E).

Abdomen with five overlapping ventrites (Fig. 4E, 5F); ventrites 3, 4, and 5 about 0.9, 0.8, and 2.3 times as long as ventrite 2, respectively.

***Notocupes daohugouensis* Li & Cai sp. nov.**
(Figs 6–8)

Material. Holotype, NIGP174675, sex unknown.

Etymology. The specific name refers to the locality of Daohugou, where the holotype was discovered.

Diagnosis. *Notocupes daohugouensis* **sp. nov.** differs from other *Notocupes* species from Daohugou in its smaller size. *Notocupes daohugouensis* **sp. nov.** differs from *Notocupes pingi* additionally in relief of middle abdominal ventrites strong.

Locality and horizon. Daohugou Village, Ningcheng County, Inner Mongolia, China. Middle Jurassic, Haifanggou Formation.

Description. Body ovate, comparatively small, about 7.6 mm long, 3.4 mm wide.

Head (Fig. 7A) subquadrate, prognathous; dorsal surface with a pair of relatively laterally situated protuberances anteriorly, probably without median protuberances posteriorly. Compound eyes

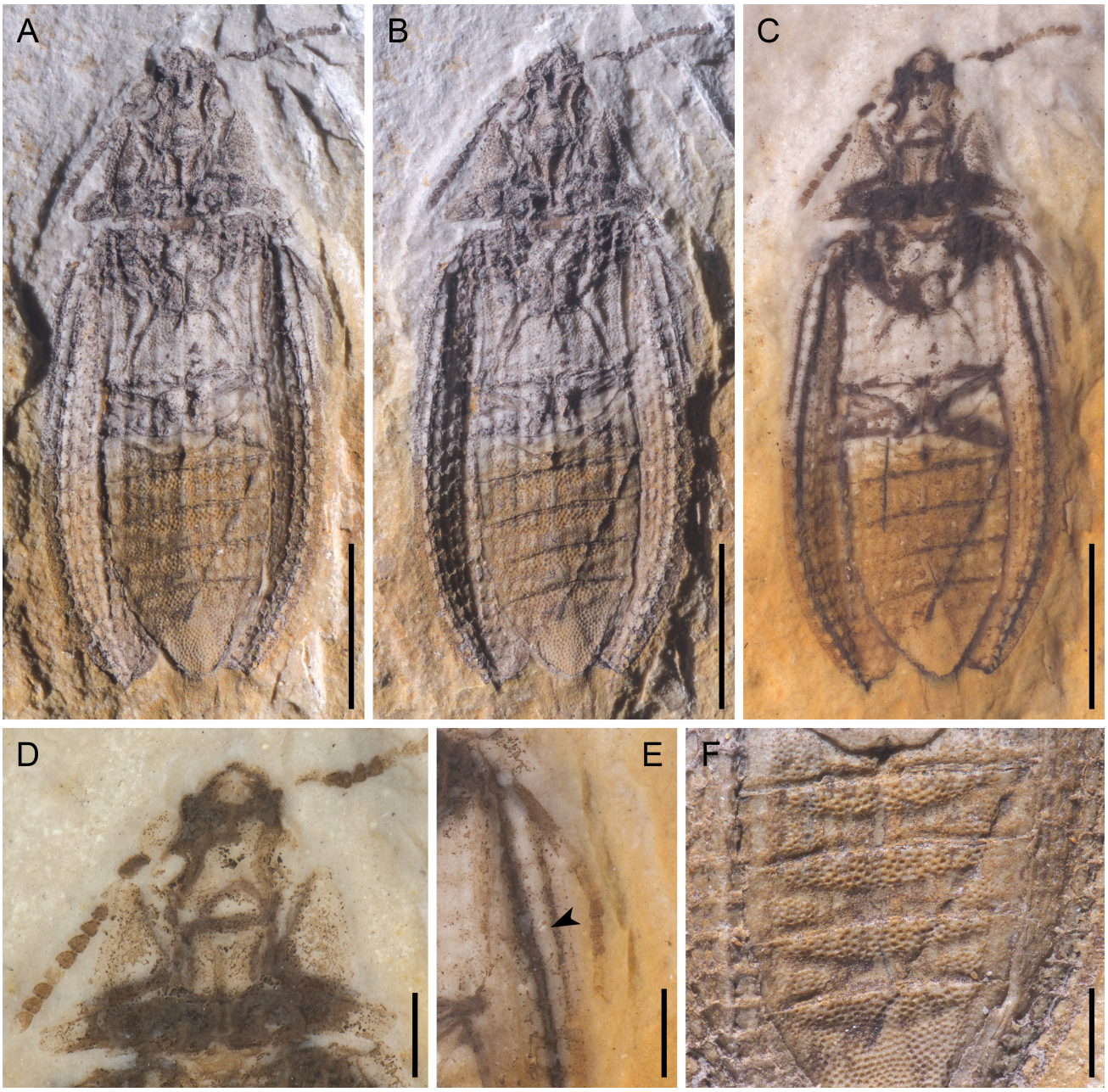

FIGURE 6. *Notocupes daohugouensis* Li & Cai **sp. nov.**, holotype, NIGP174675, under incident light. **A**, **B**, General habitus, dry. **C**, General habitus, moistened with 70% ethanol. **D**, Head and prothorax, moistened with 70% ethanol. **E**, Groove on the elytral epipleuron for housing mesotibia and -tarsus (arrowhead), moistened with 70% ethanol. **F**, Abdomen, dry. Scale bars: 2 mm in **A–C**, 600 μm in **D–F**.

hemispherical and protruding (Fig. 8A). Antennal insertions dorsolaterally situated. Antenna 11-segmented, serratiform (Fig. 7C).

Pronotal disc (Fig. 7B) approximately 1.9 times as wide as long, expanding posteriorly; anterior angles strongly extending anteriorly. Prosternum in front of coxae subquadrate; prosternal process relatively well developed, though not reaching posterior edge of procoxae (Fig. 7B). Procoxae not contiguous (Fig. 7B). Propleura probably not reaching anterior prothoracic margin. Protarsal groove present along pleurosternal and notosternal sutures (Fig. 6D).

Elytra (Figs 6A, 8B) elongate, about 1.6 times as long as width combined; each elytron with ten longitudinal rows of window punctures on disc and one row of window punctures on explanate epipleuron; anterior portion of explanate epipleura with relatively narrow longitudinal groove (Figs 6E, 7F). Mesothoracic discrimen present

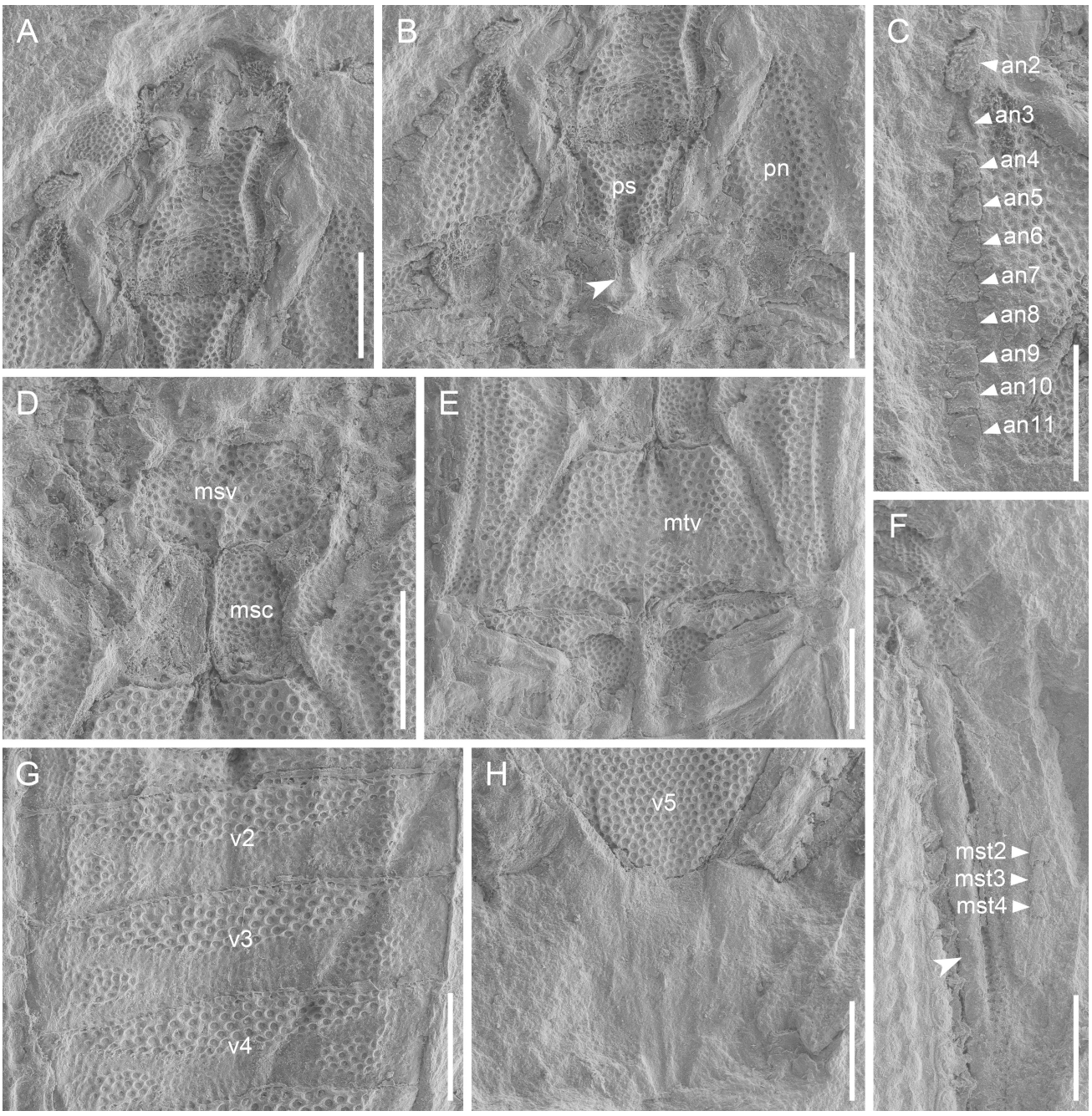

FIGURE 7. Details of *Notocupes daohugouensis* Li & Cai **sp. nov.**, holotype, NIGP174675, under scanning electron microscopy. **A**, Head. **B**, Prothorax, showing the well-developed prosternal process (arrowhead). **C**, Antenna. **D**, Mesothorax. **E**, Metathorax. **F**, Groove on the elytral epipleuron for housing mesotibia and -tarsus (arrowhead). **G**, Abdomen. **H**, Possible genitalia. Abbreviations: an2–11, antennomeres 2–11; msc, mesocoxa; msv, mesoventrite; mst2–4, mesotarsomeres 2–4; mtv, metaventrite; pn, pronotum; ps, prosternum; v2–5, ventrites 2–5. Scale bars: 500 μm.

only on posterior half. Mesocoxae contiguous (Fig. 7D). Metaventrite subtrapezoidal, with discrimen and katepisternal suture (Fig. 7E). Metepimeron exposed (Fig. 7E). Metacoxae transverse, contiguous.

Legs elongate. Femora stout. Tibiae thinner. Tarsi 5-segmented; tarsomere 5 not distinctly narrower than penultimate one (Figs 6E, 7F). Pretarsal claws simple.

Abdomen with five overlapping ventrites (Fig. 7G); ventrites 2–4 subequal in length; ventrite 5 subtriangular, about 2.3 times as long as ventrite 2.

Remarks. The trace of protruding genitalia seems to be preserved (Fig. 8C), although it is difficult to provide further description.

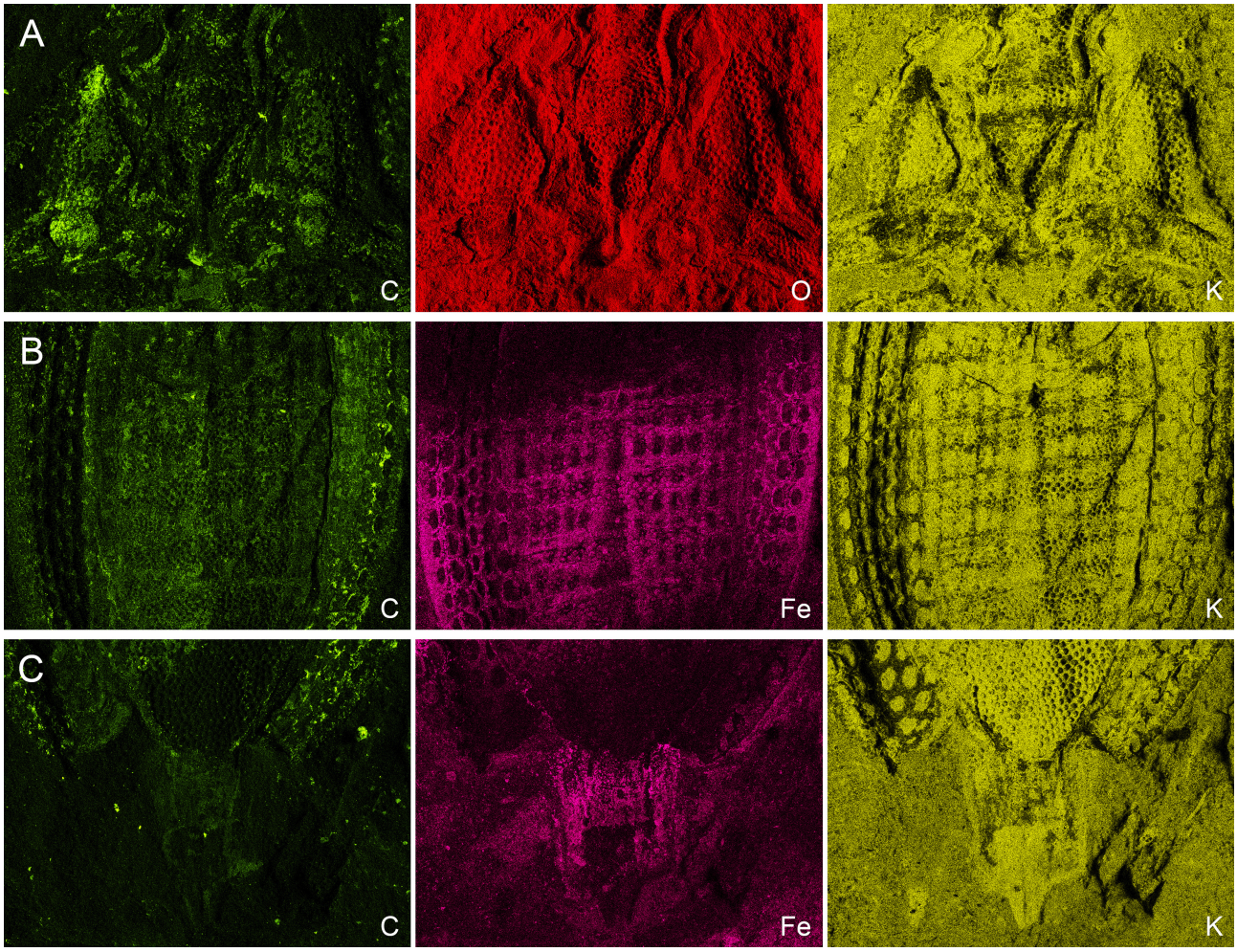

FIGURE 8. Elemental maps of *Notocupes daohugouensis* Li & Cai **sp. nov.**, holotype, NIGP174675, from energy dispersive X-ray spectroscopy. **A**, Prothorax. **B**, Abdomen and elytra. **C**, Possible genitalia.

***Notocupes* sp.** (Figs 9–12)

Material. BA202101, sex unknown.

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

Description. Body ovate, strongly dorsoventrally flattened, 13.3 mm long, 6.3 mm wide, covered with small setae/scales.

Head (Fig. 11A, B) subquadrate, prognathous; dorsal surface with a pair of distinct median protuberances posteriorly. Compound eyes hemispherical and strongly protruding. Antennal insertions dorsolaterally situated. Antenna 11-segmented, serratiform. Mandibles (Fig. 11A) relatively short, with horizontal cutting edge, gradually curved mesally with sharply acute apex. Maxillary palps (Fig. 12A) 4-segmented; apical palpomere gradually expanded distad. Labial palps 3(?)-segmented; apical palpomere gradually expanded distad. Prementum with deep central cavity. Mentum transverse, separated from gulamentum by distinct suture (Fig. 12B). Anterior part of gulamentum with subparallel longitudinal grooves extending from posterior tentorial pits. Gular sutures well separated.

Pronotal disc approximately 1.6 times as wide as long, expanding posteriorly; anterior angles strongly extending anteriorly; lateral edges denticulate, with seven denticles; dorsal surface with a pair of anterior protuberances and a single posterior protuberance (Figs 10A, 11G). Prosternum in front of coxae subquadrate (Fig. 11C); prosternal process relatively well developed, though not reaching posterior edge of procoxae (Fig. 12C). Procoxae not contiguous (Fig. 12C). Propleura probably not reaching anterior prothoracic margin (Fig. 12D). Protarsal groove present along pleurosternal and notosternal sutures (Fig. 12D).

Elytra (Fig. 10A) elongate, 1.5 times as long as width combined, mainly covered with scales; each elytron with ten longitudinal rows of window punctures

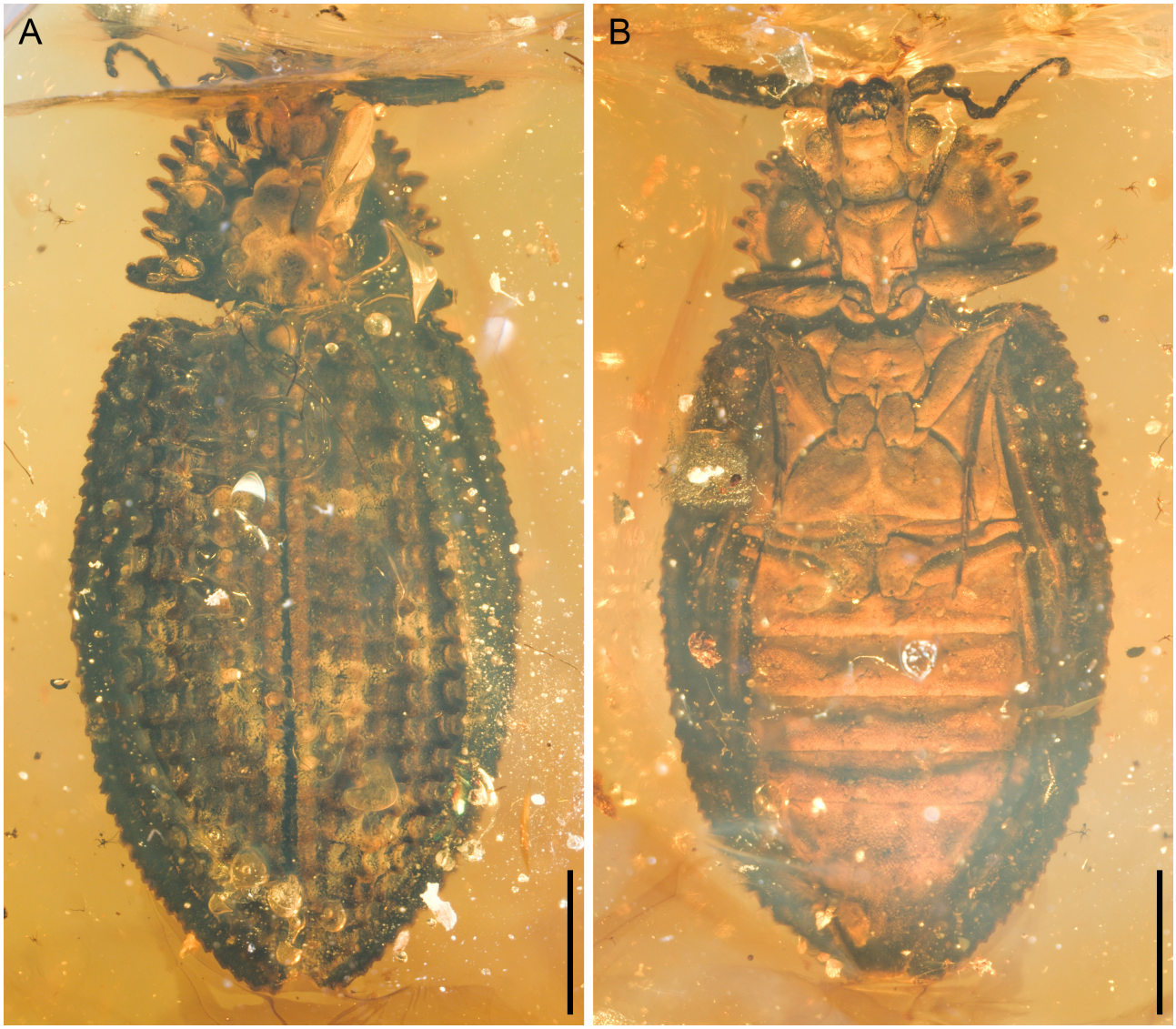

FIGURE 9. General habitus of *Notocupes* sp. in Cretaceous amber from Myanmar, BA202101, under incident light. **A**, Dorsal view. **B**, Ventral view. Scale bars: 2 mm.

on disc and one row of window punctures on explanate epipleuron (roughly 20 punctures per row); every two rows separated by distinctly raised vein; veins with coniform protuberances (spines *sensu* Kirejtshuk, 2020) (Fig. 12F); veins A1 and CuA fused before elytral apex (Fig. 11H); left elytra with posteriorly punctured sutural flange (Fig. 11H); anterior portion of explanate epipleura with longitudinal groove (Figs 10B, 11D). Mesoventrite at middle with acute anterior projection separating paired procoxal rests (Fig. 11E); mesothoracic discrimen present only on posterior quarter of mesoventrite. Mesocoxae contiguous (Fig. 11E). Region between mesepimeron and metanepisternum depressed for housing mesofemur (Figs 9B, 11E). Metaventrite subtrapezoidal, with discrimen and katepisternal suture. Metepimeron exposed (Fig. 9B). Metacoxae transverse, contiguous.

Legs elongate. Femora stout. Tibiae thinner, probably with two tibial spurs. Tarsi 5-segmented; tarsomeres (Figs 11D, 12D) covered with fine setae, with additional stout setae at apex; tarsomere 5 not distinctly narrower than penultimate one. Pretarsal claws simple.

Abdomen with five overlapping ventrites (Fig. 9B, C); ventrites 2–4 subequal in length; ventrite 5 subtriangular, about 3.3 times as long as ventrite 4, with truncate apex.

Remarks. The specimen BA202101 has a pair of anterior protuberances and a single posterior protuberance on pronotum, which differentiate it from *N. denticollis*, as the latter has only one pair of pronotal protuberances. The type specimens of *N. ohmkuhnlei* and *N. neli* are currently not available for our study. Since the differences between different *Notocupes* species are often subtle and hard to

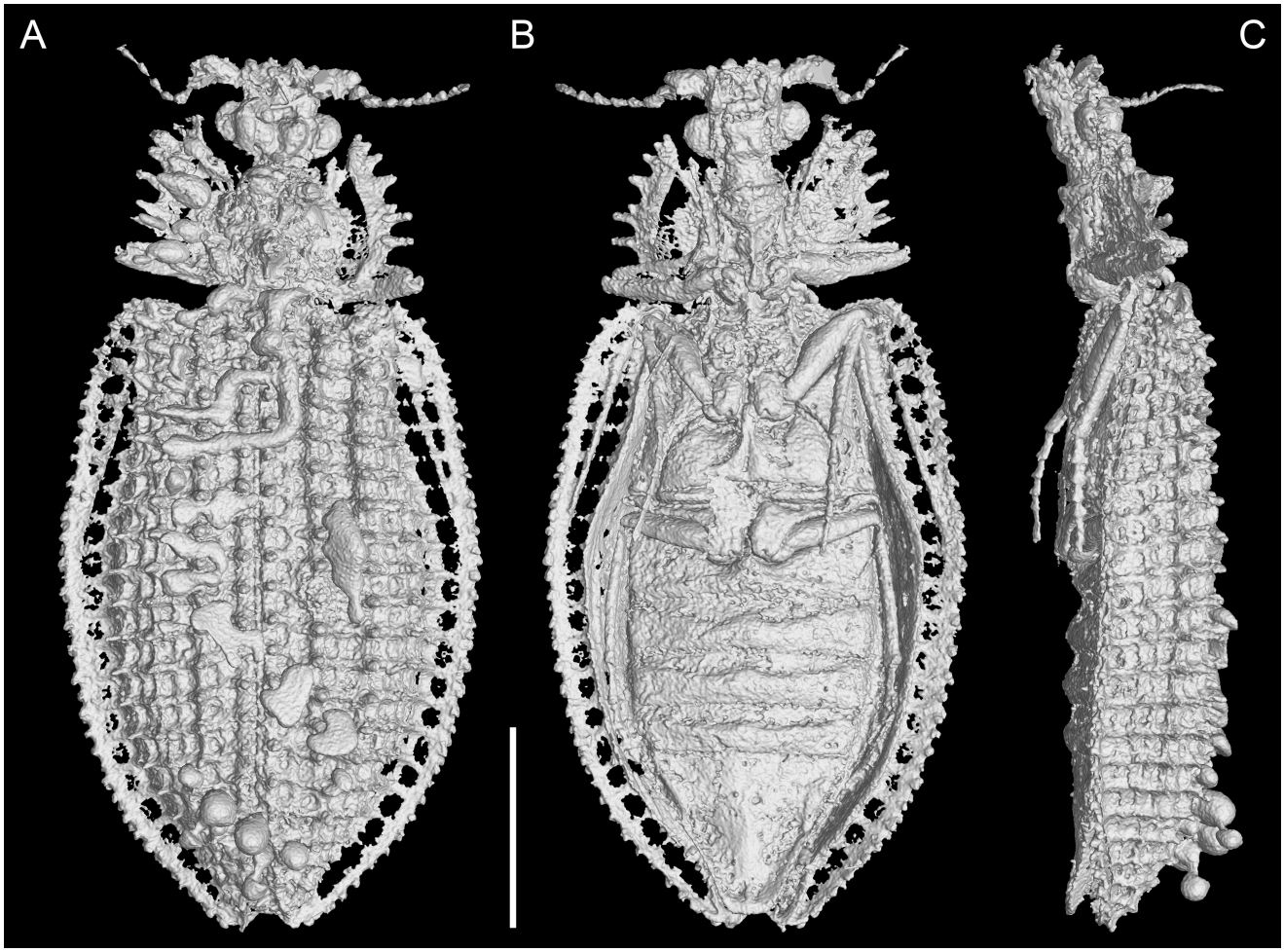

FIGURE 10. X-ray microtomographic reconstruction of *Notocupes* sp., BA202101. **A**, Dorsal view. **B**, Ventral view. **C**, Lateral view. Scale bars: 3 mm.

determine without examining the original specimens, we prefer not to establish a new species for BA202101 here.

Discussion

Circumscription of genus Notocupes

The name *Zygadenia* Handlirsch was proposed based on an isolated elytron. As elytra with similar morphology may belong to different biological taxa, we treat *Zygadenia* as a form genus, following the practice of Ponomarenko & Ren (2010) and Strelnikova & Yan (2021, 2023), while complete body fossils are placed in the genus *Notocupes*.

Due to the diversity of notocupedids in the Mesozoic fossil record, it is perhaps unsurprising that the group has a convoluted taxonomic history. The genus *Notocupes* was erected by Ponomarenko (1964) and subsequently synonymised with a number of genera including *Amblomma* Tan *et al.*, *Conexicoxa* Lin, *Forticupes* Hong & Wang, *Lupicupes* Ren, *Ovatocupes* Tan & Ren, *Picticupes* Hong & Wang, and *Sinocupes* Lin (Ponomarenko, 2006; Kirejtshuk *et al*., 2010), making it one of the largest beetle genera in the fossil record (as listed by Strelnikova & Yan, 2023). Nevertheless, some of the fossils may not belong to *Notocupes*. The only specimen of *Conexicoxa homora* Lin is so poorly preserved (Fig. 15), making it impossible to accurately determine its familial attribution (also noted by Kirejtshuk, 2020). The descriptions and line drawings of *Forticupes laiyangensis* Hong & Wang and *Picticupes tuanwangensis* Hong & Wang suggested no fusion between A1 and CuA (or Cu and M under the original elytral vein terminology by Hong & Wang, 1990), thus they are unlikely to be *Notocupes* if the drawings of Hong & Wang (1990) were correct. According to the original description and illustration by Zhang (1986), *Notocupes dischides* Zhang has nine rows of small and weak punctures on the elytra. We believe that "*N.*"

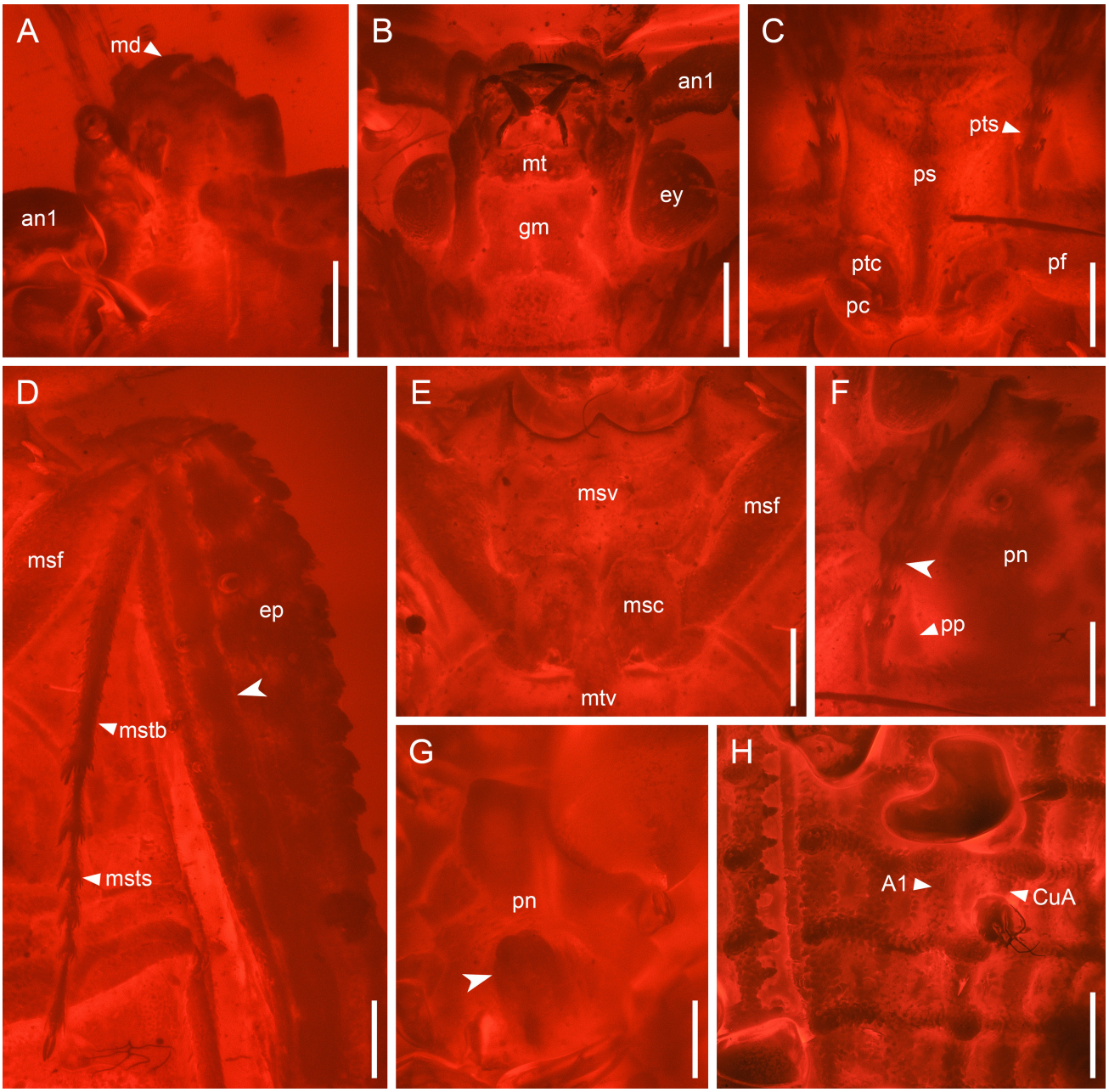

FIGURE 11. Details of *Notocupes* sp., BA202101, under widefield fluorescence. **A**, Anterior portion of head, dorsal view. **B**, Head, ventral view. **C**, Prothorax, ventral view. **D**, Groove on the elytral epipleuron for housing mesotibia and -tarsus (arrowhead), ventral view. **E**, Mesothorax, ventral view. **F**, Protarsus in the protarsal groove (arrowhead), ventral view. **G**, Prothorax, dorsal view, showing the single posterior protuberance (arrowhead). **H**, Elytron, dorsal view. Abbreviations: an1, antennomere 1; ep, epipleuron; ey, compound eye; gm, gulamentum; md, mandible; mt, mentum; msc, mesocoxa; msf, mesofemur; mstb, mesotibia; msts, mesotarsus; msv, mesoventrite; mtv, metaventrite; pc, procoxa; pf, profemur; pn, pronotum; pp, propleuron; ps, prosternum; ptc, protrochanter; pts, protarsus. Scale bars: 500 μm.

dischides is definitely not a member of Archostemata, but more likely a member of Polyphaga.

Echinocups *as a junior synonym of* Notocupes

Recently, Kirejtshuk & Jarzembowski (in Kirejtshuk, 2020) transferred all three *Notocupes* species described from Burmese amber to a newly established genus *Echinocups*. Our observations do not support a division between *Notocupes* and *Echinocups* and we retain the three species from Burmese amber in the genus *Notocupes*.

In Kirejtshuk (2020), the elytral venation of *Notocupes* (= *Zygadenia*) was described as having "A1 and Cu fused before apex and common vein ending on suture", while *Echinocups* was described as having "CuA and M fused and curved towards 1A subapically", probably based on the description and line drawing for *N.*

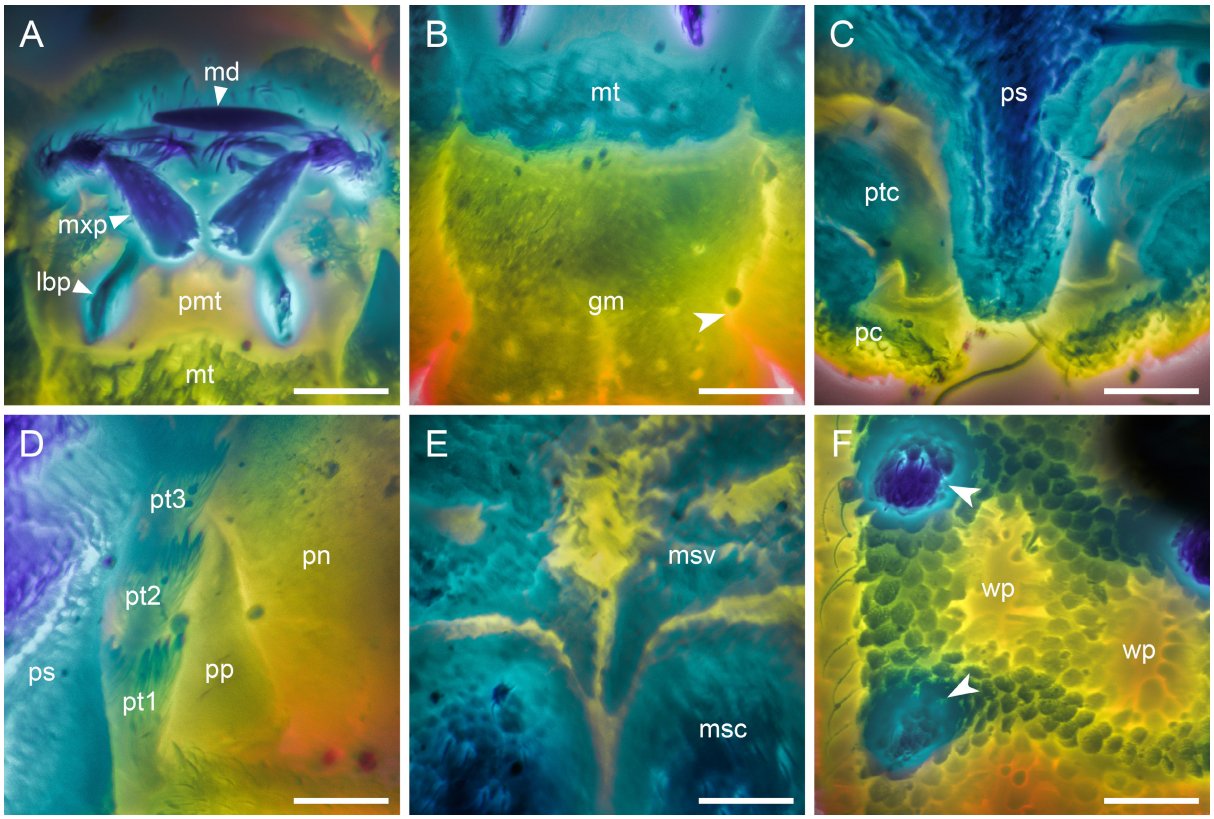

FIGURE 12. Details of *Notocupes* sp., BA202101, under confocal microscopy. **A**, Mouthparts, ventral view. **B**, Mentum and gulamentum, ventral view, showing the tentorial pit (arrowhead). **C**, Prothorax, ventral view. **D**, Protarsus in the protarsal groove, ventral view. **E**, Mesothorax, ventral view. **F**, Elytron, dorsal view, showing the coniform protuberances covered with scales (arrowheads). Abbreviations: gm, gulamentum; lbp, labial palp; md, mandible; mt, mentum; msc, mesocoxa; msv, mesoventrite; mxp, maxillary palp; pc, procoxa; pmt, prementum; pn, pronotum; pp, propleuron; ps, prosternum; pt1–3, protarsomeres 1–3; ptc, protrochanter; wp, window punctures. Scale bars: 200 μm.

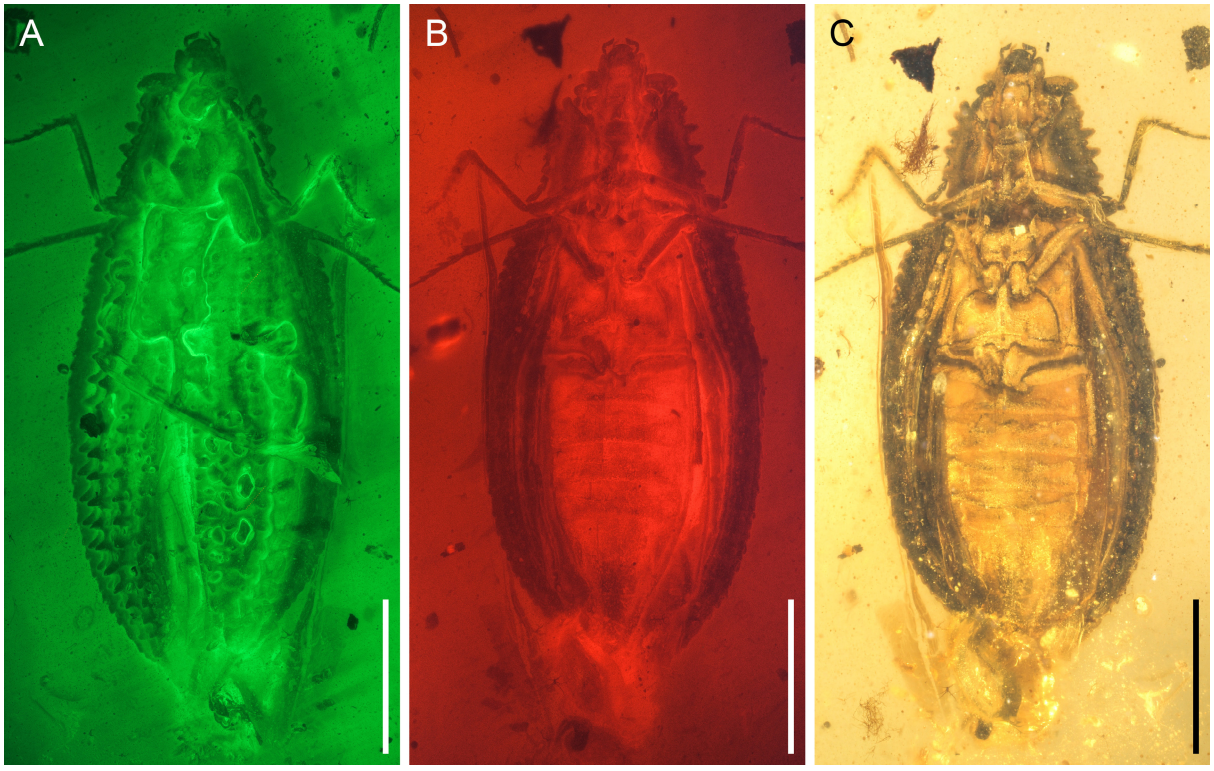

FIGURE 13. General habitus of *Notocupes denticollis* Jiang *et al.*, holotype, STJ311. **A**, Dorsal view, under widefield fluorescence. **B**, Ventral view, under widefield fluorescence. **C**, Ventral view, under incident light. Scale bars: 3 mm.

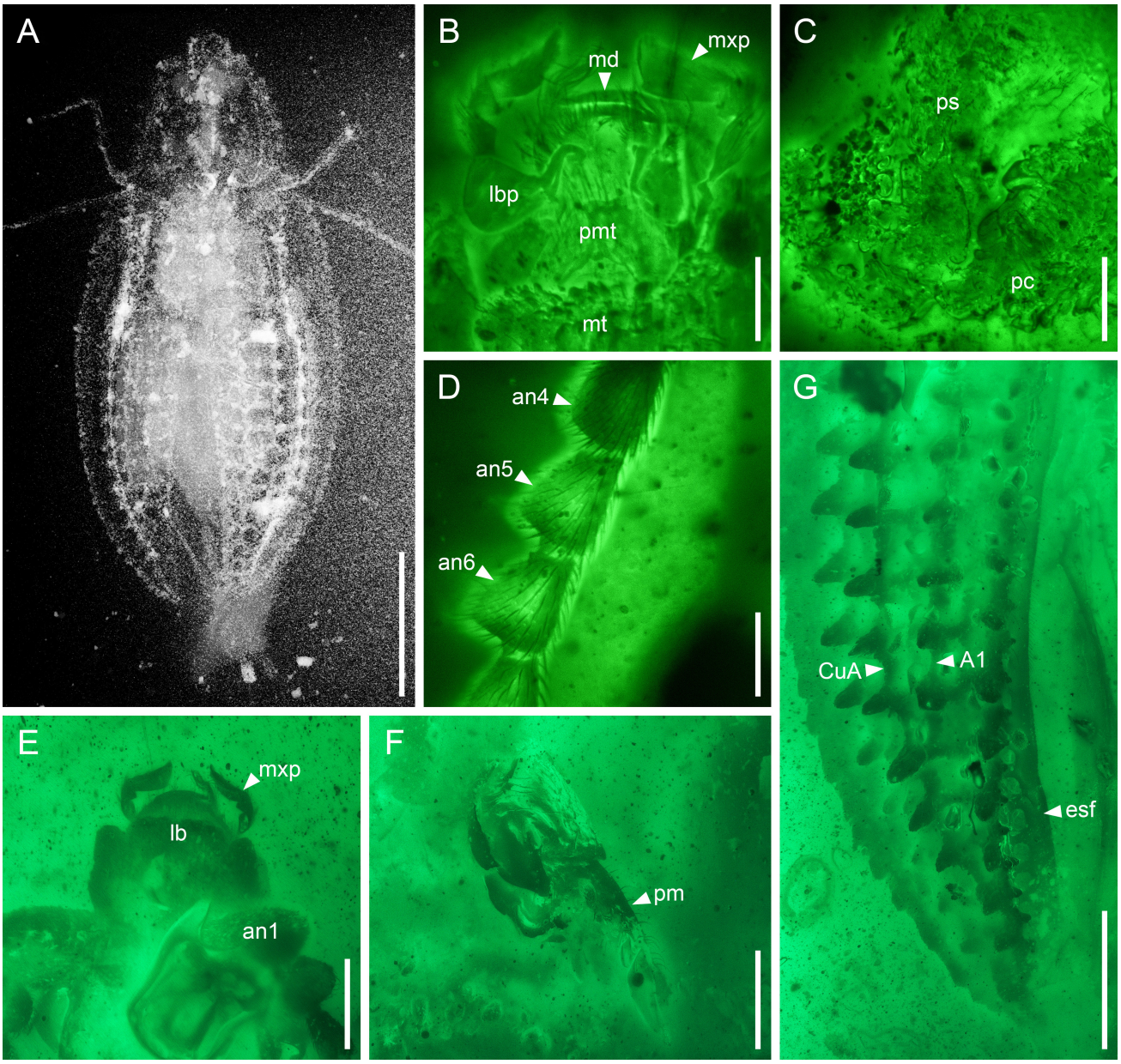

FIGURE 14. *Notocupes denticollis* Jiang *et al.*, holotype, STJ311. **A**, X-ray microtomographic reconstruction, rendered under "X-ray" mode. **B–D**, Under confocal microscopy. **B**, Mouthparts, ventral view. **C**, Prothorax, ventral view. **D**, Left antenna, dorsal view. **E**, Anterior portion of head, dorsal view. **F**, Aedeagus. **G**, Left elytron, dorsal view. Abbreviations: an1–6, antennomeres 1–6; esf, elytral sutural flange; lb, labrum; lbp, labial palp; md, mandible; mt, mentum; mxp, maxillary palp; pc, procoxa; pm, paramere; pmt, prementum; ps, prosternum. Scale bars: 3 mm in **A**, 1 mm in **G**, 500 μm in **E**, **F**, 200 μm in **B–D**.

ohmkuhnlei in Jarzembowski *et al*. (2020). However, the description in Jarzembowski *et al*. (2020) is problematic. First, the posterior region of elytra is not preserved in the *N. ohmkuhnlei* specimen, and thus the description and drawing are purely speculative and probably based on other *Notocupes* fossils (*e.g.*, *Amblomma* spp. in Tan & Ren, 2009, which were later transferred into *Notocupes*). Secondly, Jarzembowski *et al*. (2020) followed a different nomenclature (as Lubkin, 2007 and Tan & Ren, 2009 did) to define the elytral veins; thus although the description looks different, it refers to the same structures. Actually, Tihelka *et al.* (2019) clearly figured the venation of *N. neli* and described it as "veins A1 and CuA joining before apex", and Jiang *et al*. (2020) illustrated the venation of *N. denticollis* as A1 and CuA fused. Kirejtshuk (2020) somehow ignored the former, and treated the latter as erroneous without re-examining the specimens. Besides, as Kirejtshuk (2020) mentioned, the elytral venation of *Notocupes* has been described and illustrated inconsistently by previous researchers, and thus this character alone should not be used to differentiate *Notocupes* from similar genera.

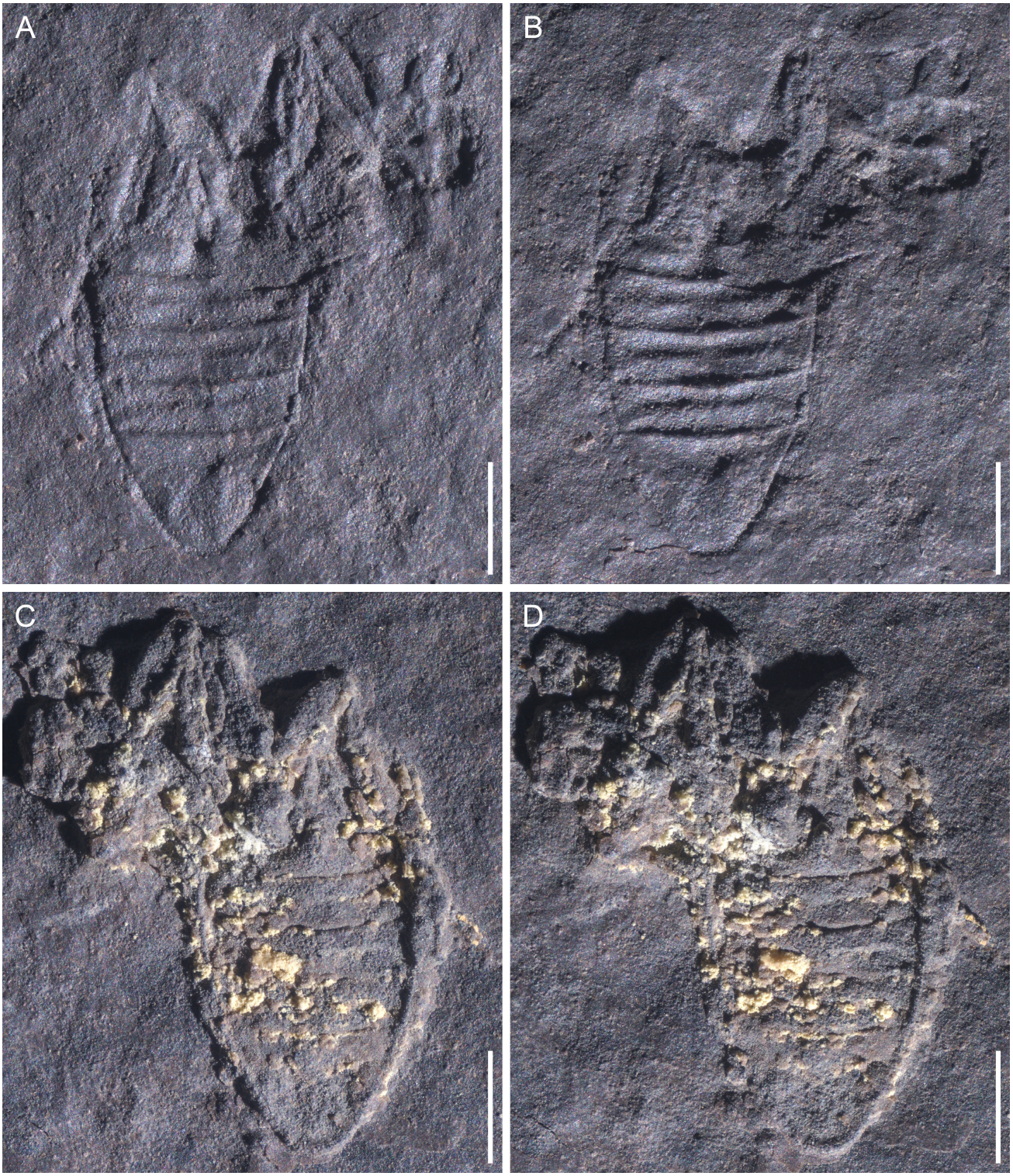

FIGURE 15. General habitus of *Conexicoxa homora* Lin, holotype, NIGP70058, under incident light. **A** and **B**, NIGP70058b. **C** and **D**, NIGP70058a. Scale bars: 1.5 mm.

Kirejtshuk (2020) suggested that the arrangement of abdominal ventrites could be used to separate *Echinocups* from *Notocupes*. He claimed that "the co-planar abdominal ventrites are characteristic of most ommatines [ommatids], including relatives of *Notocupes*", while the ventrites of *Echinocups* are overlapping. The non-overlapping ventrites of Notocupedini were also noted by Tan & Ren (2009). However, based on our observations, all *Notocupes* (or *Notocupes*-like) fossils in our collection have overlapping abdominal ventrites, which is also supported by Ponomarenko (1969, 2006), Ponomarenko & Ren (2010), Tan *et al*. (2012), and Strelnikova (2019), who suggested that overlapping abdominal ventrites may be a diagnostic character of *Notocupes* (or Notocupedini).

Kirejtshuk (2020) additionally listed the strongly dentate lateral edges of the pronotum and sharp spines on elytra as features differentiating *Echinocups* from *Notocupes.* Similar sharp spines on elytra are well-preserved in *N. spinosus* **sp. nov.** (Fig. 3D). However, since elytral spines are quite fine structures, they may not be easily preserved in adpression fossils. The presence of elytral spines in all *Notocupes* specimens from Burmese amber suggests that they might be widely distributed across the genus. The dentate pronotal edges are known in our *N. robustus* **sp. nov.** and various *Notocupes* species previously placed in *Amblomma* (Tan & Ren, 2009). The extent of dentation could also be interpreted as variability within a genus, and in itself is not sufficient to maintain *Echinocups* as a separate genus. Therefore, we treat *Echinocups* **syn. nov.** as a junior synonym of *Notocupes*. A phylogenetic analysis with a wide sampling of *Notocupes* species in future studies may however support division into multiple subgenera.

The position of genera Notocupoides*,* Rhabdocupes *and* Eurydictyon

Notocupes has recently been suggested as the sister group of Cupedidae *s.s.* (Li *et al*., 2023). However, the systematic placement of the enigmatic genera *Notocupoides* Ponomarenko, *Rhabdocupes* Ponomarenko and *Eurydictyon* Ponomarenko assigned to Notocupedini by Ponomarenko (1969) remains uncertain. Considering their somewhat *Notocupes*-like habitus and overlapping abdominal ventrites, it may be possible that they are closely related to *Notocupes*. However, in the illustrations by Ponomarenko (1966, 1969), they appeared to have contiguous procoxae. In contrast, *Notocupes* has procoxae separated by the prosternal process (Lee *et al*., 2022; Li *et al*., 2023; but also see Strelnikova & Yan, 2023). Nevertheless, sometimes this character cannot be reliably determined from adpression fossils. The discovery of better-preserved fossils or re-study of existing material might be helpful to clarify their position. If these genera indeed form a monophyletic group together with *Notocupes*, it might be appropriate to unit them in a new family (Notocupedidae).

Data availability

The following original data are available in Zenodo repository: confocal and micro-CT data of BA202101 (*Notocupes* sp.) [https://doi.org/10.5281/zenodo.4737035]; confocal and micro-CT data of STJ311 (*Notocupes denticollis*) [https://doi.org/10.5281/zenodo.4362697]; energy dispersive X-ray spectroscopy data of NIGP174673 (*Notocupes spinosus*) and NIGP174675 (*Notocupes daohugouensis*) [https://doi.org/10.5281/zenodo.7909737].

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