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The first record of disruptive colouration in holometabolan larvae from about 100 million-year-old Kachin amber is a lacewing larva with dark stripes on the legs

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Animals have evolved various strategies to avoid being eaten (*e.g.*, Howland, 1974; Peterson *et al.*, 2021). Such strategies are especially important in groups of animals that represent a large biomass and are therefore attractive aims for predators (Lindstedt *et al.*, 2019). Holometabola, the group including beetles, bees, butterflies, and all their closer relatives, represents a vast biomass in continental ecosystems; more precisely their larval forms represent this vast biomass (Husler & Husler, 1940). These larvae are important food sources for many other groups of animals and are hence central points within the food web.

This situation is not only like that in the modern fauna, but has been similar already in the past. The fossil record has provided numerous examples of holometabolan larvae exhibiting morphologies indicating anti-predator strategies as known from modern-day larvae, for example, types of camouflage, mimicry, or defensive spines (Pérez-de la Fuente *et al.*, 2012, 2016; Wang *et al.*, 2016; Haug & Haug, 2021; Haug *et al.*, 2022). Amber especially provides the preservation of such details, and among the different amber types, the about 100 million-year-old Kachin amber from Myanmar has provided numerous examples of holometabolan larvae with morphologies indicating anti-predator strategies (Haug *et al.*, 2024). Despite a rich record, some strategies known from extant holometabolan larvae have so far not yet been recorded from Kachin amber. One of these is the presence of camouflaging stripes, a form of disruptive colouration (Merilaita & Lind, 2005; Schaefer & Stobbe, 2006). Although amber provides many details of a fossil, bright colour preservation can often be challenging, but is well known for example in wings (Chen *et al.*, 2019). As wings are absent in larvae, aspects of colour in holometabolan larvae in amber have rarely been considered. Aposematic stripes on the body have also been reported (Xu *et al.*, 2022), but not yet on larval specimens.

Here we report a lacewing larva from Kachin amber that shows dark stripes on the legs. Such stripes are also known in modern relatives and seem to provide camouflage in certain cases.

Material and methods. A single specimen is the focus of this study. It is preserved in Kachin amber from Myanmar, which is about 100 million years old (Upper Cretaceous). The specimen was legally purchased on the trading platform ebay.com from the trader burmite-researcher. The specimen is deposited in the Palaeo-Evo-Devo Research Group Collection of Arthropods, Ludwig-Maximilians-Universität München (LMU Munich), Germany under repository number PED 3903. The specimen was documented on a Keyence VHX-6000 digital microscope. Images were recorded as stacks and panoramas. In addition, the HDR function was used for some images.

Results. Description of specimen PED 3903. Small larva (Fig. 1A). Body organised into head and trunk. Sclerite posterior to head (cervix) long, narrow elongate.

Head segments (presumably) forming capsulate head. In dorsal view inverse horseshoe-shaped outline. Anterior rim slightly concave. Entire head capsule bearing numerous short setae. Setae simple, with distinct sockets. Ocular segment indicated by larval eyes (stemmata), at least three stemmata on each side of the head, positioned on antero-lateral projections. Post-ocular segment 1 indicated by its pair of appendages, antennae. Antennae arising antero-dorso-laterally from head capsule. Antennae thin, short, filiform, about 50% of head capsule length. No externally visible structures of post-ocular segment 2. Post-ocular segments 3 and 4 indicated by their pairs of appendages, mandibles and maxillae. Each mandible and maxilla conjoined to form compound mouthparts, stylets. Stylets incomplete, very distal parts missing. Preserved part longer than head capsule. Stylets gently curved with at least three teeth along the inner (median) margin. Most proximal tooth short, shorter than width of stylet, distal two teeth longer, longer than width of stylet. Stylets with numerous short setae. Setae simple, with elevated sockets. Post-ocular segment 5 indicated by its pair of appendages forming the labium. Labium largely continuous

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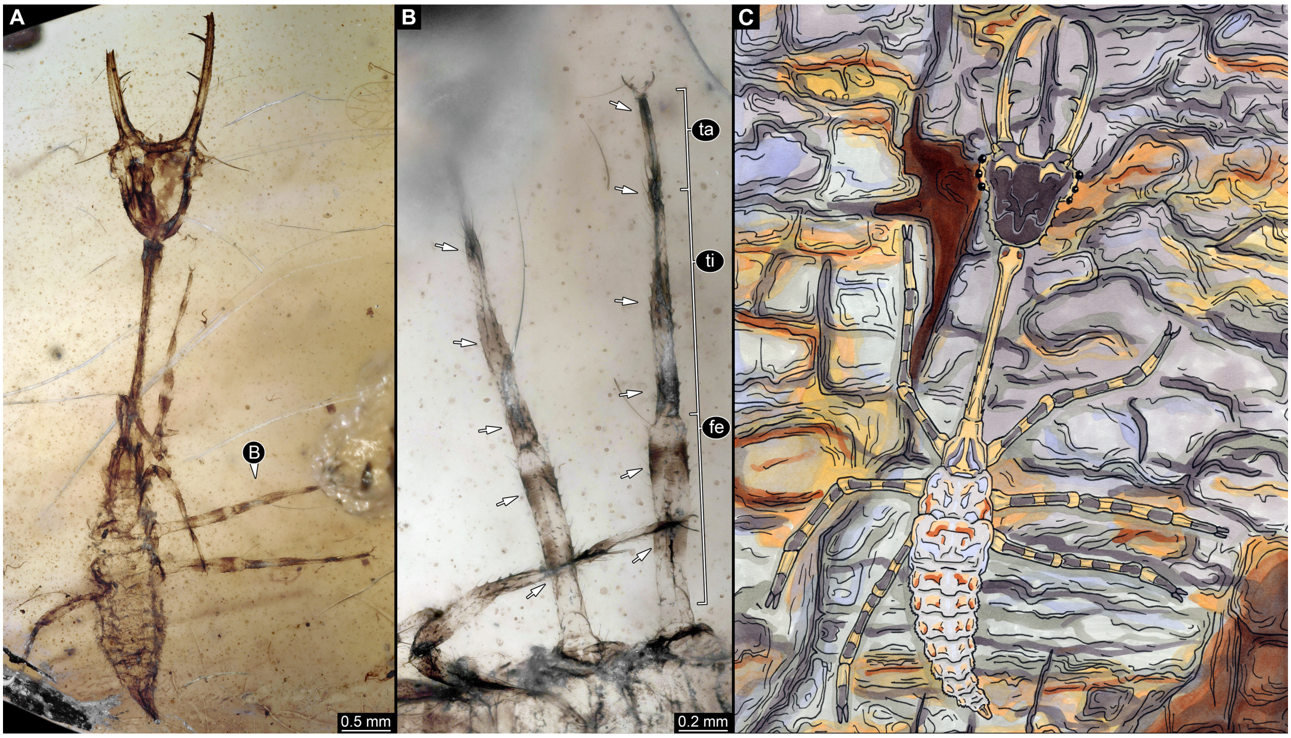

FIGURE 1. Long-necked antlion with disruptive colouration, PED 3903. **A**, Overview of the specimen. **B**, Detail of the legs, highlighting six dark stripes on each leg (marked by arrows). Abbreviations: fe, femur; ta, tarsus; ti, tibia. **C**, Palaeo-artistic interpretation of how the larva may have camouflaged on tree bark. Drawing and colouration by hand by one of the authors (GTH). Colour of body based on extant counterparts.

with head capsule, only distal parts recognisable, palps. Palps short, shorter than antennae, exact number of elements unclear, distal element elongate lanceolate.

Exact number of trunk segments not well discernible (presumed 14). First sclerite of trunk (cervix; anterior part of prothorax?) very long, forming distinct neck region. Cervix longer than head capsule, about 2×. Anterior region calyx-shaped, then tapering, widening again posteriorly. Remaining trunk spindle-shaped, about as long as head capsule plus cervix, indistinct subdivision of trunk indicated by folds. Three segments (prothorax, mesothorax, metathorax) more distinct due to the presence of pairs of locomotory appendages, legs. Legs subsimilar, about as long as cervix, also about as wide. Leg with five major elements: coxa, trochanter, femur, tibia, tarsus. Coxa short, stout. Trochanter also short, but narrower than coxa. Femur longer than trochanter, about 5×, with two distinct dark stripes banded by three areas of brighter colour (Fig. 1B). Tibia longer, about as long as trochanter plus femur, narrower than femur, tapering distally. With three dark stripes, one proximally, one medially, one distally, banded by two areas of brighter colour (Fig. 1B). Tarsus shorter than tibia, about 50%, as wide as tibia distally. Proximal region bright, distal region with a dark stripe (Fig. 1B). Distally with a pair of curved claws. All leg elements with numerous setae. Setae simple, with distinctly elevated sockets. Most setae short, shorter than diameter of leg. Medio-distally on tibia with a pair of longer, more prominent setae. Entire trunk (including cervix) with numerous small setae. Setae simple with distinct sockets. Setae on trunk end longer.

Discussion. The overall arrangement of the mouthparts, although not fully preserved, directly identifies the animal as a larva of a lacewing: conjoined mandible and maxilla forming a stylet, no palp of maxilla, proximal part of labium continuous with head capsule (*e.g.*, Aspöck & Aspöck, 2007). Among lacewing larvae, teeth on the mandible occur only in antlion-like lacewing larvae (Myrmeleontiformia; Badano *et al.*, 2018). The long neck of the new fossil is already a strong indicator that the larva is a representative of Crocinae (thread-winged lacewings), hence a long-necked antlion. Characters not known in modern forms likely represent plesiomorphies (see discussion in Haug *et al.*, 2021; *contra* Bechly, 2023).

Long-necked antlions have regularly been depicted in the literature. Yet, so far not much attention seems to have been paid to stripes on the legs, at least most drawings do not depict such stripes (Schaum, 1857: fig. 1, pl. I; Maxwell-Lefroy, 1909: top fig., p. 1006; Imms, 1911: figs 1, 2, pl. 32; Imms, 1930: fig. 395, p. 403; Riek, 1970: fig. 29.12A, p. 491; Mansell, 1976: fig. 1, p. 155; Mansell, 1980: fig. 4, p. 349; Mansell, 1981a: figs 2, 3, p. 94; Mansell, 1981b: fig. 3, p. 251; Mansell, 1983a: figs 53, 54, p. 622; Monserrat, 1983a: fig. 2, p. 42), or the depictions remain unclear concerning whether darker areas are stripes or shades (Ghosh, 1910: figs 1, 2; Pierre, 1952: figs 7, 24). Stripes on legs have rarely been indicated in drawings, but there are exceptions (Roux, 1833: fig. 3, pl. 7; Mansell, 1977: fig. 9, p. 198; Mansell, 1980: fig. 5, p. 349; Mansell, 1983b: figs 14, 15, 25, pp. 119, 128; Monserrat, 1983a: fig. 6, p. 44; Monserrat, 1983b: figs 4, 5, pp. 111, 113; Hölzel, 1999: fig. 4, p. 132). The absence of stripes may be coupled to the fact that stripes seem absent in material which was stored in ethanol for a longer time (Herrera-Flórez *et al*., 2020). Stripes are well apparent in photographs of living or freshly sacrificed individuals (Miller & Stange, 1989: fig. 1, p. 69; Suludere *et al*., 2006: fig. 7, p. 525; Aspöck & Aspöck, 2007: fig. 38, p. 465; Monserrat, 2008: fig. 9i, p. 19; Aspöck & Aspöck, 2014: fig. left middle, p. 7; Tusun & Satar, 2016: fig. 2, p. 146; Badano *et al*., 2017: fig. 1C, p. 96; Badano *et al*., 2018: fig. 1d, p. 3; Haug *et al*., 2021: fig. 5A–D, p. 443). Especially in cases in which the larvae sit on grainy sandy background, the function of the stripes becomes well apparent: providing the long legs effective camouflage (*e.g*., Haug *et al*., 2021: fig. 5C, p. 443).

Quite a few specimens interpreted as long-necked antlions have been reported from Kachin amber (reviewed in Haug *et al*., 2021). Yet, none of these larvae show any signs of stripes on the legs. In the here reported specimen, the stripes are well apparent, not only on one leg, but on several ones with a re-occurring pattern. It is therefore unlikely that the stripes represent a preservation artefact. We assume that in the other specimens this colour pattern might have been present, but was not preserved.

The life style of the fossil larvae was interpreted as quite different from their modern counterparts (Haug *et al*., 2021). While modern larvae live on (and partly buried in) sandy ground, the fossils very likely lived associated to trees. Yet, such stripes do not only provide camouflage on sandy ground, but also on bark (Fig. 1C). It remains unclear whether the stripes evolved on bark and later also provided camouflage on sand, or the other way round.

The case reported here adds another anti-predator strategy to the known ones for holometabolan larvae in Kachin amber. The find underpins how complex and diverse the strategies and interactions were already 100 million years ago.

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