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

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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 superfamily “Cucujoidea” (Forrester and McHugh 2010). Sphindidae are represented in the Recent fauna by only nine genera and approximately 66 valid extant species.
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(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; Burakows-ki 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 Sphindidae (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 previous 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 Noije Bum (26°20’ N, 96°36’ E), Hakawng 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 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. 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 “elypeus deeply embedded in head with one-third length or less projecting beyond anterior margin of head”. In fact, the elypeus 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

Genus Trematosphindus Li & Cai gen. nov.

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

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., Biphyllidae, Cryptophagidae, Boganidae, and Protocucujidae) in the general habitus, shape of antennal club, or the presence of cavities/glandular pores. Boganidae 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). Biphyllidae (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 monogenic 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 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 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 facettled, 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
(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; scutellar striole relatively reduced, with three punctures; strial 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 (Carinisphindus 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...
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 antenna (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 (Forster 2003). In other sphindids, the pygidium either en-

Figure 2. Details of Trematosphindus newtoni gen. et sp. nov., holotype, NIGP175114, under confocal microscopy. A: Head, anteroventral 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; mts, metatarsus; mtv, metaventrite; mxp, maxillary palp; pc, procoxa; pf, profemur; pn, pronotum; ps, prosternum; ptb, protibia; sc, scutellum; v1–5, ventrites 1–5. Scale bars: 200 μm.
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 sphindids, 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 Cryptophagidae (Bousquet 1989; Otero and Johnson 2013; Otero and

**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 μm.
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 beetles, 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 scare, 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 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 μm.
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.
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

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**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.
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).

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