Current Research in Insect Science 5 (2024) 100075

Contents lists available at ScienceDirect

Current Research in Insect Science

journal homepage: www.elsevier.com/locate/cris

An enigmatic Cretaceous beetle with possible affinity to Erotylidae (Coleoptera: Cucujiformia)

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ARTICLE INFO

Keywords:
Cucujiformia
Burmese amber
Fossil
Phylogenetic analysis
Parsimony

ABSTRACT

The morphology of beetles of the recently defined superfamilies Erotyloidea, Nitiduloidea and Cucujoidea is varied. Determining the systematic positions of Mesozoic fossils within these groups can often be challenging. Here we describe and illustrate a puzzling cucujiform beetle, *Isocryptophilus exilipunctus* Li & Cai **gen. & sp. nov.**, based on an individual from mid-Cretaceous Burmese amber. While we cannot definitively pinpoint the exact phylogenetic position of *Isocryptophilus*, its possible affinity to Erotylidae is discussed in light of our phylogenetic analyses. A broader-sampled morphological matrix, coupled with a robust molecular phylogeny of these groups, will be promising for clarifying the systematic placement of the fossil.

Introduction

Cucujiformia is the most diversified series in Coleoptera. As defined by the most recent phylogenomic study (Cai et al., 2022), there are nine superfamilies in Cucujiformia. Most of these superfamilies have well-characterized apomorphies. However, Erotyloidea, Nitiduloidea and Cucujoidea, which were traditionally included in a united "Cucujoidea" *sensu lato* (e.g., Leschen et al. 2005, Robertson et al. 2015), lack well-defined diagnostic characters (Cai et al., 2022). Due to frequent morphological convergence, previous studies have shown that it is difficult to resolve the phylogeny of these groups using morphological information (Leschen et al., 2005; Lawrence et al., 2011).

Many fossils belonging to Erotyloidea, Nitiduloidea and Cucujoidea have been described from mid-Cretaceous Burmese amber. Some of them can be confidently placed in certain extant families based on distinct apomorphies (e.g., *Cretoparacucujus* Cai & Escalona in Boganiidae based on the setose cavities on mandibles; *Lobatihelota* Li et al. in Helotidae based on the submental furrows; *Cretolenax* Liu et al. in Monotomidae based on the antennomere 11 withdrawn and fused with antennomere 10; *Electroxyra* Gimmel et al. in Cyclaxyridae based on the epipleural foveae; Cai et al., 2018; Gimmel et al., 2019; Liu et al., 2020; Li et al., 2023a). However, the placements of some others are more controversial and harder to determine. The recently reported *Alloterocucus* Li et al. has an unusual combination of characters, and was suggested to be possibly related to Lamingtoniidae (Li et al., 2022). The case of *Pleuroceratos* Poinar & Kirejtshuk is even more complicated, which has been suggested to belong to Silvanidae, Sphindidae, or Phloeostichidae (Poinar et al., 2008; Liu et al., 2019; Kirejtshuk et al., 2019; Tihelka et al., 2020).

Here we report another enigmatic fossil of the "traditional cucujoid group" from Burmese amber. Although the placement of the fossil cannot be confidently determined, its possible affinities are discussed in light of the results of formal phylogenetic analyses.

Material and methods

Material

The Burmese amber (Kachin amber) specimen studied herein (Figs. 1–5) originated from amber mines near Noije Bum (26°20′ N, 96°36′ E), Hukawng Valley, Kachin State, northern Myanmar. The specimen is deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China. The amber piece was trimmed with a small table saw, ground with emery papers of different grit sizes, and finally polished with polishing powder.

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https://doi.org/10.1016/j.cris.2024.100075
Received 1 October 2023; Received in revised form 3 February 2024; Accepted 5 February 2024
Available online 6 February 2024

Fossil imaging

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 488 nm (Argon) laser excitation line (Fu et al., 2021). Images under incident light and widefield fluorescence were stacked with Helicon Focus 7.0.2 and Zerene Stacker 1.04. Confocal images were stacked with Helicon Focus 7.0.2 and Adobe Photoshop CC. Microtomographic data were obtained with a Zeiss Xradia 520 Versa 3D X-ray microscope at the micro-CT laboratory of NIGP and analyzed in VGStudio MAX 3.0. Scanning parameters were as follows: isotropic voxel size, 3.3808 μm; power, 3 W; acceleration voltage, 40 kV; exposure time, 6 s; projections, 2801. Images were further processed in Adobe Photoshop CC to adjust brightness and contrast.

Phylogenetic analyses

To evaluate the systematic placement of the new fossil, we conducted constrained morphology-based phylogenetic analyses under parsimony (e.g., Fikáček et al. 2020, Li et al. 2023a, 2023b). The data matrix was derived from the previously published dataset by Leschen et al. (2005). *Cavognatha* Crowson has been synonymized with *Taphropiestes* Reitter (Ślipiński and Tomaszewska, 2010). Thus, this tip name was modified accordingly. Li et al. (2022) also used the matrix by Leschen et al. (2005) to determine the position of another cucujiform fossil through a constrained analysis, in which the backbone tree regarding the relationships among extant taxa was constructed based on the synthesized molecular tree (their Fig. 2) in McKenna et al. (2019). The constraining backbone tree in the present analysis was the same as the one used by Li et al. (2022). During the analysis, only the fossil was allowed to move freely across the backbone tree.

The analyses were performed under both equal and implied weights, using R 4.1.0 (R Core Team, 2019) and the R package TreeSearch 1.3.1 (Smith, 2023). The concavity constant in weighted analysis was set to 12, following the suggestion by Goloboff et al. (2018) and Smith (2019).

Fig. 1. General habitus of *Isocryptophilus exilipunctus* Li & Cai **gen. et sp. nov.**, holotype, NIGP203274, under incident light. (A) Dorsal view. (B) Ventral view. Scale bars: 500 μm.

In order to perceive the uncertainty of the fossil placement, the parsimony scores of the trees with alternative placements of the fossil were mapped to the corresponding branches of the backbone tree. The results were visualized with the R package ggtree 6.5.2 (Yu et al., 2017; Yu, 2020) and graphically edited with Adobe Illustrator CC 2017.

Nomenclatural acts

This published work and the nomenclatural acts it contains have been registered in ZooBank. The LSID for this publication is urn:lsid:zoobank.org:pub:63B2E92B-D30F-40AE-B173-E287265AAA54.

Systematic paleontology

Order Coleoptera Linnaeus, 1758
Suborder Polyphaga Emery, 1886
Series Cucujiformia Lameere, 1938
Superfamily (?) Erotyloidea Latreille, 1802

Genus ***Isocryptophilus*** Li & Cai gen. nov.

Type species. Isocryptophilus exilipunctus sp. nov.

Etymology. The generic name is formed based on the Greek "*isos*", similar, and *Cryptophilus Reitter*, a genus in Erotylidae, referring to the overall similar dorsal appearance to the latter. The name is masculine in gender.

Diagnosis. Neck abruptly constricted; temples essentially absent (Fig. 1A). Compound eyes without interfacetal setae. Frontoclypeal suture absent (Fig. 4D). Subantennal grooves absent (Fig. 3A). Round cavity developed between antennal insertion and anterior margin of compound eye (Fig. 3A). Genae unprojected (Fig. 3A). Pronotal disc transverse; lateral pronotal carinae complete (Fig. 4A–C). Prosternum in front of coxae long (Fig. 3B). Procoxal cavities externally open (Fig. 3B). Protrochantins concealed (Fig. 3B). Scutellar shield not abruptly elevated (Fig. 3I). Elytral punctation fine, irregular (Fig. 3I); epipleura incomplete (Fig. 2B). Mesocoxal cavities narrowly separated (Fig. 5B), laterally open (Fig. 5A). Abdominal ventrite 1 without postcoxal lines (Fig. 3D).

Isocryptophilus exilipunctus Li & Cai sp. nov.
(Figs. 1–5)

Fig. 2. General habitus of *Isocryptophilus exilipunctus* Li & Cai **gen. et sp. nov.**, holotype, NIGP203274, under widefield fluorescence. (A) Dorsal view. (B) Ventral view. Scale bars: 500 μm.

Material. Holotype, NIGP203274, female.

Etymology. The specific name is formed based on the Latin "*exilis*", small, and "*punctus*", referring to the fine punctation on elytral surface.

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 elongate, flattened, about 2.0 mm long, 0.8 mm wide; surface with fine hairs.

Head prognathous, abruptly constricted immediately behind eyes, without distinct temples. Frontoclypeal suture absent. Compound eyes prominent, moderately coarsely facetted, without interfacetal setae. Subantennal grooves absent. A round cavity present between antennal insertion and anterior margin of compound eye. Genae not projected. Antennae 11-segmented, submoniliform; terminal three antennomeres longer than proceeding ones, forming indistinct club. Mandibles bidentate apically (in the left mandible the lower tooth is further subdivided). Maxillae with well developed, setose galea; maxillary palp 4-

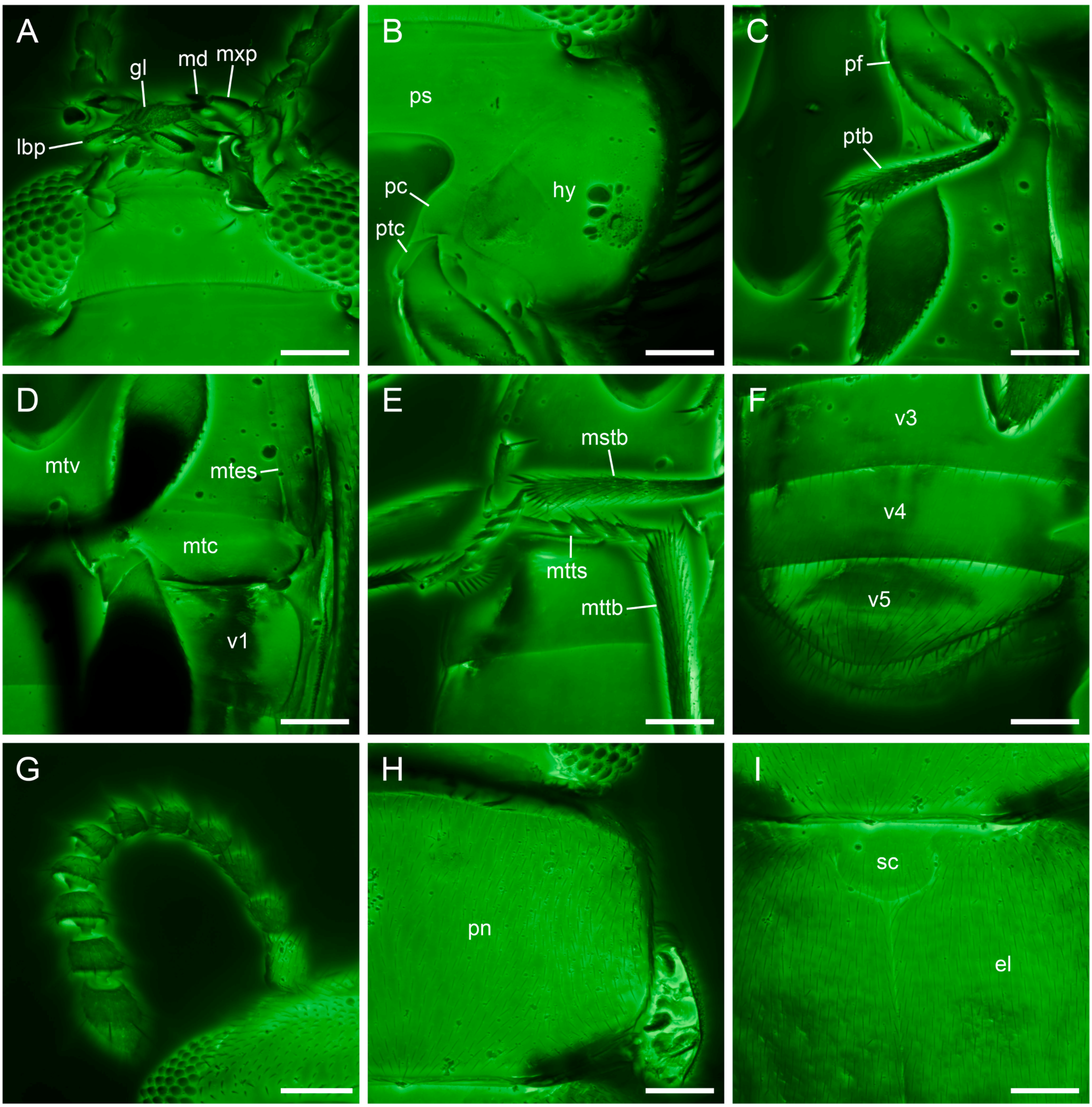

Fig. 3. Details of *Isocryptophilus exilipunctus* Li & Cai **gen. et sp. nov.**, holotype, NIGP203274, under confocal microscopy. (A) Head, ventral view. (B) Prothorax, ventral view. (C) Fore leg. (D) Abdominal base, ventral view. (E) Mid and hind legs. (F) Abdominal apex, ventral view. (G) Antenna. (H) Prothorax, dorsal view. (I) Elytral base, dorsal view. Abbreviations: el, elytron; gl, galea; hy, hypomeron; lbp, labial palp; md, mandible; mstb, mesotibia; mtc, metacoxa; mtes, metanepisternum; mttb, metatibia; mtts, metatarsus; mtv, metaventrite; mxp, maxillary palp; pc, procoxa, pf, profemur; pn, pronotum; ps, prosternum; ptb, protibia; ptc, protrochanter; sc, scutellum; v1–5, ventrites 1–5. Scale bars: 100 µm.

segmented; apically palpomere coniform. Mentum wider than long, widest at base. Apical labial palpomere strongly expanded.

Pronotal disc subrectangular, transverse, about as wide as combined elytral width; anterior and posterior angles not produced, rounded; lateral pronotal carinae complete, mainly simple (very finely serrulate); disc surface smooth, without protuberances or impressions. Prosternum in front of coxae long. Notosternal suture anteriorly incomplete. Procoxal cavities externally open. Protrochantins concealed.

Scutellar shield not abruptly elevated, transverse, posteriorly broadly rounded. Elytra about 1.6 times as long as combined width; surface with fine, confused punctation; epipleura incomplete. Mesocoxal cavities narrowly separated, bordered by mesoventrite, mesepimeron and metaventrite. Metaventrite likely without discrimen; posterior metaventral notch present. Exposed portion of metanepisternum long and narrow. Metacoxae transverse, narrowly separated, laterally not meeting elytral epipleura; coxal plate absent.

Legs relatively long and slender. Tibiae slightly and gradually widened distally; tibial spurs paired. Tarsi 5–5–5; all tarsomeres simple. Pretarsal claws simple.

Abdomen with five ventrites. Ventrite 1 not much longer than 2; postcoxal lines absent; intercoxal process acute, narrowly rounded.

Discussion

Isocryptophilus has a typical appearance of cucujiforms. Within Cucujiformia, it could be easily ruled out from Cleroidea (except for Byturidae and Biphyllidae) by the metacoxae laterally not meeting elytral epipleura, from Lymexyloidea by the unprojecting procoxae, from Tenebrionoidea and Coccinelloidea by the unreduced 5–5–5 tarsi, and from Chrysomeloidea and Curculionoidea by the simple (not pseudotetramerous) tarsi. We therefore conducted a phylogenetic analysis to test its placement in the remaining cucujiforms, i.e., Erotyloidea, Nitiduloidea and Cucujoidea, plus the cleroid families Byturidae and Biphyllidae.

Under equal weighting, the tree requires minimum number of evolutionary steps when *Isocryptophilus* is inserted to Biphyllidae, Erotylidae, Silvanidae, Agapythidae, Cavognathidae or Phloeostichidae (Fig. 6A). Previously all these families were classified in Cucujoidea. However, based on molecular evidence, Biphyllidae was transferred to Cleroidea (Hunt et al., 2007; Bocak et al., 2014; Robertson et al., 2015), and Erotylidae was separated into Erotyloidea during the further break-up of the traditional Cucujoidea (Cai et al., 2022).

Isocryptophilus shares with Agapythidae, Cavognathidae and Phloeostichidae the absence of frontoclypeal suture (except for *Bunyastichus* Leschen et al.) and subantennal grooves, externally open

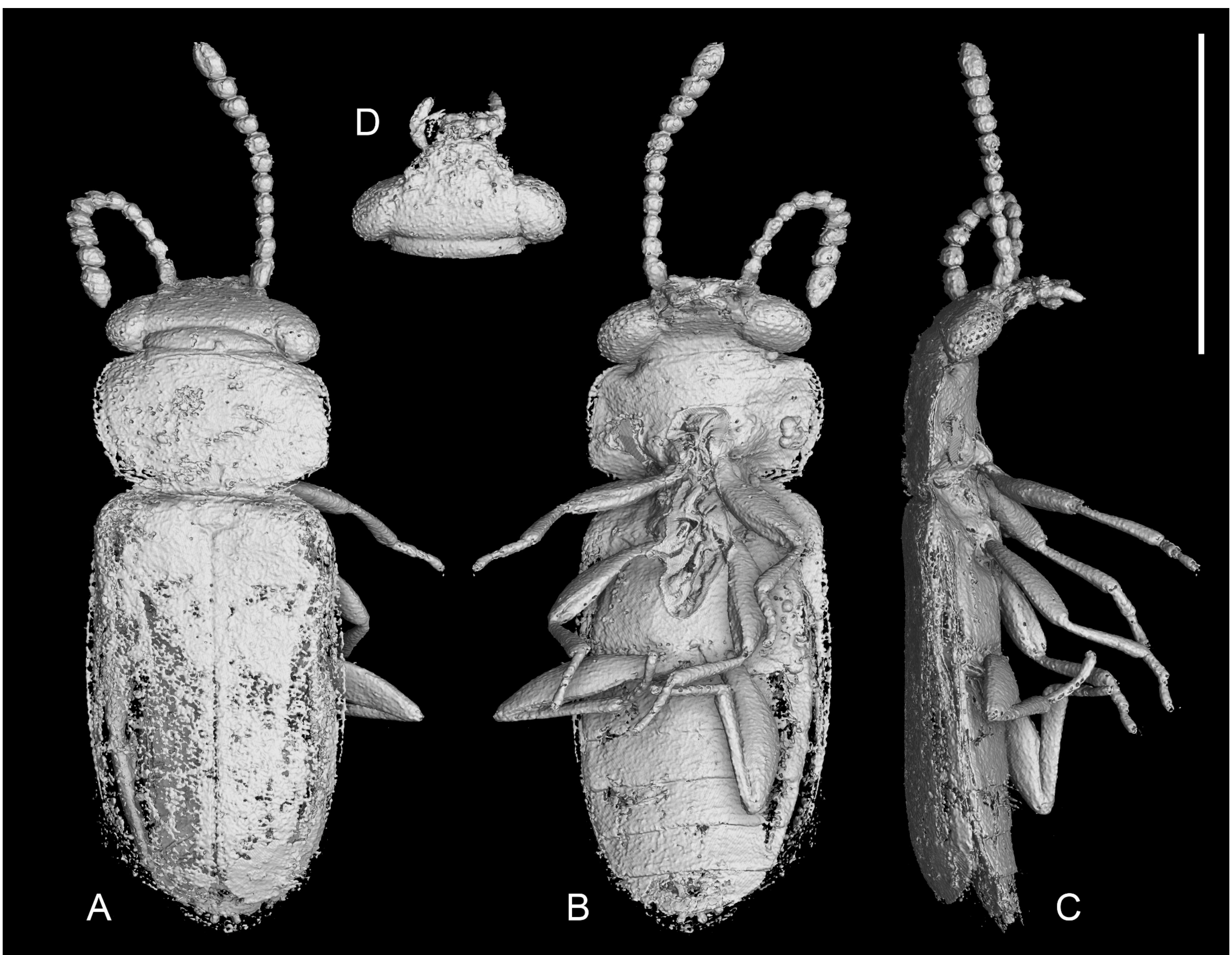

Fig. 4. X-ray microtomographic reconstruction of *Isocryptophilus exilipunctus* Li & Cai **gen. et sp. nov.**, holotype, NIGP203274. (A) Dorsal view. (B) Ventral view. (C) Lateral view. (D) Head, dorsal view. Scale bar: 1 mm.

procoxal cavities (except for *Bunyastichus*), and laterally open mesocoxal cavities. It additionally shares with Agapythidae the unprojected genae, long prosternum, fine and irregular elytral punctation, and incomplete elytral epipleura, and with Cavognathidae the transverse pronotal disc, concealed protrochantins, not abruptly elevated scutellar shield, and fine and irregular elytral punctation. Characters such as complete lateral pronotal carinae, long prosternum, irregular elytral punctation, and incomplete elytral epipleura may also be found in at least some species of Phloeostichidae. However, Agapythidae differs from *Isocryptophilus* in having distinct temples, exposed protrochantins, subquadrate pronotal disc, incomplete pronotal lateral carinae, and scutellar shield abruptly elevated (Leschen et al., 2005); Cavognathidae differs from *Isocryptophilus* in frontoclypeal region usually with paired pits, genae anteriorly projecting, pregular region with pair of oblique grooves, prosternum shorter, and elytral epipleura complete (Ślipiński and Tomaszewska, 2010); Phloeostichidae differs from *Isocryptophilus* in having laterally produced genae, usually narrower pronotal disc (base distinctly narrower than elytral bases), exposed protrochantins, and usually abruptly elevated scutellar shield (Leschen et al., 2005).

The tree appears to be more parsimonious when *Isocryptophilus* is inserted to Biphyllidae, Erotylidae or Silvanidae under implied weighting (Fig. 6B). *Isocryptophilus* shares with Biphyllidae the absence of frontoclypeal suture, transverse pronotum disc with well-developed lateral margins, concealed protrochantins, and narrowly separated and laterally open mesocoxal cavities. However, Biphyllidae differs from *Isocryptophilus* in eyes with interfacetal setae, subantennal grooves present, procoxal cavities externally closed, elytra with distinct puncture striae, tarsomeres 2 and 3 ventrally lobed, and abdominal ventrite 1 with postcoxal lines (Goodrich and Springer, 1992). Silvanidae shares with *Isocryptophilus* the unprojected genae, abruptly constricted neck, concealed protrochantins, and laterally open mesocoxal cavities. The tribe Brontini of Silvanidae also has externally broadly open procoxal cavities (Thomas, 2003). However, Silvanidae differs from *Isocryptophilus* in eyes with interfacetal setae, scutellar shield abruptly elevated, elytra with striate punctation, and epipleura usually broad and complete.

Erotylidae is a large and morphologically diverse family (Węgrzynowicz, 2002; Leschen, 2003; Leschen and Buckley, 2007). The general appearance of *Isocryptophilus* may resemble some members of Xenoscelinae, Pharaxonothinae or Cryptophilinae (e.g., Leschen and Wegrzynowicz, 2008; Skelley et al., 2017; Esser, 2017). Although the character combination of *Isocryptophilus* is very unusual for Erotylidae, most of the character states present in *Isocryptophilus* can be found individually in some subgroups of the family. For example, in Erotylidae, the frontoclypeal suture, interfacetal setae, and subantennal grooves may either be present or absent; the prosternum in front of coxae may be short or long; the procoxal cavities may be variably closed or open; and the elytral punctation may be confused to striate (Leschen et al., 2010). Even though in most erotylids the mesocoxal cavities are moderately to widely separated and laterally closed, they may be narrowly separated in *Chasmatodera* Arrow, and laterally open in *Chinophagus* Lyubarsky (Lyubarsky, 1997). Similarly, incomplete elytral epipleura may be found in *Loberonotha* Sen Gupta & Crowson even though most others have complete ones (Leschen, 2003). Besides, Boganiidae, the only other family in Erotyloidea (Cai et al., 2022), has laterally open mesocoxal cavities and incomplete elytral epipleura (Escalona et al., 2015).

Concluding remarks

Based on the above analyses and comparison of characters, we argue that *Isocryptophilus* is most likely to belong to Erotyloidea, possibly closer to Erotylidae. However, other possibilities cannot be confidently ruled out. The analyses in the present study are only preliminary and unable to accurately determine the position of *Isocryptophilus*. In the backbone tree, most families are only represented by one or two genera, which cannot fully reflect the morphological variability of the families. A morphological matrix designed with more comprehensive taxon sampling, as well as a robust molecular phylogeny covering these taxa, might be helpful for clarifying the systematic placement of this fossil in the future.

CRediT authorship contribution statement

Yan-Da Li: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Zhen-Hua Liu:** Investigation, Writing – review & editing. **Di-Ying Huang:** Funding acquisition, Resources, Writing – review & editing. **Chen-Yang Cai:** Conceptualization, Funding acquisition, Investigation, Resources, Supervision, Writing – review & editing.

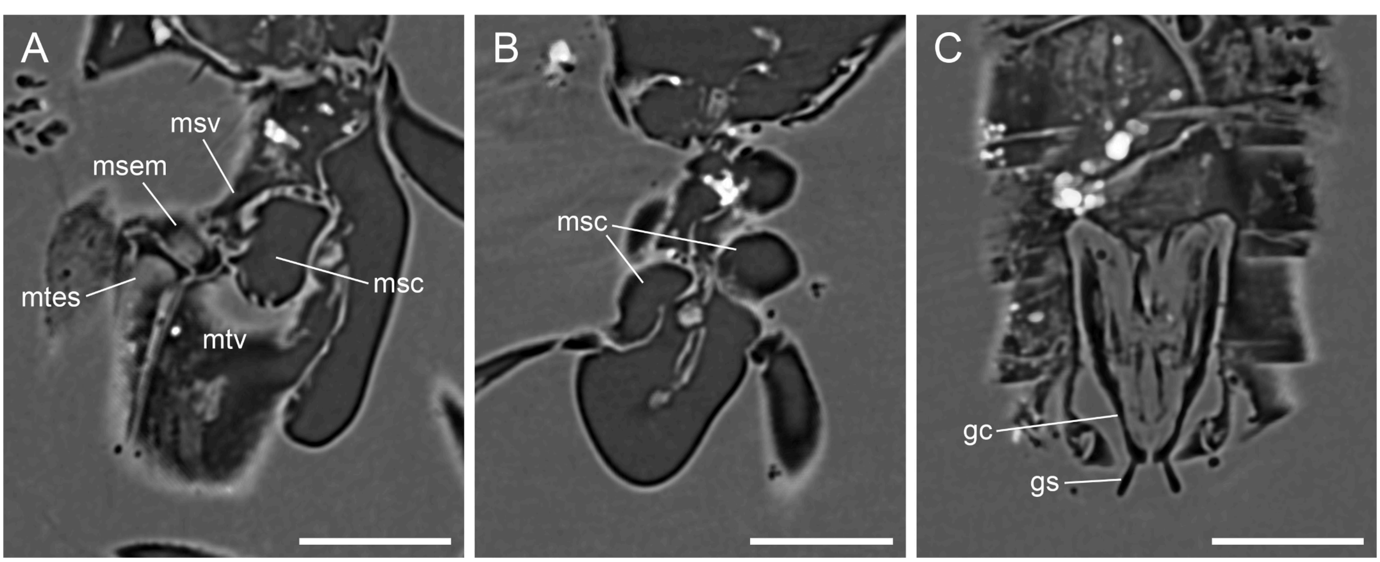

Fig. 5. *Isocryptophilus exilipunctus* Li & Cai **gen. et sp. nov.**, holotype, NIGP203274, weighted average stacking of micro-CT slices. (A) Mesothorax, ventrolateral view. (B) Mesothorax, ventral view. (C) Ovipositor, ventral view. Abbreviations: gc, gonocoxite; gs, gonostylus; msc, mesocoxa; msem, mesepimeron; msv, mesoventrite; mtes, metanepisternum; mtv, metaventrite. Scale bars: 200 μm.

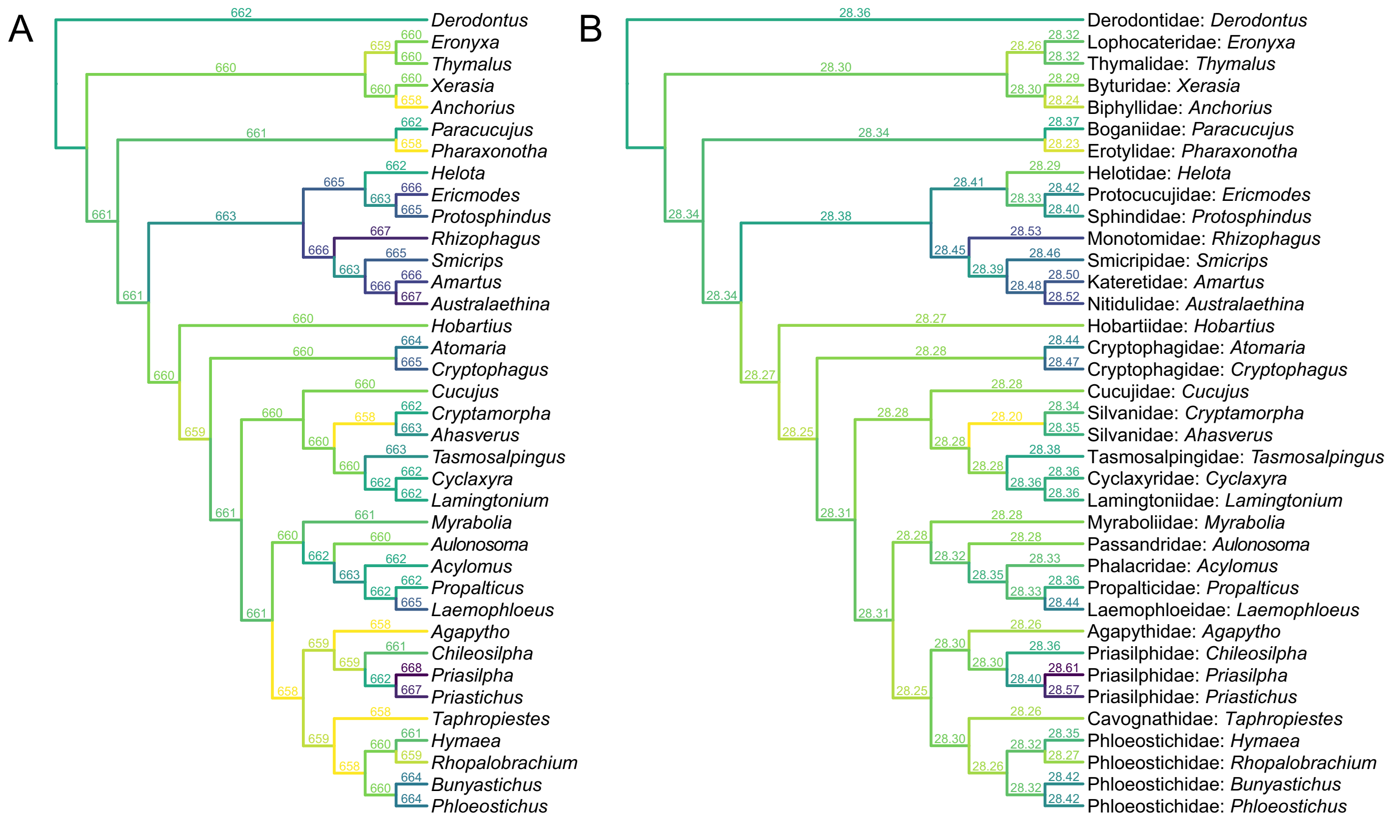

Fig. 6. Constrained parsimony analyses showing alternative placements of *Isocryptophilus* Li & Cai **gen. nov.** The score above each branch represents the parsimony score of the topology in which *Isocryptophilus* is inserted to that branch. (A) Analysis under equal weights. (B) Analysis under implied weights.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data matrix and the R script for the phylogenetic analyses are available in the Supplementary Material. The original confocal and micro-CT data are available in the Zenodo repository (https://doi.org/10.5281/zenodo.10395896).

Acknowledgements

We are grateful to Richard Leschen for helpful discussion, Su-Ping Wu for help with micro-CT reconstruction, Rong Huang and Yan Fang for help with confocal microscopy, and Jing-Jing Tang for help with widefield microscopy. Two anonymous reviewers provided helpful comments on the manuscript. 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).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.cris.2024.100075.

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