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Rhomeocalpsua torosa gen. et sp. nov., a unique lineage of Endomychidae from mid-Cretaceous Burmese amber (Coleoptera: Coccinelloidea)

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Abstract

A new fossil genus and species of the family Endomychidae, *Rhomeocalpsua torosa* Li, Tomaszewska & Cai, **gen. et sp. nov.**, is described and illustrated from the mid-Cretaceous Burmese amber. The new genus is characterised by the relatively elongate body, antennae composed of nine antennomeres with unique club morphology, unmodified pronotum, mesocoxal cavities broadly closed laterally, femora with deep and long grooves, and 3-3-3 tarsi. Detailed morphological comparisons between the Cretaceous fossil and extant relatives suggest that its unique character combination does not fit into any existing subfamilies of Endomychidae, Mycetaeidae, Eupsilobiidae or Anamorphidae.

Keywords: Endomychidae, Merophysiinae, Anamorphidae, fossil, Cretaceous, Burmese amber

Introduction

The family Endomychidae, or handsome fungus beetles, is a diverse group of widespread beetles belonging to the polyphagan superfamily Coccinelloidea (Robertson *et al.*, 2015; McKenna *et al.*, 2019; Cai *et al.*, 2022), with about 1,600 described species (not including Mycetaeinae, Eupsilobiinae and Anamorphinae, which were removed from Endomychidae by Robertson *et al.*, 2015) (Shockley *et al.*, 2009a). As their common name suggests, almost all endomychids are exclusively mycophagous, and adults and larvae are often found feeding on fungal spores or hyphae (Shockley *et al.*, 2009b), although at least one endomychid, *Saula japonica* Gorham, 1847 is known to be predaceous (Sasaji, 1978a).

Mesozoic endomychids that are important for elucidating the origin and early evolution of the family are very sparse (Tomaszewska *et al.*, 2018), while several endomychids have been formally described from Cenozoic ambers of Europe (*e.g.*, Shockley & Alekseev, 2014; Alekseev & Tomaszewska, 2018; Reike *et al.*, 2020; see also the list by Shockley *et al.*, 2009a). The mid-Cretaceous Burmese amber has offered invaluable well-preserved fossils for our understanding of character evolution, phylogeny, biogeography, and palaeoecology of beetles (*e.g.*, Cai *et al.*, 2017a, b, 2018, 2019a, b; Gimmel *et al.*, 2019; Tihelka *et al.*, 2021a). Burmese amber fossils also provide critical evidence of palaeodiversity of beetle families that are either currently extinct (*e.g.*, Li *et al.*, 2021a, b), relictual (*e.g.*, Li *et al.*, 2019, 2021c; Tihelka *et al.*, 2019, 2021b), or confined to the Southern Hemisphere (*e.g.*, Li *et al.*, 2020, 2021d). Tomaszewska *et al.* (2018) reported the oldest definitive fossil members of the Endomychidae entombed in the Burmese amber. Four genera and four new species belonging to three endomychid subfamilies were described: *Burmalestes albertalleni* Tomaszewska & Ślipiński, *Cretolestes niger* Tomaszewska, Ślipiński & Ren (Leiestinae), *Cretaparamecus tarsalis* Tomaszewska, Ślipiński, Bai & Zhang (Merophysiinae), and *Palaeomycetes foveolatus* Tomaszewska, Ślipiński & Ren (Xenomycetinae). This discovery highlights the unexpected palaeodiversity of Endomychidae preserved in one source of amber locality, and it confirmed that the origin of crown-group Coccinelloidea can be traced back to at least Jurassic as suggested by McKenna *et al.* (2019) and Cai *et al.* (2022).

Here we report a new genus and species of

Endomychidae, *Rhomeocalpsua torosa* Li, Tomaszewska & Cai, **gen. et sp. nov.**, from mid-Cretaceous amber of northern Myanmar. We discuss the systematic position of the new genus by comparing it with extant endomychid subfamilies, and demonstrating that the combination of characters of *Rhomeocalpsua* does not correspond perfectly with any existing endomychid subfamilies. Therefore, the newly discovered fossil is placed as *incertae sedis* in Endomychidae.

Material and methods

The Burmese amber specimen studied herein (Figs 1–5) originated from amber mines near Noiye Bum (26°20' N, 96°36' E), Hukawng Valley, Kachin State, northern Myanmar. The amber 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 paper of different grit sizes, and finally polished with polishing powder.

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) or 561 nm (DPSS 561-10) laser excitation lines (Fu *et al.*, 2021). 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 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 analysed in VGStudioMax 3.0. Scanning parameters were as follows: isotropic voxel size, 1.9324 μm ; power, 4 W; acceleration voltage, 50 kV; exposure time, 1.5 s; projections, 3001. Images were further processed in Adobe Photoshop CC to adjust brightness and contrast.

Systematic palaeontology

Order Coleoptera Linnaeus, 1758

Suborder Polyphaga Emery, 1886

Superfamily Coccinelloidea Latreille, 1807



FIGURE 1. General habitus of *Rhomeocalpsua torosa* Li, Tomaszewska & Cai, **gen. et sp. nov.**, holotype, NIGP180054, under incident light. **A**, Dorsal view. **B**, Ventral view. Scale bars = 500 μm .

Family Endomychidae Leach, 1815

Subfamily *incertae sedis*

Genus *Rhomeocalpsua* Li, Tomaszewska & Cai, **gen. nov.**

Type species. *Rhomeocalpsua torosa* **sp. nov.**

Etymology. The generic name is an anagram of *Holoparamecus*, a genus in Endomychidae: Merophysiinae. The name is feminine in gender.

Diagnosis. Body relatively elongate. Head with antennal sockets visible from above (Fig. 5C). Antennae composed of nine antennomeres, with club built of three antennomeres; antennomere 7 strongly asymmetrical; antennomere 8 strongly enlarged (Figs 4C, D, 5F). Apical labial palpomeres apparently enlarged (Fig. 4B). Prothorax posteriorly constricted; pronotal disc without pits, sulci or carinae (Fig. 3A). Mesocoxal cavities broadly closed (Fig. 4E). Mesotrochantins concealed (Fig. 4E). Femora with deep and long grooves along inner side (Fig. 4E, F). Tarsi simple, 3-3-3 (Fig. 4H, I).

Rhomeocalpsua torosa Li, Tomaszewska & Cai, **sp. nov.**

(Figs 1–5)

Material. Holotype, sex unknown, NIGP180054.

Etymology. The specific name refers to its distinctly enlarged antennal club.

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 relatively elongate, rather flattened, about 1.3 mm long, 0.5 mm wide, moderately densely setose.

Head prognathous, not retracted into prothorax. Eyes well developed, moderately protuberant, coarsely faceted, without interfacetal setae (Fig. 4A, D). Antennal grooves absent (Fig. 4B, D). Antennal sockets visible from above (Fig. 5C). Antennae (Figs 4C, D, 5F) composed of nine antennomeres; antennomere 2 oblong; antennomeres 3–6 moniliform; antennomeres 7–9 forming a distinct club; antennomere 7 strongly asymmetrical, short and strongly transverse; antennomere 8 strongly enlarged. Maxillary palps (Fig. 4B) 4-segmented, palpomere 1 smallest; palpomeres 2–4 narrowing progressively; palpomere 4 about as long as 2 and 3 combined, conical. Labial palps (Fig. 4B) 3-segmented, with apical palpomere apparently enlarged.

Pronotum (Fig. 3A) transverse, widest near the middle, narrower at base than elytral bases; lateral pronotal carinae complete, without raised margin (Fig. 5D); anterior angles not produced; disc without pits, sulci or carinae.

Elytra about 1.8 times as long as width combined, completely covering abdomen; sides weakly rounded; disc irregularly punctate; epipleura comparatively narrow, incomplete towards apices. Mesocoxal cavities circular, moderately widely separated, laterally broadly closed by meeting of meso- and metaventrites (Fig. 4E);

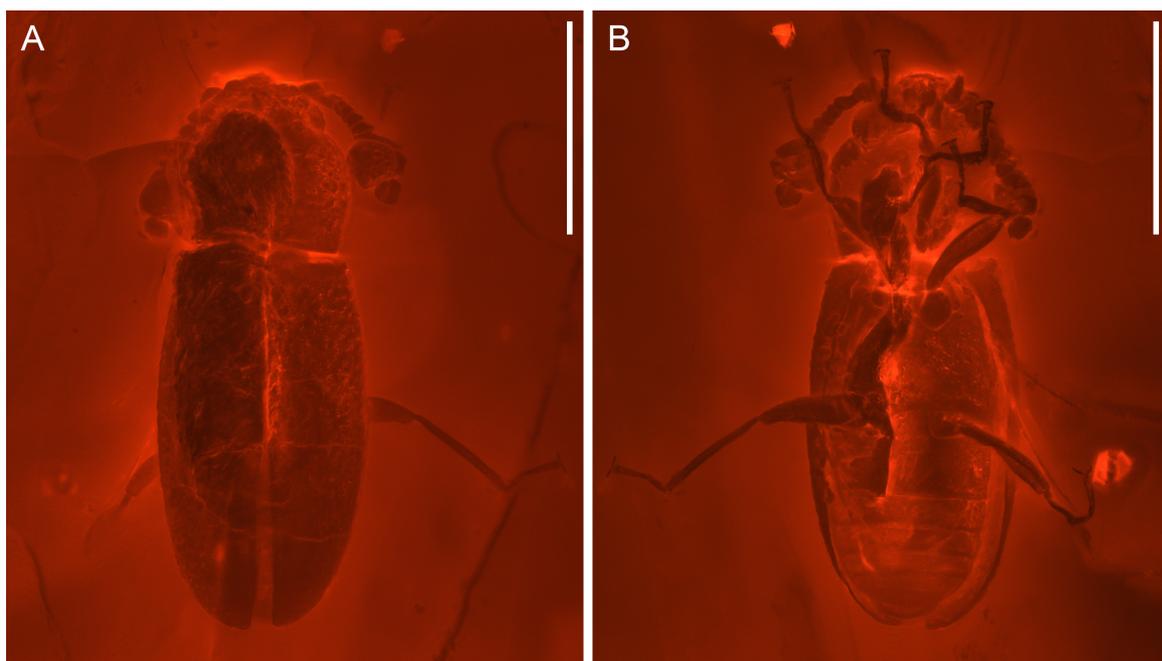


FIGURE 2. General habitus of *Rhomeocalpsua torosa* Li, Tomaszewska & Cai, **gen. et sp. nov.**, holotype, NIGP180054, under widefield fluorescence. **A**, Dorsal view. **B**, Ventral view. Scale bars = 500 μ m.

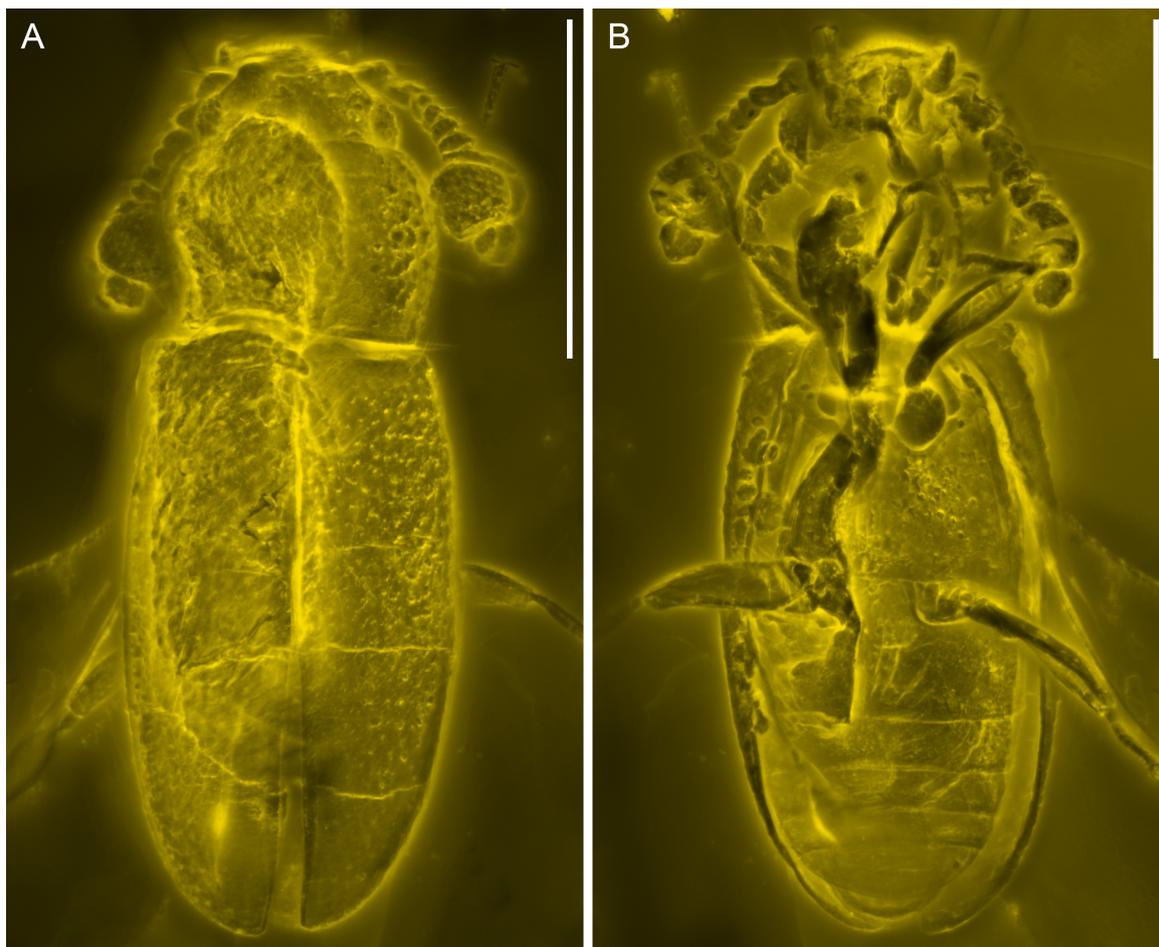


FIGURE 3. General habitus of *Rhomeocalpsua torosa* Li, Tomaszewska & Cai, **gen. et sp. nov.**, holotype, NIGP180054, under confocal microscopy. **A**, Dorsal view. **B**, Ventral view. Scale bars = 500 μ m.

mesotrochantins concealed; mesoventral process narrower than coxal cavity, narrowing between coxae towards apex, without apparent carinae or grooves (Fig. 4E). Mesometaventral junction as straight line with meso- and metaventrites contiguous (Fig. 4E). Metaventrite without postcoxal lines; postcoxal pits not apparent. Metacoxae (Fig. 4F) widely separated, transverse. Hind wings well developed.

Legs relatively long and slender. Trochanterofemoral joint oblique. Femora with deep and long groove (nearly throughout their length) for receiving tibiae (Fig. 4E, F). Tibiae without apical spurs, with short spines surrounding apex (Fig. 4H). Tarsi 3-3-3; tarsomeres simple (Fig. 4H, I). Pretarsal claws simple.

Abdomen (Fig. 4F, G) with six ventrites; ventrite 1 slightly longer than ventrite 2–4 combined, without postcoxal lines.

Discussion

Based on the results of molecular analyses, Robertson

et al. (2015) removed Mycetaeinae, Eupsilobiinae, and Anamorphinae from Endomychidae, and recognised them as separate families. Mycetaeidae and Eupsilobiidae clearly differ from *Rhomeocalpsua* in having antennae composed of 11 or 10 antennomeres, tarsi 4-4-4 and mesocoxal cavities open laterally (Pakaluk & Ślipiński, 1990; Tomaszewska, 2000a, 2010, 2011) (antenna with nine antennomeres, tarsi 3-3-3, mesocoxal cavities laterally closed in *Rhomeocalpsua*). Eupsilobiidae additionally differs by the presence of antennal grooves on head and postcoxal lines on abdominal ventrite 1 (antennal grooves absent, abdominal postcoxal lines absent in *Rhomeocalpsua*), and Mycetaeidae additionally differs by the pronotal disc with lateral raised carinae (pronotal lateral margins simply bordered without raised carinae in *Rhomeocalpsua*). Anamorphidae shares the simple 3-segmented tarsi (occurring in many Anamorphidae) and widely closed mesocoxal cavities with *Rhomeocalpsua* (Sasaji, 1978b, 1987, 1990; Tomaszewska, 2000a). Antennae built of nine antennomeres also occur in some Anamorphidae. However, the general appearance and other characters of *Rhomeocalpsua* do not fit well with

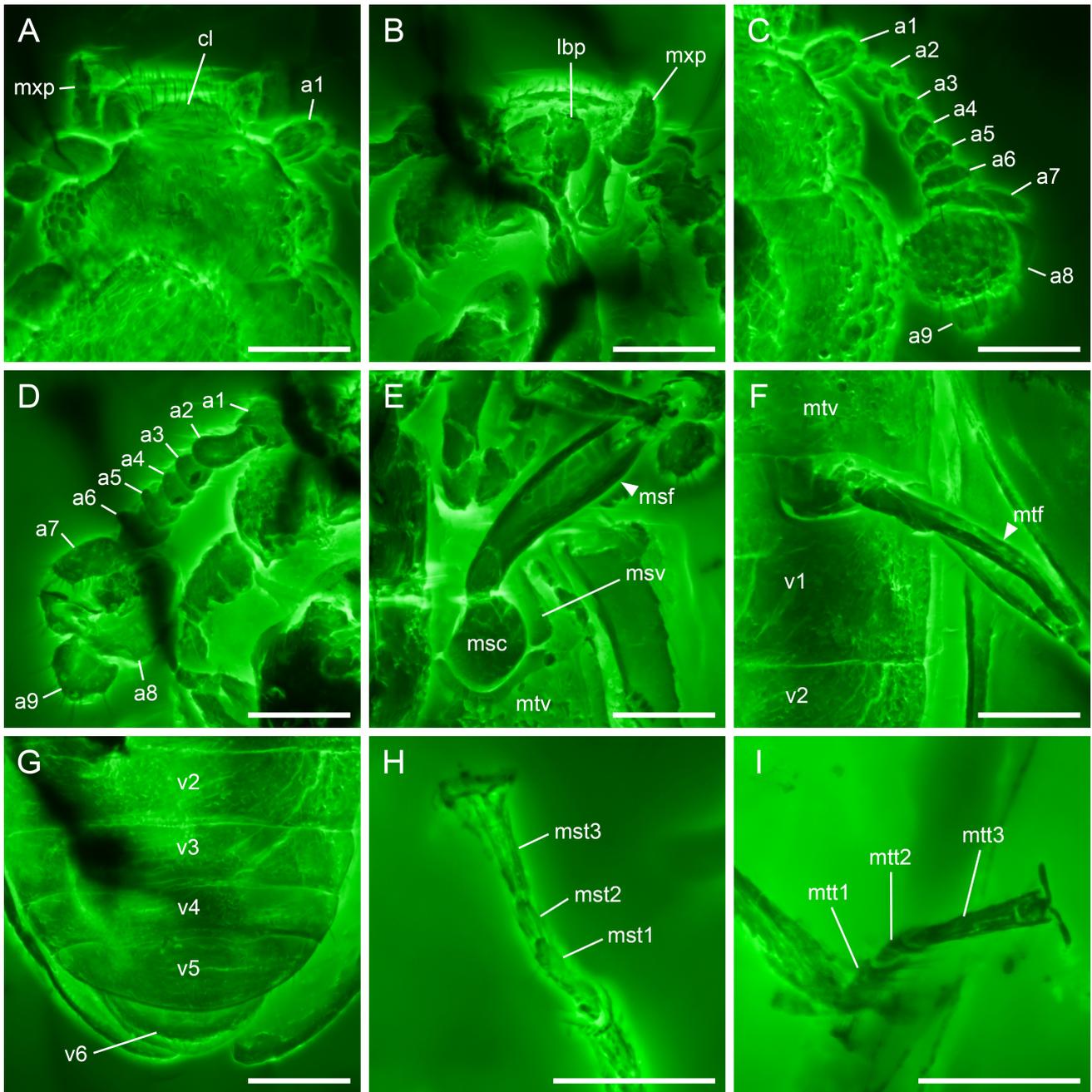


FIGURE 4. Details of *Rhomeocalpsua torosa* Li, Tomaszewska & Cai, **gen. et sp. nov.**, holotype, NIGP180054, under confocal microscopy. **A**, Head, dorsal view. **B**, Head, ventral view. **C**, Antenna, dorsal view. **D**, Antenna, ventral view. **E**, Mesothorax, ventral view. **F**, Abdominal base, ventral view. **G**, Abdominal apex, ventral view. **H**, Mesotarsus, ventral view. **I**, Metatarsus, dorsal view. Abbreviations: a1–9, antennomeres 1–9; cl, clypeus; lbp, labial palp; msc, mesocoxa; msf, mesofemur; mst1–3, mesotarsomeres 1–3; msv, mesoventrite; mtf, metafemur; mtt1–3, metatarsomeres 1–3; mtv, metaventrite; mxp, maxillary palp; v1–6, ventrites 1–6. Scale bars = 100 μ m.

Anamorphidae, including the posteriorly constricted and unmodified pronotal disc, elytra without distinct parasutural striae, strongly modified antennal club, and the relatively elongate body (pronotal disc usually widest posteriorly and with sulci or lateral carinae, parasutural striae usually present, antennae usually not modified, body usually short oval in Anamorphidae, although these characters can be variable in some anamorphid lineages).

Thus, we believe *Rhomeocalpsua* is more likely to belong to Endomychidae *sensu stricto*.

According to Robertson *et al.* (2015), Endomychidae can be divided into two major clades, the merophysiine complex and the endomychine complex (Danascelinae and Xenomycetinae not sampled in that study). The endomychine complex (the higher Endomychidae *sensu* Tomaszewska, 2005), composed of Cyclotominae,

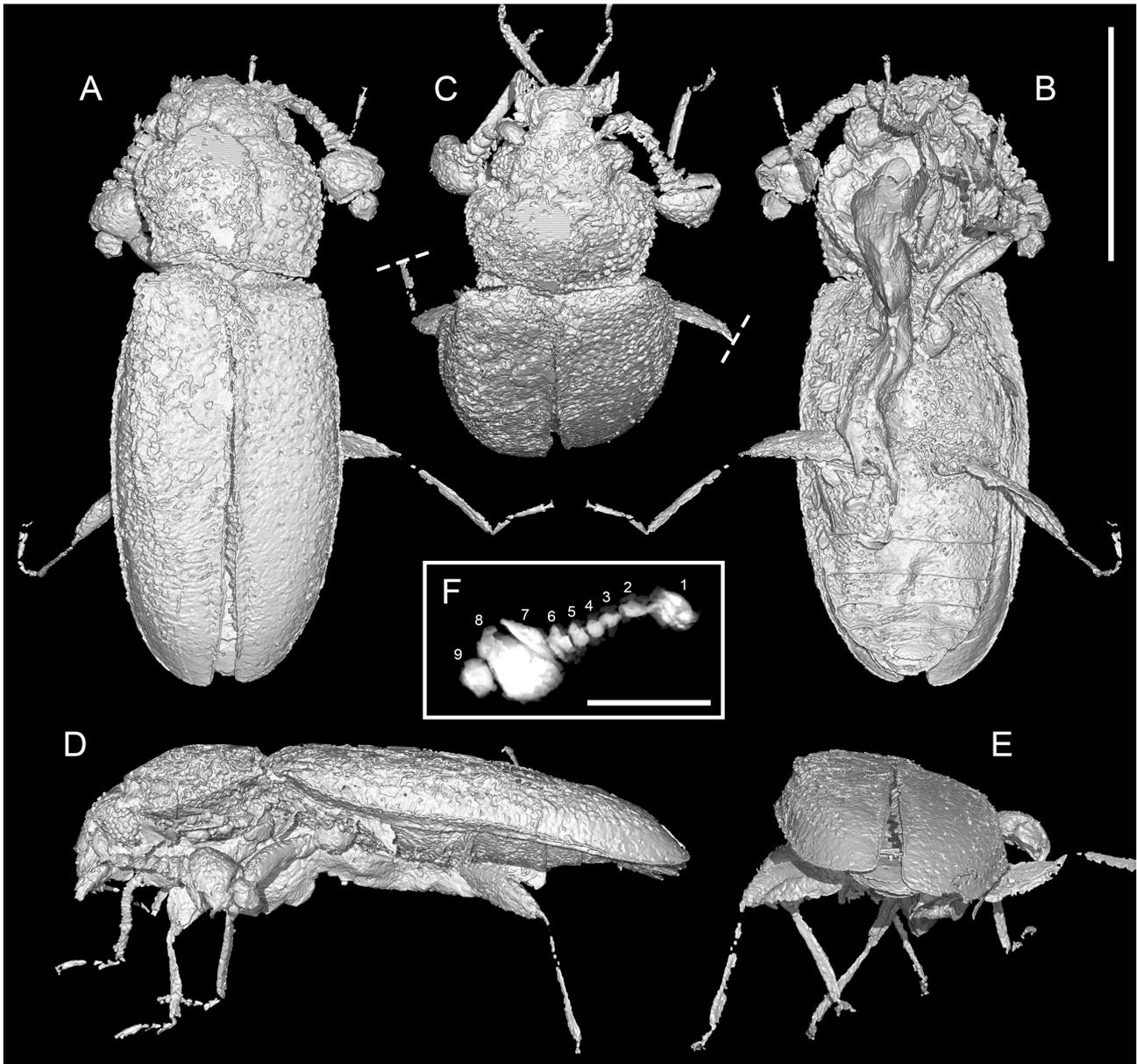


FIGURE 5. X-ray microtomographic reconstruction of *Rhomeocalpsua torosa* Li, Tomaszewska & Cai, **gen. et sp. nov.**, holotype, NIGP180054. **A**, Dorsal view. **B**, Ventral view. **C**, Anterodorsal view. **D**, Lateral view. **E**, Posterior view. **F**, Antenna, rendered under “Sum along Ray” mode. Scale bars = 500 µm in **A–E**, 200 µm in **F**.

Endomychinae, Epipocinae and Lycoperdininae, can be easily ruled out as close relatives of *Rhomeocalpsua*, primarily based on their pseudotrimerous tarsi, laterally open mesocoxal cavities, and exposed mesotrochantin (Tomaszewska, 2000a, 2005). The remaining subfamilies have tarsi more or less simple, and three of five subfamilies (Leiestinae, Pleganophorinae and Merophysyiinae) have concealed mesotrochantin (exposed in Xenomycetinae and Danascelinae). Leiestinae, Danascelinae and Xenomycetinae differ from *Rhomeocalpsua* in having 4-4-4 tarsi, laterally open mesocoxal cavities, and variously modified pronotum (with triangular lateral sulci in Leiestinae; with paired oval cavities in Danascelinae; widely bordered laterally and anteriorly in

Xenomycetinae) (Tomaszewska, 1999, 2000a, b, 2005) (tarsi 3-3-3, mesocoxal cavities laterally closed, pronotum unmodified in *Rhomeocalpsua*). Pleganophorinae has a somewhat similar body shape (especially *Trochoideus*, Westwood) with *Rhomeocalpsua* and closed mesocoxal cavities (although only narrowly), however, this subfamily differs in the 4-4-4 tarsi and antenna with usually 4–5 (never exceeding 7) antennomeres (Strohecker, 1978; Tomaszewska, 2000a, 2005).

Among the currently recognised endomychid subfamilies, Merophysyiinae appears to be most similar to *Rhomeocalpsua*, sharing the simple 3-3-3 tarsi, closed mesocoxal cavities (although narrowly closed in Merophysyiinae), and often a reduced number of

antennomeres (Tomaszewska, 2000a, 2005; Arriaga-Varela *et al.*, 2018). Additionally, the *Holoparamecus* lineage shares similarly elongate body shape and the absence of antennal grooves on the head (present in other Merophysiinae), but it has more or less distinct grooves/tubercles on the pronotum. Members of Merophysiinae also have inflated labial palpomere 2 (in *Rhomeocalpsua* the enlarged labial palpomere seems to be the apical one) and antennal sockets are invisible from above (visible from above in *Rhomeocalpsua*). Moreover, *Rhomeocalpsua* has deep and long grooves along the inner side of femora, which is often seen in related coccinelloid families, but never in such an extent in Endomychidae (Tomaszewska, 2000a, 2005). Based on the above discussion, the character combination of *Rhomeocalpsua* does not correspond perfectly with any endomychid subfamily, and therefore we prefer to place the newly discovered fossil in Endomychidae *incertae sedis*.

Data availability

The original confocal and micro-CT data are available in the Zenodo repository (<https://doi.org/10.5281/zenodo.6467721>).

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