



A new species of *Elodophthalmus* from Lower Cretaceous Lebanese amber unravels the systematic placement of Elodophthalmidae and reconciling phylogenetic conflicts within Tenebrionoidea

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Abstract

Elodophthalmidae, represented by the sole genus *Elodophthalmus* Kirejtshuk & Azar, is an extinct beetle family described from Lower Cretaceous Lebanese amber. Elodophthalmidae has been hypothesized to share close affinities with the extant superfamily Scirtoidea, but their exact systematic position remains elusive. Here, we describe a new species of *Elodophthalmus*, *Elodophthalmus maksoudae* **sp. nov.**, based on a well-preserved fossil from Early Cretaceous amber collected in Hammana/Mdeyrj, Central Lebanon, the same locality as other congeneric species. Using improved imaging technologies, we reveal detailed morphological characters of the fossil, providing critical evidence for a more robust systematic placement of *Elodophthalmus*. Our findings present compelling evidence supporting the placement of Elodophthalmidae within the superfamily Tenebrionoidea. Furthermore, we highlight that conflicts in the interfamilial relationships within Tenebrionoidea across various datasets can, at least partially, be mitigated by adopting the site-heterogeneous CAT-GTR+G model. We suggest that the traditional reliance on site-homogeneous models in Sanger sequencing-based studies may fail to capture the complexities of nucleotide substitution patterns. With the increasing recognition of the importance of modeling among-site compositional heterogeneity, our study points to the necessity for more rigorous model testing in the phylogenetic studies of ancient lineages such as Tenebrionoidea.

Key words: Elodophthalmidae, phylogenomics, fossil, Cretaceous, Lebanese amber, model

Introduction

Lebanese amber is renowned for its exceptional palaeontological significance, with over 500 outcrops identified across the region (Maksoud & Azar 2020; Maksoud *et al.* 2022). It represents the oldest amber containing abundant biological inclusions, offering invaluable insights into continental palaeobiodiversity during the Lower Cretaceous—a pivotal period for the coevolution of flowering plants (angiosperms) and insects. Most of Lebanon's amber deposits date back to the Early Cretaceous (early Barremian, with approximately 500 outcrops), while others date to the Late Jurassic (Kimmeridgian, with 19 outcrops). Notably, 36 Cretaceous outcrops have yielded fossil insects preserved either in amber or as impressions and compressions in rock. These discoveries have significantly advanced palaeoentomology, deepening our understanding of insect evolution and the biodiversity of ancient terrestrial ecosystems (Maksoud & Azar 2020, 2022; Hakim *et al.* 2022; Maksoud *et al.* 2022, 2024).

Lebanese amber has yielded a rich diversity of beetle fossils (Coleoptera), representing multiple families. These fossils include at least 14 extant beetle families that have been formally described, providing critical information about the diverse insect fauna of the Early Cretaceous. Notably, some fossils represent the oldest known records for families such as Anthicidae, Clambidae, Kateretidae, Micromalthidae, and Sphindidae (Kirejtshuk & Azar 2008). Lebanese amber has also preserved exceptionally small beetles—such as those belonging to Clambidae and

Micromalthidae—that are typically difficult to preserve as compression fossils. This unique preservation offers complementary evidence for understanding insect evolution during the Angiosperm Terrestrial Revolution (Benton *et al.* 2022) and the assembly of modern terrestrial ecosystems.

Given the antiquity of the Lebanese amber inclusions, some fossils with unusual characters are challenging to place within the current framework of beetle classification. For example, *Lebanophytum excellens* Kirejtshuk & Azar was originally assigned to the elateroid family Cerophytidae by Kirejtshuk & Azar (2008) and later to its own family, Lebanophytidae, by Kirejtshuk & Azar (2013). However, based on more comprehensive phylogenetic analyses and character-based discussions, *Lebanophytum* was reclassified as a member of the cucujoid family Cryptophagidae (Yu *et al.* 2019). Similarly, Kirejtshuk *et al.* (2016) described a new family, Ptismidae, based on a single species, *Ptisma zasukhae*, from the Lower Cretaceous Lebanese amber and placed it within the superfamily Staphylinoidea. They compared the traits of this new taxon with a variety of staphylinoid groups. However, a comparative study of extant and extinct clambid beetles by Cai *et al.* (2019) suggested that *P. zasukhae* is a crown clambid, closely related to extant *Calyptomerus*. As a result, Ptismidae is now regarded as a synonym of Clambidae, with *Ptisma zasukhae* placed as *incertae sedis* within Clambidae.

Elodophthalmidae, represented by a single genus *Elodophthalmus* Kirejtshuk & Azar and two species, is an extinct family described from Lebanese amber. Elodophthalmids exhibit the greatest resemblance to and are likely closely related to the extant family Scirtidae and are recognized as a fifth family within Scirtoidea, albeit this superfamily was recently redefined by Cai *et al.* (2022). *Elodophthalmidae* is diagnosed by the following combination of characters: 1) an elongate and convex body with steeply sloping sides; 2) long elytra with diffuse puncturation; 3) very large and coarsely faceted eyes, emarginate at the antennal insertion; 4) long antennae with strongly modified antennomeres 6–10 or 7–10; 5) long and narrow legs with simple tarsomeres; 6) narrow and long metepisterna; 7) raised submesocoxal lines deviating towards the middle of the metepisternum; and 8) short and slightly oblique metacoxae without a femoral plate (Kirejtshuk & Azar 2008). However, some of these characters, such as body shape, elytral puncturation, simple tarsi, and narrow metepisterna, are not particularly informative for determining the familial placement of the fossils. Additionally, the holotype of the type species is insufficiently preserved, and the number of hind tarsomeres remains unclear, despite claims that it was five-segmented.

Here, we describe a new species of *Elodophthalmus* Kirejtshuk & Azar based on a well-preserved fossil from Early Cretaceous amber, collected from Hammana/Mdeyrij, Caza Baabda, Mouhafazet Jabal Loubnan (Central Lebanon)—the same locality as other congeneric species. Using advanced photographic technologies, we were able to reveal detailed morphological characters of the fossil, providing crucial evidence for a more reliable systematic placement of *Elodophthalmus* (Elodophthalmidae). Our findings present compelling evidence that Elodophthalmidae belongs to the superfamily Tenebrionoidea. Additionally, we discuss the current knowledge and potential pitfalls in the Sanger-sequencing-based molecular phylogeny of Tenebrionoidea.

Material and methods

The study was based on a male specimen from the Lebanese Lower Cretaceous amber outcrop of Hammana-Mdeyrij (Azar *et al.* 2011). The Lebanese amber specimen examined is permanently deposited in the Natural History Museum of the Lebanese University, Faculty of Sciences II, Fanar, Lebanon. The method of preparation of the specimens for study was described in Azar *et al.* (2003).

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 lines (Cai & Huang 2014; Fu *et al.* 2021; Li *et al.* 2022b). Images were stacked with Helicon Focus 7.0.2, Zerene Stacker 1.04, and Adobe Photoshop CC and were further processed in Adobe Photoshop CC to adjust brightness and contrast.

To understand the molecular phylogeny of Tenebrionoidea, we used the most recently assembled Sanger-sequencing based matrix provided by Cosandey *et al.* (2024). The matrix (117 taxa, 4719 nucleotide sites) was composed of two mitochondrial gene fragments (*COI* and *16S*) and two nuclear ribosomal gene fragments (*18S* and *28S*), which is freely available at Zenodo: <https://zenodo.org/records/14002625>. To account for the among-site compositional heterogeneity, we used the site-heterogeneous CAT-GTR+G4 model implemented in PhyloBayes

MPI v1.9 (Lartillot *et al.* 2013). The CAT-GTR+G4 model, a free finite mixture model, is a better-fitting model of nucleotide substitution for addressing among-site compositional heterogeneity, as evidenced by a recent simulation study (Bujaki *et al.* 2023). Convergence parameters for the two independent runs were assessed using the bpcomp (maxdiff < 0.3) and tracecomp (reldiff < 0.1 and minimum effsize > 300) programs implemented in PhyloBayes (Lartillot *et al.* 2013; Lartillot 2020).

Systematic palaeontology

Order Coleoptera Linnaeus, 1758

Superfamily Tenebrionoidea Latreille, 1802

Family Elodophthalmidae Kirejtshuk & Azar, 2008

Genus *Elodophthalmus* Kirejtshuk & Azar, 2008

Type species. *Elodophthalmus harmonicus* Kirejtshuk & Azar, 2008.

Elodophthalmus maksoudae sp. nov.

(Figs 1–3)

Material. Holotype, 1821, D. Azar collection, Hammana/Mdeyrij outcrop, Caza Baabda, Mouhafazet Jabal Loubnan (Central Lebanon).

Etymology. The specific name is dedicated to Professor Sibelle Maksoud, who has made great contribution of the study of Lebanese amber and palaeontology in Lebanon in general.

Diagnosis. *Elodophthalmus maksoudae* sp. nov. differs from the other two *Elodophthalmus* species (*E. gracilis* Kirejtshuk & Azar and *E. harmonicus*) primarily by the minimum dorsal distance between the compound eyes and the antennal morphology. The compound eyes of *E. maksoudae* are more closely spaced, (Ocular Index [OI] = 17, widely spaced in *E. harmonicus* (OI = 41); Campbell & Marshall 1964). More importantly, the antennae of *E. maksoudae* are much longer than those of the other species. The antennomeres 3–5 are strongly reduced and transverse (antennomeres 3–6 of *E. gracilis* are reduced, but not transverse, whereas antennomeres 3–5 of *E. harmonicus* are reduced, but not transverse). The antennomeres 6–11 of *E. maksoudae* are elongate (less elongate and triangular in *E. harmonicus*).

Locality and horizon. Hammana/Mdeyrij, Caza Baabda, Mouhafazet Jabal Loubnan (Central Lebanon); Lower Cretaceous (lower Barremian).

Description. Body *ca.* 1.14 mm long, moderately convex. Upper surfaces clothed with fine, suberect hairs (Fig. 1).

Head 0.40 mm wide, strongly declined (Fig. 2A); abruptly constricted posteriorly to form narrow neck. Transverse occipital ridge developed. Eyes (Fig. 2B) strongly protuberant and coarsely faceted, slightly emarginate, with interfacetal setae; close to each other, with OI = 17. Antennal insertions (Fig. 2C) exposed from above, located at inner edges of eyes. Subantennal grooves absent. Frontoclypeal suture absent. Labrum (Fig. 2B) free, strongly transverse, rounded apically. Antennae (Fig. 2C) *ca.* 0.92 mm long, 11-segmented, densely setose, markedly elongate; antennomere 1 subquadrate; antennomere 2 slightly longer than antennomere 1; antennomeres 3–5 strongly reduced in length, slightly narrower than antennomere 2; antennomeres 4 and 5 strongly transverse; antennomeres 6–11 slender, antennomeres 6 as long as antennomeres 1–5 combined, gradually widened apically; antennomere 7 slightly shorter than antennomere 6; antennomeres 8–10 each similar to shape and size of antennomere 7; antennomere 11 slightly longer than antennomere 10. Mandible curved. Maxillary lobes short, apically pubescent; apical maxillary palpomeres slightly expanded and truncate.

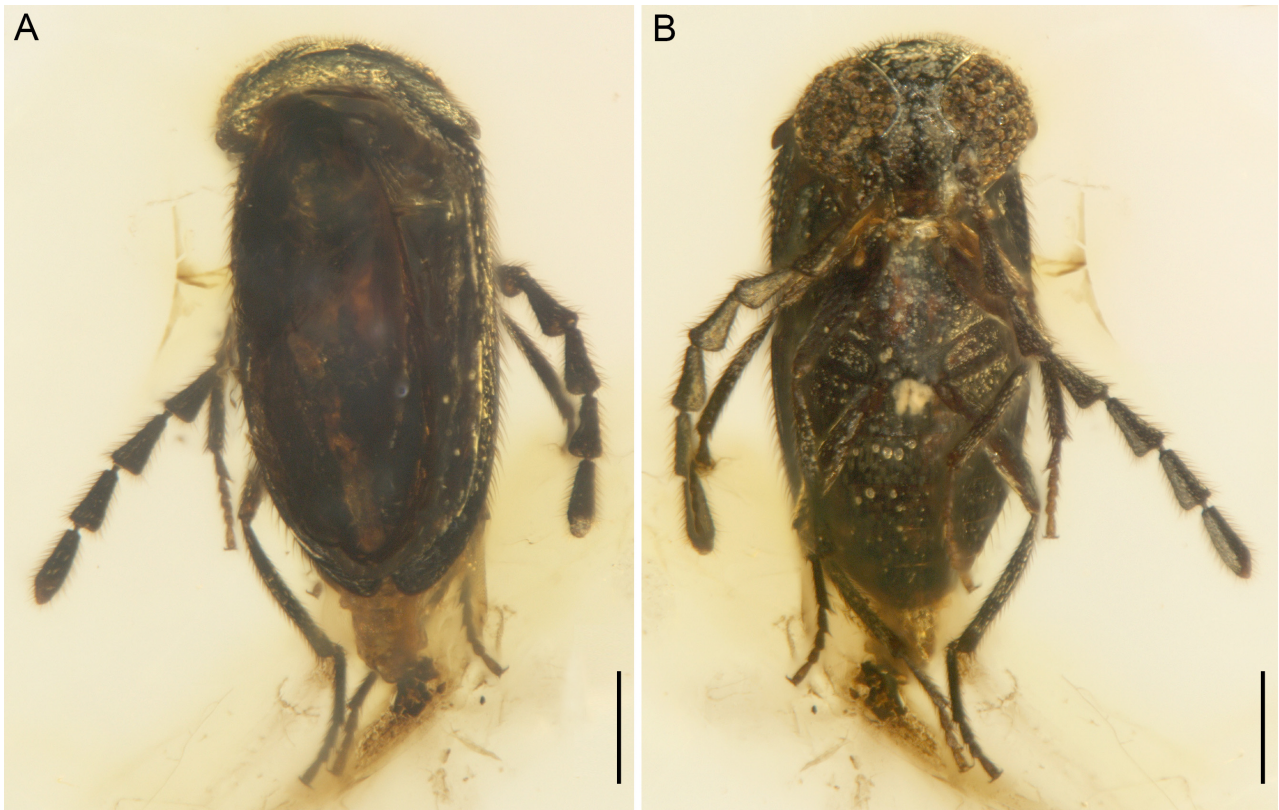


FIGURE 1. General habitus of *Elodophthalmus maksoudae* **sp. nov.**, holotype specimen 1821, D. Azar coll., under incident light. **A**, Dorsal view. **B**, Ventral view. Scale bars: 200 μ m.



FIGURE 2. General habitus of *Elodophthalmus maksoudae* **sp. nov.**, holotype specimen 1821, D. Azar coll., under confocal microscopy. Ventral view. Scale bars: 200 μ m.

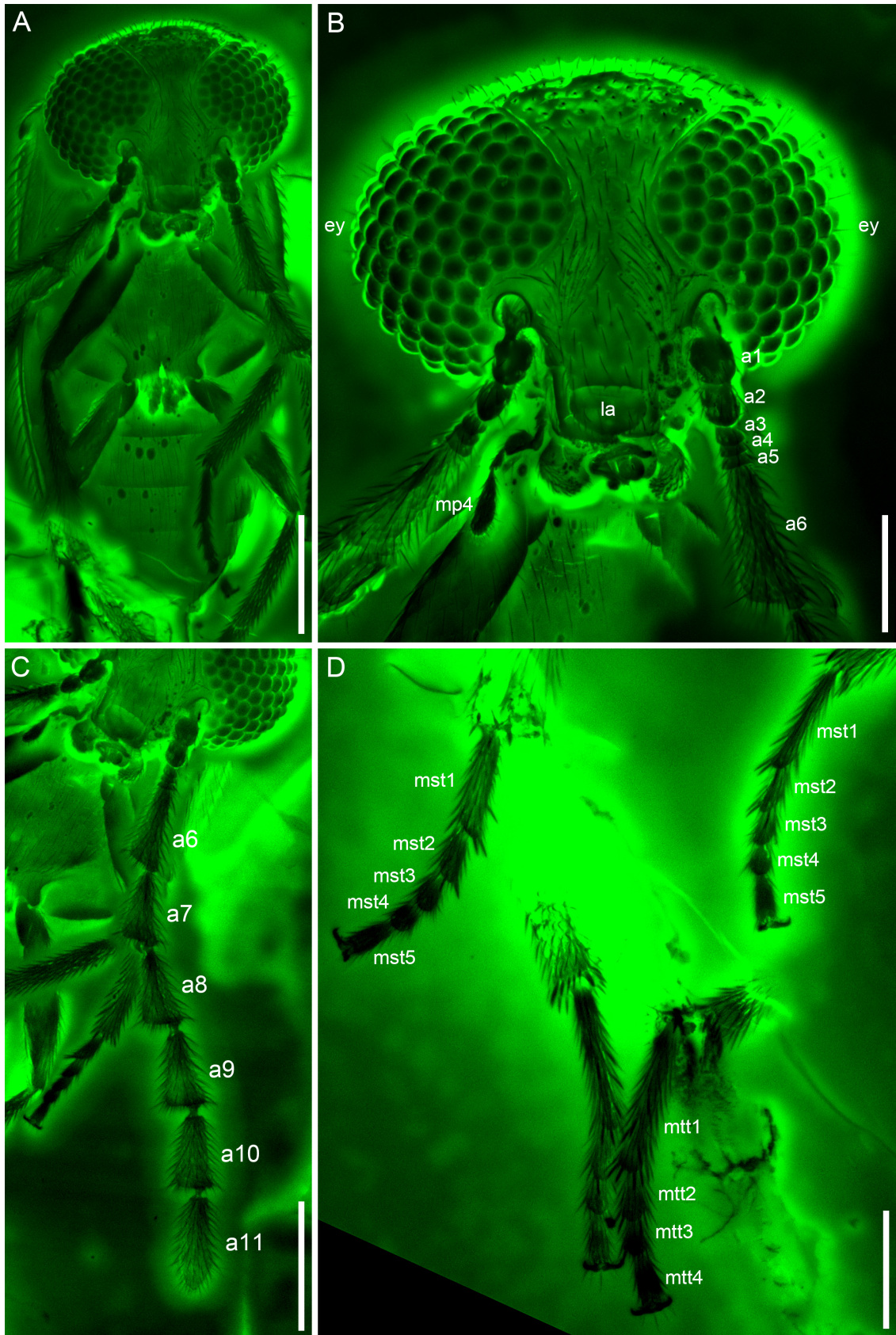


FIGURE 3. General habitus of *Elodophthalmus maksoudae* sp. nov., holotype specimen 1821, D. Azar coll., under confocal microscopy. **A**, Ventral view of body. **B**, Ventral view of head. **C**, Left antenna. **D**, Meso- and metatarsi. Abbreviations: a, antennomere; ey, compound eye; la, labrum; mp, maxillary palpomere; mst, mesotarsomere; mtt, metatarsimere. Scale bars: 200 μ m in **A** and **C**; 100 μ m in **B** and **D**.

Pronotum transverse, 0.52 mm wide; sides slightly curved; base slightly narrower than elytral bases; anterior angles not produced; posterior angles broadly rounded; posterior edge simple; disc without impressions. Scutellar shield not abruptly elevated anteriorly; posteriorly rounded. Elytron 0.89 mm long along suture, *ca.* 3.8 times as long as its width; without scutellary striole; epipleura incomplete. Metaventricle moderately convex; discrimen absent; postcoxal lines absent. Metacoxae contiguous, extending laterally to meet elytra; metacoxal plates present, small. Hind wing well developed. Trochanterofemoral joint slightly oblique with base of femur separate from coxa. Mesotibia not strongly widened; outer edge simple; outer apical angle simple. Tibial spurs developed, simple. Tarsi (Fig. 2D) 5-5-4, simple; pro- and mesotarsomeres 1–4 successively shortened; pro- and mesotarsomeres 5 elongate; metatarsomeres 1 longer than other metatarsomeres. Pretarsal claws simple.

Abdomen (Fig. 2A) with five free ventrites, first two of which not connate; ventrite 1 not much longer than 2; suture between ventrites 1 and 2 distinct; ventrite 3 slightly shorter than ventrite 2.

Discussion

Systematic position of Elodophthalmus and Elodophthalmidae

The holotype of *Elodophthalmus maksoudae* **sp. nov.** is exceptionally well preserved. Using confocal laser scanning microscopy (CLSM), many crucial characters essential for determining the family's systematic position are clearly revealed. The typical body shape and size, characteristic antennal morphology, large and coarsely faceted eyes with emargination, and the declined head are all distinctive features among all known beetles from Lebanese amber, firmly supporting its placement within *Elodophthalmus*.

The most critical character that significantly differs from the original descriptions of the genus *Elodophthalmus* and the family Elodophthalmidae is the tarsal formula. As clearly illustrated in the original line drawings of the type species of *Elodophthalmus* (Kirejtshuk & Azar 2008: fig. 11), the apical parts of the mesotarsi and metatarsi of *E. harmonicus* are not preserved, with only three visible tarsomeres in the hind tarsi. In contrast, our clear observation of four metatarsomeres is consistent with both the line drawings and the coloured figures of *E. harmonicus*. The compound eyes of the holotype of *E. maksoudae* are also well preserved, revealing important characters for systematic studies. The eyes are strongly protuberant, coarsely faceted, and slightly emarginate, as originally described for the family (Kirejtshuk & Azar 2008). However, under CLSM, we can demonstrate the presence of interfacetal setae. Based on a combination of adult characters—including 11-segmented antennae without a distinct club, a strongly declined head, coarsely faceted eyes with interfacetal setae, a 5-segmented abdomen, and a 5-5-4 tarsal formula—we can confidently place *Elodophthalmus* in the superfamily Tenebrionoidea. Within Tenebrionoidea, Elodophthalmidae shows close resemblances to some representatives of the extant families Scaptiidae, Melandryidae, and Aderidae. Elodophthalmidae differs from Scaptiidae by lacking pubescent tibial spurs and lobed penultimate tarsomeres. It differs from Aderidae by having a distinct suture between abdominal ventrites 1 and 2 (often obscured with 4 free ventrites in Aderidae), well-developed tibial spurs (weakly developed or absent in Aderidae), simple tarsi (with the penultimate tarsomere reduced and antepenultimate lobed beneath in Aderidae), and a broad prothorax (where the base is usually much narrower than the elytral bases in Aderidae). Elodophthalmidae appears to be most closely related to the heterogeneous and non-monophyletic family Melandryidae.

The most distinctive characteristic of *Elodophthalmus maksoudae* is its highly modified antennae. The strongly reduced antennomeres 3–5 and the elongate antennomeres 6–11 are, to our knowledge, unique to this species and not found in any other beetle families. The antennae of *E. maksoudae* are much longer than those of *E. harmonicus* and *E. gracilis*. Although it is not possible to determine the gender of *E. maksoudae*, the length of the antennae suggests that it may be most likely a male.

Elodophthalmidae was originally placed in the superfamily Scirtoidea, an early-diverging lineage of polyphagan beetles (Cai *et al.* 2022), and was suggested to share the most similarities with the extant Scirtidae (Kirejtshuk & Azar 2008). However, scirtoid beetles always have five-segmented tarsi, and Scirtidae features a lobed tarsomere 4. Key characters such as the tarsal morphology and the emarginate eyes with interfacetal setae rule out Elodophthalmidae as a member of Scirtoidea. Furthermore, Elodophthalmidae possesses some plesiomorphic characters not found in morphologically similar families like Scaptiidae and Aderidae,

including weakly developed metacoxal plates, simple paired tibial spurs, simple (non-lobed) tarsi, and distinctly separated abdominal ventrites 1 and 2. Given these distinctions and the fact that the interfamilial relationships of Tenebrionoidea remain controversial, it is currently challenging to place *Elodophthalmus* within any existing extant beetle families. However, we propose that Elodophthalmidae likely represents one of the early-diverging lineages within Tenebrionoidea.

Molecular phylogeny of Tenebrionoidea

The superfamily Tenebrionoidea is one of the most challenging lineages of beetles due to its ancient evolutionary history, vast species richness, and complex taxonomic history (Kergoat *et al.* 2014; Cosandey *et al.* 2024). Our understanding of the molecular phylogeny of Tenebrionoidea has improved significantly over the past decades. However, the monophyly of Tenebrionoidea has not been universally supported by studies based on a limited number of gene markers. Some studies have recovered Lymexyloidea (Lymexylidae) as a sister group to Tenebrionoidea (Bocak *et al.* 2014; Gunter *et al.* 2014), while others have not (Hunt *et al.* 2007; McKenna *et al.* 2015). Recent phylogenomic studies of beetles, based on dozens to thousands of protein-coding genes, consistently support the conclusion that Lymexyloidea (Lymexylidae) is the sister group to Tenebrionoidea (Zhang *et al.* 2018; McKenna *et al.* 2019; Cai *et al.* 2022), and the monophyly of Tenebrionoidea, as defined by Cai *et al.* (2022), is strongly supported. Unfortunately, studies on the interfamilial relationships within Tenebrionoidea are limited, often yielding poorly supported trees, which hinders a clearer understanding of its evolutionary history. The most comprehensive molecular phylogeny of Tenebrionoidea (Kergoat *et al.* 2014; Cosandey *et al.* 2024) revealed that of the 18 families included, five were found to be either paraphyletic or polyphyletic. Melandryidae has long been understudied, and its systematic classification remains poorly understood (Li *et al.* 2022a). Cosandey *et al.* (2024) presented the most comprehensive phylogeny of Melandryidae to date, based on available molecular sequence data. As in previous studies, they found the polyphyly of Melandryidae, revealing three distinct clades within Tenebrionoidea. In light of these molecular phylogenetic findings, they proposed a revised classification for Melandryidae and reinstated the family Osphyidae.

Our phylogenetic analysis, based on the matrix assembled by Cosandey *et al.* (2024) under the CAT-GTR+G model, yielded a quite different topology compared to that of the partitioned model used in the original study (Cosandey *et al.* 2024). As shown in Fig. 4, Lymexyloidea (Lymexylidae) was recovered as a sister group to Tenebrionoidea (Bayesian Posterior Probability [BPP] = 0.63), rather than being sister to Stenotrachelidae as in Cosandey *et al.* (2024). Within Tenebrionoidea, Stenotrachelidae and the clade Ripiphoridae-Mordellidae formed the first diverging lineage, followed by the clade Scaptiidae + Osphyidae. In the higher groups of Tenebrionoidea, Ischaliidae was weakly supported as sister to Aderidae (BPP = 0.32), rather than to Meloidae as in Cosandey *et al.* (2024). Pyrochroidae was weakly supported as sister to Anthicidae + Meloidae (BPP = 0.54), rather than to the clade including Scaptiidae, Osphyidae, and Salpingidae. Although the shallower phylogenetic relationships at the familial level were largely similar to the original study (Cosandey *et al.* 2024), many aspects of the interfamilial relationships differed.

It is noteworthy that under the site-heterogeneous CAT-GTR+G model, the Sanger-sequencing data produced a tree that was more congruent with recent phylogenomic studies. For instance, phylogenomic studies (Zhang *et al.* 2018; McKenna *et al.* 2019; Cai *et al.* 2022) have shown that Lymexyloidea is the sister lineage to Tenebrionoidea; the clade Ripiphoridae-Mordellidae (with Stenotrachelidae not sampled in all studies) represents the first diverging lineage within Tenebrionoidea (Batelka *et al.* 2016); Ischaliidae is closely related to Aderidae; and Pyrochroidae is a sister group to Anthicidae + Meloidae. All of these key relationships were recovered in our CAT-GTR+G tree, although the support values were often low due to the lack of sufficient phylogenetic signal.

As evidence accumulates in the phylogeny of Tenebrionoidea and Coleoptera (Zhang *et al.* 2018; McKenna *et al.* 2019; Cai *et al.* 2022), it appears that the better-fitting site-heterogeneous CAT-GTR+G model (Bujaki *et al.* 2023; Cai *et al.* 2023) is more suitable for modeling the molecular evolution of ancient beetle lineages like Tenebrionoidea. Since the CAT-GTR+G model has rarely been tested in molecular phylogenies of insects based on Sanger-sequencing data (Tihelka *et al.* 2020c; Li *et al.* 2021), we caution that previous studies based on similar data (a few gene markers) and the widely used partitioned (site-homogeneous) model may be plagued by systematic errors. The conflicting results between these studies and phylogenomic data could stem from model misspecification (Cai *et al.* 2023; Cai 2024). More extensive exploration of this topic is needed to further clarify this issue.

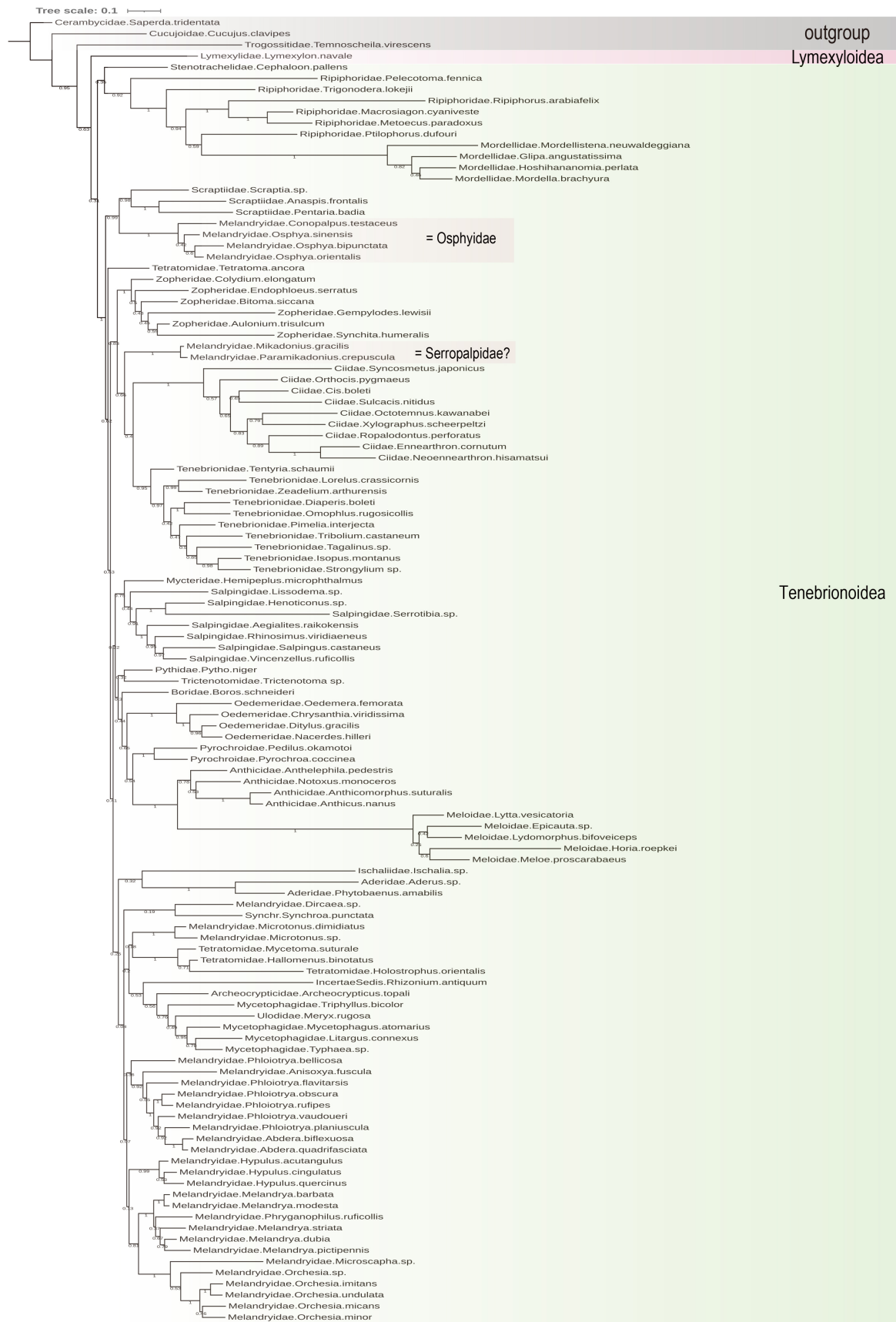


FIGURE 4. Phylogenetic relationships of Lymexyloidea and Tenebrionoidea based on Sanger sequencing data from Cosandey *et al.* (2024) under the site-heterogeneous CAT-GTR+G model. The tree is more congruent to the recent phylogenomic studies, although the support is generally low due to the lack of sufficient phylogenetic signal.

Given the growing recognition of the importance of modeling among-site compositional heterogeneity (Cai *et al.* 2020, 2022, 2023; Kapli *et al.* 2020; Tihelka *et al.* 2020a, 2020b, 2021; Lozano-Fernandez 2022; Li *et al.* 2021, 2023; Cai 2024), our study emphasizes the need for more rigorous testing of molecular models in the phylogenetic analysis of ancient and evolutionarily complex lineages such as Tenebrionoidea. The traditional use of site-homogeneous models in Sanger-sequencing-based studies, while computationally simpler, may fail to adequately capture the complexities of nucleotide substitution patterns across diverse lineages. Many of the existing conflicts regarding the interfamilial relationships of Tenebrionoidea across different datasets can, at least in part, be reconciled by adopting the site-heterogeneous CAT-GTR+G model. While the support values for some clades remain low due to the limited phylogenetic signal in the small dataset, our study lays the groundwork for future research using larger, more comprehensive data matrices.

Data availability

The high-resolution figure plates and data generated in our phylogenetic analysis are available in the Science Data Bank repository (<https://doi.org/10.57760/sciencedb.18640>).

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