



Earliest fossil record of Corylophidae from Burmese amber and phylogeny of Corylophidae (Coleoptera: Coccinelloidea)

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Abstract

The family Corylophidae is a moderately diverse coccinelloid beetle family. The fossil record of corylophid beetles is extremely sparse, with only one species formally described from the Eocene Baltic amber. Here we report a new corylophid genus and species, *Xenostanus jiangkuni* Li, Szawaryn & Cai **gen. et sp. nov.**, from mid-Cretaceous amber from northern Myanmar (ca. 99 Ma). *Xenostanus* is most distinctly characterized by the antenna with 10 antennomeres and the presence of metaventral and abdominal postcoxal lines. Our phylogenetic analysis suggested *Xenostanus* as sister to tribe Stanini. Based on its distinctive morphology and the phylogenetic results, *Xenostanus* is placed in the tribe Xenostanini Li, Szawaryn & Cai **trib. nov.**

Key words

Corylophidae, Mesozoic, Myanmar, site-heterogeneous model, constrained phylogenetic analysis

1. Introduction

Corylophidae, also known as the minute hooded beetles, is a moderately diverse and cosmopolitan family in the superfamily Coccinelloidea (Robertson et al. 2015), with about 285 extant species in 27 genera (Robertson et al. 2013). Corylophids generally have a minute body, and the ones with further miniaturization occur in several inde-

pendent lineages (Robertson et al. 2013; Polilov 2016; Yavorskaya and Polilov 2016). Both larvae and adults of corylophids feed on fungal spores and hyphae (Ślipiński et al. 2010).

The internal classification and phylogeny of Corylophidae have been generally satisfactorily studied. Bow-

estead (1999) conducted a major revision of the family, and produced a preliminary cladogram. Following the transfer of *Periptyctus* Blackburn (originally in Endomychidae) and *Cleidostethus* (originally in Coccinellidae) to Corylophidae (Bowstead et al. 2001; Ślipiński et al. 2001), Ślipiński et al. (2009) performed a morphology-based cladistic analysis and recognized two subfamilies, Periptyctinae and Corylophinae, with the latter divided into 10 tribes. Robertson et al. (2013) further revised the phylogeny of the family based on the incorporation of molecular evidence, with a new tribe, Stanini, separated from Aenigmaticini.

The fossil record of Corylophidae is extremely sparse. The only fossil species formally described was a member of *Clypastraea* Haldeman from the Eocene Baltic amber (Alekseev 2016). An occurrence of Corylophidae in the Late Cretaceous amber was mentioned by Rasnitsyn and Quicke (2002), although no further information was provided.

In the present study, we describe a well-preserved corylophid species from the mid-Cretaceous Burmese amber, which represent the earliest record of this family. The robustness of the corylophid phylogeny by Robertson et al. (2013) is also tested under a site-heterogeneous model. The placement of the new fossil is finally evaluated under implied weights parsimony with a constraining backbone based on molecular evidence.

2. Materials and methods

2.1. Materials

The Burmese amber specimens studied herein (Figs 1–5, S1) originated from amber mines near Noije Bum (26°20' N, 96°36' E), Hukawng Valley, Kachin State, northern Myanmar. The holotype is deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. The two paratypes are deposited in the Leibniz-Institut zur Analyse des Biodiversitätswandels (formerly the Geologisch-Paläontologisches Institut und Museum der Universität Hamburg), Germany. 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 or a Leica M205A stereomicroscope. Confocal images were obtained with a Zeiss LSM710 confocal laser scanning microscope, using the 488 nm Argon laser excitation line. Images under incident light were stacked in 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 VG-Studio MAX 3.0. Scanning parameters were as follows: isotropic voxel size, 1.6106 µm; power, 3 W; acceleration voltage, 40 kV; exposure time, 1.5 s; projections, 3001. Images were further processed in Adobe Photoshop CC to adjust brightness and contrast.

2.3. Molecular phylogenetic analysis

To test the robustness of the molecular phylogeny of Corylophidae, we reanalyzed the data compiled by Robertson et al. (2013) with a site-heterogeneous model. Eight genes were included, namely the nuclear genes 18S, 28S, H3 and CAD, and the mitochondrial 12S, 16S, COI and COII. All sequences were obtained from GenBank using the Batch Entrez tool. The accession numbers were the same as provided by Robertson et al. (2013). Sequence alignment generally followed the procedure of Robertson et al. (2013), though with slight modifications. In brief, the translated alignments of protein-coding genes were done using MUSCLE (Edgar 2004) module in Geneious 4.8.4 with default parameters. The rRNA genes were aligned using MAFFT 7.49 (Katoh and Standley 2013) Q-INS-i option. The ambiguously aligned regions of 28S (bp 2081–3196 in the alignment result) and CAD (bp 241–360 in the alignment result) were removed.

The site-heterogeneous mixture model CAT-GTR+G4 was run in PhyloBayes mpi 1.7 (Lartillot et al. 2009). Two independent Markov chain Monte Carlo (MCMC) chains were run until convergence (maxdiff <0.3). Convergence was assessed by using the bpcomp program to generate output of the largest (maxdiff) and mean (meandiff) discrepancies observed across all bipartitions.

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

2.4. Morphological phylogenetic analysis

To evaluate the systematic placement of the new species, a morphology-based phylogenetic analysis was performed. The data matrix was mainly derived from a previously published dataset (Ślipiński et al. 2009; Robertson et al. 2013).

The unconstrained 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.

Since the morphology-based phylogeny of Corylophidae was somewhat discordant with the molecular phylogeny, we additionally conducted a constrained analysis

(e.g., Slater 2013; Fikáček et al. 2020). For taxa with both morphological and molecular data, their interrelationships were fixed according to the molecular tree. The fossil and other extant taxa without molecular data were allowed to move freely across the reference tree. The constrained parsimony analysis was performed under implied weights ($K = 12$) with R 4.1.0 (R Core Team 2021) and the R package TreeSearch 1.0.1 (Smith 2021).

Character states were mapped onto the trees using unambiguous optimization with WinClada 1.0 (Nixon 2002).

2.5. Abbreviations

The following abbreviations of institution are used: **CCGG** – Collection Carsten Gröhn, Glinde. **GPIH** – Geologisch-Paläontologisches Institut und Museum der Universität Hamburg. **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. The following abbreviation is used in the phylogenetic analysis: **PP** – posterior probability.

3. Systematic paleontology

Order Coleoptera Linnaeus, 1758

Suborder Polyphaga Emery, 1886

Superfamily Coccinelloidea Latreille, 1807

Family Corylophidae LeConte, 1852

Tribe *Xenostanini* Li, Szawaryn & Cai
trib. nov.

<http://zoobank.org/F879CF29-9E7A-4E63-8585-441F9A-C242AA>

Type genus. *Xenostanus* gen. nov.

Diagnosis. Body elongate (oval to circular in most Corylophidae except for Foadiini, Aenigmaticini and Stanini). Head partially exposed and visible from above (concealed by produced pronotum in Peltinodini, Cleidostethini, Sericoderini, Parmulini, Corylophini, Teplinini and Rypobiiini). Antennae 10-segmented, with 3-segmented club (antennae 8-, 9-, or 11-segmented, or with 5-segmented club in some other tribes). Pronotum widest basally (narrowed posteriorly in Aenigmaticini and some Foadiini); anterior pronotal margin straight (produced or emarginate in various corylophid groups except for Aenigmaticini and Stanini). Prosternum in front of coxae as long as procoxal longitudi-

nal diameter (distinctly longer or shorter in various corylophid groups except for Aenigmaticini, Stanini and Cleidostethini); prosternal carinae absent (present in Periptycinae). Procoxal cavities externally closed (open in Peltinodini). Elytra somewhat truncate apically, exposing pygidium (conjointly rounded and concealing all abdominal tergites in many Corylophidae except for Foadiini, Aenigmaticini, Stanini, Sericoderini and some Parmulini). Transverse mesoventral carina absent (present in Stanini). Mesocoxal cavities laterally closed (laterally open in Cleidostethini, Orthoperini and Teplinini). Metaventricle with distinct postcoxal lines (metaventral postcoxal lines absent in most Corylophidae except for Peltinodini and Orthoperini). Tibiae with two small apical spurs. Abdominal ventrite 1 with strongly arcuate postcoxal lines (abdominal postcoxal lines absent in most Corylophidae except for Foadiini, Peltinodini, and some Corylophini; such lines straight in Foadiini).

Genus *Xenostanus* Li, Szawaryn & Cai gen. nov.

<http://zoobank.org/D85AF7C9-9BE5-4BBA-9F00-E066B2D085B0>

Type species. *Xenostanus jiangkuni* sp. nov.

Etymology. The generic name is composed of the Greek “*xenos*”, strange, and the generic name *Stanus* Ślipiński et al. The name is masculine in gender.

Diagnosis. As for the tribe.

***Xenostanus jiangkuni* Li, Szawaryn & Cai
sp. nov.**

<http://zoobank.org/DF781A4B-9A46-460E-AD27-BDC09B-CB1958>

Figs 1–5, S1

Etymology. The species is named after Mr. Kun Jiang, who kindly donated many fossils for our research.

Type materials. *Holotype*: NIGP177782. Two *paratypes*, GPIH no. 5058 (CCGG no. 11948), GPIH no. 5059 (CCGG no. 11105).

Type locality and horizon. Amber mine located near Noiye Bum Village, Tanai Township, Myitkyina District, Kachin State, Myanmar; unnamed horizon, mid-Cretaceous, Upper Albian to Lower Cenomanian.

Diagnosis. As for the tribe.

Description. Body elongate, widest at middle of elytra, very weakly convex. Surface with hair-like setae. — **Head** partially exposed and visible from above (Fig. 5F). Eyes coarsely faceted, without interfacetal setae (Fig. 3B,C). Frontoclypeal suture absent (Fig. 3B). Labrum free, trans-



Figure 1. General habitus of *Xenostanus jiangkuni* Li, Szawaryn & Cai **gen. et sp. nov.**, holotype, NIGP177782, under incident light. **A** Dorsal view. **B** Ventral view. Scale bars: 400 μm .

verse (Fig. 3B). Subantennal grooves absent. Antennae (Fig. 4C,D) with 10 antennomeres; scape distinctly longer and wider than pedicel; antennomeres 3–7 small, subquadrate to transverse; club (antennomeres 8–10) asymmetrical, as long as antennomeres 3–7 combined. Mandibles short (Fig. 3A). Maxillary palps (Fig. 3A) 3-segmented; apical palpomere about twice as long as penultimate one, conical. Labial palps (Fig. 3A) 2-segmented; apical palpomere about as long as basal one. Ventral head surface seemingly with a pair of parallel subgenal ridges (Figs 3A, 5E). — **Prothorax:** Pronotal disc (Fig. 5F) widest at base; anterior margin straight; lateral margins bordered in posterior part; posterior angles pointed; posterior margin bisinuate. Prosternum (Figs 3A, 5E) in front of coxae about as long as longitudinal coxal diameter, anteriorly not produced forward; prosternal carinae absent; prosternal process broad, widened beyond front coxae, meeting postcoxal hypomeral projections, truncate at apex. Procoxal cavities externally closed, ovaloid, without lateral slit (Fig. 5E). — **Meso- and metathorax:** Scutellar

shield strongly transverse. Elytra covering entire abdomen except for part of pygidium (Fig. 1A). Mesoventrite flat, without transverse carina (Figs 1B, 5A). Mesocoxal cavities circular, outwardly closed (Figs 1B, 5A). Meso-metaventral junction nearly straight (though with a small projection medially). Metaventrite with distinct postcoxal lines (Figs 1B, 2B, 5A); discrimen visible in posterior third of metaventrite. Metacoxae transverse, broadly separated. — **Legs:** Femora flattened. Tibiae simple, not strongly widened, apically with small denticles; tibial spurs 2-2-2 (Fig. 3D). Tarsi 4-4-4 (Fig. 3D); tarsomeres 1 and 2 ventrally lobed; tarsomere 3 smaller and simple; tarsomere 4 elongate, as long as 1–3 combined. Pretarsal claws simple, with small basal angulation. — **Abdomen** with six freely articulated ventrites. Ventrite 1 longer than 2–4 combined, with strongly arcuate postcoxal lines (Figs. 1B, 2B, 5A), anteriorly complete; intercoxal process very broad and truncate.

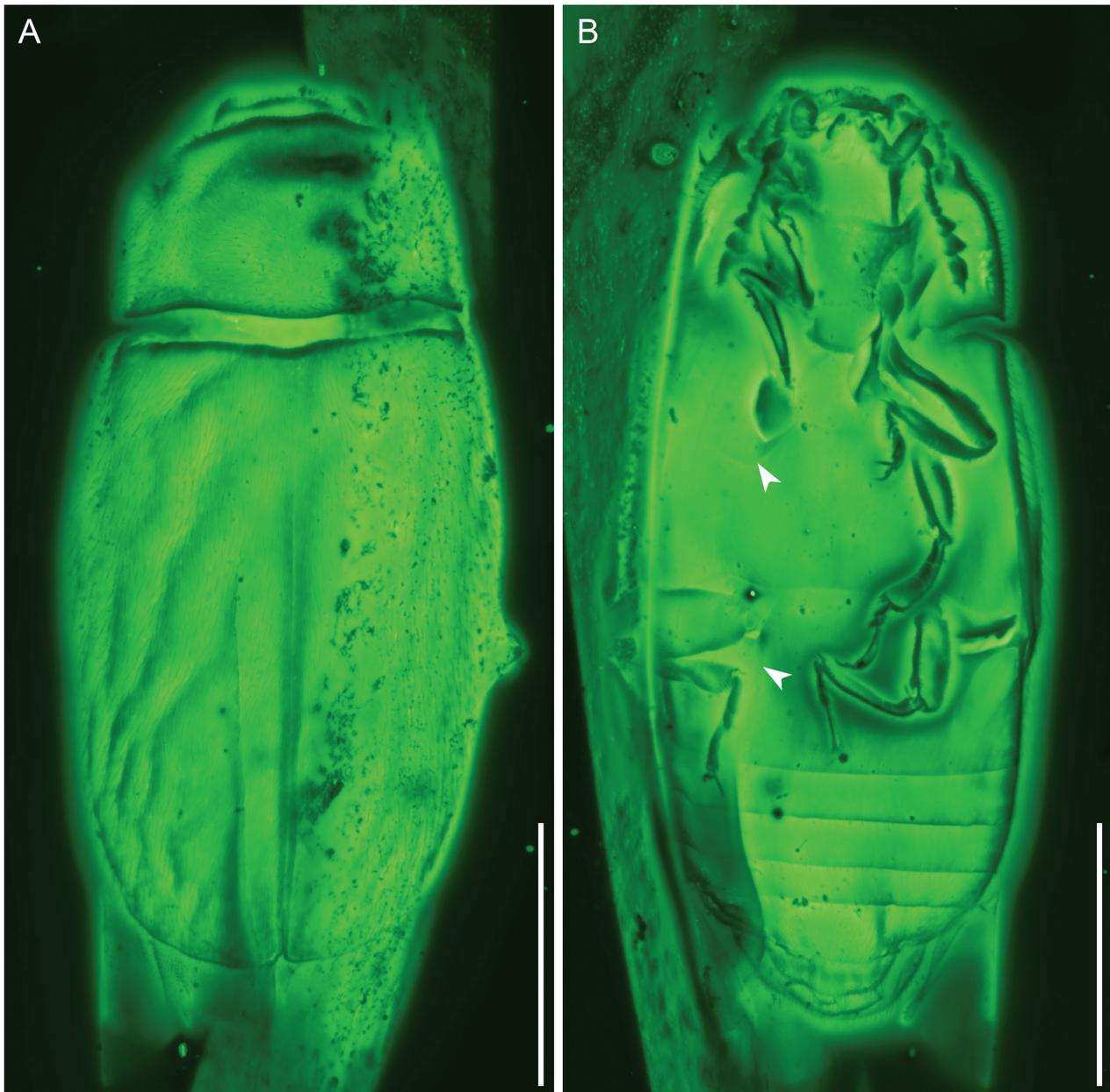


Figure 2. General habitus of *Xenostanus jiangkuni* Li, Szawaryn & Cai **gen. et sp. nov.**, holotype, NIGP177782, under confocal microscopy. **A** Dorsal view. **B** Ventral view, with arrowheads indicating the metaventral and abdominal postcoxal lines. Scale bars: 400 μm .

Measurements. NIGP177782: **BL** 1.42 mm, **BW** 0.63 mm, **HL** 0.27 mm, **HW** 0.31 mm, **PL** 0.34 mm, **PW** 0.51 mm, **EL** 0.96 mm. GPIH no. 5058: **BL** 1.88 mm, **BW** 0.74 mm. GPIH no. 5059: **BL** 1.30 mm, **BW** 0.62 mm

4. Results

4.1. Molecular phylogenetic analysis

The result under site-heterogeneous model (Fig. S2) was well consistent with the result under site-homogeneous model by Robertson et al. (2013). The monophyly of Corylophidae was strongly supported (PP = 1.00). Corylophi-

nae excluding *Holopsis* Broun (Peltinodini) was strongly supported (PP = 1.00), while Corylophinae as a whole was only moderately supported (PP = 0.83). All currently recognized tribes (*sensu* Robertson et al. 2013) were recovered as monophyletic groups. Foadiini (represented by *Foadia* Pakaluk and *Priamima* Pakaluk & Lawrence) was moderately supported (PP = 0.74), while all other tribes were strongly supported (PP = 1.00).

4.2. Morphological phylogenetic analysis

The result of unconstrained analysis (Fig. S3) is very similar to that of Ślipiński et al. (2009), only with the position of Sericoderini changed. *Xenostanus* was resolved as

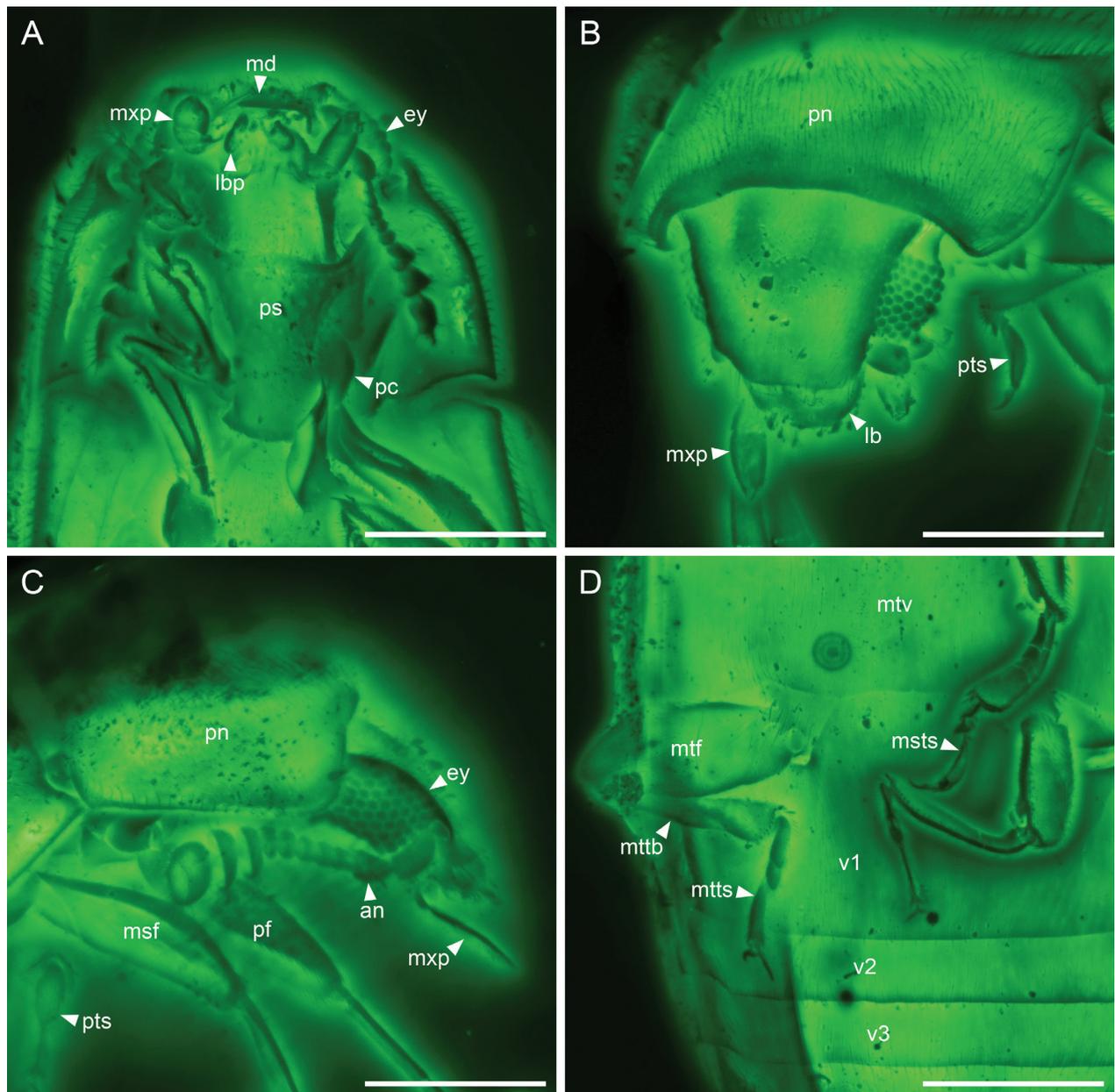


Figure 3. Details of *Xenostanus jiangkuni* Li, Szawaryn & Cai **gen. et sp. nov.**, holotype, NIGP177782, under confocal microscopy. **A** Head and prothorax, ventral view. **B** Head, dorsal view. **C** Head and prothorax, lateral view. **D** Abdominal base, ventral view. Abbreviations: an, antenna; ey, compound eye; lb, labrum; lbp, labial palp; md, mandible; msf, mesofemur; msts, mesotarsus; mtf, metafemur; mttb, metatibia; mtts, metatarsus; mtv, metaventricle; mxp, maxillary palp; pc, procoxa; pf, profemur; pn, pronotum; ps, prosternum; pts, protarsus; v1–3, ventrites 1–3. Scale bars: 200 μ m.

sister to the group consisting of Othoperini, Peltinodini, Sericoderini, Corylophini, Teplinini and Rypobiini. The tribes Aenigmaticini and Stanini were clustered together.

In the constrained analysis (Fig. 6), Aenigmaticini and Stanini were only distantly related in the reference

tree. Partly affected by this topology, *Xenostanus* was recovered as the sister group of Stanini. Teplinini grouped together with Rypobiini, and Cleidostethini grouped together with Orthoperini.

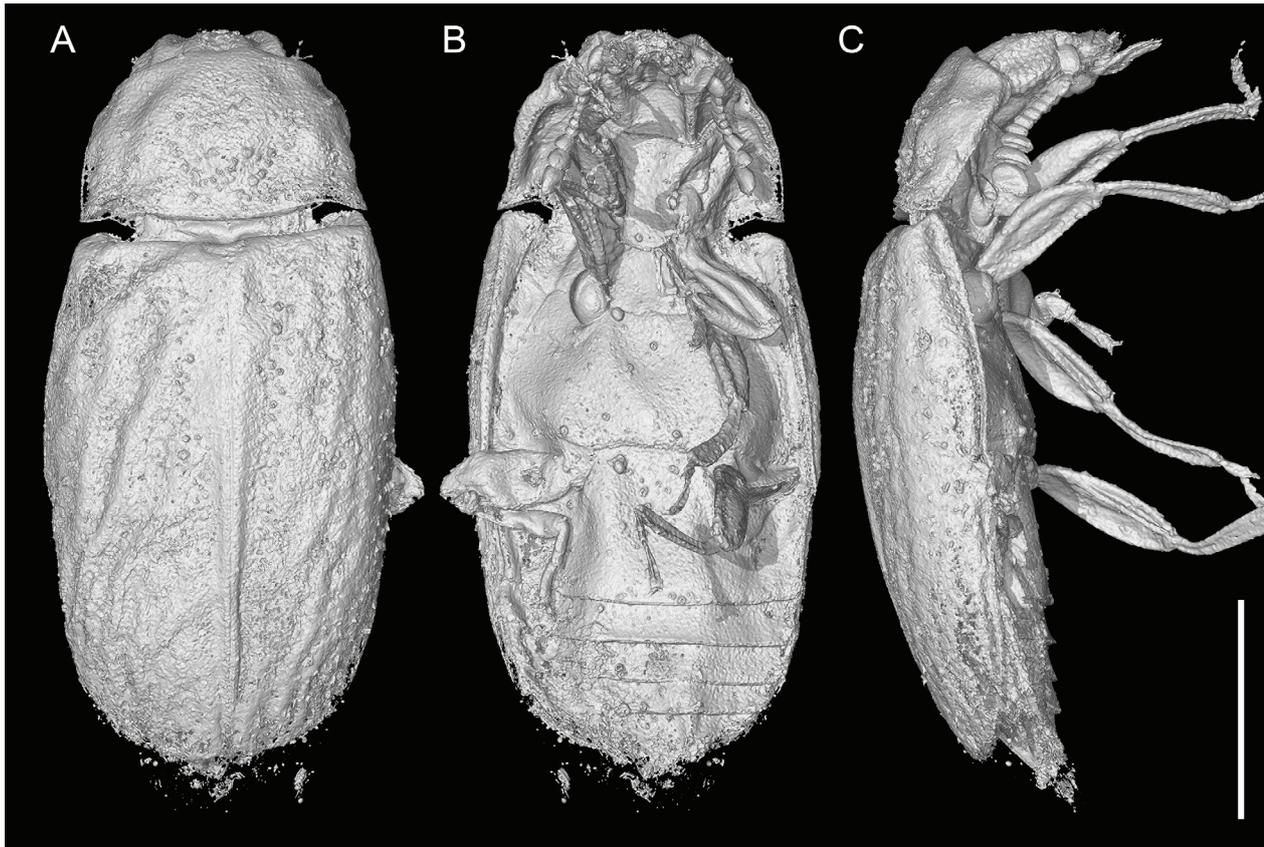


Figure 4. X-ray microtomographic reconstruction of *Xenostanus jiangkuni* Li, Szawaryn & Cai gen. et sp. nov., holotype, NIGP177782. **A** Dorsal view. **B** Ventral view. **C** Lateral view. Scale bar: 400 μ m.

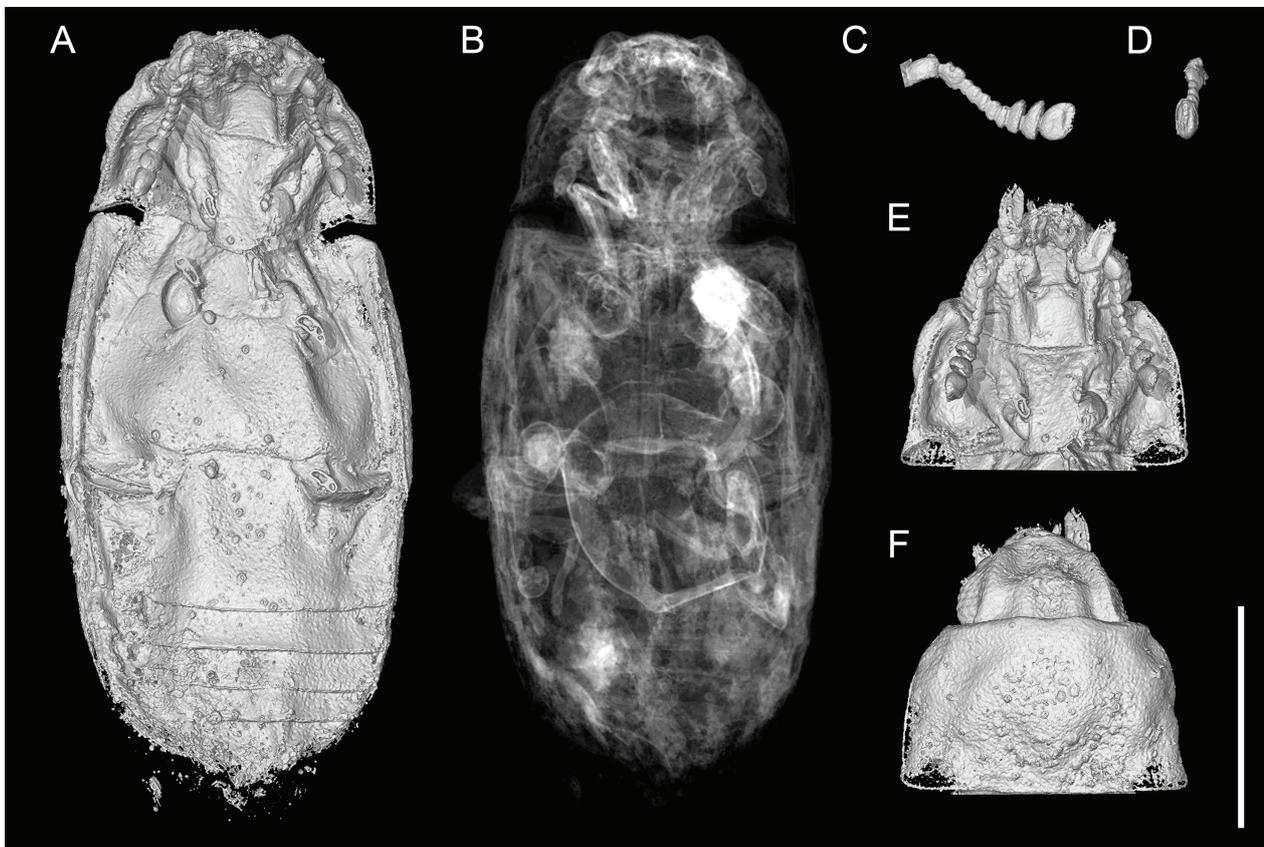


Figure 5. X-ray microtomographic reconstruction of *Xenostanus jiangkuni* Li, Szawaryn & Cai gen. et sp. nov., holotype, NIGP177782. **A** Ventral view, with legs removed. **B** Ventral view, rendered under “Sum along Ray” mode. **C**, **D** Antenna. **E** Head and prothorax, ventral view. **F** Head and prothorax, dorsal view. Scale bar: 400 μ m.

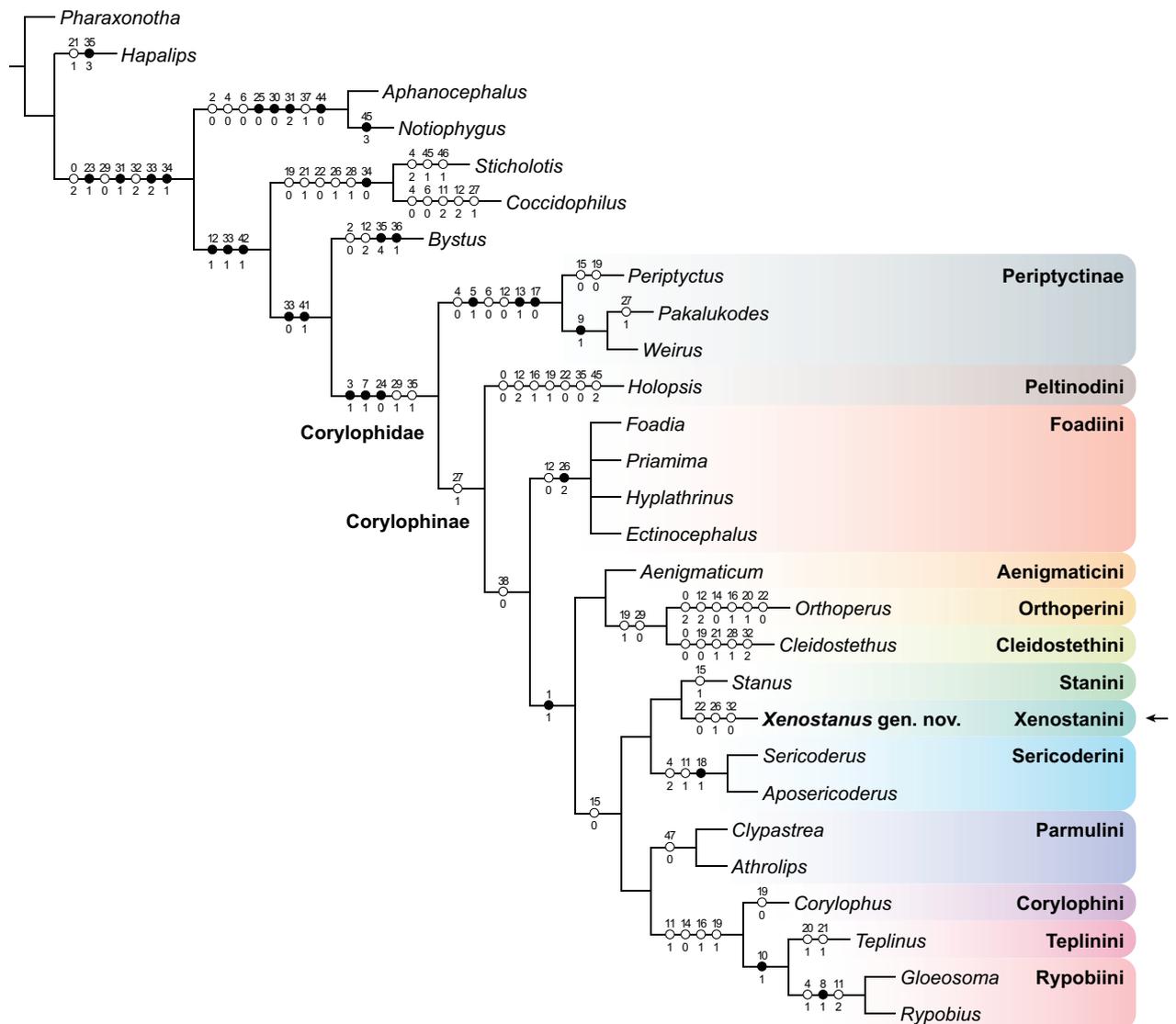


Figure 6. Suggested placement of *Xenostanus* Li, Szawaryn & Cai **gen. nov.** within Corylophidae. Tree resulting from the morphological parsimony analysis constrained by a molecular backbone tree. Black circles indicate nonhomoplasious changes; white circles indicate homoplasious characters.

5. Discussion

5.1. Sister group of Corylophidae

In the combined morphological and molecular data analyses by Robertson et al. (2013), Coccinellidae was sister to Corylophidae. However, in both phylogenies based on molecular data alone (present study; Robertson et al. 2013), Anamorphidae (represented by *Bystus* Guérin-Méneville and *Symbiotes* Redtenbacher) was resolved as the sister group of Corylophidae. The sister-group relationship between Anamorphidae and Corylophidae have been further supported by the large-scale phylogenomic study (McKenna et al. 2019). Thus, the frequently advocated combined analysis may not be an ideal solution to utilize the information from both morphological and molecular data as it seems to be.

5.2. Phylogeny of Corylophidae

Compared with the site-homogeneous models, site-heterogeneous models account for the unequal rate of evolution in sequences and have been proved to be more insensitive to phylogenetic artifacts such as long branch attraction (Lartillot et al. 2007; Pisani et al. 2015; Cai et al. 2020, 2022). Site-heterogeneous models may generate improved results even for analyses with limited gene fragments sampled (Li et al. 2021). For the present study, the internal phylogeny of Corylophidae generated with the site-heterogeneous model (Fig. S2) was essentially identical to that generated with a site-homogeneous model by Robertson et al. (2013). Thus, the current classification scheme of Corylophidae based on this phylogeny is generally satisfactory, and could serve as a framework for determining the position of the *Xenostanus* fossil.

As discussed by Robertson et al. (2013), the unconstrained morphology-based phylogeny of Corylophidae is largely inconsistent with the molecular one and therefore unreliable. Nevertheless, morphology may still provide some valuable information in cases where molecular sequences are hard or impossible to obtain. The positions of Teplinini and Cleidostethini were not evaluated by Robertson et al. (2013) due to the lack of molecular data. In our constrained morphological analysis, Teplinini was resolved as sister to Rypobiini, which is consistent with the unconstrained analysis by Ślipiński et al. (2009). However, the aberrant tribe Cleidostethini turned out to be the sister group of Orthoperini, and they together were sister to Aenigmaticini, while in the unconstrained analysis Cleidostethini was sister to the whole Corylophinae except Foadiini, suggesting the requirement for further analyses.

5.3. Placement of *Xenostanus*

Corylophidae is currently divided into two subfamilies, Periptyctinae and Corylophinae (Ślipiński et al. 2009; Robertson et al. 2013). Periptyctinae is composed of only three genera, and was once placed in family Endomychidae (Ślipiński et al. 2001, 2009). *Xenostanus* clearly does not belong to Periptyctinae, based on its pedicel shorter than scape (pedicel longer in Periptyctinae), absence of prosternal carinae (prosternal carinae present in Periptyctinae), and anterior pronotal margin unemarginated (anterior pronotal margin deeply emarginate in Periptyctinae). Based on the morphological and molecular phylogenetic analyses, 11 tribes have been recognized within Corylophinae (Ślipiński et al. 2009; Robertson et al. 2013). The unique character combination of *Xenostanus* does not fit well into any of the existing tribes. *Xenostanus* has an elongate body shape. While most corylophids have an oval to circular body, the tribes Foadiini, Aenigmaticini and Stanini also have an elongate body, and are sometimes referred to as latridiid-like taxa. *Xenostanus* can be distinguished from Foadiini in the straight anterior margin of pronotum (medially emarginate in Foadiini), and from Aenigmaticini in the antennae with 10 antennomeres (with nine antennomeres in Aenigmaticini; Pakaluk 1985) and the basally widest prothorax (posteriorly narrowed in Aenigmaticini). The phylogenetic analysis suggests a close relationship between *Xenostanus* and Stanini (Fig. 6). Both taxa share a similar pronotal shape (not constricted posteriorly). Nevertheless, *Xenostanus* can also be distinguished from Stanini based on the antennae (with 11 antennomeres in Stanini) and the absence of transverse mesoventral carina (present in Stanini).

The postcoxal lines on metaventrite and abdominal ventrite 1 are important diagnostic characters for *Xenostanus*. These postcoxal lines are usually present in Coccinellidae and some other related taxa (Ślipiński and Tomaszewska 2010; Robertson et al. 2015). However, most corylophids do not possess such lines (e.g., Furukawa 2010: fig. 4D). In extant Corylophidae, only *Holopsis* (Peltinodini) is known to have metaventral and

abdominal postcoxal lines at the same time (e.g., Furukawa 2012). Considering the basal position of *Holopsis* within Corylophidae, the presence of postcoxal lines have been suggested to be plesiomorphic for it (Robertson et al. 2013). By contrast, *Xenostanus* occupied a more derived position in Corylophidae, and its postcoxal lines are therefore likely gained secondarily.

Based on the results of phylogenetic analysis and the above discussion on the morphological characters, we suggest that *Xenostanus* should be placed in a new tribe, Xenostanini **trib. nov.** The discovery of *Xenostanus* greatly extends the earliest record of Corylophidae, which implies this family had already been diversified by mid-Cretaceous.

6. Data availability

The original confocal and micro-CT data are available in Zenodo repository (<https://doi.org/10.5281/zenodo.6801815>).

7. Competing interests

The authors have declared that no competing interests exist.

8. Acknowledgements

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9. References

- Alekseev VI (2016) *Clypastraea primainterparens* sp. nov. – the first fossil minute hooded beetle (Coleoptera: Coccinelloidea: Corylophidae) from Baltic amber (Eocene, Tertiary). *Baltic Journal of Coleopterology* 16: 21–26.
- Bowstead S (1999) A revision of the Corylophidae (Coleoptera) of the West Palaearctic Region. *Instrumenta Biodiversitatis* 3: 1–203.
- Bowstead S, Booth RG, Ślipiński A, Lawrence JF (2001) The genus *Cleidostethus* Arrow, 1929 reappraisal and transfer from Coccinellidae to Corylophidae (Coleoptera: Cucujoidea). *Annales Zoologici* 51: 319–323.
- Cai C, Tihelka E, Pisani D, Donoghue PCJ (2020) Data curation and modeling of compositional heterogeneity in insect phylogenomics: a case study of the phylogeny of Dytiscoidea (Coleoptera: Adephaga). *Molecular Phylogenetics and Evolution* 147: 106782. <https://doi.org/10.1016/j.ympev.2020.106782>
- Cai C, Tihelka E, Giacomelli M, Lawrence JF, Ślipiński A, Kundrata R, Yamamoto S, Thayer MK, Newton AF, Leschen RAB, Gimmel

- ML, Lü L, Engel MS, Bouchard P, Huang D, Pisani D, Donoghue PCJ (2022) Integrated phylogenomics and fossil data illuminate the evolution of beetles. *Royal Society Open Science* 9: 211771. <https://doi.org/10.1098/rsos.211771>
- Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797. <https://doi.org/10.1093/nar/gkh340>
- Fikáček M, Beutel RG, Cai C, Lawrence JF, Newton AF, Solodovnikov A, Ślipiński A, Thayer MK, Yamamoto S (2020) Reliable placement of beetle fossils via phylogenetic analyses – Triassic *Leehermania* as a case study (Staphylinidae or Myxophaga?). *Systematic Entomology* 45: 175–187. <https://doi.org/10.1111/syen.12386>
- Furukawa K (2010) Descriptions of two *Catoptyx* species (Coleoptera, Corylophidae) from Japan. *Elytra*, Tokyo 38: 11–17.
- Furukawa K (2012) A revision of the genus *Holopsis* Broun (Insecta: Coleoptera: Corylophidae) from Japan. *Species Diversity* 17: 177–186. <https://doi.org/10.12782/sd.17.2.177>
- Goloboff PA, Catalano SA (2016) TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 32: 221–238. <https://doi.org/10.1111/cla.12160>
- Goloboff PA, Farris JS, Nixon KC (2008) TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786. <https://doi.org/10.1111/j.1096-0031.2008.00217.x>
- Goloboff PA, Torres A, Arias JS (2018) Weighted parsimony outperforms other methods of phylogenetic inference under models appropriate for morphology. *Cladistics* 34: 407–437. <https://doi.org/10.1111/cla.12205>
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780. <https://doi.org/10.1093/molbev/mst010>
- Lartillot N, Brinkmann H, Philippe H (2007) Suppression of long-branch attraction artefacts in the animal phylogeny using a siteheterogeneous model. *BMC Evolutionary Biology* 7: S4. <https://doi.org/10.1186/1471-2148-7-S1-S4>
- Lartillot N, Lepage T, Blanquart S (2009) PhyloBayes 3: A Bayesian software package for phylogenetic reconstruction and molecular dating. *Bioinformatics* 25: 2286–2288. <https://doi.org/10.1093/bioinformatics/btp368>
- Letunic I, Bork P (2019) Interactive Tree Of Life (iTOL) v4: recent updates and new developments. *Nucleic Acids Research* 47: W256–W259. <https://doi.org/10.1093/nar/gkz239>
- Li Y-D, Tihelka E, Leschen RAB, Yu Y-L, Ślipiński A, Pang H, Huang D-Y, Kolibáč J, Cai C-Y (2021) An exquisitely preserved tiny bark-gnawing beetle (Coleoptera: Trogossitidae) from mid-Cretaceous Burmese amber and the phylogeny of Trogossitidae. *Journal of Zoological Systematics and Evolutionary Research* 59: 1939–1950. <https://doi.org/10.1111/jzs.12515>
- 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. <https://doi.org/10.1073/pnas.1909655116>
- Nixon KC (2002) Winclada ver. 1.0000. Published by the author, Ithaca, NY.
- Pisani D, Pett W, Dohrmann M, Feuda R, Rota-Stabelli O, Philippe H, Lartillot N, Wörheide G (2015) Genomic data do not support comb jellies as the sister group to all other animals. *Proceedings of the National Academy of Sciences, USA* 112: 15402–15407. <https://doi.org/10.1073/pnas.1518127112>
- Polilov AA (2016) Structure of the principal groups of microinsects. IV. Hooded beetles (Coleoptera: Corylophidae). In: *At the Size Limit – Effects of Miniaturization in Insects*. Springer International Publishing, Cham, 135–167. https://doi.org/10.1007/978-3-319-39499-2_6
- R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org>.
- Rasnitsyn AP, Quicke DLJ (Eds) (2002) *History of insects*. Kluwer Academic Publishers, Dordrecht, 517 pp.
- Robertson JA, Ślipiński A, Hiatt K, Miller KB, Whiting MF, Mchugh JV (2013) Molecules, morphology and minute hooded beetles: a phylogenetic study with implications for the evolution and classification of Corylophidae (Coleoptera: Cucujoidea). *Systematic Entomology* 38: 209–232. <https://doi.org/10.1111/j.1365-3113.2012.00655.x>
- 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. <https://doi.org/10.1111/syen.12138>
- Slater GJ (2013) Phylogenetic evidence for a shift in the mode of mammalian body size evolution at the Cretaceous-Palaeogene boundary. *Methods in Ecology and Evolution* 4: 734–744. <https://doi.org/10.1111/2041-210X.12084>
- Ślipiński A, Tomaszewska W (2010) Coccinellidae Latreille, 1802. 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, 454–472. <https://doi.org/10.1515/9783110911213.454>
- Ślipiński A, Lawrence JF, Tomaszewska W (2001) The placement of *Periptyctus* Blackburn in Corylophidae (Coleoptera: Cucujoidea) with descriptions of a new genus and subfamily. *Annales Zoologici* 51: 311–317.
- Ślipiński A, Tomaszewska W, Lawrence JF (2009) Phylogeny and classification of Corylophidae (Coleoptera: Cucujoidea) with descriptions of new genera and larvae. *Systematic Entomology* 34: 409–433. <https://doi.org/10.1111/j.1365-3113.2009.00471.x>
- Ślipiński A, Lawrence JF, Cline AR (2010) Corylophidae LeConte, 1852. 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, 472–481. <https://doi.org/10.1515/9783110911213.472>
- Smith MR (2019) Bayesian and parsimony approaches reconstruct informative trees from simulated morphological datasets. *Biology Letters* 15: 20180632. <https://doi.org/10.1098/rsbl.2018.0632>
- Smith MR (2021) TreeSearch: morphological phylogenetic analysis in R. *bioRxiv*. <https://doi.org/10.1101/2021.11.08.467735>
- Yavorskaya MI, Polilov AA (2016) Morphology of the head of *Sericoderus lateralis* (Coleoptera, Corylophidae) with comments on the effects of miniaturization. *Entomological Review* 96: 395–406. <https://doi.org/10.1134/S0013873816040023>

Supplementary material 1

Figures S1–S3

Authors: Li Y-D, Zhang Y-B, Szawaryn K, Huang D-Y, Cai C-Y (2022)

Data type: .pdf

Explanation note: **Figure S1.** *Xenostanus jiangkuni* Li, Szawaryn & Cai gen. et sp. nov., paratypes, under incident light. **A–D:** GPIH no. 5059. **E, F:** GPIH no. 5058. — **Figure S2.** Tree resulting from molecular Bayesian analysis with the site-heterogeneous CAT-GTR+G4 model. — **Figure S3.** Tree resulting from unconstrained morphological parsimony analysis.

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Link: <https://doi.org/asp.80.e81736.suppl1>

Supplementary material 2

List of characters

Authors: Li Y-D, Zhang Y-B, Szawaryn K, Huang D-Y, Cai C-Y (2022)

Data type: .rtf

Explanation note: List of characters used in the phylogenetic analyses (adapted from Ślipiński et al. 2009; Robertson et al. 2013).

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Link: <https://doi.org/asp.80.e81736.suppl2>

Supplementary material 3

Morphological dataset

Authors: Li Y-D, Zhang Y-B, Szawaryn K, Huang D-Y, Cai C-Y (2022)

Data type: .tnt

Explanation note: Morphological dataset used for the analyses.

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Link: <https://doi.org/asp.80.e81736.suppl3>

Supplementary material 4

R code

Authors: Li Y-D, Zhang Y-B, Szawaryn K, Huang D-Y, Cai C-Y (2022)

Data type: .R

Explanation note: R code for the constrained parsimony analysis.

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Link: <https://doi.org/asp.80.e81736.suppl4>

Supplementary material 5

Molecular dataset

Authors: Li Y-D, Zhang Y-B, Szawaryn K, Huang D-Y, Cai C-Y (2022)

Data type: .zip

Explanation note: Data for the molecular analysis and the output files.

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