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First Artematopodidae from mid-Cretaceous amber of northern Myanmar (Coleoptera: Elateroidea)

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Abstract

Artematopodid fossils from the mid-Cretaceous Burmese amber are reported for the first time, represented by three species in two genera. *Bipogonia* Li, Kundrata & Cai **gen. nov.** with two species, *B. trivialis* Li, Kundrata & Cai **sp. nov.** and *B. fortis* Li, Kundrata & Cai **sp. nov.**, is mainly characterized by the distinctly serrate antennae, mandibles with both apical and subapical teeth, and prosternum without paired longitudinal ridges. *Carinibipogonia xiai* Li, Kundrata & Cai **gen. et sp. nov.** shares with *Bipogonia* the distinctly serrate antennae and mandibles with both apical and subapical teeth but differs mainly in the prosternum with short paired longitudinal ridges. Based on their morphology, the two new genera might be related to the extant *Allopogonia*; however, this needs to be tested in the future with a phylogenetic framework.

Key words: taxonomy, fossil, Burmese amber, Cretaceous, Mesozoic

Introduction

Artematopodidae are a small but widespread family in superfamily Elateroidea, with approximately 70 described extant species (Kundrata *et al.* 2013; Gimmel & Bocakova 2015; Wang & Liu 2021). Adults of Artematopodidae can be easily recognized based on the interlocking tongue on the apicoventral region of the elytra (Lawrence 2010; Cai *et al.* 2015). Additional useful characters for identifying artematopodids include the ventrally bilobed tarsomere 4, the completely connate abdominal ventrites, the paired ridges of prosternum and the strongly curved suture between abdominal ventrites 4 and 5 (though the latter two are present only in some genera).

In the morphology-based phylogeny by Lawrence *et al.* (2011), Artematopodidae were revealed as the lineage sister to the remainder of Elateroidea. Although phylogenies of Elateroidea based on molecular and morphology differ dramatically, the basal position of Artematopodidae was also supported by recent molecular studies (e.g., Zhang *et al.* 2018; McKenna *et al.* 2019; Douglas *et al.* 2021; Cai *et al.* 2022). According to Kundrata *et al.* (2014) and McKenna *et al.* (2015), Artematopodidae constitute the basal-most branch of Elateroidea together with Omethidae (including Telegeusidae).

No molecular studies have been conducted to deduce the intergeneric relationships within Artematopodidae. Based on a morphological cladistic analysis, Lawrence (2005) recognized three subfamilies in Artematopodidae, namely Electribiinae (*Electribius* Crowson, only), Allopogoniinae (*Allopogonia* Cockerell, only), and Artematopodinae. However, the position of *Allopogonia* varied dramatically in different studies with similar character lists (Lawrence 2005; Cai *et al.* 2015, 2020), which might have been caused by the different selection of outgroup taxa.

Most fossils of Artematopodidae were reported from the Eocene Baltic amber (Crowson 1973; Hörnschemeyer 1998; Háva 2015). A species of *Electribius* was reported from the Miocene Mexican amber (Wu *et al.* 2015). Cai *et*

al. (2015) reported the earliest artematopodid fossil, *Sinobrevipogon* Cai *et al.*, from the Middle Jurassic Daohugou beds in Northeast China. *Tarsomegamerus* Zhang from the same deposit was also transferred to Artematopodidae (Cai *et al.* 2015). Cai *et al.* (2020) reported *Cretobrevipogon* Cai *et al.* from the Lower Cretaceous Yixian Formation in Northeast China. Recently, "*Notocupes*" *undatabdominus* Lin (originally placed in Archostemata) from the Lower Cretaceous of South China was also suggested to be an artematopodid (Li *et al.* 2021). In the present study, we report the first members of Artematopodidae from the mid-Cretaceous amber of northern Myanmar.

Materials and methods

The Burmese amber specimens studied herein (Figs 1–10) originated from amber mines near Noije Bum (26°20' N, 96°36' E), Hukawng Valley, Kachin State, northern Myanmar. Jewellery-grade Burmese amber specimens are commonly carried and sold legally in Ruili, Dehong Prefecture on the border between China and Myanmar. The specimens in this study were purchased in 2016–2017, and are permanently deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China. All 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 paper of different grit sizes, and finally polished with polishing powder.

Photographs under incident light were taken with a Zeiss Discovery V20 stereo microscope. Widefield fluorescence images were captured with a Zeiss Axio Imager 2 light microscope combined with a fluorescence imaging system. Confocal images were obtained with a Zeiss LSM710 confocal laser scanning microscope, using the 561 nm (DPSS 561-10) laser excitation line. 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 Helicon Focus 7.0.2 and Adobe Photoshop CC. Images were further processed in Adobe Photoshop CC to adjust brightness and contrast.

The elytra are partially open in some specimens; thus the measurements of body width were taken as the maximum width of abdomen. Other measurements were taken as follows: body length as the apparent distance from the mandibular apex to the apex of abdominal ventrite 5; prosternal width as the maximum width of prosternum (near the anterior prosternal edge); prosternal length as the distance from the anterior prosternal edge to the apex of prosternal process along the middle. These measurements are more or less affected by the conformation of the beetle body and should only be regarded as rough approximations.

Systematic paleontology

Order Coleoptera Linnaeus, 1758

Suborder Polyphaga Emery, 1886

Superfamily Elateroidea Leach, 1815

Family Artematopodidae Lacordaire, 1857

Subfamily incertae sedis

Remarks. We place the below described genera in Artematopodidae based on the following combination of characters: head slightly deflexed, antennae serrate, with 11 antennomeres, prosternum transverse in front of coxae, procoxal cavities broadly open posteriorly, elytral apex ventrally with the interlocking tongue (Figs 3F, 7E, 10D), tarsal formula 5-5-5, and abdomen with five ventrites, which are presumably all connate (Lawrence 2010). Although the genera described below are similar to *Allopogonia* in some characters, e.g., serrate antennae or missing or reduced prosternal ridges, we prefer to classify them as *incertae sedis* as they differ in several characters from *Allopogonia* and also from all remaining artematopodids (see Remarks for individual genera).

Genus Bipogonia Li, Kundrata & Cai gen. nov.

Type species. Bipogonia trivialis sp. nov., here designated.

Etymology. The generic name combines the prefix "*bi-*" referring to its bidentate mandibles (with both apical and subapical teeth) and the name *Allopogonia*. The name is feminine in gender.

Diagnosis. Antennomeres 5–10 distinctly serrate, less than twice as long as wide (Figs 3H, 7F). Anterior edge of frontoclypeus dentate (Figs 3G, 7G). Mandibles with subapical tooth (Figs 3G, 7G). Apical maxillary palpomere not clearly expanded apically (Figs 4C, 7A). Prosternum in front of coxae without paired longitudinal ridges (Figs 3B, 7B). Elytra with 10 puncture rows (Fig. 3I). Inner posterobasal angle of radial cell almost right (Fig. 6E).

Description. Body moderately broad to broad, 2.1–2.6 times as long as wide, surface punctate.

Antennal insertions dorsally exposed. Subantennal groove absent. Frontoclypeal suture absent; anterior clypeal margin multidentate. Antennomeres 2–4 simple, moderately slender; antennomere 5 moderately serrate; antennomeres 6–10 strongly serrate, about as long as wide. Mandibles with one apical and one subapical teeth. Maxillary palps 4-segmented; apical palpomere not clearly expanded apically. Mentum subtriangular, apically broadly rounded.

Pronotal disc subtrapezoidal, widest at base; anterior margin weakly trisinuate; anterior angles somewhat produced; surface without transverse groove. Prosternum in front coxae transverse, without paired ridges or deep pits. Prosternal process with subparallel sides, apically broadly rounded, fitting into mesoventral cavity.

Scutellar shield widely pentagonal. Elytra elongate; surface with puncture rows; epipleura developed only in anterior third. Mesoventrite short, anteriorly with well-developed mesoventral cavity. Mesocoxal cavities separated by about twice or more the shortest diameter of coxal cavity. Metaventrite more than half as long as wide, with sides widest posteriorly. Metacoxae strongly transverse, almost contiguous, extending laterally to epipleura; metacoxal plate weakly developed but complete to lateral edge.

Legs slender; tibiae slightly longer than respective femora, with two tibial spurs; tarsomeres 1 and 5 elongate; tarsomeres 3 and 4 with well-developed, bilobed membranous ventral process. Pretarsal claws simple.

Abdominal ventrites with margins denticulate. Sutures between all ventrites complete and distinct; suture between ventrites 4 and 5 only weakly curved. Ventrites 1–4 subequal in length; ventrite 5 about 1.6–1.7 times as long as ventrite 4.

Remarks. Among previously reported genera of Artematopodidae, only *Allopogonia* is known to possess strongly serrate antennae and prosternum without paired ridges (Lawrence 2005; Fig. 11A, B). In other genera, the antennae are more filiform (if slightly serrate, antennomere more than twice as long as wide), and there is a pair of longitudinal ridges on the prosternum in front of coxae continuous with the lateral margins of prosternal process. *Bipogonia* gen. nov. is similar to *Allopogonia* in having strongly serrate antennae and lacking prosternal ridges. *Allopogonia*, however, differs from *Bipogonia* in mandibles without a subapical tooth (Fig. 11L), which is a unique character state in Artematopodidae (Lawrence 2005). *Bipogonia* has the anterior edge of frontoclypeus dentate, while in most other artematopodids the anterior clypeal margin is rounded. Extant artematopodids have 11 or 12 puncture rows on each elytron (Lawrence 2005; fig. 3G in Wang & Liu 2021). However, there are probably only 10 elytral puncture rows in *Bipogonia* gen. nov. (as seen in *B. trivialis*), as well as *Carinibipogonia* gen. nov.

Bipogonia trivialis Li, Kundrata & Cai sp. nov.

(Figs 1-4)

Material. Holotype, sex unknown, NIGP179428 (NIGP). Two paratypes, sex unknown, NIGP179429, NIGP179430 (NIGP).

Etymology. The specific name refers to its relatively common occurrence.

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 approximately 2.6 times as long as wide (versus 2.1 times as long as wide in *Bipogonia fortis* **sp. nov.**). Prosternum moderately broad, about 1.2–1.3 times as wide as long (versus 1.7 times as wide as long in *B. fortis* **sp. nov.**). Metaventral discrimen distinct only posteriorly (Figs 3E, 4B).



FIGURE 1. General habitus of *Bipogonia trivialis* Li, Kundrata & Cai **gen. et sp. nov.**, holotype, NIGP179428, under incident light. **A**, Dorsal view. **B**, Ventral view. Scale bars: 1.5 mm.



FIGURE 2. General habitus of *Bipogonia trivialis* Li, Kundrata & Cai gen. et sp. nov., holotype, NIGP179428, under widefield fluorescence. A, Dorsal view. B, Ventral view. Scale bars: 1.5 mm.



FIGURE 3. Details of *Bipogonia trivialis* Li, Kundrata & Cai **gen. et sp. nov.**, holotype, NIGP179428, under confocal microscopy. **A**, Head, ventral view. **B**, Prothorax, ventral view. **C**, Mesothorax, ventral view. **D**, Mid leg. **E**, Metathorax and abdominal base, ventral view. **F**, Elytral and abdominal apices, showing the interlocking tongue (arrowhead). **G**, Head, dorsal view. **H**, Pronotum and antenna, dorsal view. **I**, Elytron, dorsal view. Abbreviations: a1–11, antennomeres 1–11; cl, clypeus; ep, elytral epipleuron; ey, compound eye; md, mandible; mstb, mesotibia; msts, mesotarsus; msv, mesoventrite; mt, mentum; mtc, metacoxa; mttc, metatrochanter; mtv, metaventrite; pn, pronotum; ps, prosternum; ptb, protibia; pts, protarsus; v1–5, ventrites 1–5. Scale bars: 300 μm.

Description. As for the genus, except for the following characters: Body moderately broad, 4.4–4.6 mm long, 1.7–1.8 mm wide. Eyes well-developed, without interfacetal setae. Prosternum moderately broad. Surface of elytron with 10 puncture rows. Mesocoxal cavities separated by about twice the shortest diameter of coxal cavity. Metaventral discrimen distinct only near posterior end, not clearly visible anteriorly. Abdominal ventrite 5 about 1.7 times as long as ventrite 4.



FIGURE 4. *Bipogonia trivialis* Li, Kundrata & Cai gen. et sp. nov., paratypes. A, B, NIGP179429, under incident light. A, Dorsal view. B, Ventral view. C, D, NIGP179430, under widefield fluorescence. C, Head, dorsal view. D, Elytral apices, dorsal view. Scale bars: 1 mm.

Bipogonia fortis Li, Kundrata & Cai sp. nov.

(Figs 5–7)



FIGURE 5. General habitus of *Bipogonia fortis* Li, Kundrata & Cai gen. et sp. nov., holotype, NIGP179431, under incident light. A, Dorsal view. B, Ventral view. Scale bars: 1.5 mm.

Material. Holotype, sex unknown NIGP179431 (NIGP).

Etymology. The specific name refers to the robust appearance of the species.

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 approximately 2.1 times as long as wide (versus 2.6 times as long as wide in *Bipogonia trivialis* **sp. nov.**). Prosternum moderately broad, about 1.7 times as wide as long (versus 1.2–1.3 times as wide as long in *B. trivialis* **sp. nov.**). Metaventral discrimen (almost) complete (Fig. 6D).

Description. As for the genus, except for the following characters: Body broad, 5.2 mm long, 2.5 mm wide. Prosternum broad. Elytral surface with puncture rows (their number cannot be counted due to visibility problems). Mesocoxal cavities separated by more than two times the shortest diameter of coxal cavity. Metaventral discrimen (almost) complete. Hind wing well-developed. Radial cell moderately elongate, about 2.3 times as long as wide; inner posterobasal angle almost right. Abdominal ventrite 5 about 1.6 times as long as ventrite 4.



FIGURE 6. Details of *Bipogonia fortis* Li, Kundrata & Cai **sp. nov.**, holotype, NIGP179431, under widefield fluorescence. **A**, Head and prothorax, dorsal view. **B**, Head and prothorax, ventral view. **C**, Elytron, dorsal view. **D**, Posterior body, ventral view. **E**, Elytron and hind wing, ventral view. **F**, Abdominal apex, dorsal view. Abbreviations: an, antenna; el, elytron; md, mandible; mtv, metaventrite; mxp, maxillary palp; pn, pronotum; ps, prosternum; R, radial cell; v1–5, ventrites 1–5. Scale bars: 500 μm.



FIGURE 7. Details of *Bipogonia fortis* Li, Kundrata & Cai **sp. nov.**, holotype, NIGP179431, under confocal microscopy. **A**, Head, ventral view. **B**, Prothorax, ventral view. **C**, Mesothorax, ventral view. **D**, Meso- and metatarsi. **E**, Elytral apex, showing the interlocking tongue (arrowhead). **F**, Antenna. **G**, Head, dorsal view. **H**, Scutellar shield, dorsal view. **I**, Abdominal apex, dorsal view. Abbreviations: a1–11, antennomeres 1–11; cl, clypeus; el, elytron; md, mandible; msts, mesotarsus; msv, mesoventrite; mtc, metacoxa; mtts, metatarsus; mtv, metaventrite; mxp, maxillary palp; pn, pronotum; ps, prosternum; pts, protarsus; sc, scutellum; t8, tergite VIII; v5, ventrite 5. Scale bars: 300 µm.

Remarks. Extant Artematopodidae may display some degree of sexual dimorphism in body robustness, antennal length/serration, or pronotal shape (sinuation of lateral pronotal margin) (Hopping 1936; Sakai 1982; Lawrence; 2005; Yoshitomi 2018). Usually, the body is slightly more thickened in females than males. However, the specimen of *B. fortis* here is distinctly wider than *B. trivialis*. Besides, no dimorphic prosternum or metaventral discrimen as seen in our fossils has been reported before. Thus, we believe that *B. fortis* is more likely to represent a separate species, rather than a specimen of the opposite sex of *B. trivialis*.

Genus Carinibipogonia Li, Kundrata & Cai gen. nov.

Type species. Carinibipogonia xiai sp. nov., here designated.

Etymology. The generic name is based on the latin "*carina*" referring to its paired prosternal carinae and the name *Bipogonia*. The name is feminine in gender.

Diagnosis. Antennomeres distinctly serrate, less than twice as long as wide (Fig. 10G). Anterior edge of frontoclypeus dentate (Fig. 10F). Mandibles with subapical tooth (Fig. 10F). Apical maxillary palpomere not clearly expanded apically (Fig. 10A, F). Prosternum in front of coxae with paired longitudinal ridges; ridges not extending to anterior half of prosternum (Fig. 10B). Elytra with 10 puncture rows. Inner posterobasal angle of radial cell almost right (Fig. 9C).

Description. Since this genus is monotypic, see the species description below.

Remarks. *Carinibipogonia* **gen. nov.** is generally very similar to *Bipogonia* **gen. nov.** Both genera share the anteriorly dentate frontoclypeus, strongly serrate antennae, and mandibles with a subapical tooth. The only major difference between them appears to be the presence of paired prosternal ridges in *Carinibipogonia*. The prosternal ridges generally extend to the anterior margin of prosternum in other artematopodids with prosternal ridges. However, in *Carinibipogonia*, the ridges disappear in the anterior half of prosternum. *Carinibipogonia xiai* **sp. nov.** differs from *B. fortis* **sp. nov.** additionally in having a more elongated radial cell. However, this character state cannot be observed in *B. trivialis* **sp. nov.** since the hind wings are not exposed in the available specimens.

Carinibipogonia xiai Li, Kundrata & Cai sp. nov. (Figs 8–10)

Material. Holotype, female, NIGP179432 (NIGP).

Etymology. The species is named after Mr. Fang-Yuan Xia, who kindly allowed us to study many valuable fossil specimens in his collection.

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. As for the genus.

Description. Body moderately broad, 4.4 mm long, 1.7 mm wide; surface punctate.

Eyes well-developed, without interfacetal setae. Antennal insertions dorsally exposed. Subantennal groove absent. Frontoclypeal suture absent; anterior clypeal margin multidentate. Antennomeres 2–4 simple; antennomere 5 moderately serrate; antennomeres 6–10 strongly serrate, about as long as wide. Mandibles with one apical and one subapical teeth. Maxillary palps 4-segmented; apical palpomere seemingly cylindrical, not clearly expanded apically. Labial palps 3-segmented; apical palpomere widened apically. Mentum subtriangular, apically slightly emarginate.

Pronotal disc subtrapezoidal, widest at base; surface without transverse groove. Prosternum in front coxae transverse, with paired incomplete ridges; ridges not extending to anterior half of prosternum; deep pits absent; prosternal process with subparallel sides. Procoxal cavities broadly open posteriorly.

Elytra elongate; surface of each elytron with 10 puncture rows; epipleura developed only in anterior third.

Legs slender; tibiae slightly longer than respective femora, with two tibial spurs; tarsomeres 1 and 5 elongate; tarsomeres 3 and 4 with well-developed, bilobed membranous ventral process. Pretarsal claws simple.

Hind wing well-developed. Radial cell elongate, about 4.2 times as long as wide; inner posterobasal angle almost right.

Abdominal ventrites with margins denticulate. Sutures between all ventrites complete and distinct; suture between ventrites 4 and 5 only weakly curved. Ventrite 5 about 1.3 times as long as ventrite 4 (might be affected by distortion).



FIGURE 8. General habitus of *Carinibipogonia xiai* Li, Kundrata & Cai **sp. nov.**, holotype, NIGP179432, under incident light. **A**, Dorsal view. **B**, Ventral view. Scale bars: 1.5 mm.



FIGURE 9. Details of *Carinibipogonia xiai* Li, Kundrata & Cai **gen. et sp. nov.**, holotype, NIGP179432, under widefield fluorescence. **A**, Head and prothorax, dorsal view. **B**, Head and prothorax, ventral view. **C**, Hind wing, dorsal view. **D**, Abdomen, ventral view. **E**, Elytron, ventral view. Abbreviations: an, antenna; el, elytron; lbp, labial palp; md, mandible; mt, mentum; mxp, maxillary palp; pn, pronotum; ps, prosternum; ptb, protibia; R, radial cell; v1–5, ventrites 1–5. Scale bars: 500 μm.



FIGURE 10. Details of *Carinibipogonia xiai* Li, Kundrata & Cai **gen. et sp. nov.**, holotype, NIGP179432, under confocal microscopy. **A**, Head, ventral view. **B**, Prothorax, ventral view, showing the paired longitudinal ridges (arrowhead). **C**, Fore and mid legs. **D**, Elytral apex, showing the interlocking tongue (arrowhead). **E**, Abdominal apex, ventral view. **F**, Head, dorsal view. **G**, Antenna, dorsal view. **H**, Elytron, dorsal view. **I**, Ovipositor, dorsal view. Abbreviations: a1–11, antennomeres 1–11; cl, clypeus; gs, gonostylus; lbp, labial palp; md, mandible; mstb, mesotibia; msts, mesotarsus; mt, mentum; ps, prosternum; ptb, protibia; pts, protarsus; v5, ventrite 5. Scale bars: 300 μm.

Discussion

Artematopodidae are among the basalmost splits in Elateroidea and hence they represent a lineage with a long evolutionary history which can be traced back to the Mesozoic (Kundrata *et al.* 2014; Zhang *et al.* 2018; McKenna *et al.* 2019; Douglas *et al.* 2021; Cai *et al.* 2022). Several artematopodids have been reported from Jurassic and Cretaceous deposits (e.g., Cai *et al.* 2015, 2020; Li *et al.* 2021). Thus, it is somewhat unexpected that no artematopodids have yet been described from likely the most fossil-rich Cretaceous deposit, Burmese amber (Ross

2019, 2020, 2021, 2022). All previously reported Mesozoic fossils of Artematopodidae have complete ridges on prosternum. Therefore, the discovery of *Bipogonia* gen. nov. with no such ridges, and *Carinibipogonia* gen. nov. with only short ridges on prosternum, expands our knowledge on the Mesozoic morphological disparity of this family, and implies a possibly high diversity of Artematopodidae in Burmese amber.



FIGURE 11. Details of extant *Allopogonia villosa* (Horn), NHMUK010189601, dissection prepared by R. A. Crowson. Photo credit: ©The Trustees of the Natural History Museum, London, licensed under CC BY 4.0. **A**, Head. **B**, Prothorax. **C**, **D**, Fore legs. **E**, Mesothorax. **F**, Elytron. **G**, Metathorax. **H**, Abdomen. **I**, **J**, Hind wings. **K**, Hind leg. **L**, Mandible. **M**, Labium. **N**, Maxilla. Abbreviations: msf, mesofemur; mstb, mesotibia; mtf, metafemur; mttb, metatibia; mtv, metaventrite; pf, profemur; ps, prosternum; ptb, protibia; pts, protarsus; v2–5, ventrites 2–5. Scale bars: 500 µm.

Extant *Allopogonia* (Fig. 11), the sole member of the subfamily Allopogoniinae, is currently the only other known genus in Artematopodidae without ridges on prosternum (Lawrence 2005). Although its phylogenetic position has not yet been settled (Cai *et al.* 2015), there are some indications that this group might represent a sister-group to the remaining Artematopodidae. If both new genera described here are closely related to *Allopogonia* (which is supported by strongly serrate antennae and no or short ridges on prosternum), then we could assume that the short prosternal ridges which disappear in the anterior half of prosternum in *Carinibipogonia*, could represent an intermediate state between the lineages without ridges and other artematopodids with complete prosternal ridges. However, this hypothesis as well as the validity of the current suprageneric classification of the family should be tested in the future using a combination of molecular and morphological data, including fossils.

Data availability

The original confocal data of *Bipogonia* and *Carinibipogonia* are available in Zenodo repository (https://doi. org/10.5281/zenodo.6390097).

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