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OPINION PAPER

The 'first fossil tumbling flower beetle' larva is a symphytan (Hymenoptera)

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Abstract. A correction is provided regarding the identity of a fossil larva recently reported to represent the first Cretaceous record of its kind for the tenebrionoid family Mordellidae (Coleoptera, tumbling flower beetles). A review of the description of the specimen, however, reveals it to be a larval symphytan (order Hymenoptera), and likely of the family Pamphiliidae. The evidence for the revised identification is summarized.

Key words. Coleoptera, Mordellidae, Hymenoptera, Pamphiliidae, Mesozoic, Burmese amber

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Introduction

As may happen from time to time, the conclusions of paleontological studies may be found wanting and require commentary and revision. Such is the nature of science. Along these lines, a recent article published on 3 March 2022 in *PalZ* by Ana Zippel et al. reporting what was dubbed as the, 'first fossil tumbling flower beetle-type larva', from Kachin amber contains some errors of interpretation that necessitates constructive commentary. While the work presents the description of a fossil larva putatively of the beetle family Mordellidae, it is evident that the specimen in question is neither a mordellid nor a beetle. In fact, an analysis of the content of the study reveals that the larva is that of a symphytan (Hymenoptera), and likely of the family Pamphiliidae (a.k.a., the leaf-rolling or web-spinning sawflies today well known as sometimes gregarious herbivores of conifers or Rosaceae).

Systematics

Perhaps the origin of the difficulty stemmed from the seemingly automatic assertion that the larva was a beetle and that the abdominal apical process indicated Mordellidae, an assumption then exacerbated by exclusively making comparisons with extant Mordellidae. Regardless, the authors compared their fossil with extant Mordellidae, suggesting the two shared a, 'general appearance', while simultaneously noting dramatic differences most of the prominent characters they discussed. In actuality, as can be observed in their figures, the fossil resembles little the extant mordellid larva presented (Zippel et al. 2022). A number of critical differences highlight these distinctions. Foremost, the putative presence of 'eight' antennomeres (note that the number of antennomeres is misinterpreted, see below) does not correspond with the groundplan of core Polyphaga, to which Tenebrionoidea (and Mordellidae therein) belong (Zhang et al. 2018, Cai et al. 2022). Furthermore, the antenna is of a completely different morphology (e.g., the sensorium is lacking), the number of antennomeres is too great (in Polyphaga there are usually three or fewer, only rarely four or five in some Staphylinoidea and Scarabaeoidea, while more antennomeres are only known in Scirtidae) (Lawrence et al. 2011). Additionally, the occurrence of four maxillary palpomeres, as recorded for their fossil (Zippel et al. 2022), is known again only in Scirtidae, and not in Tenebrionoidea. The only remaining putatively mordellid-like feature is the, 'specific single process at the posterior end of the abdomen' (Zippel et al. 2022). However, the structure of these processes and related terminal structures are, in fact, not similar, that of the mordellid being a conical spine surrounded by small, blunt tubercles, while in the fossil the apicalmost tergum is compressed, broadened, with large, slightly upcurved, spine, significantly broader than that of extant Mordellidae.

The putative homology argued by Zippel et al. (2022) is lacking, and the simple presence of an apical spine is, in and of itself, insufficient evidence of relationship as spines of various form occur in many unrelated holometabolan larvae. Beutel & Friedrich (2005) proposed two externally visible synapomorphies for larvae of Tenebrionoidea: posteriorly diverging gula with well-developed gular ridges and asymmetric mandibles. Neither of these characters are described nor mentioned in the original account of the fossil larva. It is clear that the fossil larva lacks similarities with Mordellidae and lacks diagnostic features of Polyphaga, or even Coleoptera.

From the available evidence, the fossil larva belongs to the order Hymenoptera, where has typical characters of many groups of Symphyta, the sawflies and woodwasps. Before exploring this attribution further, a few corrections are necessary (terminology that follows is that of Viitasaari (2002a), and particular for Symphyta; special terms in italics): the antennae are misinterpreted as 'eight segmented', as the authors apparently misidentified the membranous *antacorium* as antennomere I (the *antacorium* is quite distinct in their images and identical to that of Symphyta); the *ocularium* is visible in their figures 3a,b and was seemingly overlooked in their discussion; the three simple legs (typical for Pamphiliidae and some other symphytan lineages) are labeled and described as having two tarsal elements, but no pretarsus (claw), when in the setaceous legs of pamphiliids there is a simple claw, sometimes unrecognizably fused to the tarsus and seemingly forming a single podite (as is the condition in their figures); the abdomen is described as nine-segmented but in Coleoptera as well in Symphyta the abdomen is 10-segmented (Lawrence et al. 2011, Viitasaari 2002b). In fact, what they label as the 'terminal end' is actually the modified segment X (Zippel et al. 2022: figs 2b, 3f), which in many, but not all, pamphiliids is broadened, typically rounded apically, but sometimes somewhat scoop- or spade-shaped (somewhat like in the fossil), sometimes bearing a thickened apical rim, and often with a *postcornus* or *suranal hook* (e.g., Eidt 1969). Additionally, what the authors label as the 'urogomphus' (Zippel et al. 2022: figs 3f, g) is actually the subanal appendage typical of Pamphiliidae (on segment X), Blasticotomidae (on segments IX and X), and Cephidae (present but greatly reduced on segment X). Quite peculiarly, the terminology employed is that for Crustacea, rather than for holometabolan larvae, and this perhaps misleads or even confuses the interpretation of key characters.

Definitive placement as to family is not attempted here given that we have not been able to examine the fossil firsthand to look for further diagnostic traits. Nonetheless, the absence of prolegs, the presence of distinct thoracic legs with seven podomeres, the seven antennomeres on a pronounced *antacorium*, the well sclerotized head capsule that is distinctly separated from the thorax by a constriction (not the case in mordellid larvae), the enlarged and modified abdominal tergum X, the presence of well-developed and seemingly trimerous subanal appendages on segment X, and the presence of a *postcornus* (albeit dramatically enlarged in the fossil), are all consistent with Pamphiliidae. It is possible that further pamphiliid characters could be uncovered upon closer examination of the fossil.

The former suborder 'Symphyta' has been long recognized as a paraphyletic group (e.g., Sharkey et al. 2012, Peters et al. 2017). Although topologies for early diverging Hymenoptera vary, one of the more recent phylogenomic studies (Peters et al. 2017) recovered a monophyletic 'Eusymphyta' composed of Xyeloidea, Pamphilioidea, and Tenthredinoidea, putatively with pamphiliids basal therein. Alternatively, these three superfamilies form a paraphyletic group sister to all remaining Hymenoptera (i.e., Unicalcarida *sensu* Schulmeister et al. 2002, Sharkey et al. 2012), followed by the remaining superfamilies of 'Symphyta', and ultimately a monophyletic Euhymenoptera (Orussoidea + Apocrita). All three of these early diverging superfamilies are abundant in the Mesozoic fossil record. Xyeloidea are represented since the Late Triasic (e.g., Engel 2005, Lara et al. 2014), Pamphilioidea since the Middle Jurassic (e.g., Wang et al. 2016), and Tenthredinoidea since the Early Jurassic (Nel et al. 2004). A taxonomic match of the fossil hymenopteran larva with possible adults in the fossil record is unlikely, aside from noting that the fossil is likely a pamphiliid. In fact, holometabolous larvae can only rarely be matched with conspecific or congeneric adults because of their wholly different morphology and typically different microhabitat preferences. Indeed, such matches between holometabolan life stages can only be made under the most special of circumstances, and requiring that the stages are discovered together, as in, for example, some parasitoid beetles with a complex life cycle or some eusocial insects (Batelka et al. 2021, Boudinot et al. 2022). The described Mesozoic larvae of 'Symphyta' from the Lower Cretaceous, *Vitimilarva paradoxa* Rasnitsyn, 1969 and *Kuengilarva inexpectata* Rasnitsyn, 1990, are currently considered of uncertain familial placement within Tenthredinoidea (Nel et al. 2004).

Conclusion

The larva reported as a tumbling flower beetle by Zippel et al. (2022) does not possess characters of Coleoptera and particularly lacks those traits of Polyphaga, to which Mordellidae belongs. Instead, its habitus and morphology (antennae, legs, number of abdominal segments, modified segment X, subanal appendages, and unusually prolonged *postcornus*) clearly indicate its placement among the early diverging Hymenoptera. Furthermore, the combination of characters present is most indicative of the Pamphiliidae (as noted above). Accordingly, it would be worthwhile to undertake a new revision of the fossil, specifically looking for additional traits that may shed further light on its phylogenetic placement, particularly among pamphiliids. Pamphiliids include a lineage of conifer-feeding species, as well as angiosperm-associated genera. Thus, this fossil from a pivotal period in the floral shift between a gymnosperm- to an angiosperm-dominated world could prove insightful into the transition between hosts in this lineage of sawflies. Unfortunately, no repository for the specimen is mentioned in the text (Zippel et al. 2022), although according to the accession number it originated from and is likely stored in the private collection of Patrick Müller. It is hoped that the fossil will be available to future hymenopterists for a fuller study of this unique inclusion.

Given the misidentification, the hypotheses presented by Zippel et al. (2022) regarding a possible association of the larva with wood or fungi and its contribution to the decomposition of plant matter are unfounded. The larvae of most sawflies, particularly those of the early diverging families, have phytophagous larvae that live externally on their host, feeding on plant foliage or the needles of conifers, and in the case of pamphiliids include species that may roll leaves or build tents from leaves united by silk, and can at times live gregariously. The comparatively long legs of the fossil larva are anatomically unsuitable for tunneling in any kind of wood or herbaceous tissues, and are instead typical of a pamphiliid, which uses these to move about as well as to help bring together plant material to be rolled or spun together into a tent. It is only the more derived lineages of symphytans, such as the stem sawflies (Cephidae) or the woodwasps (Siricidae and Xiphydriidae) that live within stems or wood, while the Orussidae are parasitic on xylophagous insects. These families can be excluded on the basis of many traits, most notably the reduction or absence of true legs owing to the movement of the larvae within plant tissues or wood, or because of their parasitoidism.

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