

Limnomma, a new genus of Ommatidae from the Middle Jurassic Daohugou beds (Coleoptera, Archostemata)

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Abstract

The relictual archostematan beetle family Ommatidae attained high diversity during the Mesozoic. Despite their once high taxonomic diversity and morphological disparity, many Mesozoic ommatid taxa remain poorly understood, partly due to limited preservation. Here we report an exceptionally well-preserved fossil, which we describe as a new ommatid genus and species, *Limnomma daohugouense* **gen. et sp. nov.**, from the mid-Jurassic Daohugou Lagerstätte in Northeast China. The new genus can be most easily distinguished from other ommatids by the presence of a circular non-tuberculate region on ventrite 5. The new taxon is discussed in relation to the classification of the Mesozoic genera *Brochocoleus* and *Burmocoleus*.

Key Words

Archostemata, Daohugou, Jurassic, *Limnomma*, Ommatidae

Introduction

Ommatidae is a small family in the beetle suborder Archostemata. While the group has been historically treated as a subfamily of the superficially similar-looking Cupedidae by some authors (e.g. Ponomarenko 1969), recent transcriptomic analyses have recovered ommatids as the sister group of Micromalthidae, hence supporting their status as a separate family (McKenna et al. 2019). Only three extant genera and seven species of Ommatidae are known from Australia and South America (Hörschemeyer and Beutel 2016, Escalona et al. 2020). However, this currently relictual family had a high diversity in the Mesozoic. Numerous fossil genera have been discovered from fossil sites across the continents of Europe and Asia (e.g. Ponomarenko 1969, Tan and Ren 2009, Kirejtshuk 2020). Though many fossil archostematans (including ommatids) have been found in China in the 20th century (e.g. Hong 1982, 1983, Ren 1995),

most of them are rather poorly preserved and are, therefore, of limited taxonomic and phylogenetic value. The discovery of well-preserved ommatid in compression-impression fossils in northeastern China (Tan and Ren 2009, Tan et al. 2012) and in amber from northern Myanmar (e.g. Yamamoto 2017, Jarzembowski et al. 2018, Li et al. 2020a, Tihelka et al. 2020) over the last decade greatly enhanced our understanding of the family's diversity.

The Middle Jurassic Daohugou beds represent a famous Jurassic Lagerstätte in Northeast China (Huang 2016). The fossil-bearing deposits at Daohugou have been correlated with the Haifanggou Formation at Beipiao (as summarised in Lian et al. 2021). Based on isotope analyses, the Daohugou beds have been dated to approximately 165 Ma (Chen et al. 2004, Yang and Li 2008). More than 700 insect species have been described from Daohugou beds over the past 20 years, including representatives of 23 orders (Lian et al. 2021). Many fossils from the

Daohugou beds are exceptionally well-preserved with remarkably fine details, providing invaluable information on the biology of these extinct organisms (e.g. Gao et al. 2012, Huang et al. 2013, Cai et al. 2014).

Considering the high biodiversity of Ommatidae in the Mesozoic, the ommatids from the Daohugou beds remain insufficiently studied, with only six species reported to date (Tan and Ren 2009, Tan et al. 2012). In this study, we report a new genus of Ommatidae from Daohugou, which further extends our knowledge on the morphological diversity of Mesozoic Ommatidae.

Materials and methods

The compression fossil studied herein (Figs 1–5) originates from Daohugou Village, Ningcheng County, Inner Mongolia, China (~ 165 Ma). Additional fossil ommatids from Burmese amber (Noije Bum, Hukawng Valley, Kachin State, northern Myanmar; ~ 99 Ma) were also ex-

amined for comparison. 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 specimen CNU-COL-BR2014808 (*Burmo-coleus zhiyuani*) is deposited in the Capital Normal University, Beijing, 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, compression fossils were moistened with 70% ethanol to improve the contrast of morphological characters. Widefield fluorescence images were captured with a Zeiss Axio Imager 2 light microscope combined with a fluorescence imaging system. Images under incident light and widefield fluorescence were stacked in Helicon Focus 7.0.2 or Zerene Stacker 1.04. Scanning electron microscopic (SEM) images were obtained with a Hitachi SU 3500 scanning electron microscope, operating with an accelerating voltage of 15 kV and a pressure of 80 Pa.



Figure 1. General habitus of *Limnomma daohugouense* gen. et sp. nov., holotype, NIGP176015, dry, under low-angle incident light. A. Part, NIGP176015a; B. Counterpart, NIGP176015b. Scale bars: 4 mm.



Figure 2. General habitus of *Limnomma daohugouense* gen. et sp. nov., holotype, NIGP176015, moistened with 70% ethanol, under incident light. **A.** Part, NIGP176015a; **B.** Counterpart, NIGP176015b. Scale bars: 4 mm.

The following specimens were examined for this study:

Limnomma daohugouense gen. et sp. nov.: NIGP176015 (holotype).

Burmocoleus zhiyuani (Liu et al., 2017): CNU-COL-BR2014808 (holotype).

Burmocoleus prisnyi Kirejtshuk, 2020: NIGP176016.

Burmocoleus sp.: NIGP176017.

Systematic palaeontology

Order Coleoptera Linnaeus, 1758

Suborder Archostemata Kolbe, 1908

Family Ommatidae Sharp & Muir, 1912

Genus *Limnomma* Li & Cai, gen. nov.

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Type species. *Limnomma daohugouense* sp. nov.

Etymology. The generic name is derived from the Greek “limne”, meaning lake, referring to its habitats around the Daohugou palaeolakes, and the generic name “Omma”, the type genus of Ommatidae. The name is neuter in gender.

Diagnosis. Head elongate, without distinct protuberances. Antennae subfiliform; antennomere 3 more than twice as long as 4. Antennal grooves absent. Gula sutures long, almost reaching posterior edge of head. Pronotal disc subtrapezoidal, with maximum width near base; lateral edges dentate. Elytra with distinct explanate epipleura; each epipleuron with only two rows of window punctures. Abdominal ventrites abutting; ventrite 5 with a slightly raised circular non-tuberculate region.

Remarks. The circular non-tuberculate region on ventrite 5 is the most important character differentiating *Limnomma* from all other extant or extinct ommatids. The shape of head, prothorax, and elytral epipleura could serve as additional characters differentiating *Limnomma* from other *Brochocoleus*-like fossils.

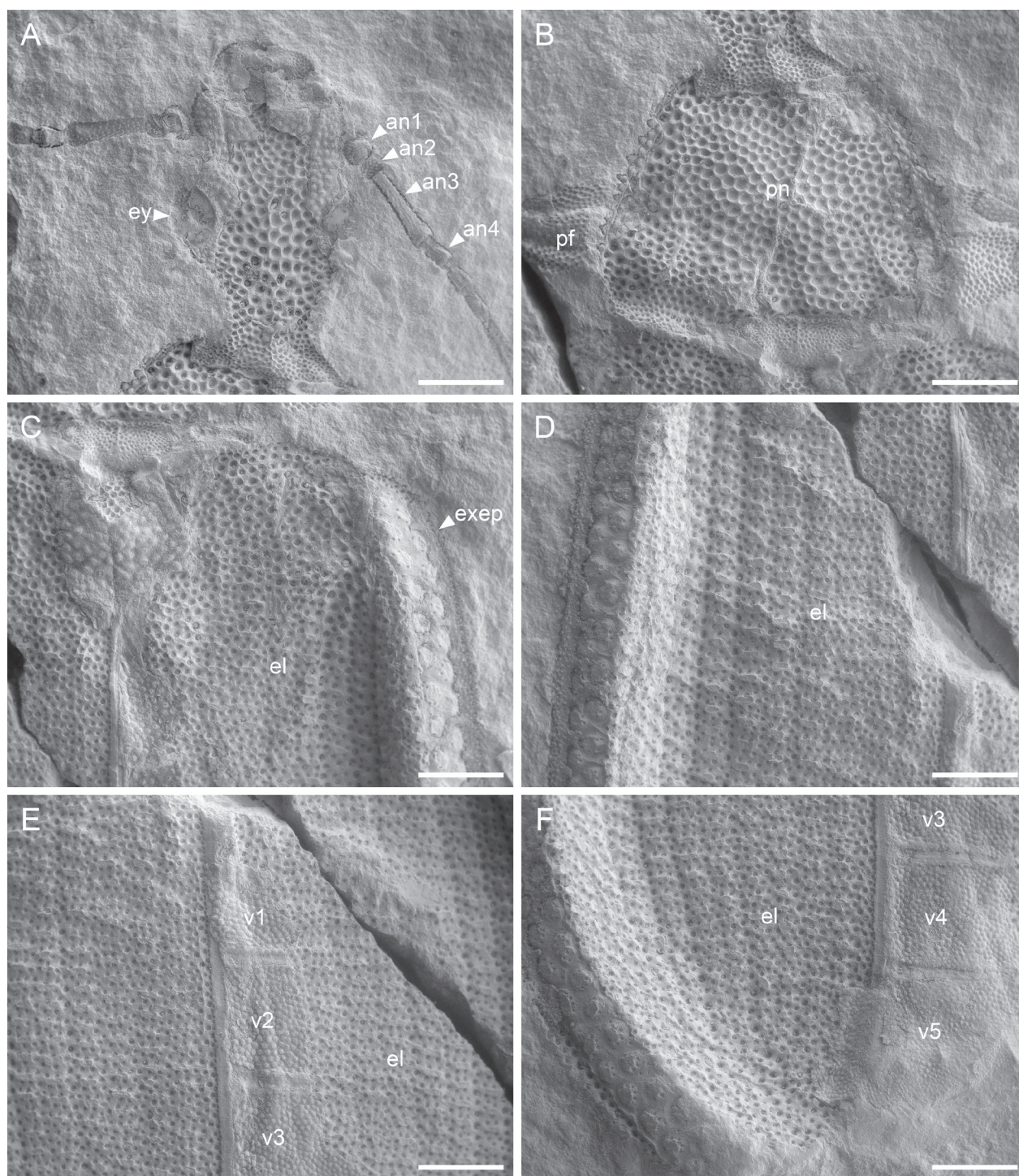


Figure 3. Details of *Limnomma daohugouense* gen. et sp. nov., holotype, NIGP176015a, under scanning electron microscopy. **A.** Head; **B.** Prothorax; **C.** Elytral base; **D.** Middle part of elytra; **E.** Elytra, with carbon film of abdominal ventrites partially showing; **F.** Elytral apex. Abbreviations: an1–4, antennomeres 1–4; el, elytron; exep, explanate epipleuron; ey, compound eye; pf, profemur; pn, pronotum; v1–5, ventrites 1–5. Scale bars: 1 mm.

***Limnomma daohugouense* Li & Cai, sp. nov.**

<https://zoobank.org/92EE1D83-E65B-4345-A343-694ECB200884>

Figures 1–5

Material. *Holotype*, NIGP176015.

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

Diagnosis. As for the genus.

Description. Body elongate, covered with rounded tubercles.

Head prognathous, elongate, constricted posteriorly to form a neck; dorsal surface without prominent posterior protuberances (Fig. 3A). Compound eyes protruding laterally (Fig. 5H). Antennal insertion area located antero-laterally. Antennal grooves absent. Postocular temples

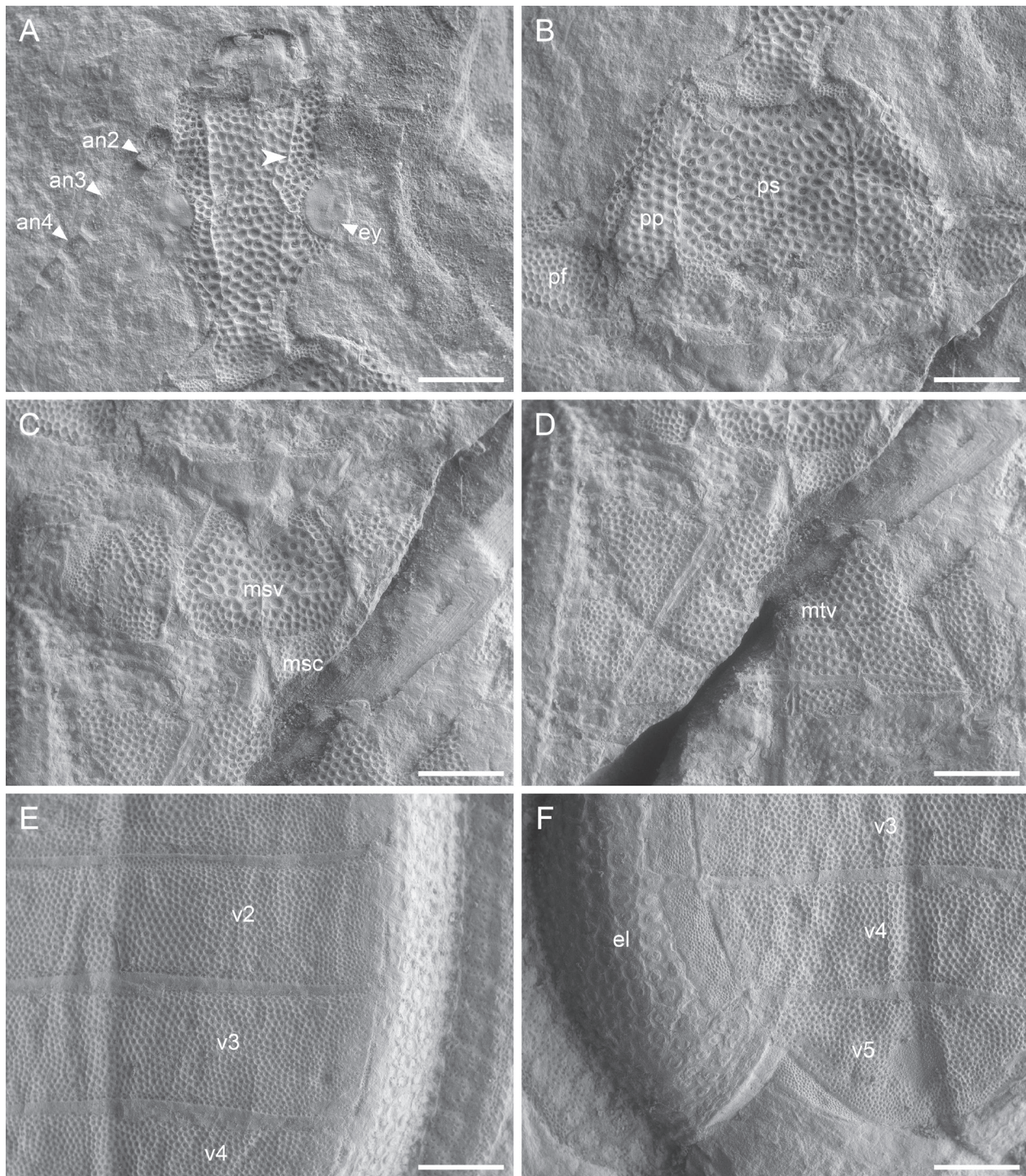


Figure 4. Details of *Limnomma daohugouense* gen. et sp. nov., holotype, NIGP176015b, under scanning electron microscopy. **A.** Head, with gula sutures highlighted (arrowhead); **B.** Prothorax; **C.** Mesothorax; **D.** Metathorax; **E.** Middle part of abdomen; **F.** Abdominal apex. Abbreviations: an2–4, antennomeres 2–4; el, elytron; ey, compound eye; msc, mesocoxa; msv, mesoventrite; mtv, metaventrite; pf, profemur; pp, propleuron; ps, prosternum; v2–5, ventrites 2–5. Scale bars: 1 mm.

not prominent. Antenna 11-segmented, short, extending beyond anterior prothoracic margin when posteriorly directed, but not reaching posterior prothoracic margin, with thin and short setae; antennomere 1 wider than other antennomeres; antennomere 2 distinctly small, subquadrate, about as wide as long; antennomere 3 elongate, 2.6 times as long as 4; antennomeres 4–10 short, subequal in length; antennomere 11 tapering apically. Mandibles probably

with vertical cutting edges (Fig. 5A). Gula sutures long, (almost) reaching posterior edge of head (Fig. 4A).

Pronotal disc subtrapezoidal, with maximum width near base, distinctly narrower than hind body (Fig. 3B); lateral edges dentate (Fig. 5D). Pronotal hypomeron very narrow. Propleura reaching anterior margin of prothorax (Fig. 4B). Prosternum (Fig. 4B) comparatively large, quadrate; prosternal process short. Procoxae contiguous.

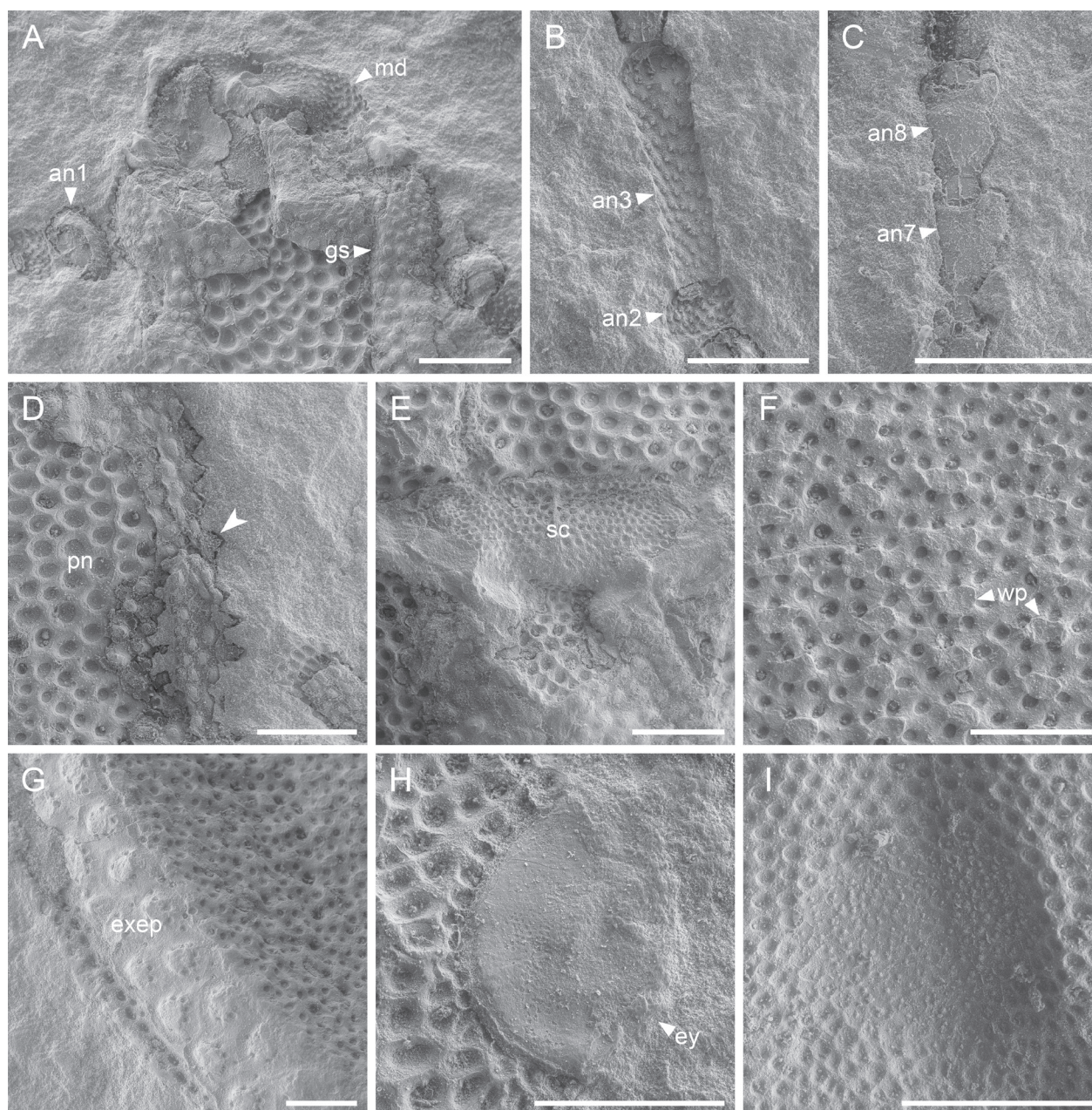


Figure 5. Details of *Limnomma daohugouense* gen. et sp. nov., holotype, NIGP176015, under scanning electron microscopy. A–G. NIGP176015a; **A.** Mouthparts; **B.** Antennomeres 2 and 3; **C.** Antennomeres 7 and 8; **D.** Dentate lateral edge of pronotal disc (arrowhead); **E.** Scutellum; **F.** Elytral disc; **G.** Explanate epipleuron; **H–I.** NIGP176015b; **H.** Compound eye; **I.** Non-tuberculate circular region on ventrite 5. Abbreviations: an1–8, antennomeres 1–8; exep, explanate epipleuron; ey, compound eye; gs, gula suture; md, mandible; pn, pronotum; sc, scutellum; wp, window punctures. Scale bars: 500 μ m.

Elytra elongate; each elytron with probably ten longitudinal rows of transverse maculated window punctures on disc and two rows of larger maculated window punctures on explanate epipleuron (Fig. 3C–F); longitudinal ridges (elytral veins) indistinct, with rounded tubercles (Fig. 5F). Mesoventrite with discrimen on posterior half (Fig. 4C). Mesocoxae contiguous. Metaventrite subtrapezoidal, with discrimen and katepisternal suture (Fig. 4D). Metacoxae transverse, contiguous.

Abdomen broad, with five coplanar ventrites, separated by distinct grooves; ventrites 2–5 subequal in length (Fig. 4E, F); ventrites 5 with a slightly raised non-tuberculate circular region in the middle (Fig. 5I).

Measurements of holotype. Body length, 21.8 mm; body width, 9.7 mm; head length (including neck), 3.9 mm; head width (including eyes), 2.3 mm; pronotal length, 4.1 mm; pronotal width, 3.0 mm; elytral length, 13.8 mm; elytral width (single), 4.8 mm.

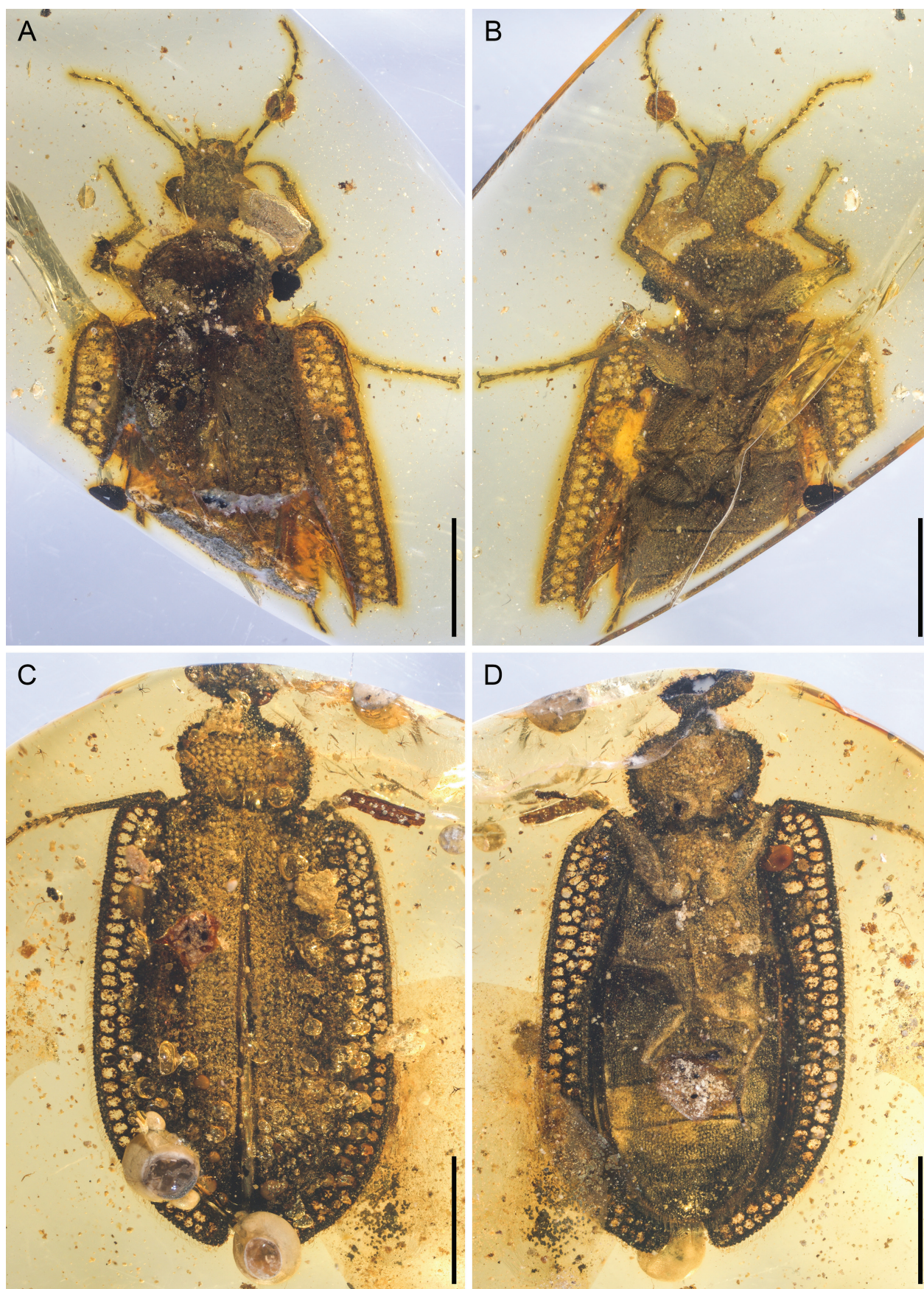


Figure 6. General habitus of *Burmocoleus*, under incident light. **A, B.** *Burmocoleus prisnyi*, NIGP176016; **A.** Dorsal view; **B.** Ventral view; **C, D.** *Burmocoleus* sp., NIGP176017; **C.** Dorsal view; **D.** Ventral view. Scale bars: 3 mm.

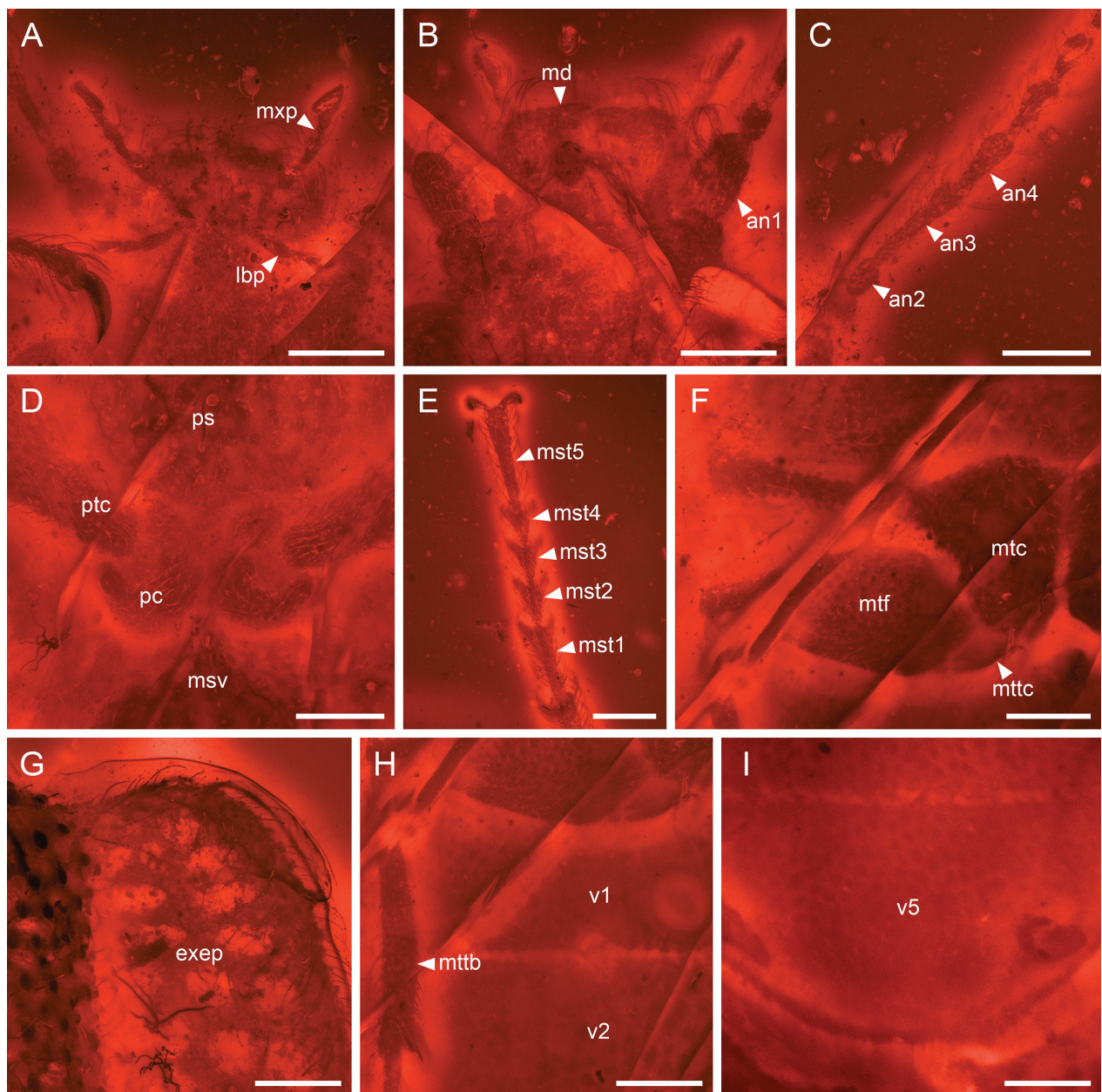


Figure 7. Morphological details of *Burmocoleus*, under widefield fluorescence. **A–H.** *Burmocoleus prisnyi*, NIGP176016; **A.** Mouthparts, ventral view; **B.** Mouthparts, dorsal view; **C.** Antenna, dorsal view; **D.** Procoxae, ventral view; **E.** Mesotarsus, ventral view; **F.** Hind leg, ventral view; **G.** Base of explanate epipleuron, dorsal view; **H.** Abdominal base, ventral view; **I.** *Burmocoleus zhiyuani*, holotype, CNU-COL-BR2014808, abdominal apex, ventral view. Abbreviations: an1–4, antennomeres 1–4; exep, explanate epipleuron; lbp, labial palp; md, mandible; mst1–5, mesotarsomeres 1–5; msv, mesoventrite; mtc, metacoxa; mtf, metafemur; mttb, metatibia; mttc, metatrochanter; mxp, maxillary palp; pc, procoxa; ps, prosternum; ptc, protrochanter; sc, scutellum; v1–5, ventrites 1–5. Scale bars: 500 µm.

Discussion

Brochocoleus Hong is a problematic fossil genus in Ommatidae. The first species assigned to this genus, *Br. punctatus* Hong, was described based on an isolated elytron (Hong 1982). Later, numerous Mesozoic fossils across Europe and Asia with wide explanate epipleura have been placed into *Brochocoleus* (e.g. Ponomarenko 1994, Tan and Ren 2009, Jarzembowski et al. 2013b). In a recent review, Kirejtshuk (2020) moved the *Brochocoleus* spe-

cies from Burmese amber to two new genera, and divided the majority of remaining species into *Brochocoleus* s.s. and *Diluticupes* Ren. This division was mainly based on differences in elytral venation. Though in some ommatids there are clear fusions between elytral veins, in many other ommatids the veins become weak and hardly traceable near the elytral apex. Thus, we think Kirejtshuk's division of *Brochocoleus* into *Brochocoleus* s.s. and *Diluticupes* is not supported by the available morphological evidence. Nevertheless, we agree that the current *Brocho-*

colemus is probably a heterogenous assemblage and needs further revision. The discovery of the aberrant ommatid *Stegocoleus* Jarzembowski and Wang demonstrated that the wide explanate epipleura could have evolved multiple times within Ommatidae (Jarzembowski and Wang 2016, Li et al. 2020b). Thus, wide epipleura alone cannot be regarded as a diagnostic character uniting the otherwise dissimilar species placed into *Brochocoleus*.

Limnomma gen. nov. is somewhat similar to the previously known fossils assigned to *Brochocoleus* in having distinct explanate epipleura. However, the new fossil can be easily differentiated from all previously-reported *Brochocoleus*-like fossils. In species assigned to *Brochocoleus*, the explanate epipleura are always wider and with more rows of window punctures in the basal region. In contrast, the explanate epipleura of *Limnomma* only have two rows of window punctures extending from the elytral base to the apex, and the epipleural width remains almost the same along the entire length. The epipleura of *Limnomma* are somewhat similar to *Burmocoleus* Kirejtshuk (Figs 6, 7), where the additional row of window punctures in the basal region is sometimes reduced and appears as a single window puncture (fig. 5C in Kirejtshuk 2020). However, the head and thoracic morphology of *Limnomma* differs distinctly from that of *Burmocoleus*. The pronotal disc of *Burmocoleus* is flattened and oval, reaching its maximum width at the middle, while the pronotal disc of *Limnomma* is subtrapezoidal, with maximum width near the base. The head of *Burmocoleus* is nearly as long as wide, while in *Limnomma*, the head is distinctly narrower. Besides, the gula sutures are present in *Limnomma*, but are absent in *Burmocoleus* (Fig. 6B).

The most notable character, differentiating *Limnomma* from all other ommatids, is the comparatively smooth circular region on the ultimate abdominal ventrite (Fig. 5I). The body surface of *Limnomma*, like other ommatids, is covered with rounded tubercles (Figs 3 and 4). However, in *Limnomma*, there is a slightly raised circular region without tubercles in the middle of ventrite 5. This character is absent in extant archostematan and has likewise not been previously reported in other fossils in this group. In the relatively well-preserved ommatids in Burmese amber we examined, we found no trace of such a smooth region (e.g. Fig. 7I). In *Lepicerus* (Myxophaga: Lepiceridae), there is a similar raised circular setose region on the last ventrite (fig. 11 in Shepard et al. 2005); however, its function has not been reported. We suppose that the raised circular region in *Limnomma* might have been involved in sensory or excretory function, although this is admittedly difficult to verify.

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