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Misidentification of fossil beetle larvae on the subordinal level – Scraptiidae (Polyphaga: Tenebrionoidea) instead of Haliplidae (Adephaga)

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Abstract

Larvae embedded in Cretaceous amber were presented in a recent study on Haliplidae (LINHART et al. 2023). However, these fossil immature stages do not belong to this family and not to the suborder Adephaga. Instead they are here attributed to the polyphagan tenebrionoid Scraptiidae (subfamily Scraptiinae) based on the conspicuous unpaired club-shaped and apically rounded terminal abdominal process. It is recommended that investigations on fossil larvae should be undertaken with adequate techniques and expert knowledge of the group(s) in question.

Key words: Coleoptera, Haliplidae, Crawling water beetles, Scraptiidae, Burmese amber.

Introduction

Numerous studies have been published on amber fossils in the last decades, especially on insects embedded in Burmese amber (see e.g., POHL et al. 2021, BEUTEL et al. 2024). It has been shown that the application of advanced techniques (e.g., micro-computed tomography) combined with taxonomic and morphological expertise of authors can lead to very detailed reconstructions of even minute fossils and a reliable systematic placement. Examples are 1st instar larvae of Strepsiptera, ca. 0.2 mm long, described and illustrated in detail by POHL et al. (2018) or tiny first instars of parasitic Ripiphoridae (BATELKA et al. 2018).

In contrast, suboptimal or inadequate methods, in some cases combined with insufficient expert knowledge, can lead to misinterpretations even on the ordinal level. SCHAWAROCH et al. (2005), for instance, identified beetle larvae as strepsipteran "triungulins", an interpretation clearly refuted in POHL et al. (2018). Another example are larvae that were attributed to the beetle family Mordellidae by ZIPPEL et al. (2022b) but in fact belong to a group of symphytan Hymenoptera (BATELKA & ENGEL 2022). BARANOV et al. (2022) assigned four unnamed "new morphotypes" of larvae to Megaloptera, described them briefly and illustrated them with photographs and interpretative reconstructions. PROKIN & BASHKUEV (2023) showed that the "new morphotype 1" from the Miocene Foulden Maar in New Zealand can be recognized as a plecopteran nymph based on the typical head shape, short pronotum, meso- and metathoracic wing pads, and legs, which were misinterpreted as gills by BARANOV et al. (2022: fig. 3B or C, gl). Likewise, the "new morphotype 2" from the Eocene Green River Formation (USA) is also not an immature stage of Megaloptera, but rather a beetle larva of the suborder Adephaga. This is indicated by the proportions of the head and thorax and preserved urogomphi, misinterpreted as a "possible terminal filament" (BARANOV et al. 2022; fig. 4B, fl) (PROKIN & BASHKUEV 2023, A. Prokin pers. comm.). Another example is an unnamed larva from Baltic amber, briefly described by ZIPPEL et al. (2022a) and assigned to the aquatic family Elmidae. It was recently classified as Holometabola incertae sedis, most likely Coleoptera, by KIREJTSHUK et al. (2023).

In the following, we will respond to some problems and misinterpretations in a recent study on Haliplidae with numerous included amber fossils which were addressed as larvae of this adephagan family by the authors (LINHART et al. 2023).

Results

The study of LINHART et al. (2023) claims to be a revision of larvae of the aquatic adephagan family Haliplidae (Fig. 1), also occasionally addressed as "crawling water beetles". All images of extant haliplid larvae presented in this contribution are based on literature sources, as for instance Spangler (1991) and Vondel (1996, 2012, 2016). In fact, some of the sources should be considered as tertiary, as Klausnitzer (1978) does not contain original images of the author, but only pictures taken from earlier studies. Obviously, no specimens of extant larvae were examined by the authors.

RIBERA et al. (2002) is cited as a molecular study confirming Haliplidae as a family of Adephaga. Aside from the outdatedness of this contribution, this placement has never been seriously questioned (e.g., BEIER 1929, CROWSON 1955, 1981). LINHART et al. (2023) note that adults of Haliplidae carry their breathing air supply under the large metacoxal plates. Even though this is not incorrect, it should have been mentioned that the air supply is carried mainly in the subelytral space as in other aquatic beetles (e.g., BEUTEL 1997). The air-storage and breathing mechanism were described in detail in BEIER (1929) and also addressed in a morphological contribution of BELKACEME (1986). Both studies are not cited in LINHART et al. (2023).





Figs. 1–2: Larvae of 1) Haliplidae, 3rd instars, lateral view; above: *Haliplus* sp., below: *Peltodytes caesus* DUFTSCHMID, 1805; 2) Scraptiidae, *Scraptia* sp., dorsal view. All photos: © P. Jałoszyński.

A shortcoming of the first part of LINHART et al. (2023) is that important relevant studies were overlooked or ignored. This includes the excellent morphological treatment of larvae of three haliplid genera of JABOULET (1960), the comprehensive treatment of aquatic adephagan larvae of BERTRAND (1972), an anatomical study on the larval head of *Haliplus lineatocollis* (MARSHAM, 1802) (BEUTEL 1986), and a phylogenetic investigation on the haliplid genera (BEUTEL & RUHNAU 1990). Excellent studies on immature stages and the ecology of Haliplidae were

published by SEEGER (1971a-c). None of them was cited by LINHART et al. (2023). The claim that the "entire record of water crawling [sic!] beetle larvae" was reviewed is certainly not justified.

Fossil coleopteran larvae, i.e., inclusions in Cretaceous Burmese amber, are treated in the second part of LINHART et al. (2023). They are implicitly addressed as larvae of Haliplidae. However, an entire series of features raises doubts about the (tentative) identification of these fossils. The authors point out the similarity with haliplid immature stages, but this morphological affinity is superficial at best and irrelevant in a phylogenetic context. Like haliplid larvae (Fig. 1), the fossils are elongate and slender, but this applies to numerous families in Adephaga and Polyphaga. It remains unclear, why the authors assign the fossils to Adephaga in the first place. The legs are 5-segmented (see LINHART et al. 2023: fig. 14) with a tibiotarsus (and single claw) like in larvae of Myxophaga and Polyphaga (e.g., LAWRENCE & NEWTON 1982, BEUTEL & HAAS 2000). This condition is unknown in immature stages of Adephaga, which consistently have legs with six segments, i.e. coxa, trochanter, femur, tibia and tarsus including claws (usually paired but not in Haliplidae). The larvae of Haliplidae are typically characterized by specific clasping apparatuses of the forelegs (absent for instance in species of the subgenus Liaphlus GUIGNOT, 1928 of Haliplus LATREILLE, 1802, possibly correlated with a switch from filamentous algae to Characeae; SEEGER 1971a), either formed by femoral (Brychius THOMSON, 1860) or by tibial extensions (e.g., JABOULET 1960, VONDEL 2016). This structural specialization is absent in the fossil larvae shown in LINHART et al. (2023). Setiferous tubercles, another characteristic derived feature of haliplid larvae, very distinct on the head but also present on other body regions, are also clearly missing in the fossil larvae. Unique breathing organs of haliplid larvae are long and thin dorsal tracheal gills (Peltodytes RÉGIMBART, 1878) or short tubercles with tracheoles (called microtracheal gills by SEEGER 1971a) (Brychius, Haliplus) (Fig. 1; JABOULET 1960, BEUTEL & RUHNAU 1987). These structures are also missing in the fossil larvae in question, which display a smooth and shiny cuticle without external breathing organs. It is very likely that these fossils were terrestrial. A derived feature of the aquatic larvae of Haliplidae is the lack of long setae inserted on the head and postcephalic body (e.g., JABOULET 1960, SEEGER 1971a). In striking contrast to this, extremely long, laterally projecting setae are present on all postcephalic segments of the fossil larvae shown in LINHART et al. (2023). This strongly suggests that these larvae did not live in aquatic environments.

Larvae of *Peltodytes* display paired slender segmented tubercles belonging to abdominal segment IX, whereas a long postanal prolongation with a forked apical part is present in the other genera (MAKAROV & PROKIN 2015). In contrast, the fossil larvae shown in LINHART et al. (2023) bear a conspicuous unpaired club-shaped and apically rounded terminal abdominal process (Fig. 2) that is unique to the subfamily Scraptiinae of the tenebrionoid Scraptiidae (Fig. 2; e.g., LAWRENCE & ŚLIPIŃSKI 2010). This conspicuous apomorphic feature leaves little doubt that the fossils in question belong to this polyphagan group. An interesting side aspect of the study of LINHART et al. (2023) is that two of the co-authors have previously published on Cretaceous larvae of Scraptiidae (HAUG & HAUG 2019). It is puzzling, why they did not assign the fossil larvae shown in LINHART et al. (2023) to this very characteristic family with a unique and conspicuous larval morphology.

Larvae of Haliplidae live in a large variety of freshwater environments, including ponds, lakes, brackish water, and also rivers or brooks (SEEGER 1971a–c, VONDEL 2016). They crawl among aquatic plants, either filamentous algae or Characeae (SEEGER 1971a–c). The possibility that the aquatic immature stages may be entrapped by resins and thus become embedded in amber appears unlikely but cannot be ruled out completely. This can happen when a puddle or trench has dried out under a relevant tree. However, in this case one would expect that there would be also inclusions of algae or other aquatic plants inhabited by the larvae and also representatives of

other groups of arthropods from the same community, notably other aquatic insects or crust-aceans. In the case of the fossil larvae treated in LINHART et al. (2023), it appears much more likely that they were more or less closely associated with wood like extant immature stages of Scraptiidae (LAWRENCE & ŚLIPIŃSKI 2010) and had thus a much better chance to become embedded in resin.

Discussion

LINHART et al. (2023) emphasize that the fossils presented in their study expand the fossil record of Adephaga. This is certainly not the case, as the larvae obviously belong to a polyphagan group. Moreover, as the adephagan fossil record dates back to the late Permian (e.g., BEUTEL et al. 2014), Cretaceous findings would be of very minor consequence. The redrawn images of extant haliplid larvae and the comments may be useful for some colleagues interested in immature stages of this family. However, the fossil larvae treated in LINHART et al. (2023) obviously belong to a completely different group, namely the tenebrionoid family Scraptiidae (Scraptiinae), with a conspicuous unpaired and apically rounded terminal abdominal appendage as a unique shared apomorphy (LAWRENCE & ŚLIPIŃSKI 2010). A re-evaluation of the fossil larvae by an expert of the group could yield interesting results. Our main conclusion is that the investigation of larvae embedded in amber (and other fossils) should be carried out with optimal techniques and with expert knowledge of the group(s) in question.

The rapid publication of studies with insufficiently investigated and documented fossils does apparently not contribute to a clarification of the evolution of beetles or other groups of insects. Erroneous interpretations potentially create confusion and require time of experts to correct morphological and/or phylogenetic misinterpretations. In addition to competent peer review as conducted in the case of the study discussed here (pers. comm. to R.G. Beutel), appropriate editorial decisions are necessary to ensure a high scientific level in publications on fossils of beetles and other organisms.

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