



New mid-Cretaceous cryptic slime mold beetles and the early evolution of Sphindidae (Coleoptera: Cucujoidea)

Yan-Da Li¹, Erik Tihelka², Zhen-Hua Liu^{3,4}, Di-Ying Huang¹, Chen-Yang Cai^{1,2}

¹ State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, Nanjing 210008, China; Yan-Da Li [ydl@pku.edu.cn]; Di-Ying Huang [dyhuang@nigpas.ac.cn]

² School of Earth Sciences, University of Bristol, Life Sciences Building, Tyndall Avenue, Bristol, BS8, United Kingdom; Erik Tihelka [wn20250@bristol.ac.uk]

³ State Key Laboratory of Biocontrol, Key Laboratory of Biodiversity Dynamics and Conservation of Guangdong Higher Education Institute, College of Ecology and Evolution, School of Life Sciences, Sun Yat-Sen University, Guangzhou, China; Zhen-Hua Liu [liuzhh22@mail2.sysu.edu.cn]

⁴ Australian National Insect Collection, CSIRO National Research Collections Australia, Canberra, Australia

<http://zoobank.org/F4F66D8B-35D3-4DE0-9467-5115C9143A73>

Corresponding author: Chen-Yang Cai (cycai@nigpas.ac.cn)

Received 8 August 2021
Accepted 18 October 2021
Published 23 November 2021

Academic Editors Ricardo Pérez-de la Fuente & Mónica M. Solórzano-Kraemer

Citation: Li Y-D, Tihelka E, Liu Z-H, Huang D-Y, Cai C-Y (2022) New mid-Cretaceous cryptic slime mold beetles and the early evolution of Sphindidae (Coleoptera: Cucujoidea). *Arthropod Systematics & Phylogeny* 79: 587–597. <https://doi.org/10.3897/asp.79.e72724>

Abstract

The cryptic slime mold beetles, Sphindidae, are a moderately diverse cucujoid beetle family, whose members are obligately tied to slime molds throughout their life. The fossil record of sphindid beetles is sparse; stem-sphindids and crown-group members of uncertain systematic placement have been reported from Cretaceous ambers. Here we review the Mesozoic fossil record of Sphindidae and report a new sphindid genus and species, *Trematosphindus newtoni* **gen. et sp. nov.**, from Albian/Cenomanian amber from northern Myanmar (ca. 99 Ma). *Trematosphindus* is set apart from all other sphindids by the presence of distinct lateral cavities on the anterior pronotal angles. Our phylogenetic analysis identifies *Trematosphindus* as an early-diverging genus within Sphindidae, sister to the remainder of the family except *Protosphindus*, or *Protosphindus* and *Odontosphindus*. The new fossils provide evidence that basal crown slime mold beetles began to diversify by the mid-Cretaceous, providing a valuable calibration point for understanding timescale of sphindid co-evolution with slime molds.

Key words

Sphindidae, *Trematosphindus*, myxomycetes, Cretaceous, Burmese amber

1. Introduction

The family Sphindidae, cryptic slime mold beetles, is a group of widespread beetles belonging to the diverse and, as currently conceived, paraphyletic polyphagan su-

perfamily “Cucujoidea” (Forrester and McHugh 2010). Sphindidae are represented in the Recent fauna by only nine genera and approximately 66 valid extant species

(J.V. McHugh, personal communication), though much of their biodiversity remains undocumented. For example, Forrester and McHugh (2007) mentioned that they have identified more than a hundred undescribed species in a single sphindid genus, *Aspidiphorus* Latreille. As their common name suggests, sphindid beetles feed exclusively on slime molds (myxomycetes) in both larval and adult stages, while most other aspects of their ecology remain elusive (Lawrence and Newton 1980; Burakowski and Ślipiński 1987). Sphindidae appears to be closely related to Protocucujidae, which is supported by multiple lines of morphological and molecular evidence (e.g., Leschen et al. 2005; Robertson et al. 2015; McKenna et al. 2019). Four extant subfamilies have been proposed within Sphindidae based on a morphological phylogenetic analysis, i.e., Protosphindinae, Odontosphindinae, Sphindiphorinae, and Sphindinae (McHugh 1993).

The fossil record of Sphindidae is very sparse. All putative pre-Quaternary sphindid fossils were reported from amber deposits. Kirejtshuk et al. (2015) described five species of *Libanopsis* Kirejtshuk from the Early Cretaceous Lebanese amber, and assigned them to a new subfamily, Libanopsinae. Later, Kirejtshuk et al. (2019) described the genus *Burmops* Kirejtshuk from the mid-Cretaceous Burmese amber, and moved the previously described genus *Pleuroceratos* Poinar & Kirejtshuk from Silvanidae to Sphindidae, treating both as members of the extant subfamily Protosphindinae. However, *Pleuroceratos* has externally open procoxal cavities (Liu et al. 2019), which is discordant with a placement in Protosphindinae. Tihelka et al. (2020) further found that the morphology of *Pleuroceratos* is actually characteristic of Phloeostichidae, and confirmed its position in Phloeostichidae with a formal phylogenetic analysis.

Here, we report a new sphindid genus and species from mid-Cretaceous Burmese amber, *Trematosphindus newtoni* **gen. et sp. nov.**, adding to our knowledge on the Mesozoic diversity of this family.

2. Material and methods

2.1. Materials

The Burmese amber specimens studied herein (Figs 1–6) originated from amber mines near Noiye Bum (26°20' N, 96°36' E), Hukawng Valley, Kachin State, northern Myanmar. The specimens are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. The amber pieces were trimmed with a small table saw, ground with emery papers of different grit sizes, and finally polished with polishing powder.

2.2. Fossil imaging

Photographs under incident light were taken with a Zeiss Discovery V20 stereo microscope. Widefield fluores-

cence 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. 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 colour coding for depth in ZEN 2.3 (Blue Edition), or without colour coding in Helicon Focus 7.0.2. 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: NIGP175114 [isotropic voxel size, 3.2569 µm; power, 4 W; acceleration voltage, 50 kV; exposure time, 1 s; projections, 2501]; NIGP175115 [isotropic voxel size, 2.3931 µm; power, 3 W; acceleration voltage, 40 kV; exposure time, 3 s; projections, 3001]. Images were further processed in Adobe Photoshop CC to enhance contrast.

2.3. Morphological phylogenetic analysis

To evaluate the systematic placement of the new species, a morphological phylogenetic analysis was performed using both parsimony and Bayesian inference. The data matrix was mainly derived from a previously published dataset (McHugh 1993) (File 1, 2). *Ericmodes sylvaticus* (Philippi) (Protocucujidae) was selected as the outgroup. Character 4 in McHugh (1993) was originally coded for *Protosphindus chilensis* Sen Gupta & Crowson as “clypeus deeply embedded in head with one-third length or less projecting beyond anterior margin of head”. In fact, the clypeus of *Protosphindus* Sen Gupta & Crowson is similar to other sphindids in having more than half of its length projecting beyond the anterior margin of the head (fig. 1 in Sen Gupta and Crowson 1979), and hence the coding of the character was amended accordingly.

Parsimony analysis was performed under implied weights using the program TNT 1.5 (Goloboff et al. 2008, 2016). Parsimony analyses achieve highest accuracy under a moderate weighting scheme (i.e., when concavity constants, K , are between 5 and 20) (Goloboff et al. 2018; Smith 2019). Therefore, the concavity constant was set to 12 here, as suggested by Goloboff et al. (2018). Most parameters were set as default in the “new technology search”, while the value for “find min. length” was changed from 1 to 100. A strict consensus tree was calculated, and standard bootstrap analysis was implemented by 10,000 pseudoreplicates, where the support values were shown as frequency differences (Goloboff et al. 2003).

A Bayesian inference for morphological traits was conducted using MrBayes 3.2.6 (Ronquist et al. 2012). Two MCMC analyses were run simultaneously, each with one heated chain and three cold chains. Trees were sampled every 10,000 generations. Analyses were stopped when the average standard deviation of split frequencies

remained below 0.01. The first 25% of sampled trees were discarded as burn-in, and the remains were used to build a majority-rule consensus tree.

Trees were drawn with the online tool iTOL 5.7 (Letunic and Bork 2019) and graphically edited with Adobe Illustrator CC 2017.

2.4. Abbreviations

The following abbreviation of institution is used: **NIGP** – Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. The following abbreviations of morphological characters are used: **BL** – apparent body length in dorsal view; **BW** – body width; **EL** – elytral length; **HL** – head length; **HW** – head width; **PL** – pronotal length; **PW** – pronotal width.

3. Systematic palaeontology

Order Coleoptera Linnaeus, 1758

Suborder Polyphaga Emery, 1886

Superfamily Cucujoidea Latreille, 1802

Family Sphindidae Jacquelin du Val, 1860

(For references of high-rank taxon names, see Bouchard et al. 2011)

Genus *Trematosphindus* Li & Cai gen. nov.

<http://zoobank.org/045EDCD5-8A8D-494F-B25B-FA48081-E1B20>

Type species. *Trematosphindus newtoni* sp. nov.

Etymology. The generic name is composed of the Greek “*trema*”, hole, and generic name *Sphindus*, in reference to the cavity at each anterior pronotal angle. The name is masculine in gender.

Diagnosis. Head without any distinct grooves. Antennae 11-segmented. Pronotum with large cavities at anterior pronotal angles. Pronotal lateral edges dentate. Procoxal cavities closed externally. Elytra without raised carinae. Pygidium with a distinct median longitudinal groove.

Remarks. *Trematosphindus* is somewhat similar to several families in (or formerly in) the broadly defined Cucujoidea (e.g., Biphylidae, Cryptophagidae, Boganiidae, and Protocucujidae) in the general habitus, shape of antennal club, or the presence of cavities/glandular pores. Boganiidae and Cryptophagidae can be easily ruled out as potential relatives of *Trematosphindus*, based on their

externally open procoxal cavities (procoxal cavities externally closed in *Trematosphindus* and Sphindidae). Biphylidae (now in Cleroidea) and also Cryptophagidae can be distinguished from *Trematosphindus* by their laterally closed mesocoxal cavities (mesocoxal cavities laterally open in *Trematosphindus* and Sphindidae). As the sister taxon of Sphindidae, the monogeneric family Protocucujidae shares many features with *Trematosphindus* (and other Sphindidae, Ślipiński 1998). However, Protocucujidae lacks the distinct elytral striae and the distinct basal row of depressions on ventrites 2–5 (elytral striae distinct and basal row of depressions on ventrites 2–5 present in *Trematosphindus* and at least most Sphindidae). Thus, we think *Trematosphindus* can be quite confidently assigned to Sphindidae, despite the presence of some characters unusual for a crown-group sphindid (e.g., supraocular grooves absent, anterior pronotal angles with cavities/glandular pores, scale-like setae; see also Discussion).

Trematosphindus newtoni Li & Cai sp. nov.

<http://zoobank.org/0FD33A15-0CF1-4A2B-9EBC-71AE503-EFC69>

Figs 1–6

Etymology. The species is named after Dr. Alfred F. Newton, an authority on coleopteran systematics.

Materials. **Holotype**, NIGP175114, female. **Paratype**, NIGP175115, sex unknown.

Locality and horizon. Amber mine located near Noi-je 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 narrowly oval, convex. Surface with moderately large, rounded punctures and hair- to scale-like setae. — **Head** (Fig. 2F) partially visible from above; dorsal surface without any distinct grooves or ridges; basal region with hair-like setae only; anterior region with distinctly thicker (somewhat scale-like) setae. Compound eyes moderately to coarsely faceted, prominent. Antennae (Fig. 2A) 11-segmented; antennomere 1 large and broad; antennomere 2 smaller; antennomere 3 elongate; antennomere 4 submoniliform; antennomeres 9–11 large, forming a densely pubescent compact club. Frontoclypeal suture arcuate. Clypeus weakly emarginate apically, with nearly straight lateral edges. Labrum slightly emarginate apically. Mandibles apparently flattened at apex. — **Prothorax:** Pronotal disc (Figs 2G, 5B) transverse, 1.4–1.5 times as wide as long; surface with scale-like and hair-like setae; anterior margin with a row of densely-arranged moderately-thick setae; lateral edges dentate; basal margin arcuate. A pair of large cavities

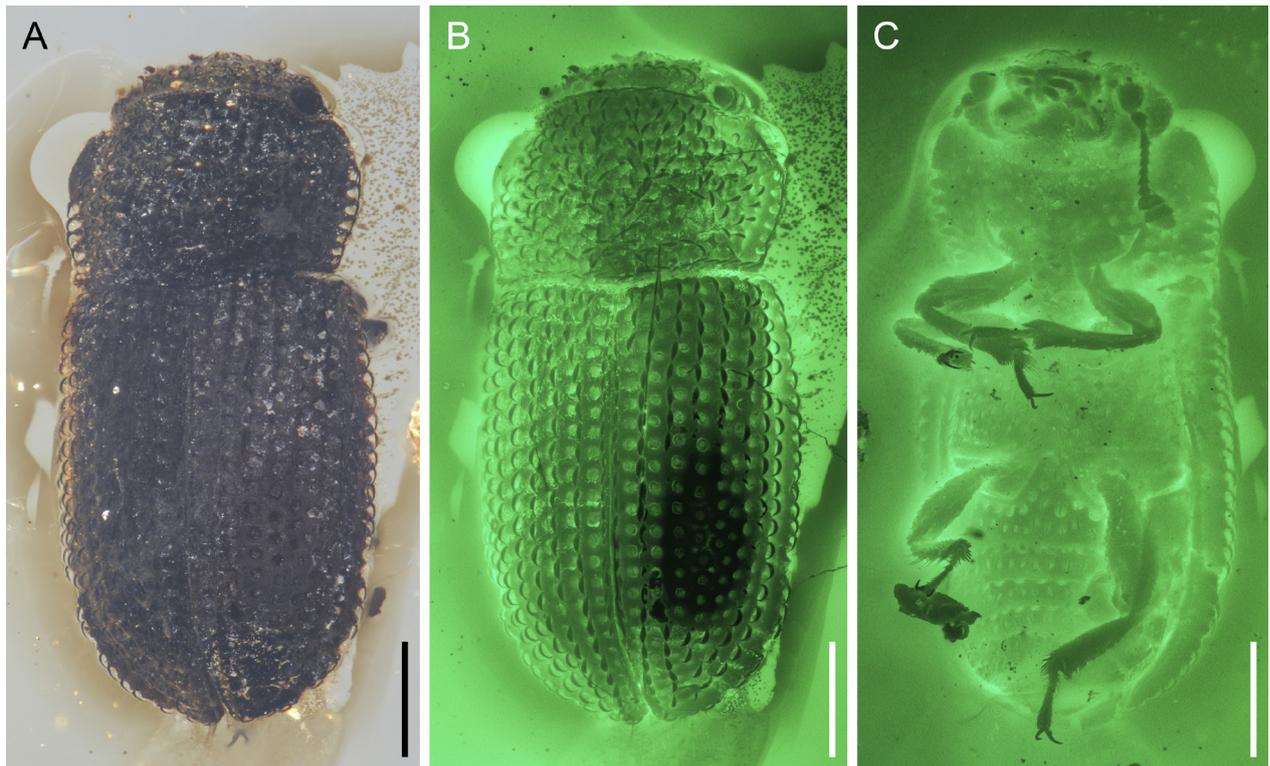


Figure 1. General habitus of *Trematosphindus newtoni* gen. et sp. nov., holotype, NIGP175114. **A:** Dorsal view, under incident light. **B:** Dorsal view, under widefield fluorescence. **C:** Ventral view, under widefield fluorescence. Scale bars: 400 μ m.

(alternatively interpreted as glandular callosities) present at anterior pronotal angles (Figs 2F, 5B). Prosternum in front of procoxae transverse, about as long as prosternal process; prosternal process relatively thick, without keel or protuberance. Procoxal cavities externally closed posteriorly by lateral extensions of prosternal process and posterior extensions of each hypomeron (Figs 2B, 3F). — **Meso- and metathorax:** Scutellum (Fig. 5C) small, transverse, without longitudinal median carina. Elytra elongate, covering abdomen, tapered posteriorly, 1.4–1.5 times as long as width combined; surface with eight rows of nearly round punctures; scutellary striole relatively reduced, with three punctures; stria interspaces convex and each with one row of scale-like thick setae. Mesosternal process flat, bilobed (Fig. 3F). Metasternum without a distinct impunctate region around notch receiving intercoxal process. — **Legs** long, slender. Coxae transverse. Femora moderately setose. Tibiae moderately setose, with apical crown of stout spurs. Tarsi with formula 5-5-5 in female, tarsomeres 5 longer than the basal four segments combined; protarsomeres 1–4 with distinctly longer hairs. Pretarsal claws simple. — **Abdomen** with 5 ventrites. Ventrite 1 with a relatively broad intercoxal process (Fig. 2D); ventrites 2–5 with a basal row of depressions. Pygidium with a distinct median longitudinal groove (Fig. 3E).

Measurements. NIGP175114: BL 2.40 mm, BW 1.12 mm, HL 0.67 mm, HW 0.77 mm, PL 0.71 mm, PW 1.05 mm, EL 1.53 mm. NIGP175115: BL 1.90 mm, BW 0.75 mm, HL 0.50 mm, HW 0.55 mm, PL 0.54 mm, PW 0.73 mm, EL 1.16 mm.

4. Results

The parsimony analysis under implied weights yielded two most parsimonious trees, where the placement of *Notosphindus* McHugh & Wheel differed (Fig. 7). The results are consistent with the parsimony analysis under equal weights by McHugh (1993). The Bayesian inference recovered the position of *Notosphindus* as sister to (*Cariniphindus* McHugh + *Sphindus* Chevrolat), though with only a low posterior probability (Fig. 7). In both analyses, the fossil *Trematosphindus newtoni*, was recovered in a relatively basal position within Sphindidae. In the implied-weighted parsimony analysis, *Trematosphindus* was recovered as sister to all extant sphindids except *Protosphindus*, while in the Bayesian inference it appeared to be sister to all extant sphindids except *Protosphindus* and *Odontosphindus* LeConte.

5. Discussion

Kirejtshuk et al. (2015) described *Libanopsis*, a genus of putative sphindids, from Lebanese amber. *Libanopsis* possesses a series of characters different from extant sphindids, including the lack of a clear frontoclypeal suture and (sub)contiguous metacoxae. Thus, *Libanopsis* may be isolated from other sphindid subfamilies, and possibly represent a stem-group of Sphindidae (Kirejtshuk et al. 2015). Unlike *Libanopsis*, *Trematosphindus*

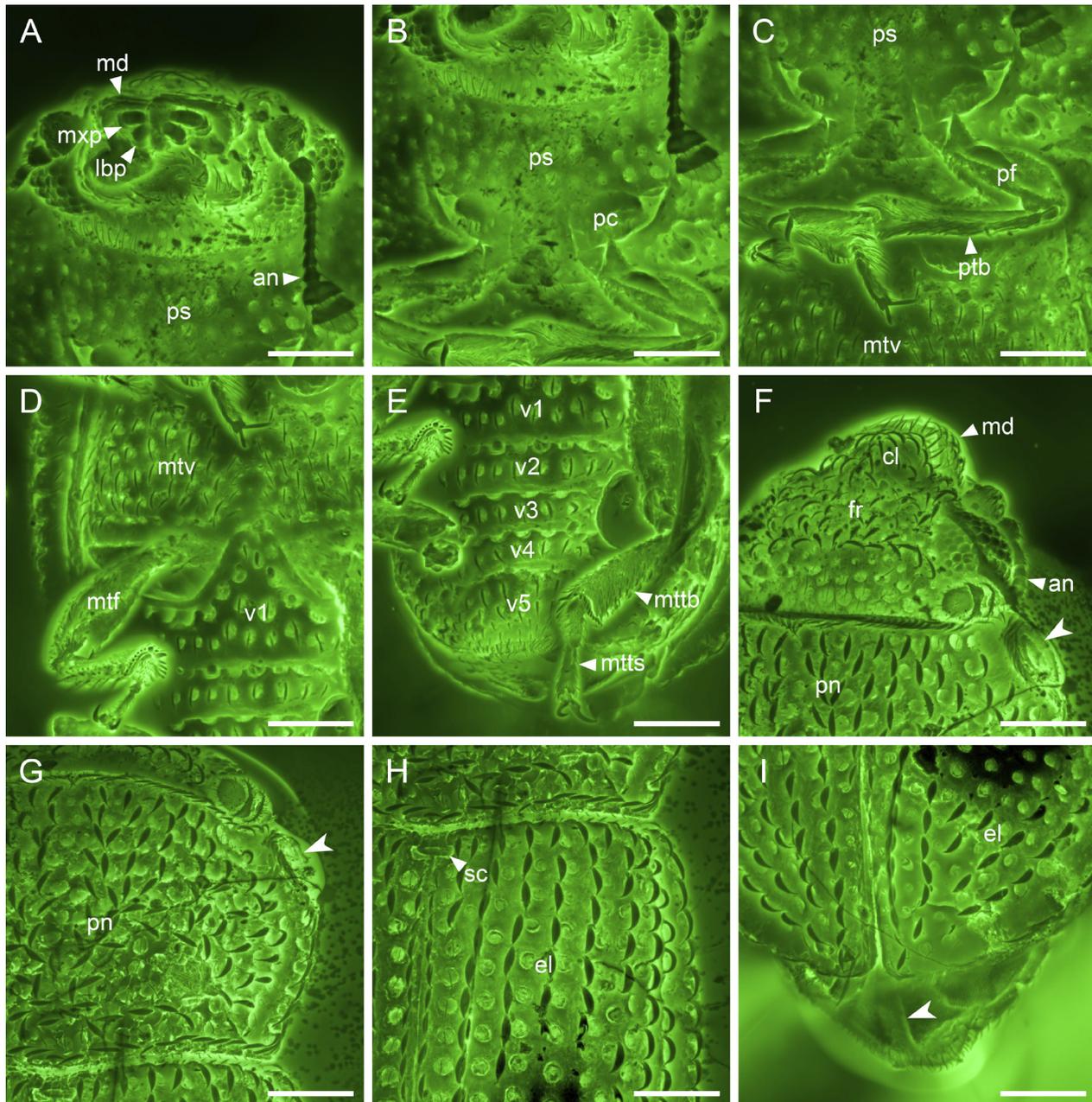


Figure 2. Details of *Trematosphindus newtoni* gen. et sp. nov., holotype, NIGP175114, under confocal microscopy. **A:** Head, anterior-ventral view. **B:** Prothorax, ventral view. **C:** Fore legs. **D:** Posterior portion of metathorax and anterior portion of abdomen, ventral view. **E:** Posterior portion of abdomen, ventral view. **F:** Head, dorsolateral view, with arrowhead showing the cavity at anterior pronotal angle. **G:** Prothorax, dorsal view. **H:** Elytral base, dorsal view. **I:** Elytral apex and pygidium, posterodorsal view, with arrowhead showing the distinct median groove on pygidium. Abbreviations: an, antenna; cl, clypeus; el, elytron; fr, frons; lbp, labial palp; md, mandible; mtf, metafemur; mttb, metatibia; mttts, metatarsus; mtv, metaventricle; mxp, maxillary palp; pc, procoxa; pf, profemur; pn, pronotum; ps, prosternum; ptb, protibia; sc, scutellum; v1–5, ventrites 1–5. Scale bars: 200 μ m.

represents a crown-group sphindid. Our phylogenetic analysis placed it as the sister taxon of all other extant sphindids except *Protosphindus* under parsimony, and as sister to all other sphindids excluding *Protosphindus* and *Odontosphindus* in the Bayesian analysis. *Trematosphindus* possesses a combination of apomorphic and plesiomorphic characters. It shares some plesiomorphic characters with *Protosphindus*, the earliest branching lineage in crown-group Sphindidae, including the absence of supraocular antennal grooves, the non-emarginate lateral margin of the clypeus, and the 11-segmented an-

tenna (also shared with *Odontosphindus* and *Sphindiphorus* Sen Gupta & Crowson). However, *Trematosphindus* differs from *Protosphindus* in abdominal ventrites 2–4 with a distinct basal band of depressions (Fig. 2E), and the absence of raised carinae on elytra. It differs from *Odontosphindus* and *Sphindiphorus*, two other basal sphindid genera, as well as *Protosphindus* in having a pygidium with a longitudinal median groove (Fig. 3E). This well-defined median groove on pygidium was previously known in *Aspidiphorus* and *Sphindiphorus* (Forrester 2003). In other sphindids, the pygidium either en-

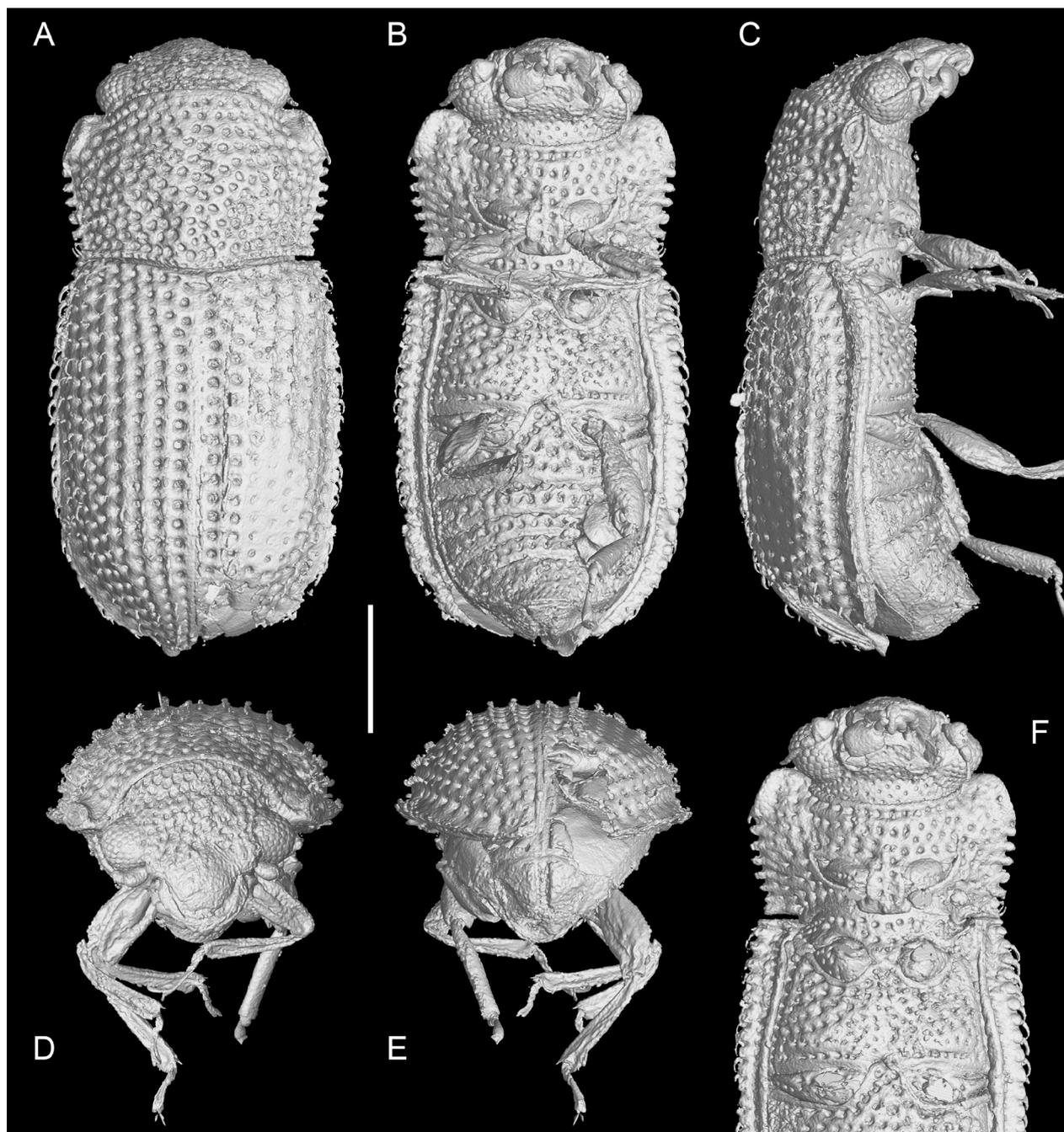


Figure 3. X-ray microtomographic reconstruction of *Trematosphindus newtoni* gen. et sp. nov., holotype, NIGP175114. **A:** Dorsal view. **B:** Ventral view. **C:** Lateral view. **D:** Anterior view. **E:** Posterior view. **F:** Ventral view, with legs removed. Scale bar: 500 μ m.

tirely lacks any depressions or grooves, or has only an indistinctly defined median depression. The mandibles of *Trematosphindus* are probably flattened at apex, while in *Protosphindus* and *Odontosphindus* the mandibles are broad at apex (McHugh 1993).

A notable character distinguishing *Trematosphindus* from all extant and fossil members of Sphindidae is the presence of a large oval cavity at each anterior pronotal angle (Figs 2F, 3C). External exoskeletal cavities have been widely reported in Coleoptera, and some of them have been suggested as a storage place for fungal transport (Grebennikov and Leschen 2010). Sphindidae are known to feed on myxomycetes (slime molds). Though these large pronotal cavities are absent in extant sphin-

dids, the surface punctures of sphindids have been associated with slime mold spores, and therefore likely play a role in transporting slime molds (McHugh 1990, 1993). As such, the large pronotal cavities in *Trematosphindus* may have fulfilled a similar function. The presence of surface punctures is a plesiomorphic for the family. *Trematosphindus* possibly evolved large lateral pronotal cavities later to further increase the efficiency of fungal transport. Alternatively, those cavities may be interpreted as glandular pores on callosity. A somewhat similar glandular callosity at anterior pronotal angles can be found in some Boganiidae (Crowson 1990; Escalona et al. 2015; Cai and Huang 2019) and some Cryptophagiidae (Bousquet 1989; Otero and Johnson 2013; Otero and

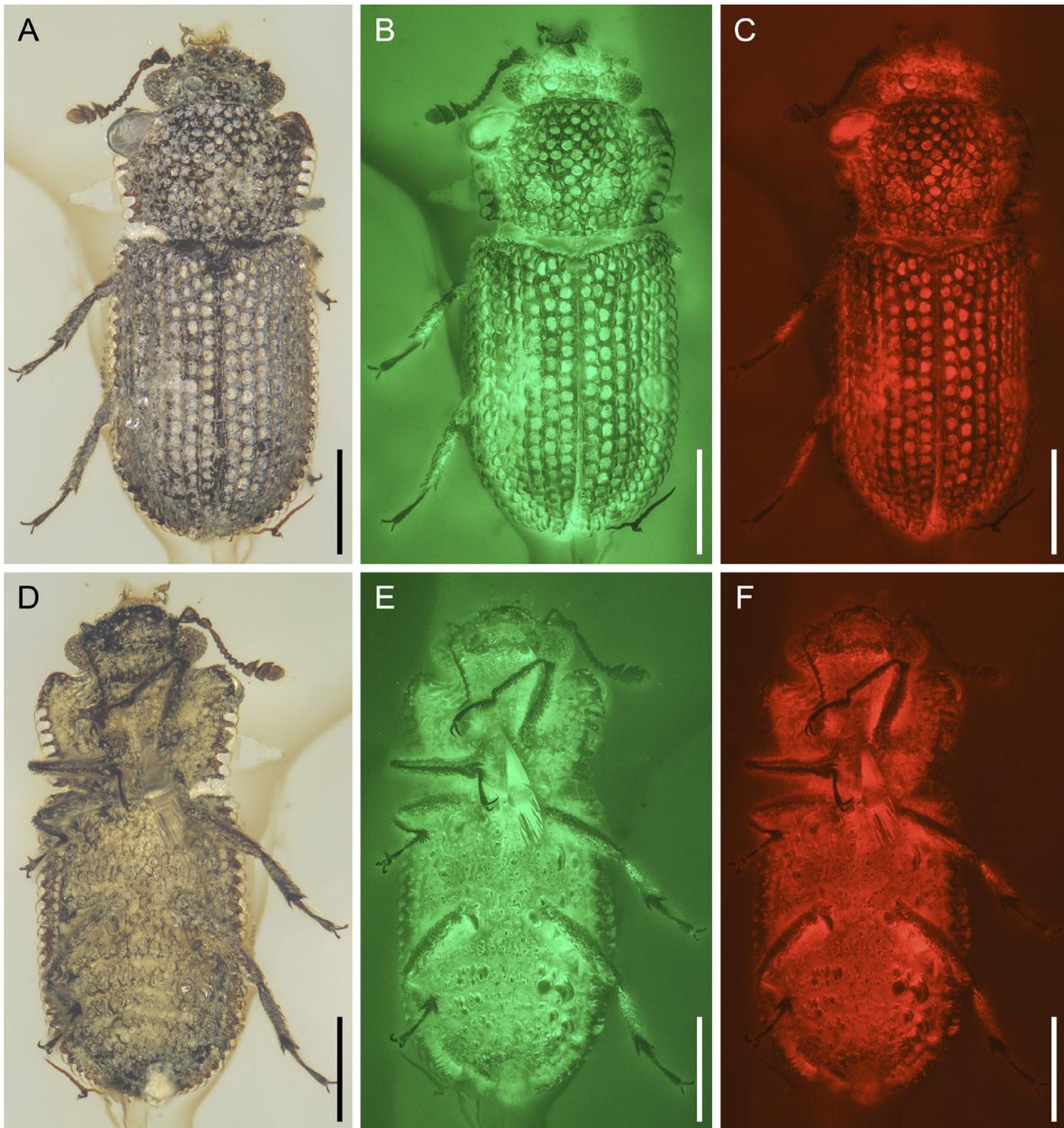


Figure 4. General habitus of *Trematosphindus newtoni* gen. et sp. nov., paratype, NIGP175115, under incident light (A, D) or widefield fluorescence (B, C, E, F). A–C: Dorsal view. D–F: Ventral view. Scale bars: 400 μ m.

Pereira 2019). Historically, Sphindidae, Boganiidae and Cryptophagidae are all placed in the superfamily Cucujoidea. However, recent phylogenetic analyses recovered that this Cucujoidea *sensu lato* is paraphyletic and contains three separate clades (McKenna et al. 2019; Cai et al., 2021). Each of the three families mentioned above is placed in a different clade, and are therefore only distantly related to each other. Therefore, the openings at the anterior pronotal angles probably evolved independently in these families.

Slime molds are ubiquitous in humid substrates such as most wood, soil, and dung worldwide (Stephenson et al. 2008). While the spores and spore-bearing structures of slime molds provide food for a diverse range of bee-

gles, sphindids stand out as the only family in which all species appear to be obligately associated with this food source (Lawrence and Newton 1980). The fossil record of slime molds is exceedingly scarce, owing to the fragile nature of their fruiting bodies. Nonetheless, recent discoveries of exceptionally preserved slime molds in Burmese amber (Poinar and Vega 2019; Rikkinen et al. 2019) suggest that the group was diverse in saproxylic habitats by the mid-Cretaceous. The growing fossil record of Cretaceous sphindids provides corroborating evidence that slime molds were important players in terrestrial ecosystems in the Mesozoic. Future discoveries of fossils sphindids can shed further light on the co-evolution between slime molds and beetles. Because some sphindids display

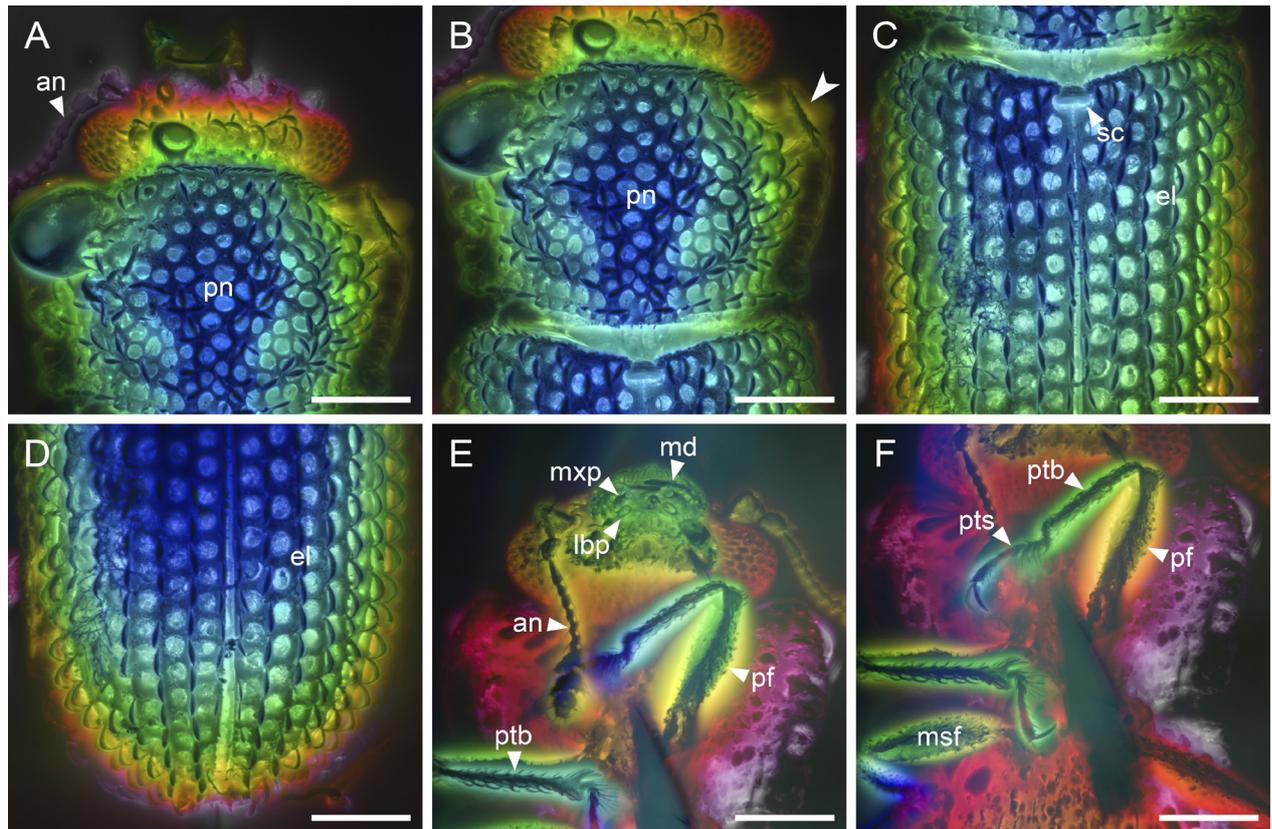


Figure 5. Details of *Trematosphindus newtoni* gen. et sp. nov., paratype, NIGP175115, under confocal microscopy, with depth color-coding. **A:** Head and prothorax, dorsal view. **B:** Prothorax, dorsal view, with arrowhead showing the cavity at anterior pronotal angle. **C:** Elytral base, dorsal view. **D:** Elytral apex, dorsal view. **E:** Head and prothorax, ventral view. **F:** Fore legs. Abbreviations: an, antenna; el, elytron; lbp, labial palp; md, mandible; msf, mesofemur; mxp, maxillary palp; pf, profemur; pn, pronotum; ptb, protibia; pts, protarsus; sc, scutellum. Scale bars: 200 µm.

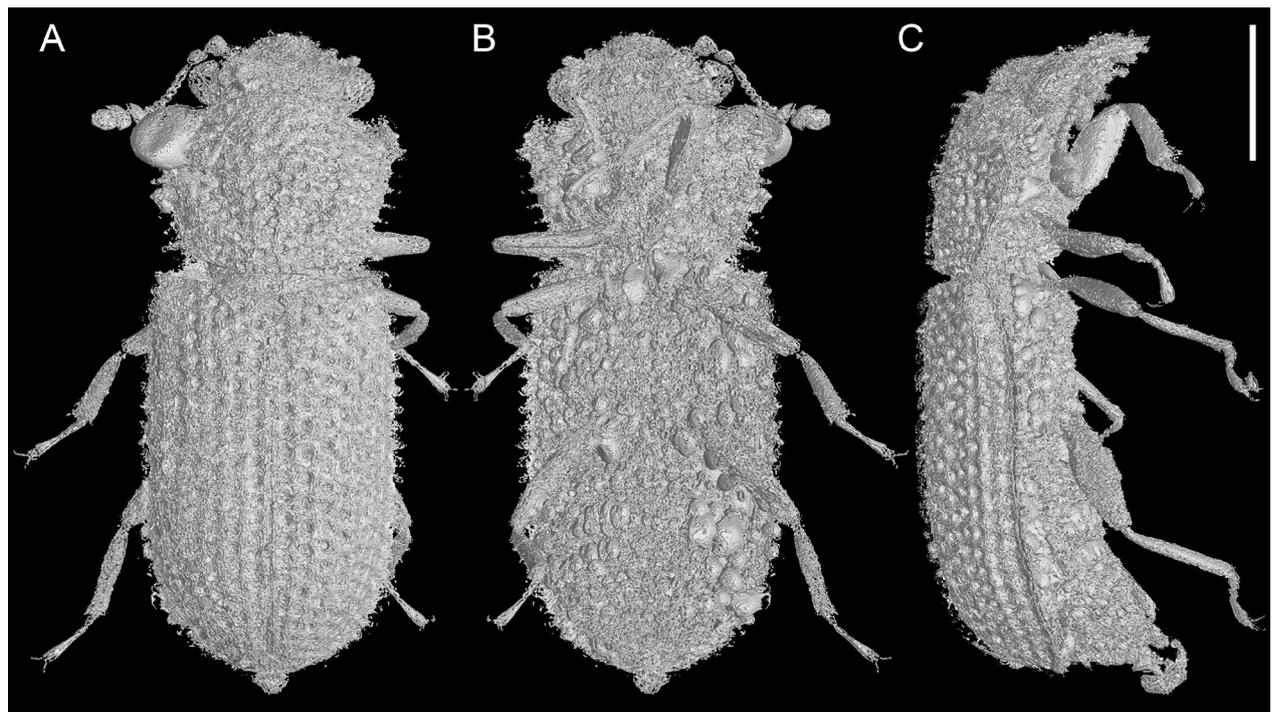


Figure 6. X-ray microtomographic reconstruction of *Trematosphindus newtoni* gen. et sp. nov., paratype, NIGP175115. **A:** Dorsal view. **B:** Ventral view. **C:** Lateral view. Scale bar: 400 µm.

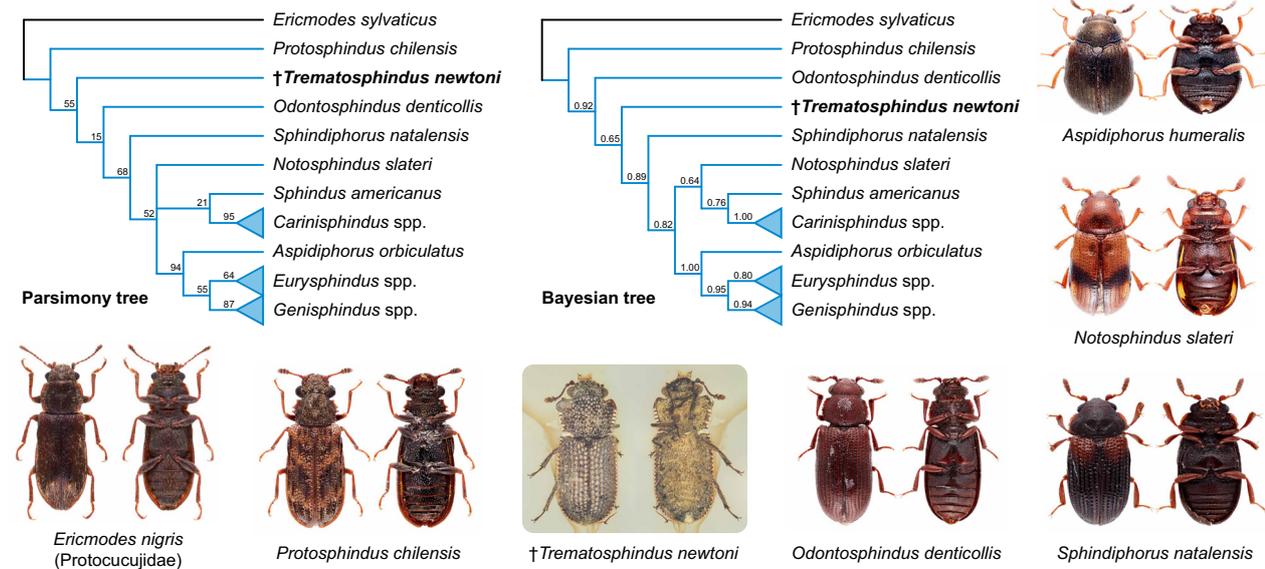


Figure 7. Suggested placement of *Trematosphindus newtoni* gen. et sp. nov. within Sphindidae. Values at nodes indicate bootstrap support (parsimony tree) or posterior probabilities (Bayesian tree). The insets show representatives of Sphindidae and Protocucujidae.

a degree of host specificity (Lawrence and Newton 1980), the fossil record of cryptic slime mold beetles can provide valuable indirect calibration points for inferring the timescale of the slime mold tree of life.

6. Data availability

The original confocal and micro-CT data are available in Zenodo repository (<http://doi.org/10.5281/zenodo.5579977>).

7. Competing interests

The authors have declared that no competing interests exist.

8. Acknowledgements

We are grateful to Richard A. B. Leschen and Steven L. Stephenson for the help discussion, and Joseph V. McHugh and one anonymous reviewer for the detailed comments on the earlier version of this paper. We also thank Su-Ping Wu for technical help in micro-CT reconstruction, and Yan Fang for technical help in confocal imaging. Financial support was provided by the Second Tibetan Plateau Scientific Expedition and Research project (2019QZKK0706), the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000 and XDB18000000), and the National Natural Science Foundation of China (41688103).

9. References

Bouchard P, Bousquet Y, Davies AE, Alonso-Zarazaga MA, Lawrence JF, Lyal CH, Newton AF, Reid CA, Schmitt M, Ślipiński SA, Smith

- AB (2011) Family-group names in Coleoptera (Insecta). *ZooKeys* 88: 1–972.
- Bousquet Y (1989) A review of the North American genera of Cryptophaginae (Coleoptera: Cryptophagidae). *The Coleopterists Bulletin* 43: 1–17.
- Burakowski B, Ślipiński SA (1987) A new species of *Protosphindus* (Coleoptera: Sphindidae) from Chile with notes and descriptions of immature stages of related forms. *Annali del Museo Civico di Storia Naturale, Genova* 86: 605–625.
- Cai C, Huang D (2019) First boganiine beetle in mid-Cretaceous amber from northern Myanmar (Coleoptera: Boganiidae). *Proceedings of the Geologists' Association* 130: 81–86.
- Cai C, Tihelka E, Giacomelli M, Lawrence JF, Slipinski A, Kundrata R, Yamamoto S, Thayer MK, Newton AF, Leschen RAB, Gimmel ML, Lü L, Engel MS, Huang D, Pisani D, Donoghue PCJ (2021) Integrated phylogenomics and fossil data illuminate the evolution of beetles. *bioRxiv*. <https://doi.org/10.1101/2021.09.22.461358>
- Crowson RA (1990) A new genus of Boganiidae (Coleoptera) from Australia, with observations on glandular openings, cycad associations and geographical distribution in the family. *Journal of the Australian Entomological Society* 29: 91–99.
- Escalona HE, Lawrence JF, Wanat M, Ślipiński A (2015) Phylogeny and placement of Boganiidae (Coleoptera, Cucujoidea) with a review of Australian and New Caledonian taxa. *Systematic Entomology* 40: 628–651.
- Forrester JA (2003) *Taxonomy of the Aspidiphorus uenoi* species group (Coleoptera: Sphindidae). University of Georgia, Athens, Georgia.
- Forrester JA., McHugh JV (2007) A review of the Sphindidae (Coleoptera: Cucujoidea) of Madagascar. *The Coleopterists Bulletin* 61: 590–603.
- Forrester JA., McHugh JV (2010) Sphindidae Jacquelin du Val, 1861. In: Leschen RAB, Beutel RG, Lawrence JF (Eds) *Handbook of Zoology, Arthropoda: Insecta, Coleoptera, beetles, Vol. 2: morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)*. Walter de Gruyter, Berlin and New York, 300–306.
- Goloboff PA, Farris JS, Källersjö M, Oxelman B, Ramirez MJ, Szumik CA (2003) Improvements to resampling measures of group support. *Cladistics* 19: 324–332.

- Goloboff PA, Farris JS, Nixon KC (2008) TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786.
- Goloboff PA, Torres A, Arias JS (2018) Weighted parsimony outperforms other methods of phylogenetic inference under models appropriate for morphology. *Cladistics* 34: 407–437.
- Goloboff PA, Catalano SA (2016) TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 32: 221–238.
- Grebennikov VV, Leschen RAB (2010) External exoskeletal cavities in Coleoptera and their possible mycangial functions. *Entomological Science* 13: 81–98.
- Kirejtshuk AG, Chetverikov PE, Azar D (2015) Libanopsinae, new subfamily of the family Sphindidae (Coleoptera, Cucujoidea) from Lower Cretaceous Lebanese amber, with remarks on using confocal microscopy for the study of amber inclusions. *Cretaceous Research* 52: 461–479.
- Kirejtshuk AG, Willig C, Chetverikov PE (2019) Discovery of a new sphindid genus (Coleoptera, Sphindidae, Protosphindinae) in Cretaceous amber of Northern Myanmar and taxonomic notes. *Palaeoentomology* 2: 602–610.
- Lawrence JF, Newton AF (1980) Coleoptera associated with the fruiting bodies of slime molds (Myxomycetes). *The Coleopterists Bulletin* 34: 129–143.
- Leschen RAB, Lawrence JF, Ślipiński SA (2005) Classification of basal Cucujoidea (Coleoptera: Polyphaga): cladistic analysis, keys and review of new families. *Invertebrate Systematics* 19: 17–73.
- Letunic I, Bork P (2019) Interactive Tree Of Life (iTOL) v4: recent updates and new developments. *Nucleic Acids Research* 47: W256–W259.
- Liu Z, Ślipiński A, Wang B, Pang H (2019) The oldest silvanid beetles from the Upper Cretaceous Burmese amber (Coleoptera, Silvanidae, Brontinae). *Cretaceous Research* 98: 1–8.
- McHugh JV (1990) *Carinisphindus*, a new genus and three new species of Neotropical Sphindidae (Coleoptera: Clavicornia). *The Coleopterists Bulletin* 44: 307–322.
- McHugh JV (1993) A revision of *Eurysphindus* LeConte (Coleoptera: Cucujoidea: Sphindidae) and a review of sphindid classification and phylogeny. *Systematic Entomology* 18: 57–92.
- McKenna DD, Shin S, Ahrens D, Balke M, Beza-Beza C, Clarke DJ, Donath A, Escalona HE, Friedrich F, Letsch H, Liu S, Maddison D, Mayer C, Misof B, Murin PJ, Niehuis O, Peters RS, Podsiadlowski L, Pohl H, Scully ED, Yan EV, Zhou X, Ślipiński A, Beutel, RG (2019) The evolution and genomic basis of beetle diversity. *Proceedings of the National Academy of Sciences, USA* 116: 24729–24737.
- Otero JC, Johnson C (2013) Species of *Cryptophagus* Herbst, 1792, belonging to the “*dentatus* group” (Coleoptera: Cryptophagidae) from the Western Palearctic region. *Entomologica Fennica* 24: 81–93.
- Otero JC, Pereira JM (2019) *Neomicrambe* subgen. nov. of *Micrambe* Thomson, 1863 (Coleoptera: Cryptophagidae) from East Africa. *Zootaxa* 4674: 57–67.
- Poinar G, Vega FE (2019) Mid-Cretaceous cellular slime mold (Eukarya: Dictyostelia?) in Burmese amber. *Historical Biology* 33: 712–715.
- Rikkinen J, Grimaldi DA, Schmidt AR (2019) Morphological stasis in the first myxomycete from the Mesozoic, and the likely role of cryptobiosis. *Scientific Reports* 9: 19730.
- Robertson JA, Ślipiński A, Moulton M, Shockley FW, Giorgi A, Lord NP, McKenna DD, Tomaszewska W, Forrester J, Miller KB, Whiting MF, McHugh JV (2015) Phylogeny and classification of Cucujoidea and the recognition of a new superfamily Coccinelloidea (Coleoptera: Cucujiformia). *Systematic Entomology* 40: 745–778.
- Ronquist F, Teslenko M, Mark PVD, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542.
- Sen Gupta T, Crowson RA (1979) The coleopteran family Sphindidae. *Entomologist’s Monthly Magazine* 113: 177–191.
- Ślipiński SA (1998) Revision and phylogeny of Protocucujidae (Coleoptera: Cucujoidea). *Annales Zoologici* 48: 275–298.
- Smith MR (2019) Bayesian and parsimony approaches reconstruct informative trees from simulated morphological datasets. *Biology Letters* 15: 20180632.
- Stephenson SL, Schnittler M, Novozhilov YK (2008) Myxomycete diversity and distribution from the fossil record to the present. *Biodiversity and Conservation* 17: 285–301.
- Strasser JF, Irisarri I, Williams TA, Burki F (2021) A molecular timescale for eukaryote evolution with implications for the origin of red algal-derived plastids. *Nature Communications* 12: 1879.
- Tihelka E, Huang D, Cai C (2020) *Pleuroceratos jiewenae* sp. nov.: A new Cretaceous phloeostichid beetle (Coleoptera: Cucujoidea: Phloeostichidae). *Palaeoentomology* 3: 248–259.

Supplementary material 1

Character list

Authors: Li et al. (2021)

Data type: .rtf

Explanation note: List of characters used in the phylogenetic analyses (adapted from McHugh 1993).

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/asp.79.e72724.suppl1>

Supplementary material 2

Morphological dataset

Authors: Li et al. (2021)

Data type: .nex

Explanation note: Morphological dataset used for the analyses.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/asp.79.e72724.suppl2>