

LETTER TO THE EDITOR

A hatching aphidlion-like lacewing larva in 100 million years old Kachin amber

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Dear Editor,

Hatching is a crucial moment in the life of an animal. The animal stops being an embryo protected by the egg and becomes a post-embryonic immature (see Haug, 2020 for difficulties in naming these stages). This must have been the case in the past as well, but the fossil record is rather sparse in the preservation of this very moment. The fossil preservation of such a case needs to facilitate not only preservation of the animal, but also of the egg. As these are often of rather different material, making the preservation of both together in many cases unlikely. Yet, there are preservation types that seem to favor such incidents. Amber has become famous for preserving cases of “frozen behaviour”, preserving a specific moment in the life of an animal in an almost life-like manner (Ariillo, 2007), including: copulations, parasite-host interactions, aggregations, group defense, brood care, egg-laying (although likely stress-induced), but also animals hatching from their eggs (examples in e.g., Weitschat & Wichard, 2002; Engel & Grimaldi, 2008; Weitschat, 2009; Boucot & Poinar, 2010; Gröhn, 2015; Hörnig *et al.*, 2016, 2019, 2020, 2022; Fischer & Hörnig, 2019; Pérez-de la Fuente *et al.*, 2019). Preserved eggs are often difficult to identify as such in amber due to the low number of characters and often being rather soft. Also the identification of the “producer” of the egg can be challenging.

This is different if organisms were captured right in the moment of hatching or during the process of egg laying, providing a link from a specific egg morphology to the corresponding animal. Known examples include assassin

bugs hatching from their highly specialised eggs with distinct “lids”, offering more characters to identify such eggs even as fossils (Hörnig *et al.*, 2019), but also lacewings. A small lacewing larva in late Cretaceous Canadian amber (redrawn in Fig. 1B) is preserved in direct proximity to a stalked egg, well known, for example, in modern green lacewings (Chrysopidae; New, 1989 fig. 125-5 p. 87; redrawn in Fig. 1A), but also in some other groups of lacewings (Lucchese, 1956 fig. LV p. 179; redrawn in Fig. 1C). The specimen in amber was initially interpreted as a representative of Chrysopidae (Engel & Grimaldi, 2008 fig. 14 p. 58; redrawn in Fig. 1B), but later reinterpreted as a larva of beaded lacewings (Berothidae). In beaded lacewings, a clutch of eggs is attached to a single stalk (Brushwein, 1987 fig. 1 p. 674) or at least fewer stalks than there are eggs in the clutch (Toschi, 1964 fig. 2 p. 23), but there are also eggs with no stalk and a well developed surface structuring (Möller *et al.*, 2006 fig. 1 p. 3; Monserrat, 2006 fig. 10a p. 194). Still, there are also species that produce individual eggs with a single stalk without strong surface sculpture, very similar to what is seen in the fossil (Tillyard, 1916 text-fig. 10 p. 320; Toschi, 1964 fig. 1 p. 22), supporting the interpretation as a beaded lacewing. More spectacular is a group of aphidlion-like larvae preserved in Cretaceous Lebanon amber (Pérez-de la Fuente *et al.*, 2019; redrawn in Fig. 1D). No less than 13 larvae (some incomplete), with remains of eleven eggs have been reported, including egg bursters in some of the eggs, indicating that the event of hatching must have occurred just before the animals became embedded in the resin. As two examples of preserved hatching involve lacewing larvae, and one example includes a dozen specimens, it is partly surprising that we have so far not seen a similar case from Kachin amber, Myanmar. This type of amber has provided by far the

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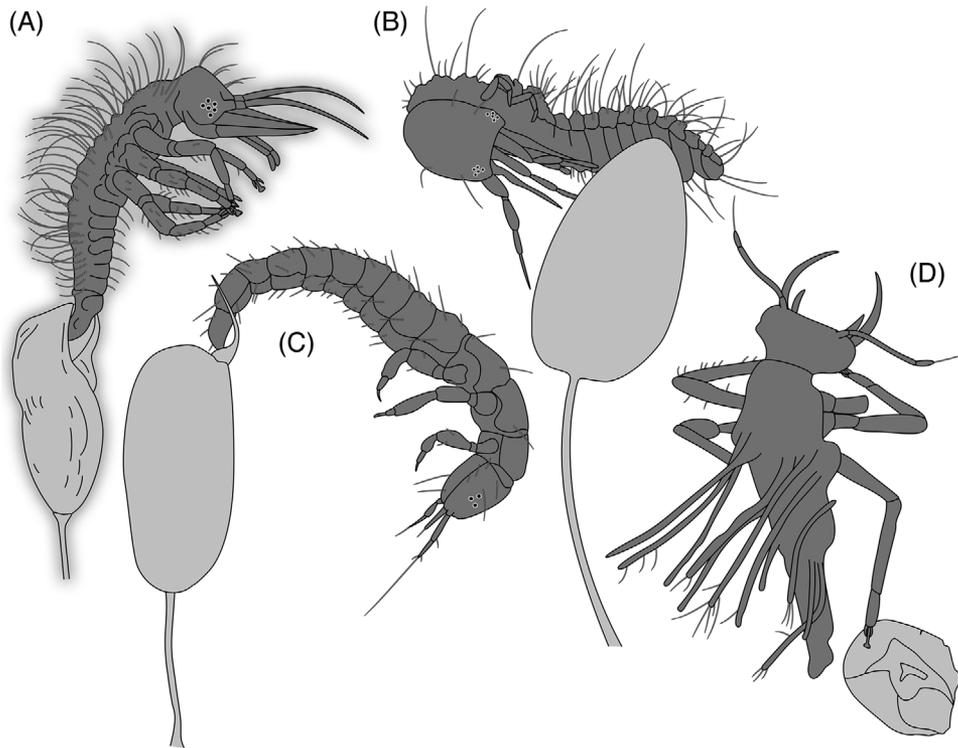


Fig. 1 Examples of hatching lacewing larvae. (A). *Chrysopa septempunctata*, extant aphidlion (simplified from New, 1989 fig. 125-5 p. 87). (B). Fossil from Canadian amber, possible beaded lacewing larva (simplified from Engel & Grimaldi, 2008 fig. 14 p. 58). (C). *Mantispa perla*, extant mantis lacewing (simplified from Lucchese, 1956 fig. LV p. 179). (D). *Tragichrysa ovoruptora*, fossil aphidlion-like larva (simplified and flipped from Pérez-de la Fuente *et al.*, 2019 fig. 1 p. 550).

majority of lacewing larvae, more than 200 specimens (Liu *et al.*, 2016, 2018; Wang *et al.*, 2016; Badano *et al.*, 2018, 2021; Haug *et al.*, 2019a–c, 2020a–c, 2021a–d, 2022a–d; Hörnig *et al.*, 2020, 2022; Pérez-de la Fuente *et al.*, 2020; Zippel *et al.*, 2021; Haug & Haug, 2022; Liu *et al.*, 2022). However, none of these included a case of hatching.

We here report a new fossil aphidlion-like larva from Myanmar amber (Fig. 2A–E). It is preserved in close proximity to an empty egg case (Fig. 2A–C), indicating that it represents a newly hatched larva. The specimen is part of the Palaeo-Evo-Devo Research Group Collection of Arthropods at the Ludwig-Maximilians-Universität München, under repository number PED 1754. It was documented on a Keyence VHX-6000 digital microscope (for details, see Haug *et al.*, 2019b). For comparison, eggs of modern green lacewings were collected on the campus of the University of Yangon, Yangon, Myanmar (Fig. 3A, B). Eggs were observed until the larvae hatched and were photographed/filmed with a Xiaomi Redmi Note 8 and under a stereo microscope (Olympus SZ 51) with an Apple iPhone 8 (Fig. 3C–L; in Supplementary Information

Video S1). For detailed descriptions, see Supplementary Information.

The mouth parts of the new specimen form prominent stylets without any teeth (Fig. 2D), and the trunk segments bear large protrusions (Fig. 2A–C; cf. MacLeod, 1964; Zimmermann *et al.*, 2019). Very similar-appearing larvae have already been reported from many Cretaceous ambers from Spain (Pérez-de la Fuente *et al.*, 2012, 2016), Lebanon (Pérez-de la Fuente *et al.*, 2018, 2019), and Myanmar (Wang *et al.*, 2016; Haug *et al.*, 2022c). All these larvae have been interpreted as relatives of modern green lacewings (Chrysopidae), which are generally termed aphidlions. The fossils therefore represent aphidlion-like larvae; also the new fossil is apparently such an aphidlion-like lacewing larva.

Wang *et al.* (2016) and Haug *et al.* (2022c) differentiated three morphotypes of aphidlion-like larvae in Myanmar amber with prominent protrusions, but the details partly differ. Based on the relative lengths of the protrusions, morphotype 1 seems to be similar in both cases. Liu *et al.* (2022) erected a new species, *Acanthochrysa langae*, based on a single aphidlion-like larvae. While

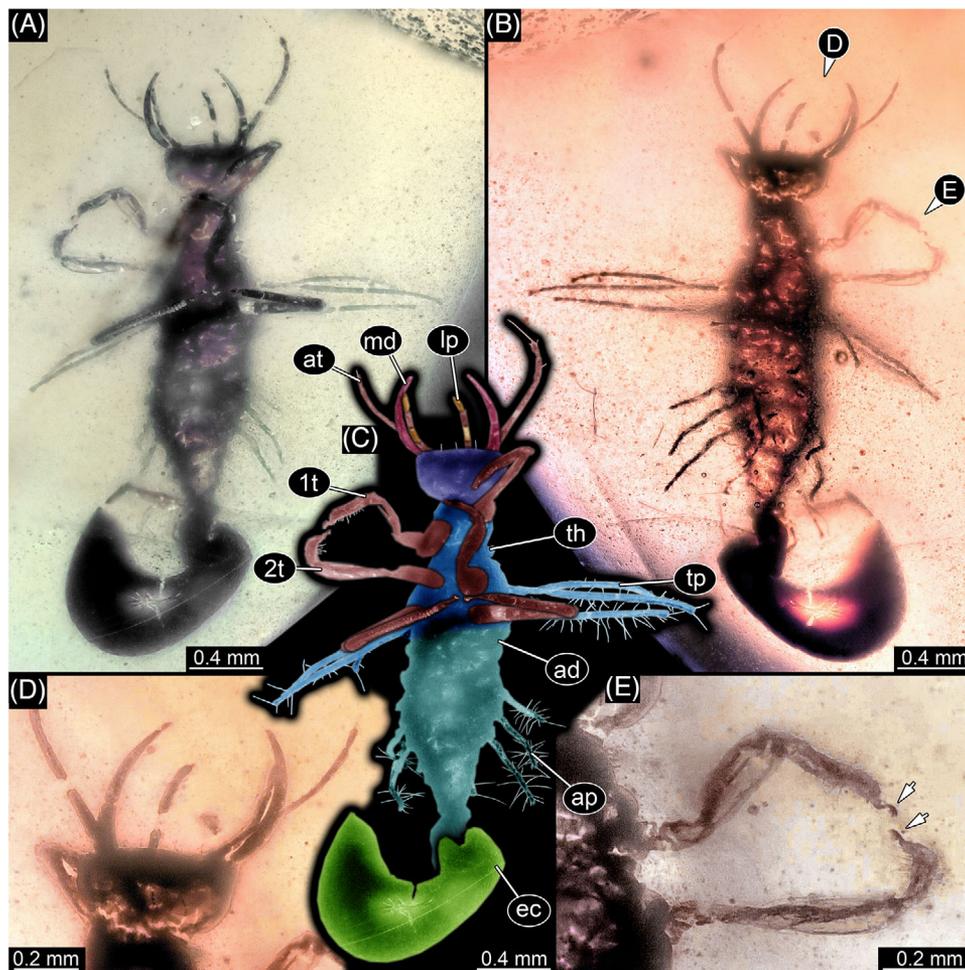


Fig. 2 New specimen, PED 1754, aphidlion-like larva with remains of egg case. (A). Ventral side, (B). Dorsal side. (C). Combined from A and B, color-marked. (D). Close-up of head region. (E). Close-up of trunk appendages (legs) with empodia (arrows). Abbreviations: 1t = trunk appendage (leg) 1; 2t = trunk appendage (leg) 2; ad = abdomen; ap = abdomen process; at = antenna; ec = remains of egg case; lp = labial palp; md = mandible; th = thorax; tp = thorax process.

generally falling into morphotype 1, Liu *et al.* (2022) pointed out differences that could be used to clearly diagnose the specimen from others: the more elongated head capsule and the longer stylets. Indeed this aspect seems to vary quite drastically among the aphidlion-like larvae in Myanmar (Haug *et al.*, 2022c), indicating that there are several species represented within (at least some of) the morphotypes. The new specimen is best interpreted as morphotype 1, but differs from *Acanthochrysa langae*.

Although not very well preserved, at the trunk end of the aphidlion-like larva an egg case is visible (Fig. 2A–C). It strongly resembles the egg cases reported by Pérez-de la Fuente *et al.* (2019). The egg case lacks signs of a stalk, similar to the egg cases from Pérez-de la Fuente *et al.* (2019). An egg burster is not preserved, but these

were only preserved in very few egg cases reported in Pérez-de la Fuente *et al.* (2019); hence the absence in the new specimen does not appear unusual. Also the morphology of the larva is very similar to that of the larvae reported by Pérez-de la Fuente *et al.* (2019). As these were interpreted as having newly hatched from their eggs, this is also plausible for the new fossil.

Most extant representatives of Chrysopidae are known to produce clusters of stalked eggs (Fig. 3B) from less than ten eggs, but usually about 200, reaching up to 600 (Hinton, 1981). It seems that the stalk of the eggs leads to a protection against predation and even cannibalism of conspecific larvae (Růžička, 1997). The eggs are usually deposited close to putative prey of the larvae, especially close to aphid colonies, resulting in a better food

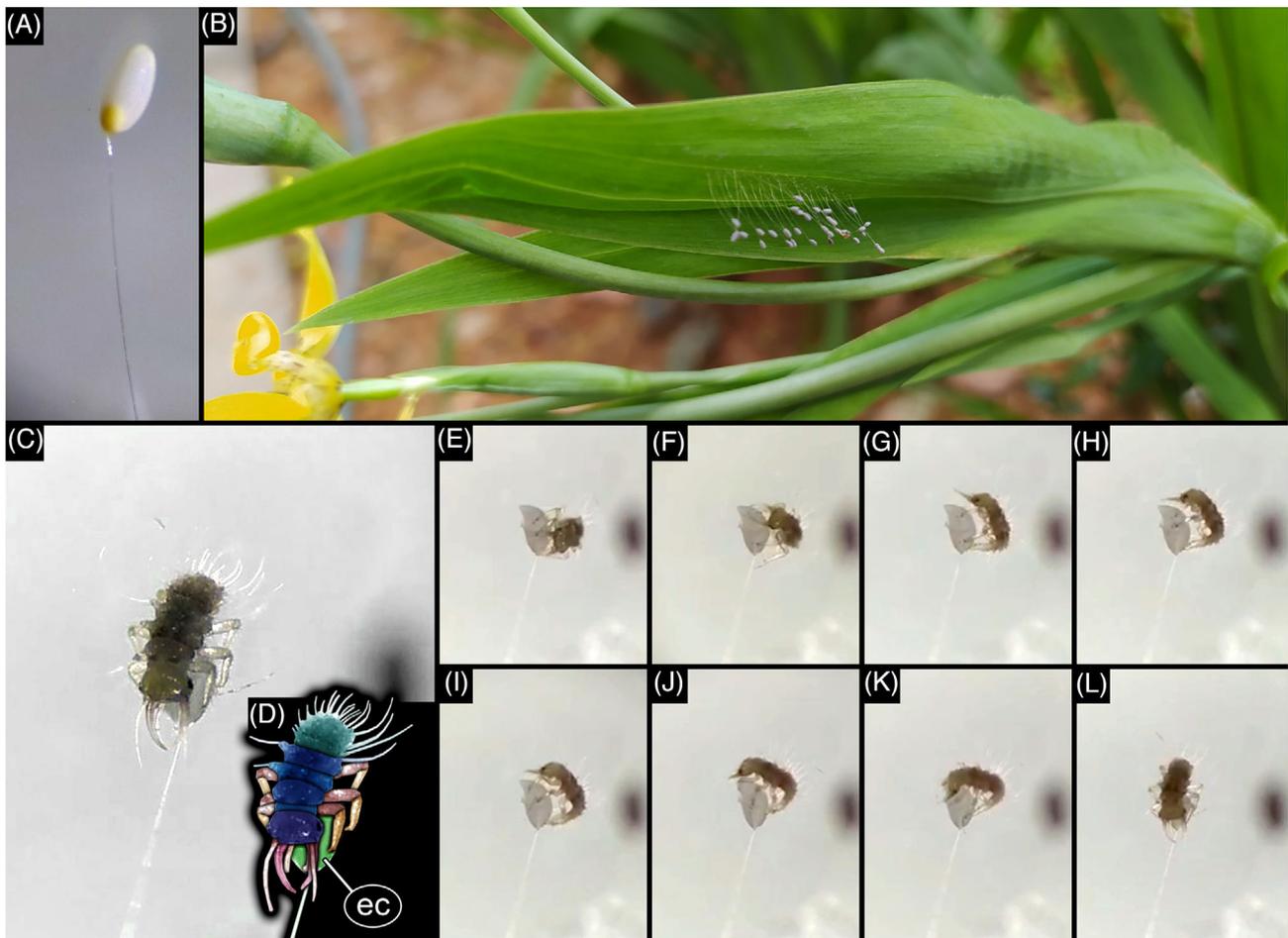


Fig. 3 Modern aphidlion larva from Myanmar. (A). Stalked egg. (B). Stalked eggs on host plant. (C). Close-up of newly hatched larva. (D). Color-marked version of C, same color-markings as in Fig. 2. (E–L). Sequence of movements after hatching. Abbreviation: ec = egg case.

availability for the freshly hatched aphid lions. The position close to aphids leads to a risk for the eggs, as aphids can be protected by ants. Hayashi and Nomura (2014) could show that the survival rate of eggs with intact stalks is distinctly higher compared to those with removed stalks in presence of ants, but not necessarily in presence of other predators (in this study *Chrysoperla nipponensis*).

However, Gepp (1990) reported at least five different deposition forms of eggs within Chrysopidae. These include also unstaked eggs, either laid in loose groups or singly. The new specimen PED 1754 does not show any remains of an egg stalk. This lack could be a preservational artefact, or it means that a stalk was simply not present in this group of aphidlion-like representatives, as also known for some modern species of Chrysopidae. The strategy of stalked eggs was already present

in lacewings in the Cretaceous as shown by the hatching beaded lacewing (Engel & Grimaldi, 2008), but not necessarily in Chrysopidae. Pérez-de la Fuente *et al.* (2019) assumed that, even if not preserved in the specimens, egg stalks might be present on eggs of *Tragichrysa ovoruptora* (Pérez-de la Fuente *et al.*, 2019, fig. 5). While stalked eggs are the “typical” deposition type in modern representatives of Chrysopidae (Fig. 3), it does not seem to be part of the ground pattern. Therefore, a stalk might not necessarily have been present in Cretaceous representatives with aphidlion-like larvae, as a stalked egg may possibly have evolved later within the group.

Hatching events for lacewing larvae have so far been reported from Canadian and Lebanon amber (Engel & Grimaldi, 2008; Pérez-de la Fuente *et al.*, 2019). In contrast to many other insect groups, fossil findings of lacewings which allow to reconstruct aspects of

behavior are comparatively common in the literature (camouflage, Engel & Grimaldi, 2007; Weitschat, 2009; Pérez-de la Fuente *et al.*, 2012, 2016, 2018; Wang *et al.*, 2016; digging behavior, Badano *et al.*, 2018; group defense, Hörnig *et al.*, 2022, different aspects of trophic interactions, Ohl, 2011; Haug *et al.*, 2018; Hörnig *et al.*, 2020; summarized in Haug *et al.*, 2022). Most of these aspects of fossilized behavior in lacewing larvae have been reported from Myanmar amber (Haug *et al.*, 2022), hence it was expectable that also a case of hatching should have been preserved. The new fossil finally fills this gap.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Supplementary information

Video S1 Extant aphidlion during hatching process.