



<https://doi.org/10.11646/palaeoentomology.5.6.6>

<https://zoobank.org/urn:lsid:zoobank.org:pub:2487ECA7-762F-427A-9E87-12299E876AC0>

Parelateriformius from the Middle–Late Jurassic of China reinterpreted as the earliest Dascillidae (Coleoptera: Dascilloidea)

YAN-DA LI^{1,2}, ZHEN-YU JIN³, ADAM ŚLIPIŃSKI⁴, DI-YING HUANG¹ & CHEN-YANG CAI^{1,2,*}

¹State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China

²Bristol Palaeobiology Group, School of Earth Sciences, University of Bristol, Life Sciences Building, Tyndall Avenue, Bristol BS8 1TQ, UK

³Institute of Entomology, Agricultural College, Yangtze University, Jingzhou 434025, China

⁴Australian National Insect Collection, CSIRO, GPO Box 1700, Canberra ACT 2601, Australia

✉ ydli@pku.edu.cn; <https://orcid.org/0000-0002-9439-202X>

✉ ahk_731@163.com; <https://orcid.org/0000-0003-0245-0622>

✉ adam.slipinski@csiro.au; <https://orcid.org/0000-0002-1216-8068>

✉ dyhuang@nigpas.ac.cn; <https://orcid.org/0000-0002-5637-4867>

✉ cycail@nigpas.ac.cn; <https://orcid.org/0000-0002-9283-8323>

*Corresponding author

Abstract

The elateriform genus *Parelateriformius* Yan & Wang from the Middle–Late Jurassic Daohugou beds has been placed previously in the extinct Lasiosynidae or the extant Eulichadidae. Our reinvestigation of the type specimens and additional materials suggests that the character combination of *Parelateriformius* (e.g., tarsomeres 2–4 distinctly lobed, posterior pronotal margin crenulate, radial cell short and with truncate base, and metakatepisternal suture complete) is not accordant with either Lasiosynidae or Eulichadidae. Instead, it should belong to the family Dascillidae and appears closely related to the extant *Petalon*. A new species of *Parelateriformius* is also described, as *P. grimaldii* Li & Cai **sp. nov.** Our discovery highlights the antiquity of Dascillidae, which is consistent with the recent fossil-calibrated molecular dating of beetles.

Keywords: *Parelateriformius*, *Petalon*, Dascillidae, Lasiosynidae, fossil, Daohugou beds

Introduction

Dascillidae is a small family in the elateriform superfamily Dascilloidea, which has a complex taxonomic history (summarised by Jin *et al.*, 2013a; Lawrence, 2016a). Crowson (1971) proposed a close relationship between Dascillidae and Rhipiceridae (collectively as Dascilloidea), which has been supported by molecular studies (e.g., Zhang *et al.*, 2018; McKenna *et al.*, 2019; Cai *et al.*, 2022). Two subfamilies are currently recognised

in Dascillidae, *i.e.*, Dascillinae and Karumiinae, although the boundary between them is somewhat vaguely defined (Lawrence, 2016a; Kundrata *et al.*, 2021). The fossil record of Dascillidae is quite scarce. Kundrata *et al.* (2021) reported *Baltodascillus* Kundrata *et al.* from Eocene Baltic amber, and tentatively assigned it to the subfamily Karumiinae. Most other Cenozoic fossils once attributed to Dascillidae have since been removed, leaving only certain Miocene members of *Lyprodascillus* Zhang and *Dascillus* Latreille possibly belonging to the family (Jin *et al.*, 2013b). *Mesodascilla* Martynov from the Jurassic of Kazakhstan, originally included in Dascillidae (Martynov, 1926), has been transferred to Lasiosynidae or Eulichadidae (Kirejtshuk *et al.*, 2010; Kirejtshuk & Azar, 2013). Currently, the only Mesozoic dascillid genus known is the monotypic *Cretodascillus* Jin *et al.* from the Lower Cretaceous Yixian Formation in China (Jin *et al.*, 2013b).

Parelateriformius Yan & Wang (Figs 1–5) is a fossil genus of elateriform beetles, known only from the Daohugou beds in Northeast China (Yan & Wang, 2010). Four species were recognised in the genus by Yan & Wang (2010). *Parelateriformius* has been treated as a member of the extinct family Lasiosynidae (Kirejtshuk *et al.*, 2010; Yan *et al.*, 2014a), or as a member of Eulichadidae along with the incorporation of the whole Lasiosynidae into Eulichadidae (Kirejtshuk & Azar, 2013). However, some characters of *Parelateriformius* do not fit well with Lasiosynidae or Eulichadidae. After a re-examination of the *Parelateriformius* specimens from Daohugou,

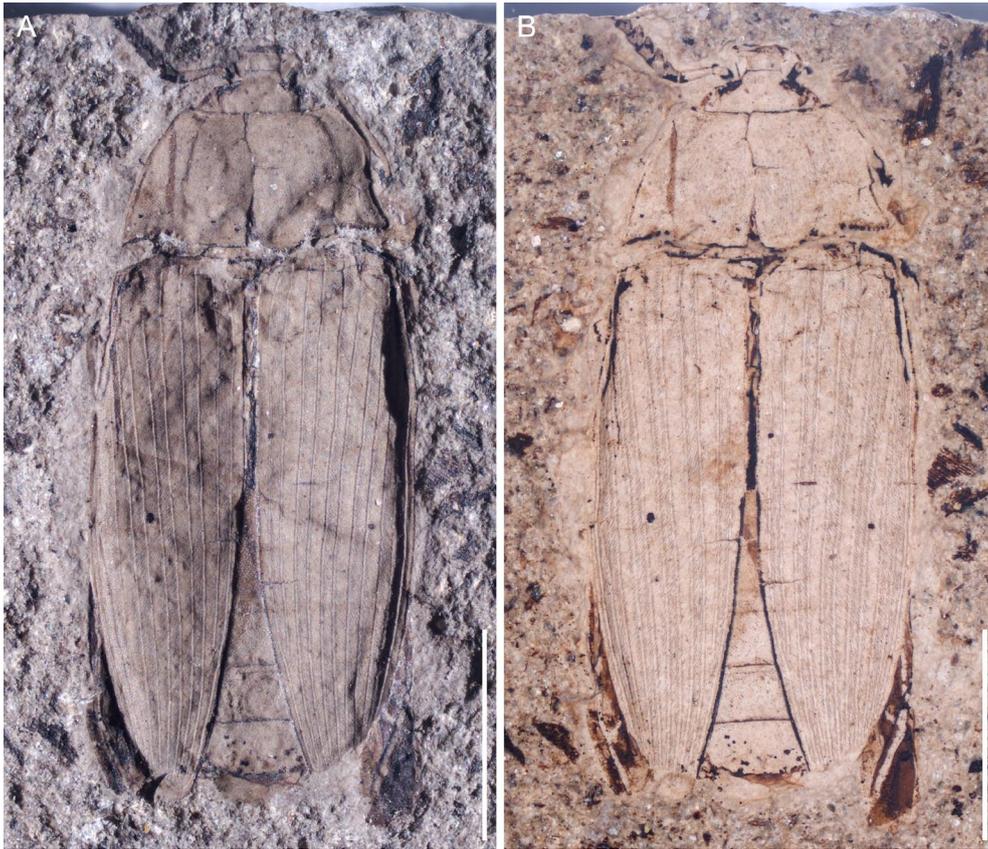


FIGURE 1. Habitus of *Parelateriformius grimaldii* Li & Cai sp. nov., holotype, NIGP200728b, under incident light, dry (A) or moistened with 70% ethanol (B). Scale bars = 4 mm.



FIGURE 2. Habitus of *Parelateriformius grimaldii* Li & Cai sp. nov., holotype, NIGP200728a, under incident light, dry (A) or moistened with 70% ethanol (B). Scale bars = 4 mm.

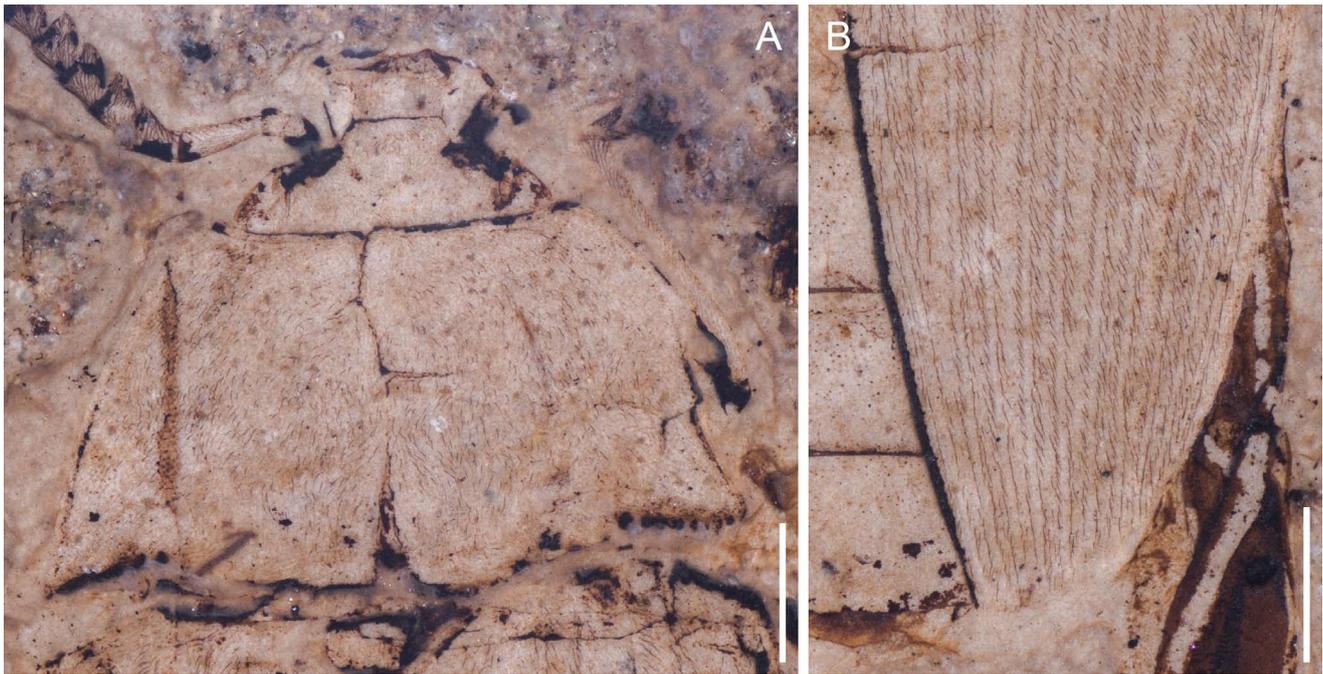


FIGURE 3. Details of *Parelateriformius grimaldii* Li & Cai **sp. nov.**, holotype, NIGP200728b, under incident light, moistened with 70% ethanol. **A.** Head and prothorax. **B.** Elytral apex. Scale bars = 1 mm.

we suggest that *Parelateriformius* clearly belongs to Dascillidae, and is closely related to the extant genus *Petalon* Schönherr of the extant subfamily Dascillinae (Fig. 6).

Materials and methods

All the fossil specimens of *Parelateriformius* studied herein originated from Daohugou Village, Ningcheng County, Inner Mongolia, China, and are deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China. The fossil-bearing Daohugou beds have produced a rich insect fauna (with more than 700 species described; Lian *et al.*, 2021).

Specimens of extant Dascillidae used for comparison are deposited in the Australian National Insect Collection (ANIC), Commonwealth Scientific and Industrial Research Organisation (CSIRO), Canberra, Australia.

Photographs under incident light were mainly taken with a Zeiss Discovery V20 stereo microscope, and were stacked in Helicon Focus 7.0.2. Where necessary, adpression fossils were moistened with 70% ethanol to improve the contrast of morphological characters. Scanning electron microscopic (SEM) images were obtained with a Hitachi SU 3500 scanning electron microscope, operating with an accelerating voltage of 20 kV and a pressure of 60

Pa. Images were further processed in Adobe Photoshop CC to adjust brightness and contrast. For the habitus photo of extant *Petalon fulvulus* (Wiedemann), due to aesthetic considerations, part of the right body was digitally replaced by the mirrored counterpart of the left body.

Systematic palaeontology

Order Coleoptera Linnaeus, 1758

Superfamily Dascilloidea Guérin-Méneville, 1843

Family Dascillidae Guérin-Méneville, 1843

Subfamily Dascillinae Guérin-Méneville, 1843

Genus *Parelateriformius* Yan & Wang, 2010

Type species. *Parelateriformius communis* Yan and Wang, 2010.

Remarks. The delimitation of species in *Parelateriformius* is quite problematic. Yan & Wang (2010) differentiated the species on the basis of the shape and size of body, head, antennomeres, pronotum and abdomen. However, these characters might be easily affected by taphonomy and could show great intraspecific variations (at least when following the species assignment by Yan & Wang, 2010), and therefore cannot sufficiently distinguish the species of *Parelateriformius*.

The most common and abundant species, *P.*

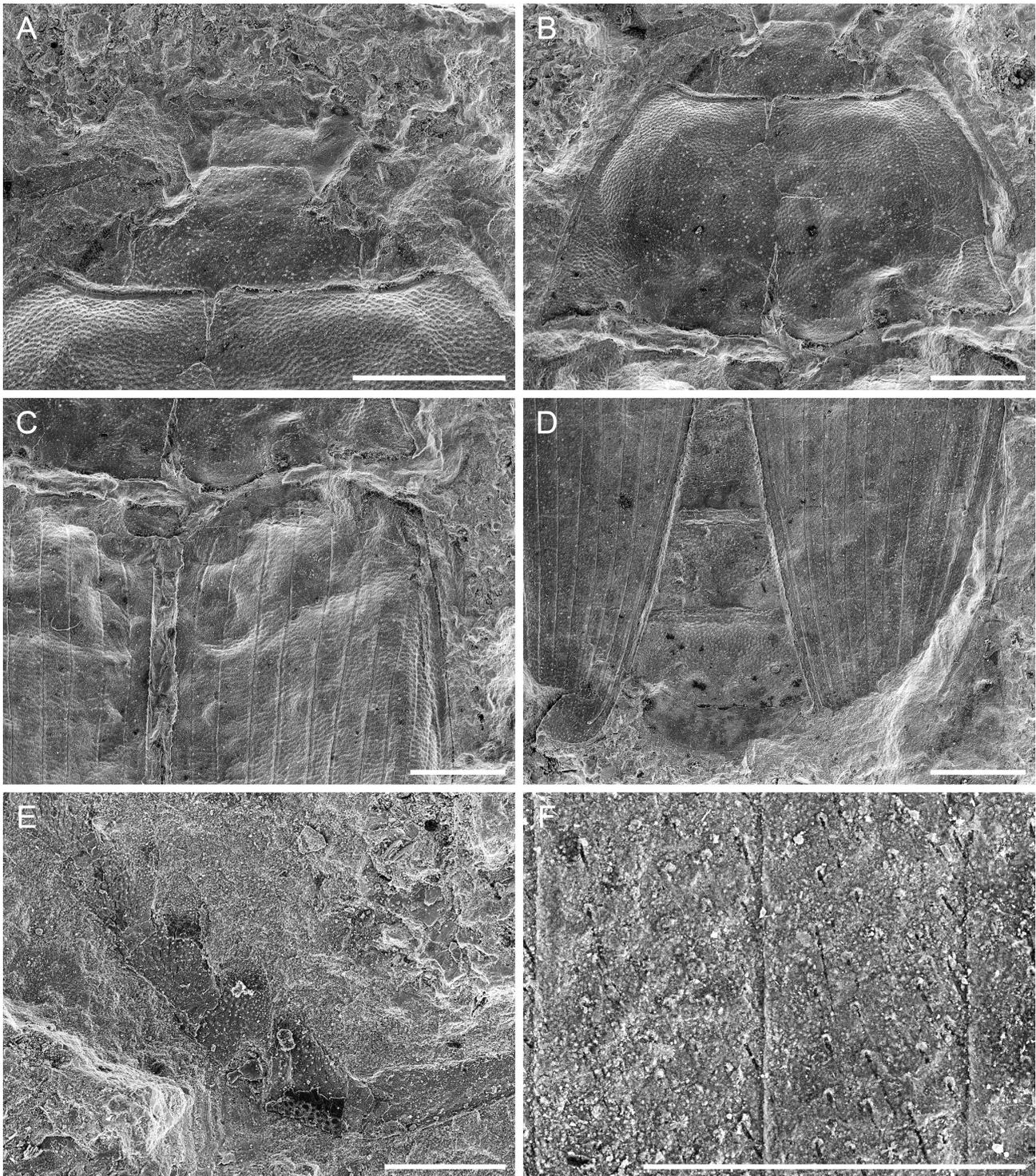


FIGURE 4. Details of *Parelateriformius grimaldii* Li & Cai **sp. nov.**, holotype, NIGP200728b, under scanning electron microscopy. **A**, Head. **B**, Prothorax. **C**, Elytral base. **D**, Elytral apex. **E**, Antenna. **F**, Hairs on elytron. Scale bars = 1 mm in **A–D**, 400 μ m in **E–F**.

communis Yan & Wang (Figs 7–19), could be well separated from *P. villosus* Yan & Wang (Figs 20–24) and *P. capitifossus* Yan & Wang (Figs 25–28) by the rather filiform (and only weakly serrate) antennae and the slenderer prosternal process. However, differentiating *P. villosus* and *P. capitifossus* would be more tricky.

The holotype of *P. villosus* (NIGP151553; Fig. 20) indeed shows a relatively weakly serrate antennae (*e.g.*, antennomeres 7–9 no more than twice as wide at apex as basal width) and a short abdominal ventrite 4 (about 0.65 time as long as ventrite 2), while the holotype of *P. capitifossus* (NIGP151558/151659; Figs 25, 26) has

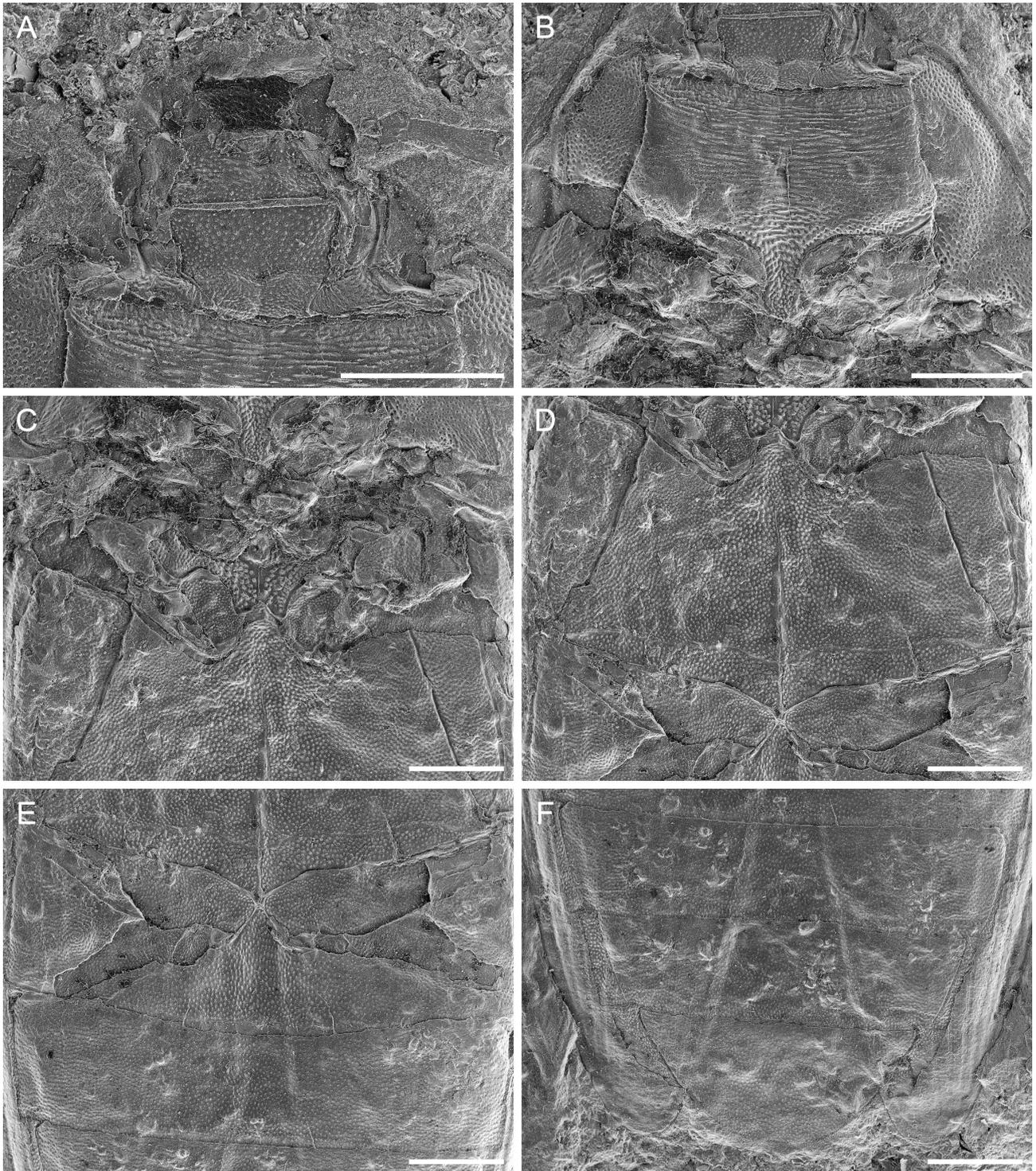


FIGURE 5. Details of *Parelateriformius grimaldii* Li & Cai **sp. nov.**, holotype, NIGP200728a, under scanning electron microscopy. **A**, Head. **B**, Prothorax. **C**, Mesothorax. **D**, Metathorax. **E**, Abdominal base. **F**, Abdominal apex. Scale bars = 1 mm.

distinctly serrate antennae (antennomeres 7–9 more than three times as wide at apex as basal width) and a longer ventrite 4 (about 0.9 time as long as ventrite 2). However, the specimen NIGP151658 (assigned to *P. villosus*; Fig. 22) has distinctly serrate antennae (antennomeres 7–9 more than three times as wide at apex as basal width), and the specimen NIGP151555 (assigned to *P. villosus*; Fig.

21) has a relatively long ventrite 4 (about 0.8 time as long as ventrite 2).

Parelateriformius mirabdominis Yan & Wang (Figs 29, 30), represented by a single poorly-preserved specimen, is the most troublesome species in the genus. Yan & Wang (2010) claimed that *P. mirabdominis* differs from all other species of *Parelateriformius* in the smaller

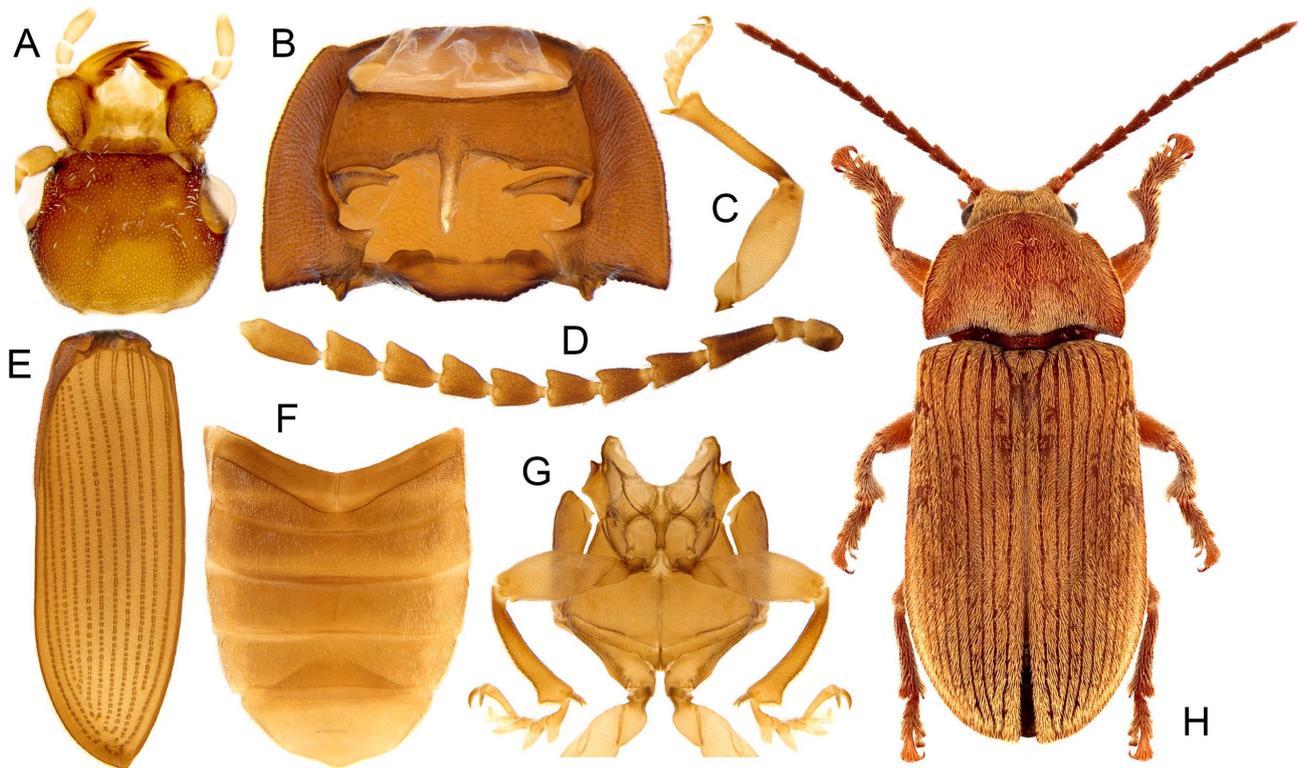


FIGURE 6. Extant *Petalon fulvulus* (Wiedemann) collected from Java, Indonesia. **A**, Head, dorsal view. **B**, Prothorax, ventral view. **C**, Fore leg. **D**, Antenna. **E**, Elytron, ventral view. **F**, Abdomen, ventral view. **G**, Meso- and metathorax, ventral view. **H**, Neotype of *Bruchus fulvulus* Wiedemann, habitus.

body size, with a body length of about 12.8 mm in the holotype (NIGP151560). However, the holotype of *P. capitifossus* (NIGP151558/151659) is even smaller than it, with a body length of about 12.5 mm (this length was erroneously measured by Yan & Wang, 2010). Yan & Wang (2010) also claimed that *P. mirabdominis* has a narrow head, but without providing quantitative definition for this character. The head (including eyes) of *P. mirabdominis* is about 0.5 time as wide as pronotal width (Fig. 29), which is not clearly narrower than that of other species. For example, the specimen NIGP151658 (assigned to *P. villosus*; Fig. 22) is only about 0.4 time as wide as pronotal width. Other characters used by Yan & Wang (2010) include the shape of the anterior margin of the pronotum and the shape of abdomen. However, these shapes could be easily affected by deformation during the formation of adpression fossils. For example, *P. villosus* was described by Yan & Wang (2010) as having a distinctly concave anterior pronotal margin, although the anterior pronotal margin is essentially straight in NIGP151658 (Fig. 22). Besides, sexual dimorphism, including variation in the shape of abdomen, is commonly recorded in extant Dascillidae (Jin *et al.*, 2013a, c, 2015, 2016, 2017; Li *et al.*, 2017; Wang *et al.*, 2020; Johnston & Gimmel, 2020). Since the antennae are not preserved in the holotype of

P. mirabdominis, we suggest that this species cannot be confidently separated from any other congeners.

Nevertheless, the primary goal of the present study is to re-evaluate the familial placement of *Parelateriformius*, rather than thoroughly revise the species within the genus. Therefore, we here simply follow the species assignments by Yan & Wang (2010) for those specimens reported in their study.

***Parelateriformius grimaldii* Li & Cai sp. nov.**
(Figs 1–5)

Material. Holotype, NIGP200728.

Etymology. The species is named after Prof. David A. Grimaldi, an entomologist extraordinaire.

Diagnosis. *Parelateriformius grimaldii* differs from all other species in having light and dark stripes on the elytra, where the dark (presumably stouter) hairs are present only in the odd-numbered interstriae space (the space between elytral suture and the first striae not counted). *Parelateriformius grimaldii* differs from *P. communis* additionally in having distinctly serrate antennae.

Locality and horizon. Daohugou Village, Ningcheng County, Inner Mongolia, China. Middle–Late Jurassic, Haifanggou Formation (Huang, 2019).

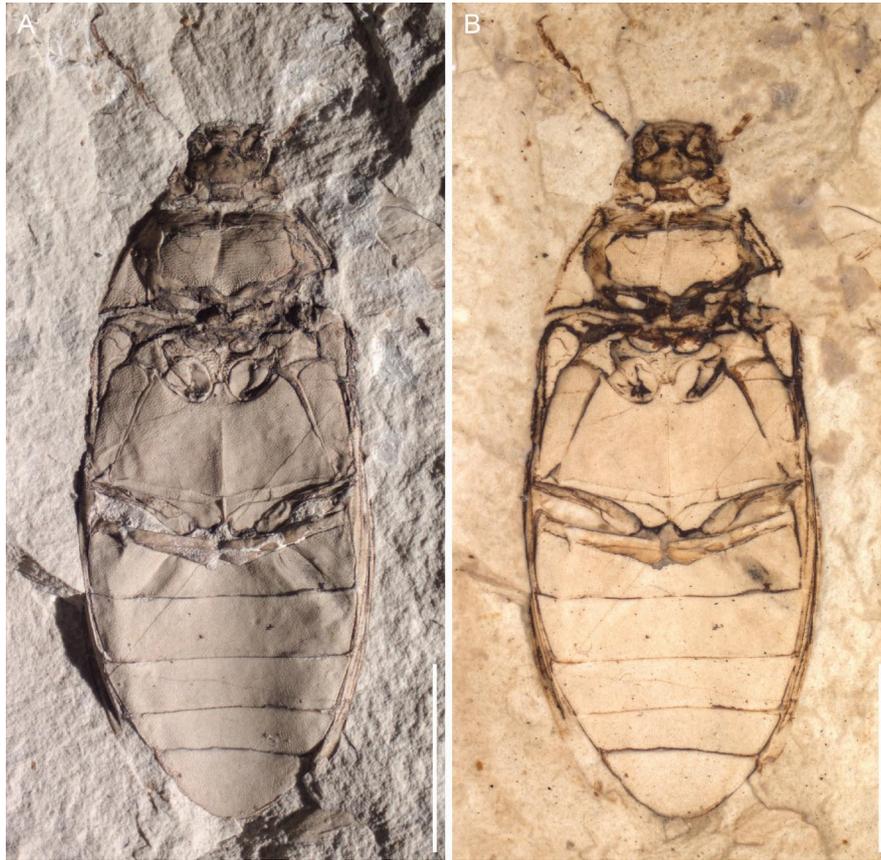


FIGURE 7. Habitus of *Parelateriformius communis* Yan & Wang, holotype, NIGP151537a, under incident light, dry (A) or moistened with 70% ethanol (B). Scale bars = 4 mm.



FIGURE 8. Habitus of *Parelateriformius communis* Yan & Wang, holotype, NIGP151537b, under incident light, dry (A) or moistened with 70% ethanol (B). Scale bars = 4 mm.



FIGURE 9. Habitus of *Parelateriformius communis* Yan & Wang, paratype, NIGP151539b, under incident light, dry (A) or moistened with 70% ethanol (B). Scale bars = 4 mm.



FIGURE 10. Habitus of *Parelateriformius communis* Yan & Wang, paratype, NIGP151539a, under incident light, dry (A) or moistened with 70% ethanol (B). Scale bars = 4 mm.

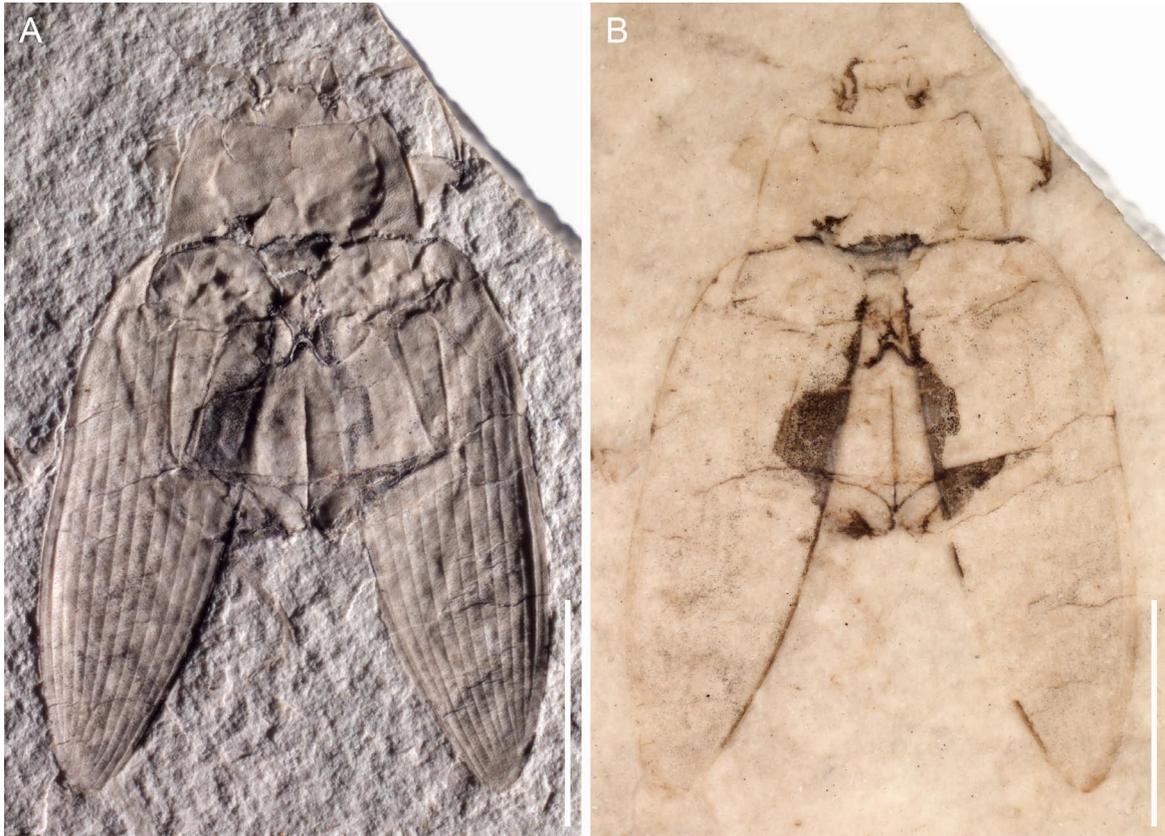


FIGURE 11. Habitus of *Parelateriformius communis* Yan & Wang, paratype, NIGP151542b, under incident light, dry (A) or moistened with 70% ethanol (B). Scale bars = 4 mm.



FIGURE 12. Habitus of *Parelateriformius communis* Yan & Wang, paratype, NIGP151542a, under incident light, dry (A) or moistened with 70% ethanol (B). Scale bars = 4 mm.



FIGURE 13. Habitus of *Parelateriformius communis* Yan & Wang, paratype, NIGP151543b, under incident light, dry (A) or moistened with 70% ethanol (B). Scale bars = 4 mm.

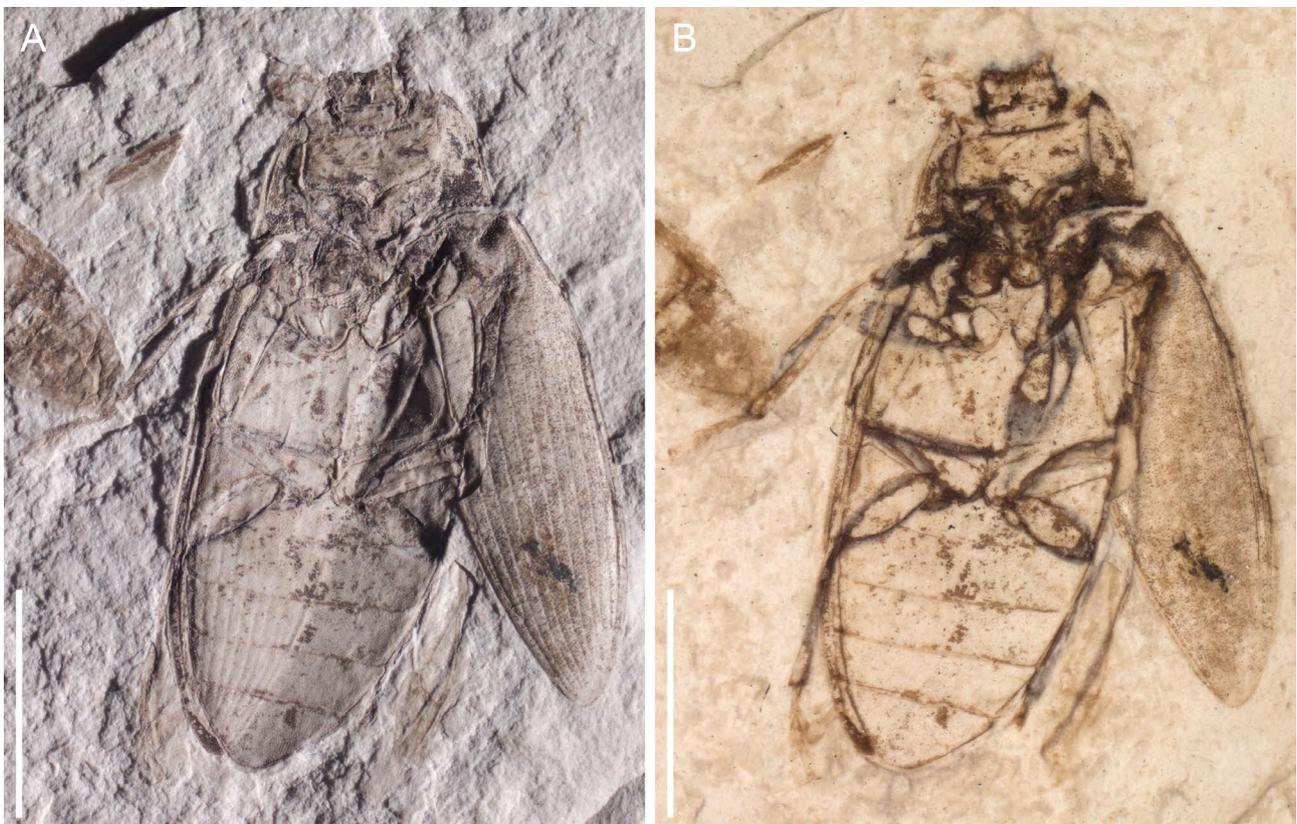


FIGURE 14. Habitus of *Parelateriformius communis* Yan & Wang, paratype, NIGP151543a, under incident light, dry (A) or moistened with 70% ethanol (B). Scale bars = 4 mm.

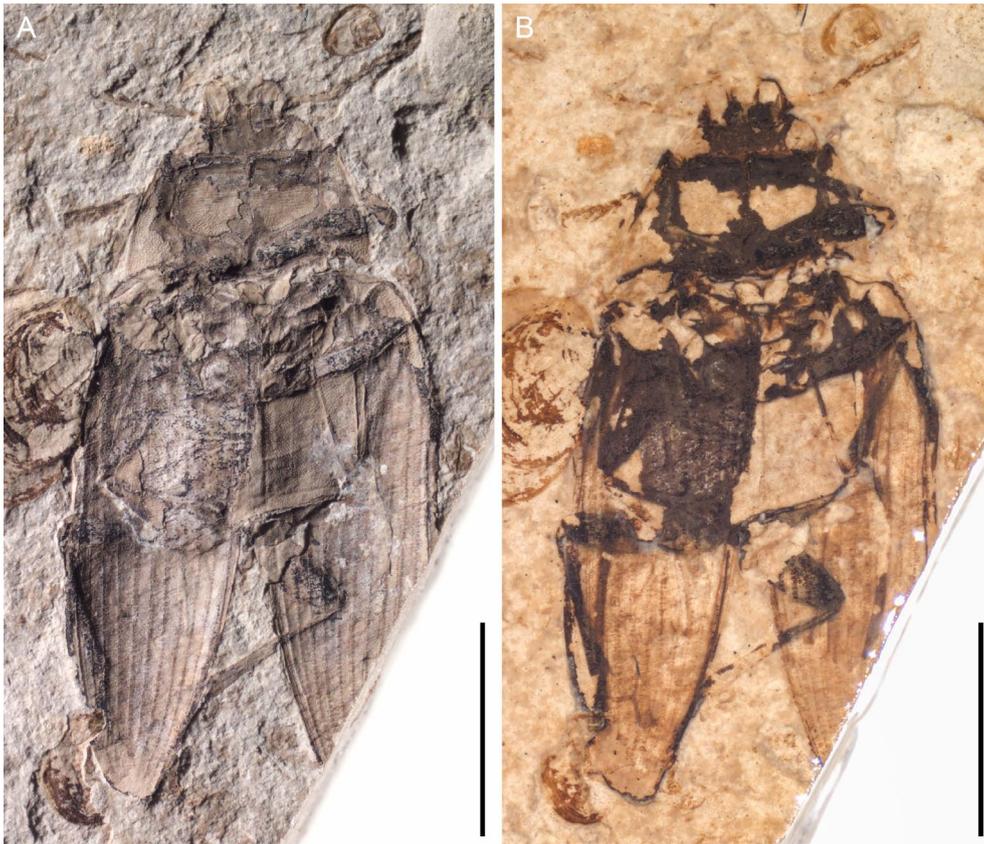


FIGURE 15. Habitus of *Parelateriformius communis* Yan & Wang, paratype, NIGP151544, under incident light, dry (A) or moistened with 70% ethanol (B). Scale bars = 4 mm.

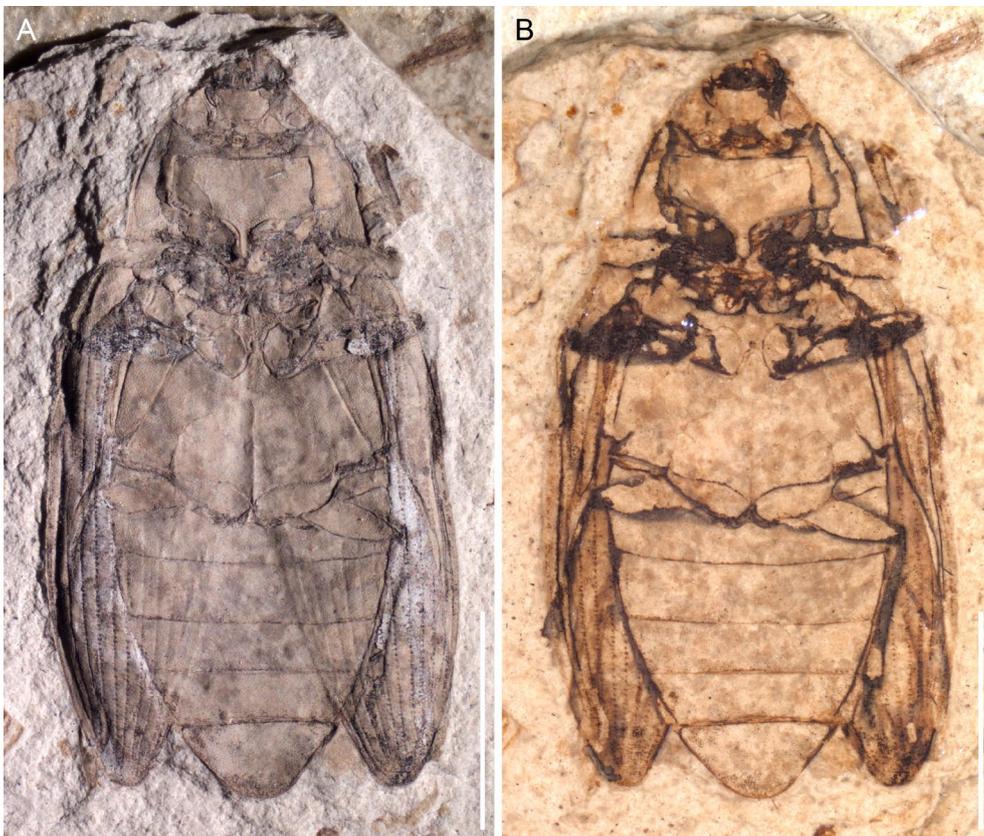


FIGURE 16. Habitus of *Parelateriformius communis* Yan & Wang, paratype, NIGP151546, under incident light, dry (A) or moistened with 70% ethanol (B). Scale bars = 4 mm.

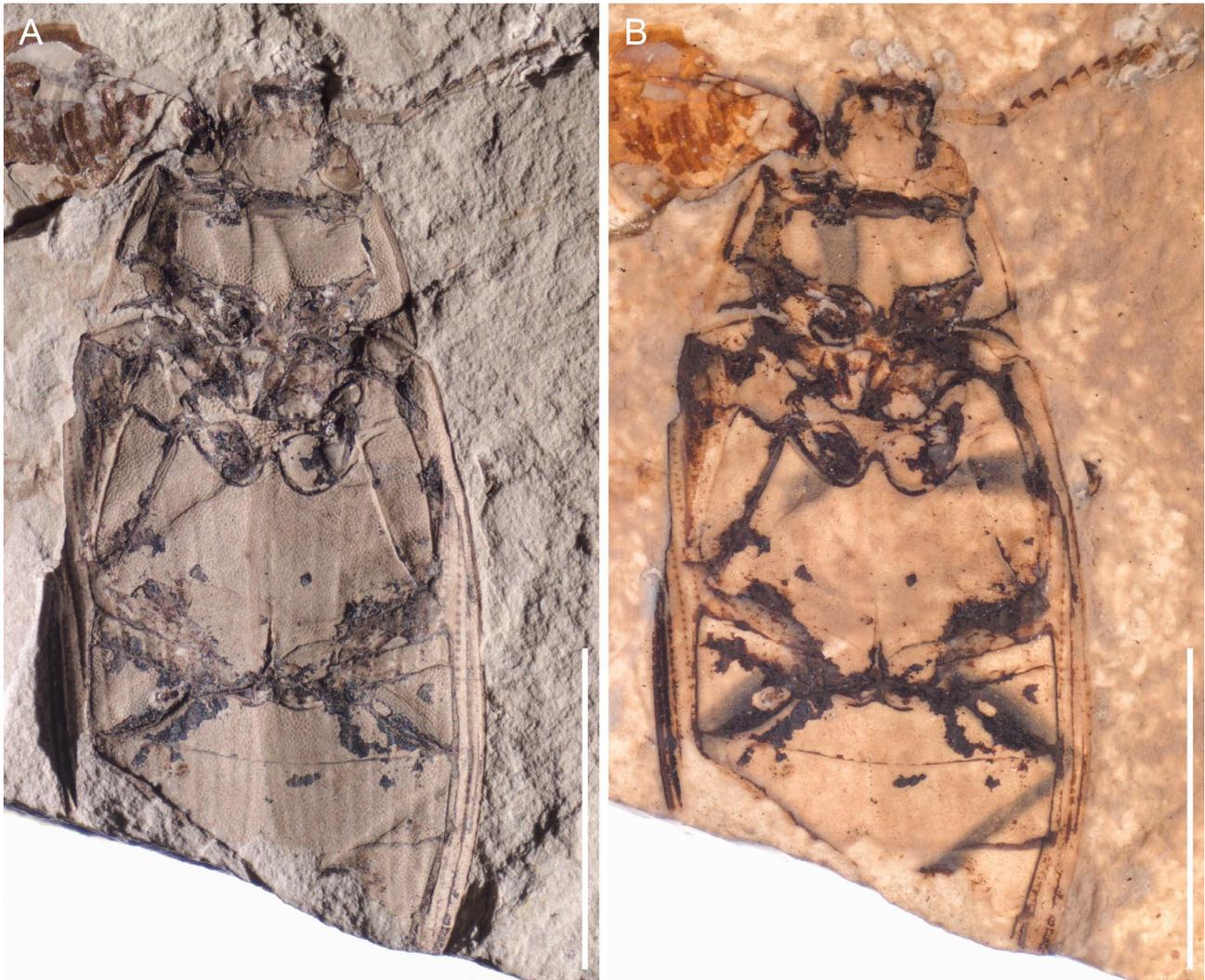


FIGURE 17. Habitus of *Parelateriformius communis* Yan & Wang, paratype, NIGP151563, under incident light, dry (A) or moistened with 70% ethanol (B). Scale bars = 4 mm.

Description. Body moderately elongate, 14.3 mm long, 6.1 mm wide; surface punctate. Head about half as wide as maximum prothoracic width (Fig. 3A). Clypeus trapeziform (Figs 3A, 4A). Labrum half as long as wide (Figs 3A, 4A). Antennomeres 1 and 2 relatively small; antennomere 2 subquadrate; antennomere 3 elongate, about 3.0 times as long as apical width; antennomeres 4–8 distinctly serrate, about as wide as long; antennomeres 9–11 not preserved (Fig. 3A). Pronotal disc about 2.0 times as wide as length along middle; posterior angles protruding posterolaterally, acute; posterior margin crenulate (Figs 3A, 4B). Prosternum in front of coxae transverse, about 2.2 times as wide as length (Fig. 5B). Prosternal process relatively wide, about 0.4 time as wide as length; apex rounded (Fig. 5B). Procoxal cavities strongly transverse (Fig. 5B). Elytron each 3.6 times as long as width, with 11 striae (Fig. 4C, D) (erroneously described as having ten striae for the genus by Yan & Wang, 2010); stria 2

interrupted at three-fourths of elytron length (Figs 3B, 4D); interstriae with light and dark patterns, with dark hairs present only in odd-numbered interstriae (Figs 1B, 3B, 4F). Mesoventrite with distinct discrimen (Fig. 5C). Metaventrite with distinct discrimen and katepisternal suture (Fig. 5D). Abdomen (Fig. 5E, F) with five ventrites; ventrite 4 about 0.9 time as long as ventrite 2; ventrite 5 apically broadly rounded.

Discussion

Parelateriformius was first reported by Yan & Wang (2010), who suggested that *Parelateriformius* should be closely related to the elateriform fossil genera *Lasiosyne* Tan *et al.*, *Brachysyne* Tan & Ren and *Pappisyne* Tan & Ren. Kirejtshuk *et al.* (2010) formally included these genera in an exclusively fossil family,

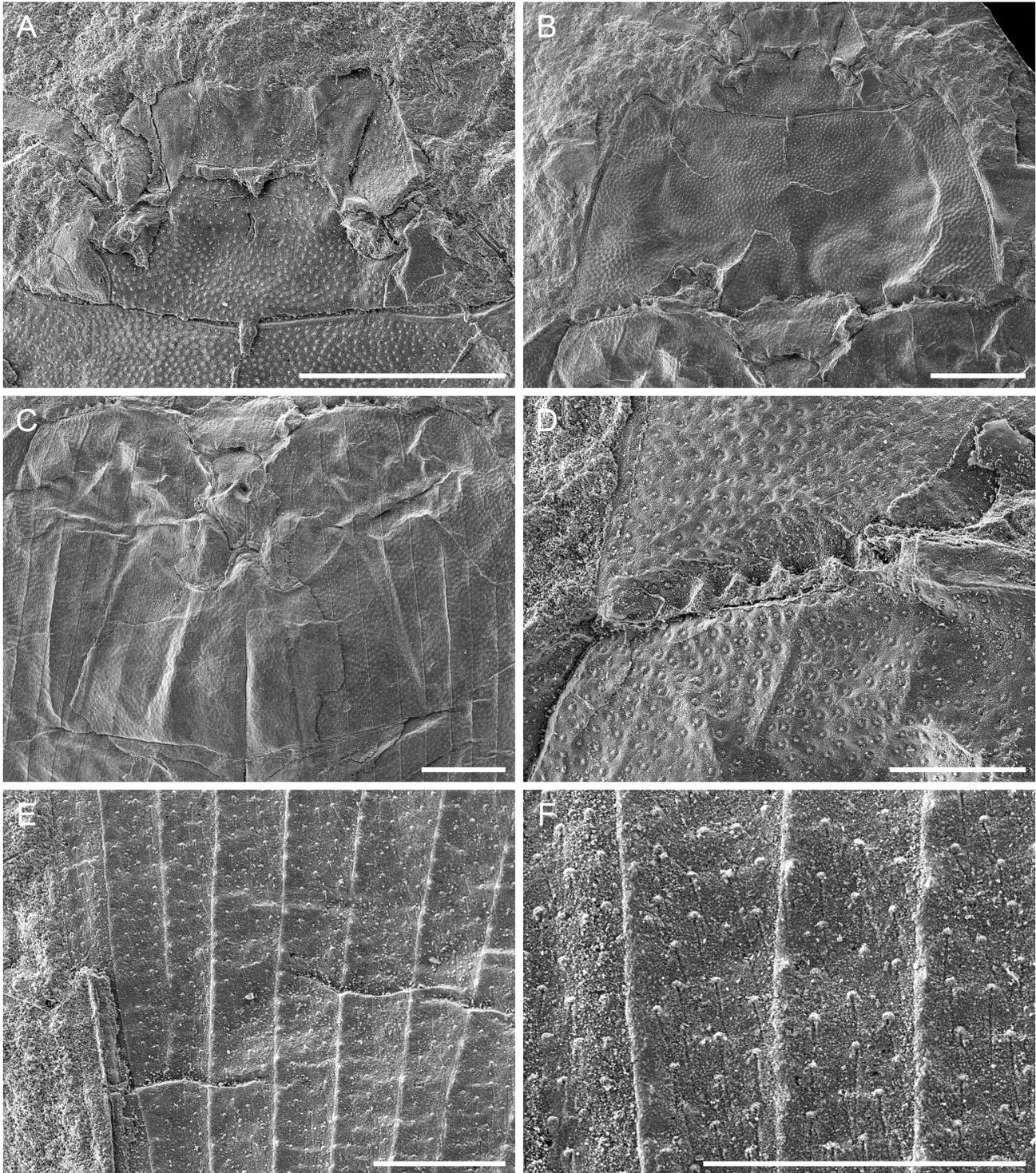


FIGURE 18. Details of *Parelateriformius communis* Yan & Wang, paratype, NIGP151542b, under scanning electron microscopy. **A**, Head. **B**, Prothorax. **C**, Meso- and metathorax. **D**, Crenulate posterior pronotal margin. **E**, **F**, Elytron. Scale bars = 1 mm in **A–C**, 400 μ m in **D–F**.

Lasiosynidae, which has characters reminiscent of modern Ptilodactylidae and Eulichadidae. Later, Kirejtshuk & Azar (2013) further proposed to merge Lasiosynidae into Eulichadidae. However, Yan *et al.* (2014a, 2015) argued that Lasiosynidae should be maintained as a separate family. Kirejtshuk & Azar

(2013) also proposed *Parelateriformius* as a junior synonym of *Tarsomegamerus* Zhang, but the synonymy was soon rejected by Yan *et al.* (2014a). Cai *et al.* (2015) transferred *Tarsomegamerus* to Armatopodidae, based on the apicoventrally-located elytral interlocking tongue, paired prosternal carinae, and curved sutures between

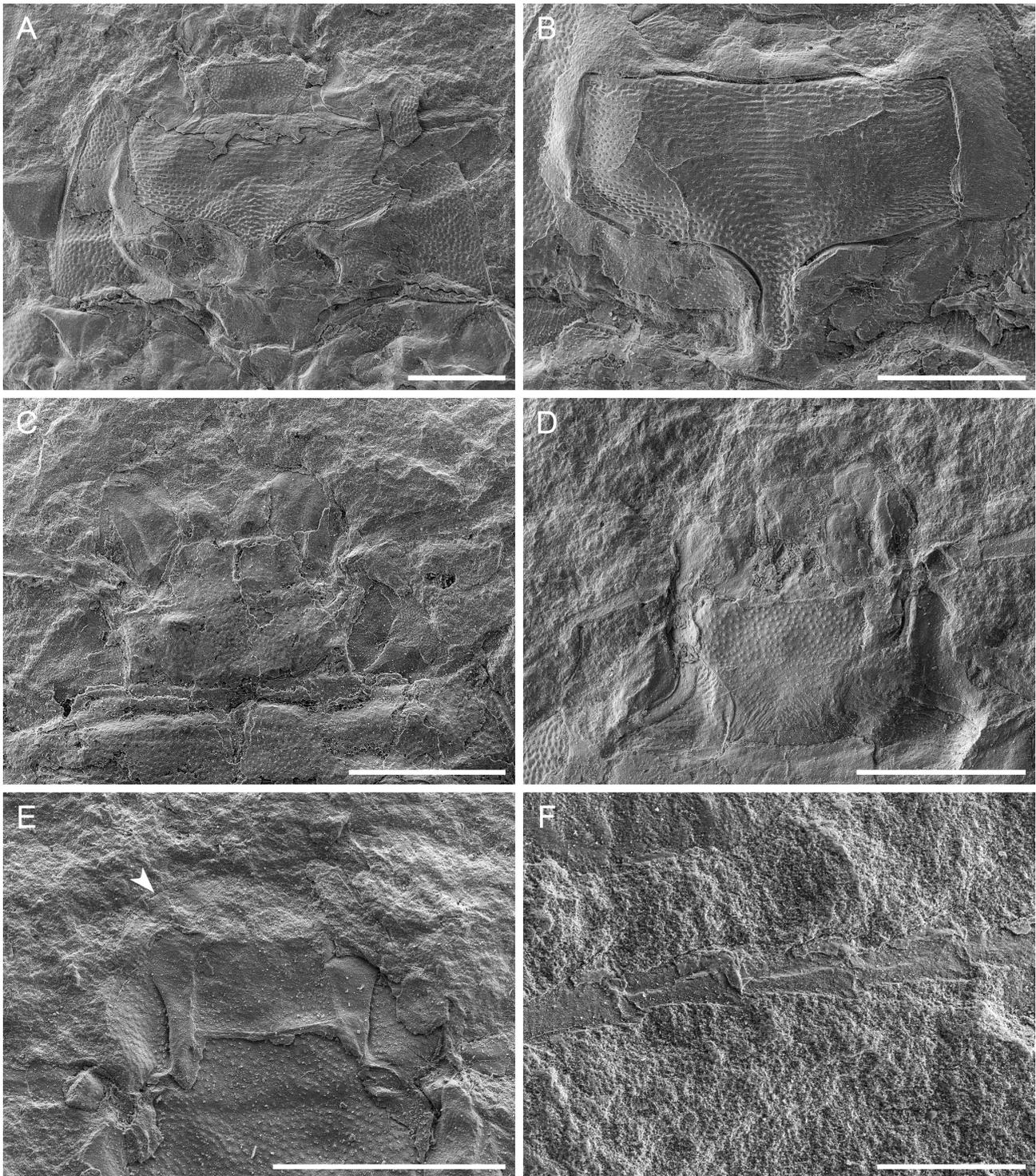


FIGURE 19. Details of *Parelateriformius communis* Yan & Wang, paratypes, under scanning electron microscopy. **A**, NIGP151542a, prothorax. **B**, NIGP151546, prothorax. **C**, NIGP151544, head. **D**, NIGP151539a, head. **E**, NIGP151539b, head, with arrowhead showing the possible apical cusp of mandible. **F**, NIGP151563, antenna. Scale bars = 1 mm in **A–E**, 400 μ m in **F**.

abdominal ventrites, whereas all these characters are absent in *Parelateriformius*.

In fact, as noticed by Yan *et al.* (2014a), *Parelateriformius* has a character combination that is quite different from the other members included in Lasiosynidae. The tarsi of *Parelateriformius* have

distinctly ventral lobes on at least tarsomeres 2–4 (e.g., Figs 20B, 25B), whereas in other lasiosynids the tarsomeres are at most weakly lobed (Yan *et al.*, 2013, 2014a, b; Guo *et al.*, 2022). *Parelateriformius* has a crenulate posterior rim of pronotum (Fig. 18D), whereas the posterior pronotal margin of other

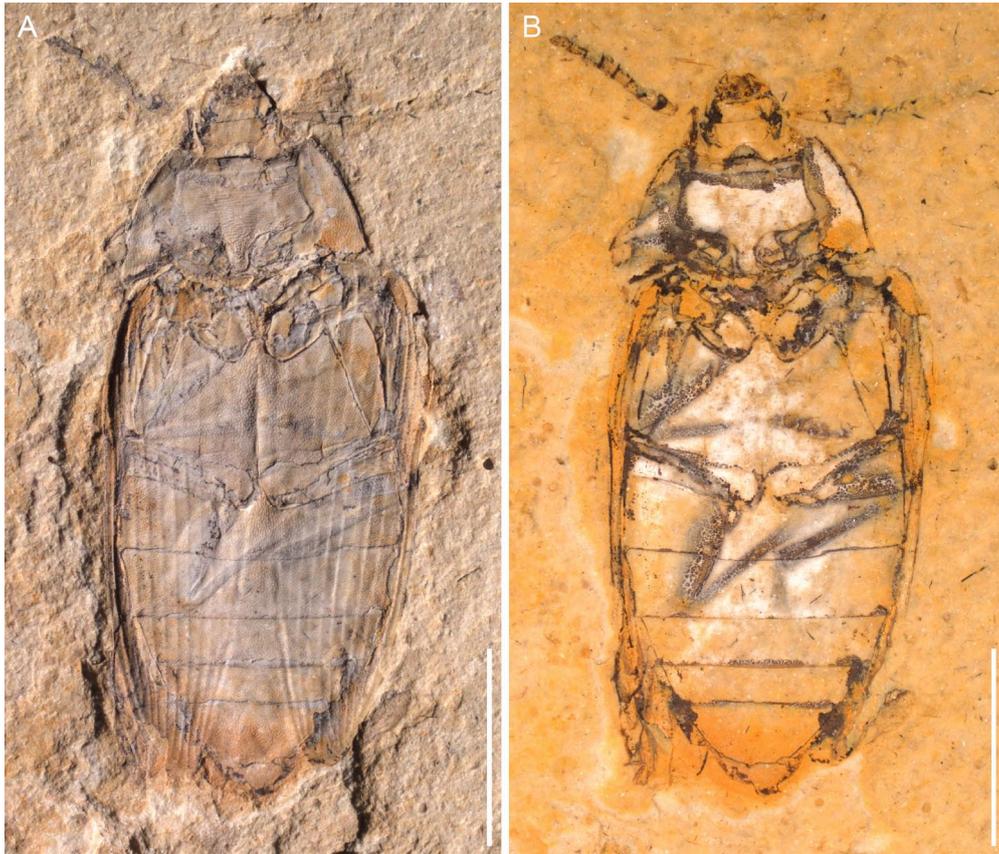


FIGURE 20. Habitus of *Parelateriformius villosus* Yan & Wang, holotype, NIGP151553, under incident light, dry (A) or moistened with 70% ethanol (B). Scale bars = 4 mm.



FIGURE 21. Habitus of *Parelateriformius villosus* Yan & Wang, paratype, NIGP151555, under incident light, dry (A) or moistened with 70% ethanol (B). Scale bars = 4 mm.



FIGURE 22. Habitus of *Parelateriformius villosus* Yan & Wang, paratype, NIGP151658, under incident light, dry (A) or moistened with 70% ethanol (B). Scale bars = 4 mm.

lasiosynids is generally smooth (Yan *et al.*, 2014a). In addition, *Parelateriformius* differs from the type genus, *Lasiosyne*, in having a subtriangular exposed portion of metanepisternum (Figs 5D, 18C), normalized metatrochanters (Fig. 5E), and elytra with stria 2 shortened posteriorly (Figs 3B, 4D, 18E, 24D, 30D) (exposed portion of metanepisternum subrectangular, metatrochanters enlarged, and elytra with striae 2 and 3 shortened posteriorly in *Lasiosyne*).

Parelateriformius appears to be more similar to extant Ptilodactylidae and Eulichadidae. In addition to the similar habitus, many Ptilodactylidae and Eulichadidae also have a crenulate posterior pronotal

margin (Lawrence, 2016b; Ivie, 2016), and in certain members of Ptilodactylidae the tarsal lobes could be present on more than one tarsomere (Lawrence, 2016b; Ivie, 2016). Nevertheless, *Parelateriformius* can still be readily separated from Ptilodactylidae and Eulichadidae. In Ptilodactylidae, the radial cell of hind wings has an oblique base, and in Eulichadidae the radial cell is strongly elongate (Lawrence *et al.*, 2021). By contrast, the radial cell of *Parelateriformius* is relatively short, no more than twice as long as wide (Fig. 21B; Yan *et al.*, 2015: fig. 5C), and the base is truncate (with nearly right basal angles; at least as seen in the well-preserved NIGP151555). The metakatepisternal suture is short or absent in Ptilodactylidae and Eulichadidae (Lawrence,

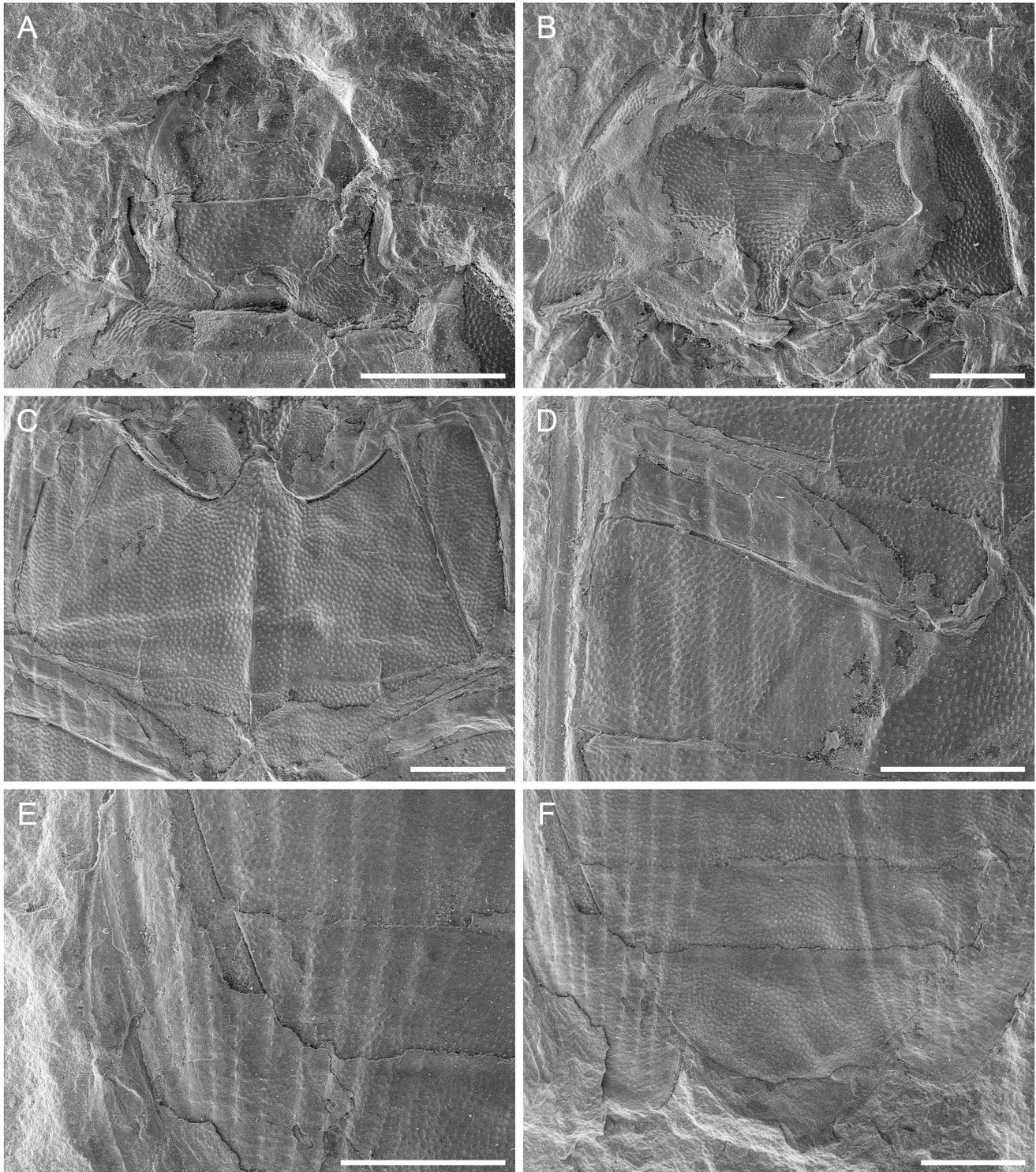


FIGURE 23. Details of *Parelateriformius villosus* Yan & Wang, holotype, NIGP151553, under scanning electron microscopy. **A**, Head. **B**, Prothorax. **C**, Metathorax. **D**, Abdominal base. **E**, Elytron and abdomen. **F**, Abdominal apex. Scale bars = 1 mm.

2016b; Ivie, 2016), while *Parelateriformius* has complete metakatepisternal suture (Figs 5D, 18C, 23C). Additionally, the scutellar shield of Ptilodactylidae is often notched anteriorly (scutellar shield with smooth anterior margin in *Parelateriformius*), and the frontoclypeal suture and the mesoventral discrimen are absent in Eulichadidae (both present in *Parelateriformius*; Yan & Wang, 2010).

Here we suggest that *Parelateriformius* is a definitive member of Dascillidae. Dascillidae shares with *Parelateriformius* the strongly transverse procoxal cavities, anteriorly simple scutellar shield, distinct metakatepisternal suture, relatively short radial cell (usually about twice as long as wide) with a generally truncate base, and often ventrally lobed tarsomeres. *Parelateriformius* is

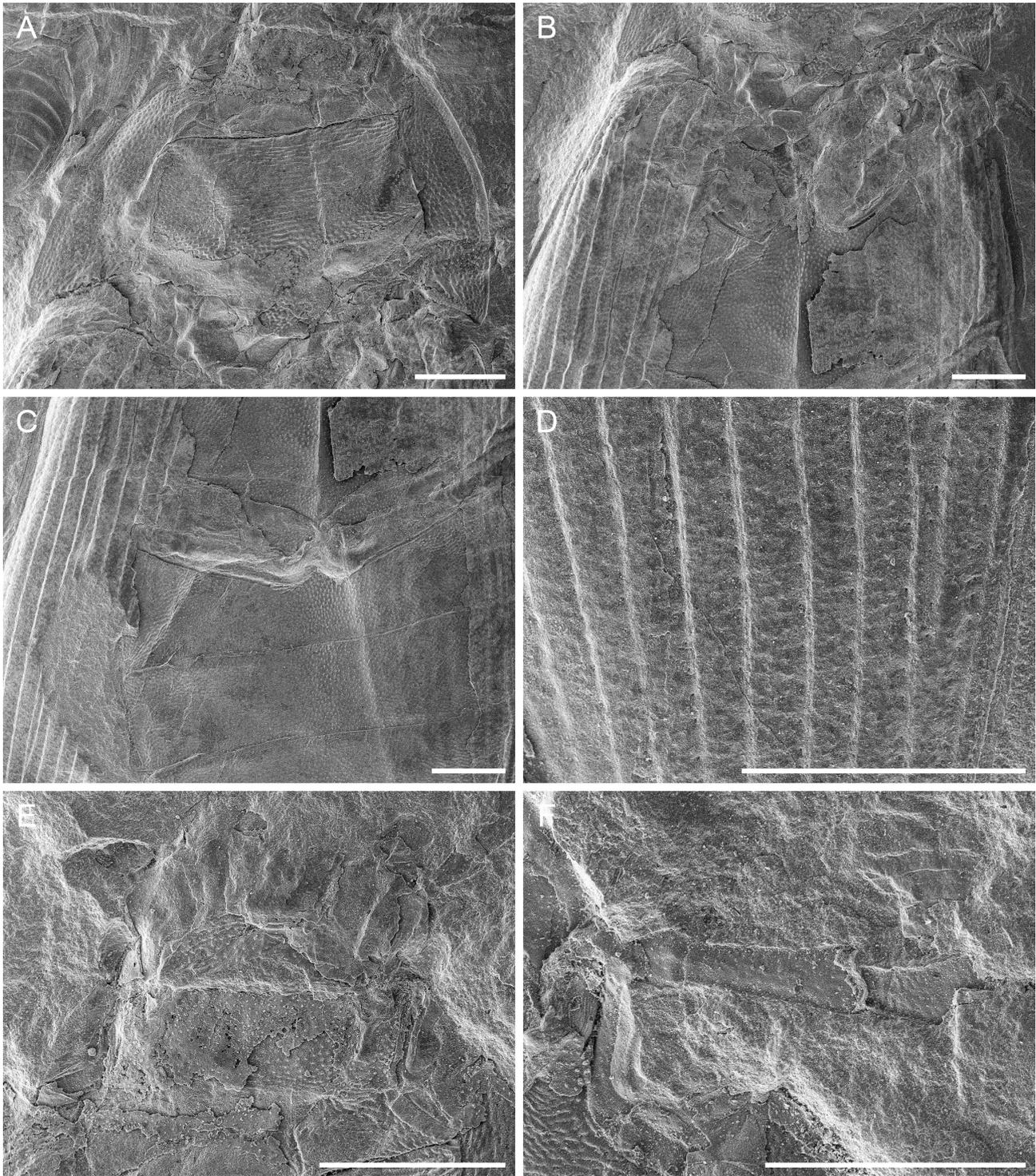


FIGURE 24. Details of *Parelateriformius villosus* Yan & Wang, under scanning electron microscopy. **A–E**, Paratype, NIGP151555. **A**, Prothorax. **B**, Meso- and metathorax. **C**, Abdominal base. **D**, Elytron. **E**, Head. **F**, Holotype, NIGP151553, antenna. Scale bars = 1 mm.

especially similar to *Petalon* in the subfamily Dascillinae. *Petalon* shares with *Parelateriformius* the serrate antennae, well-developed prosternal process, distinctly crenulate posterior pronotal margin, and grooved elytral striae, with elytral stria 2 shortened posteriorly (Jin *et al.*, 2013a). Some species of *Petalon* are unique in having

mandibles with a deciduous apical cusp (Jin *et al.*, 2013a), which rarely occurs in other groups of beetles except Curculionoidea (*e.g.*, Thompson, 1992). In these species, the apical part of mandibles was missing in most of the specimens examined, leaving only the basal part preserved (Z.-Y. Jin, personal observation; *e.g.*, Jin *et al.*, 2013a:

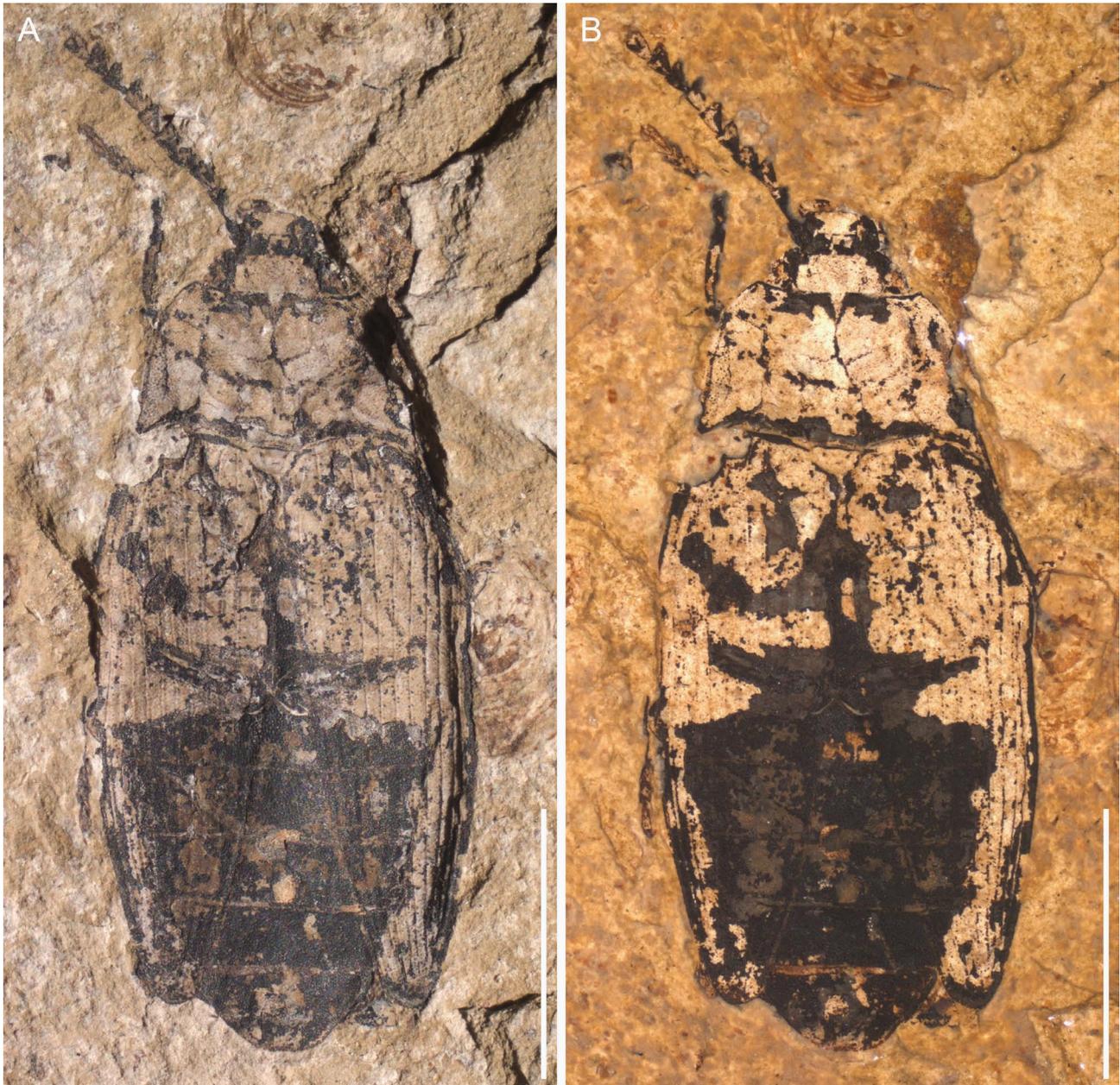


FIGURE 25. Habitus of *Parelateriformius capitifossus* Yan & Wang, holotype, NIGP151558, under incident light, dry (A) or moistened with 70% ethanol (B). Scale bars = 4 mm.

fig. 17E). In most of the *Parelateriformius* specimens we examined, the mandibles preserved appear to be relatively short and broad (e.g., Figs 3A, 18A, 19C, 28D). However, in the specimen NIGP151539, there is a curved line in front of (the basal part of) the mandible, which might be interpreted as the outer edge of an apical cusp (Fig. 19E). Considering that the apical mandibular cusp is not preserved in most of *Parelateriformius* specimens, this cusp might also be deciduous in *Parelateriformius*, as seen in many extant species of *Petalon*.

The earliest dascillid fossil previously known was *Cretodascillus* from the Early Cretaceous (Jin *et al.*,

2013b). The re-interpretation of *Parelateriformius* thus extends the fossil record of Dascillidae to the Middle Jurassic, which is critical for future dating of phylogenetic trees.

Data availability

Additional brightfield photos under different lighting conditions are available in the Zenodo repository (<https://doi.org/10.5281/zenodo.7236488>).



FIGURE 26. Habitus of *Parelateriformius capitifossus* Yan & Wang, holotype, NIGP151659, under incident light, dry (A) or moistened with 70% ethanol (B). Scale bars = 4 mm.



FIGURE 27. Habitus of *Parelateriformius capitifossus* Yan & Wang, paratype, NIGP151559, under incident light, dry (A) or moistened with 70% ethanol (B). Scale bars = 4 mm.

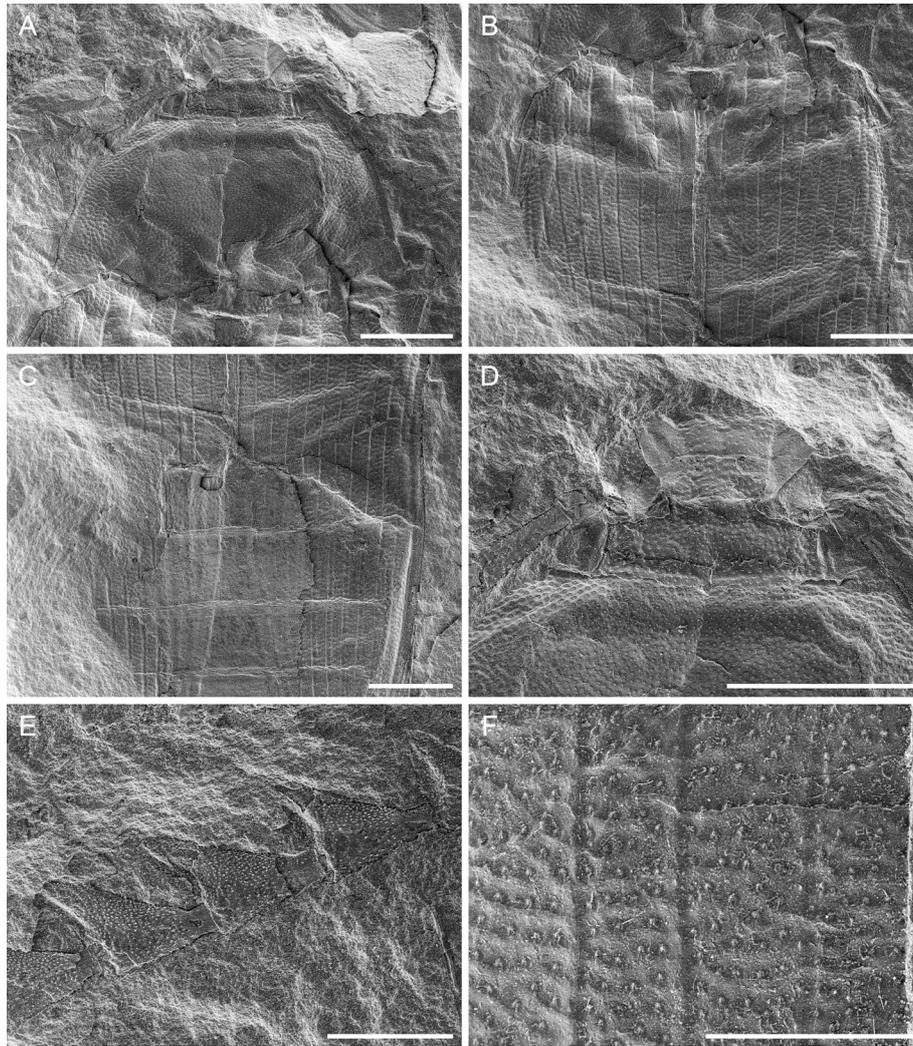


FIGURE 28. Details of *Parelateriformius capitifossus* Yan & Wang, paratype, NIGP151559, under scanning electron microscopy. **A**, Head and prothorax. **B**, Meso- and metathorax. **C**, Abdominal base. **D**, Head. **E**, Antenna. **F**, Elytron. Scale bars = 1 mm in **A–D**, 400 μm in **E–F**.



FIGURE 29. Habitus of *Parelateriformius mirabdominis* Yan & Wang, holotype, NIGP151560, under incident light, dry (**A**) or moistened with 70% ethanol (**B**). Scale bars = 4 mm.

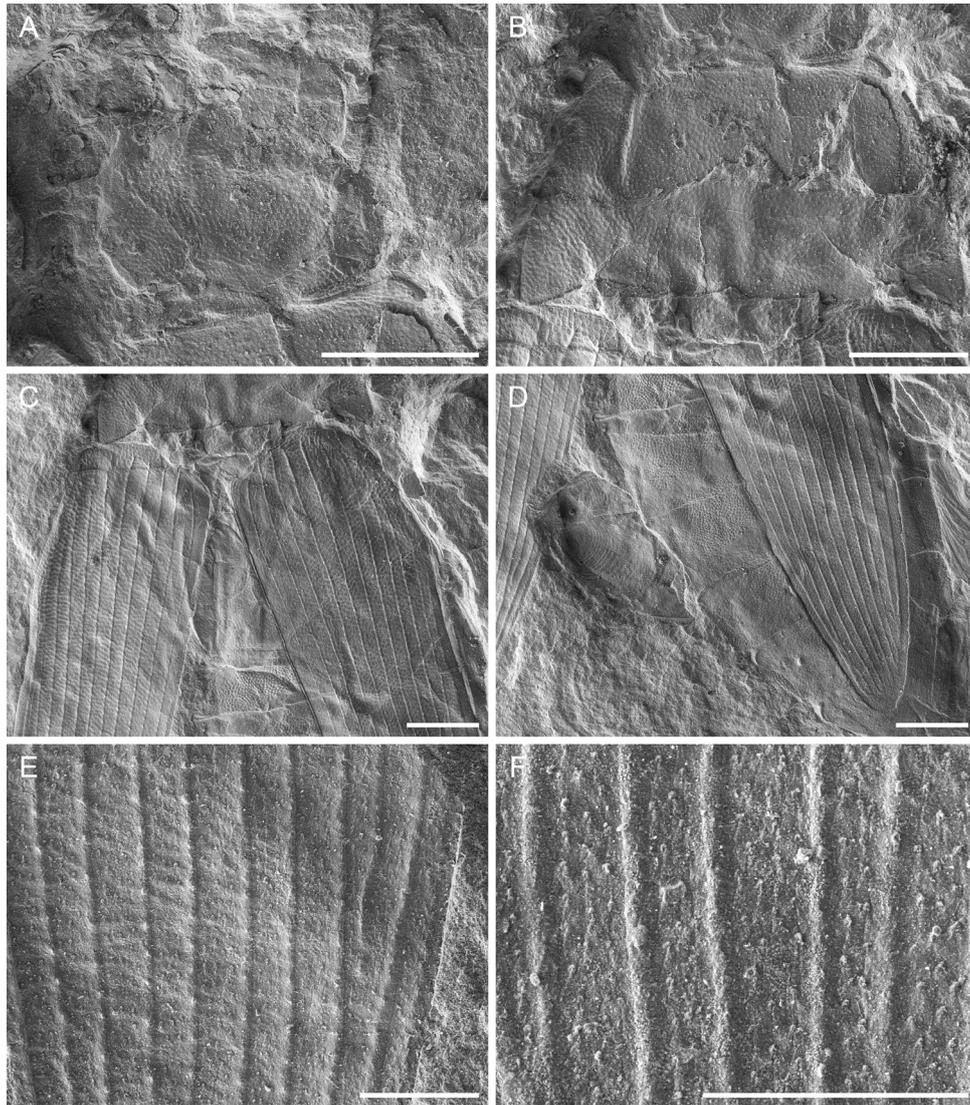


FIGURE 30. Details of *Parelateriformius mirabdominis* Yan & Wang, holotype, NIGP151560, under scanning electron microscopy. **A**, Head. **B**, Prothorax. **C**, Elytral base. **D**, Elytral apex and abdomen. **E**, **F**, Elytron. Scale bars = 1 mm in **A–D**, 400 μ m in **E**, **F**.

Acknowledgements

We are grateful to Chun-Zhao Wang for technical help with SEM imaging. The staff at the fossil repository of NIGP provided helpful assistance during the examination of specimens. Liang Lü and an anonymous reviewer provided constructive comments on the manuscript. Financial support was provided by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000), and the National Natural Science Foundation of China (42222201, 42288201). Yan-Da Li is supported by a scholarship granted by the China Scholarship Council (202108320010).

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