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. ohmkuhneni 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.
Suborder Archostemata Kolbe, 1908
Genus Notocupes 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. Procoxae probably not contiguous (Fig. 3G). Propleura probably not reaching anterior prothoracic margin. Protarsal groove present along pleurosternal and notosternal sutures (Fig. 2E).

Systematic palaeontology

Order Coleoptera Linnaeus, 1758
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.
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.
**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).

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, serriform (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 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.
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

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**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.
hemispherical and protruding (Fig. 8A). Antennal insertions dorsolaterally situated. Antenna 11-segmented, serriform (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 discernmen present

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.
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.
**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, serriform. 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 gulalementum by distinct suture (Fig. 12B). Anterior part of gulalementum 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 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.
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
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.”

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.

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.

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).

**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) 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 Ambiulamma (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 Eurydicyctyon
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 Eurydicyctyon 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 STI311 (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].

Acknowledgements
We are grateful to Margaret K. Thayer (Field Museum of Natural History, USA) for helpful discussion, Su-Ping Wu (NIGP, China) for technical help in micro-CT reconstruction, Yan Fang (NIGP, China) for technical help in confocal imaging and EDS imaging, Chun-Zhao Wang (NIGP, China) for technical help in SEM imaging, and Dao-Jun Yuan (NIGP, China) for help in inspecting the holotype of Conexicoxa homora. Financial support was provided by the National Natural Science Foundation of China (42222201, 42288201) and the Second Tibetan Plateau Scientific Expedition and Research project (2019QZKK0706). Y.-D.L. is supported by a scholarship granted by the China Scholarship Council (202108320010).

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