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Disruptive colouration is much more common in immature animals from the Myanmar amber forest than anticipated, indicating regular convergent evolution

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Abstract

Animals have evolved a wide range of traits to avoid predation, and some of these defensive strategies can be traced in the fossil record. Recently, the first case of disruptive colouration was documented in a lacewing larva from Cretaceous Kachin amber, Myanmar. Here we report additional immature specimens from the same deposit that also exhibit disruptive colouration, expressed as alternating dark and bright stripes on the legs. The examples span a broad array of lineages, including another lacewing larva (Neuroptera: Crocinae), as well as planthoppers (Fulgoromorpha), a true bug (Heteroptera), a "predatory cricket" (Ensifera), cockroach-like forms (Dictyoptera), and several praying mantises (Mantodea). The repeated appearance of leg-based disruptive colouration in such distantly related groups suggests that this trait evolved multiple times already 100 million years ago, reflecting diverse predator-prey interactions and a complex Cretaceous food web.

Keywords: Cretaceous, Burmese amber, Fulgoromorpha, Mantodea, detection avoidance

Introduction

Animals often exhibit specific colours, arranged in characteristic patterns, and among these, stripes are perhaps the most striking—familiar from both zebras and yellow-jacket wasps. These two examples immediately illustrate the two major functions stripes can serve (*e.g.*, Barnett *et al.*, 2018; Hinkelman, 2023):

1) They represent a warning colour (aposematism). In this way, they signal to possible predators that the animal is dangerous or at least not healthy to digest, as in the yellow-jacket wasp. Such a type of stripe pattern mostly involves bright colours, often yellow and red tones (Barnett *et al.*, 2018: fig. 1a right, p. 2).

2) The stripes represent disruptive colouration. In this case, they prohibit that a possible predator, parasite, or prey is able to detect the animal, comparable to other types of camouflage. The colours are often less bright in such a case (no red or yellow). This function seems to be the case for the zebra (*e.g.*, Caro *et al.*, 2019).

The functional role of stripes can, however, be more complex. The same pattern may act as aposematic at close range but serve a disruptive function at greater distances (Barnett *et al.*, 2018). Even so, striped patterns are widespread among living animals, and it is reasonable to assume that similar patterns occurred in the past. Unfortunately, colour preservation in fossils is relatively rare. Nonetheless, several examples exist, and with advanced analytical methods it is even possible to reconstruct aspects of colour patterning in fossil dinosaurs (*e.g.*, Vinther, 2015). More commonly, colours and patterns are preserved in certain exceptional fossil deposits. Amber, in particular, is well known for preserving fossils, especially of Pterygota, the group of "flying insects" (in quotation marks as many of them do not fly, and even the flying ones do that only for a short period of their lifetime) in near-life-like detail. Although, specialized techniques are sometimes required to reveal fine details (Wang *et al.*, 2022), colour and colour patterns are well documented in amber inclusions (*e.g.*, Hinkelman, 2023).

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Aposematic colouration has indeed been reported from amber fossils (Sendi & Azar, 2017; Xu *et al*., 2022; Hinkelman, 2023; Fabrikant & Novoselska, 2024), as have various forms of camouflage (Jiang *et al*., 2019), including disruptive colouration (Hinkelman, 2023). Recently, a lacewing larva with distinct leg stripes was described from ~100-million-year-old Kachin amber, representing a clear case of disruptive colouration (Haug *et al*., 2024). Here we report additional fossils from other evolutionary lineages—Fulgoromorpha (planthoppers), Heteroptera (true bugs), and Dictyoptera (cockroach-like insects), including Mantodea (praying mantises)—that also exhibit similar striped leg patterns. We discuss the occurrences of these patterns across such distantly related groups.

Material and methods

Material

Twelve new specimens are reported here, all from 100 million years old Cretaceous Kachin amber, Hukawng valley, Myanmar. The specimens were legally purchased on the trading platform ebay.com from the traders burmite-miner and burmitefossil. All are deposited in the Palaeo-Evo-Devo Research Group Collection of Arthropods, Ludwig-Maximilians-Universität München (LMU Munich), Germany under repository numbers PED 0261, 1075, 2590, 2666, 4197, 4207, 4266, 4269, 4279, 4302, 4304, and 4305. The amber surfaces were ground with abrasive paper (grain size 1200–5000) and silver polish (Poliboy) to improve optical clarity.

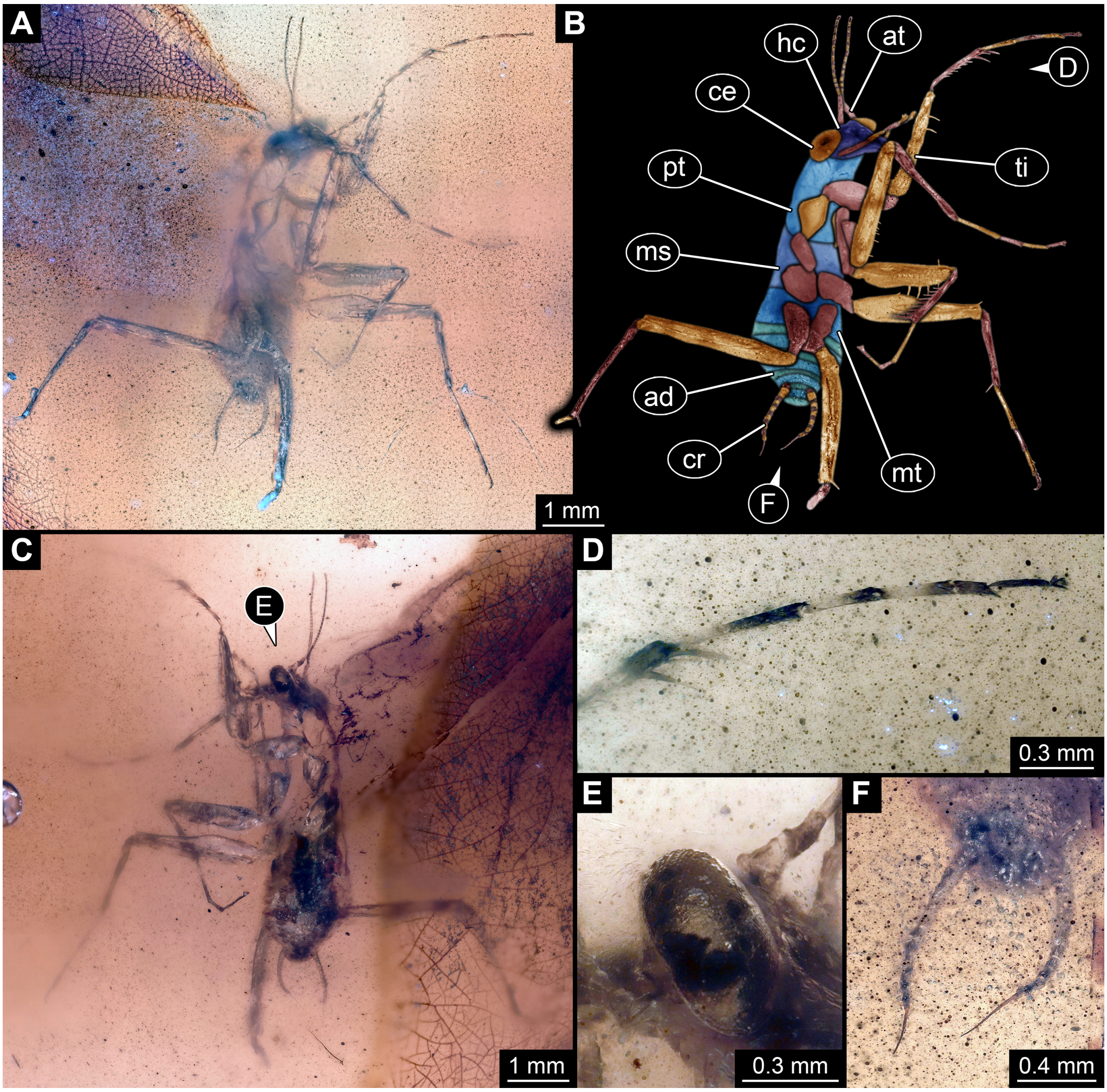

FIGURE 1. New praying mantis with stripes on appendages, PED 4207. **A**, **B**, Ventral view. **A**, Overview. **B**, Colour-marked version of **A**. **C**, Dorsal view. **D**, Detail of tarsus. **E**, Detail of compound eye. **F**, Detail of cerci. Abbreviations: ad = abdomen; at = antenna; ce = compound eye; cr = cercus; hc = head capsule; ms = mesothorax; mt = metathorax; pt = prothorax; ti = tibia.

FIGURE 2. New dictyopterans with stripes on appendages. **A**–**C**, Praying mantises. **A**, PED 2666. **B**, PED 4266. **C**, PED 2590. **D**–**F**, Non-mantodean, PED 4302. **D**, Overview in ventral view. **E**, Detail of leg. **F**, Detail of cercus.

Documentation methods

All specimens were documented on a Keyence VHX-6000 digital microscope. A drop of glycerine was placed between the amber and a cover slip to minimise optical distortion caused by the curved surface. We used the built-in optical enhancement tools for overcoming limitations in depth of field and field of view. Yet, we did not use the HDR function. While this function provides much more detail concerning spines, setae, and surface ornament, it partly obscures the colour pattern. As we were here focussing on colour patterns, we did not use this common enhancement tool.

Results

As this study focuses on the colour patterns of the specimens, the descriptions provide mostly these aspects. Other morphological aspects are summarised more briefly.

Mantodean specimen PED 4207

Small mantodean immature. The main body is not well preserved, but the eyes (Fig. 1E) and many appendages are well apparent, especially concerning the colour pattern (Fig. 1A–C).

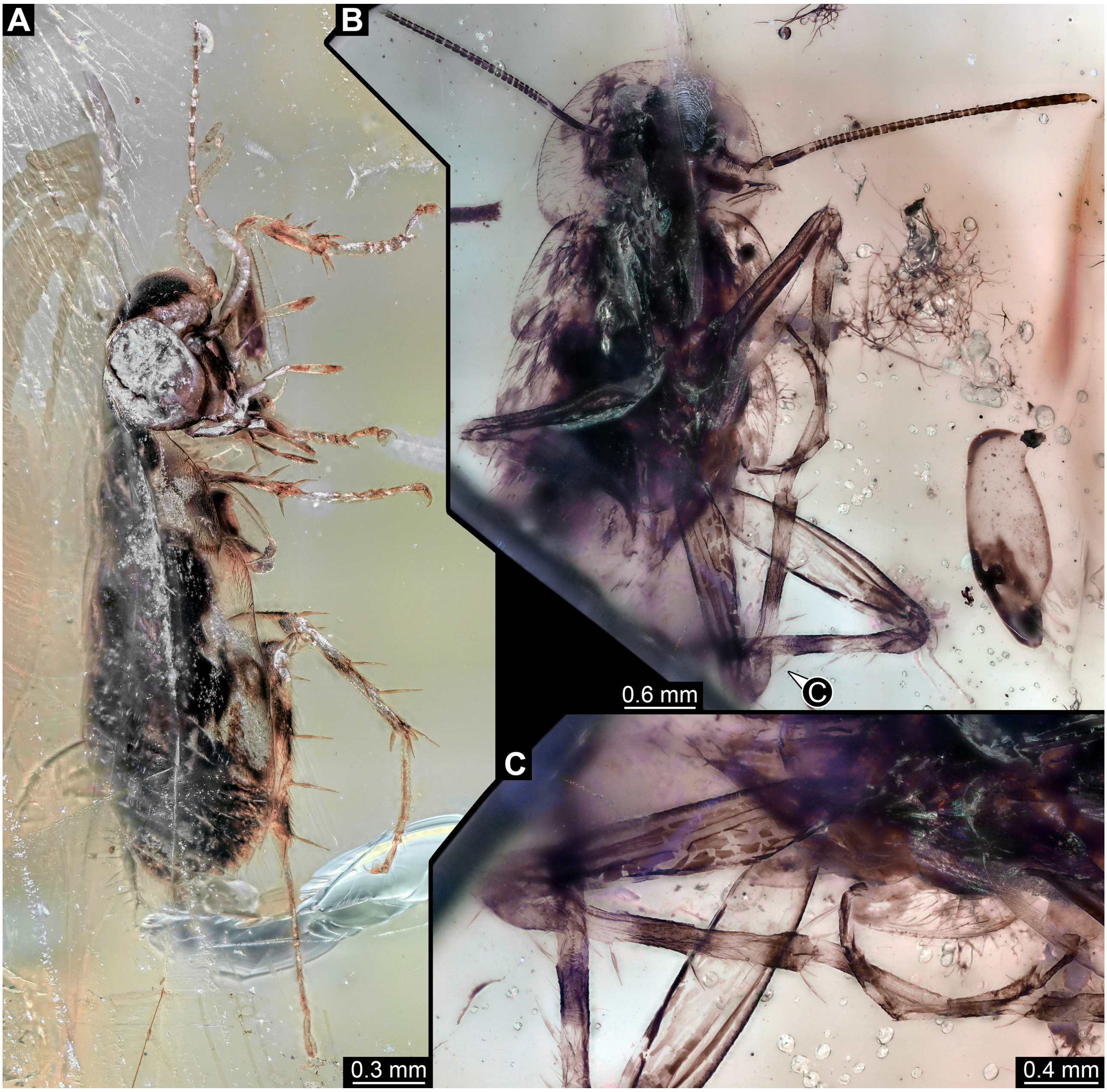

FIGURE 3. New non-mantodean dictyopterans with stripes on legs. **A**, PED 0261. **B**, **C**, PED 1075. **B**, Overview in ventral view. **C**, Detail of leg.

Of the forelegs the proximal region is not well accessible. The tibia, armed with numerous spines or setae, has two distinct dark stripes and two bright ones, from proximal to distal: bright, dark, bright, dark. Also the tarsus (composed of five elements) has bright and dark stripes (Fig. 1D). The long proximal element has one proximal bright and one distal dark stripe. The two shorter following elements have similar patterns; further distal elements are entirely dark (Fig. 1D).

For the midleg the proximal elements are not well accessible. The tibia and tarsus have a similar pattern to the foreleg (Fig. 1A), but the distal two elements of the tarsus are not preserved.

Of the hindleg mostly the femur is accessible. It has six stripes, from proximal to distal: dark, bright, dark, bright, dark, bright (Fig. 1A).

The cerci also have a certain colour pattern. The proximal elements are bright, the distal ones are dark (Fig. 1F).

Additional incomplete mantodean specimens: PED 2590, 2666, 4266

In the three incomplete specimens especially the forelegs are preserved (Fig. 2A–C). The colour pattern concerning stripes is very similar to the pattern seen in PED 4207.

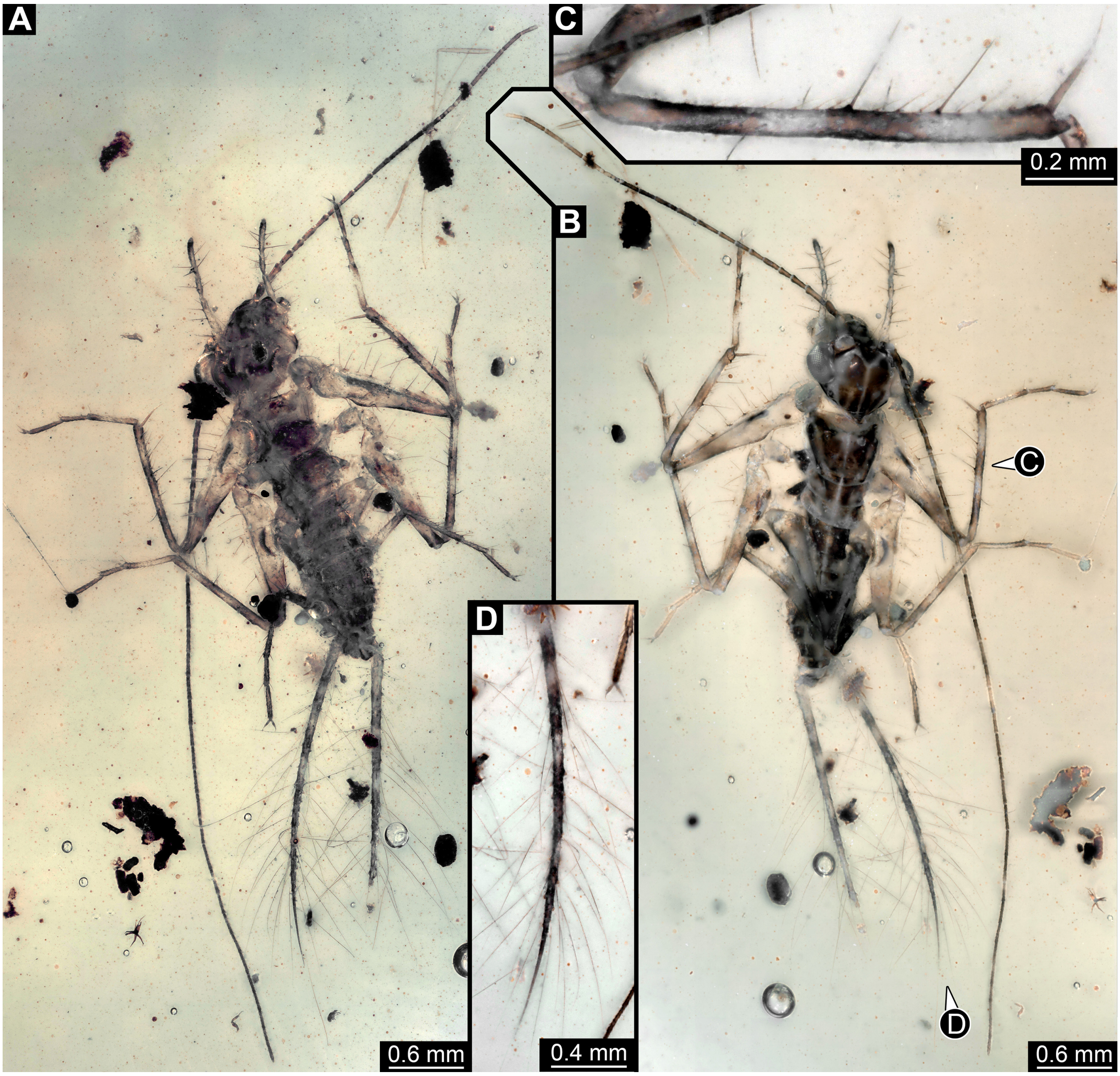

FIGURE 4. New specimen of the ensiferan *Gryllobencain patrickmuelleri* with stripes on appendages, PED 4305. **A**, Ventral view. **B**, Dorsal view. **C**, Detail of leg. **D**, Detail of cercus.

Non-mantodean dictyopteran specimen PED 4302

Small roach-like immature (Fig. 2D). The central body is incomplete, preserving traces, but no clear indications of the colour of the central body. The tibia of the midleg has five stripes, from proximal to distal: a very short bright one, followed by dark, bright, dark, bright (Fig. 2E). Three tarsus elements are preserved (the proximal one being the longest) all appear to have a dark stripe proximally and a bright one distally (Fig. 2E). Also the cerci have stripes, five from proximal to distal: dark, bright, dark, bright, dark (Fig. 2F).

Non-mantodean dictyopteran specimen PED 0261

Small roach-like immature. Accessible in lateral view. Colour pattern on front and midleg indistinct. Hindleg tibia with five stripes, from proximal to distal: bright, dark, bright, dark, bright (Fig. 3A).

Non-mantodean dictyopteran specimen PED 1075

Larger roach-like immature. Accessible in ventral view (Fig. 3B). Indistinct colour pattern on dorsal side. Leg colouration of proximal parts unclear. Tibia of foreleg and midleg with five stripes, from proximal to distal: dark, bright, dark, bright, dark (Fig. 3C). Tarsus in both legs appears to have six stripes, from proximal to distal: bright, dark, bright, dark, bright, dark (Fig. 3C).

Orthopteran specimen PED 4305

Small orthopteran immature (Fig. 4A). The central body dorsally shows clear indications of colour pattern (dark

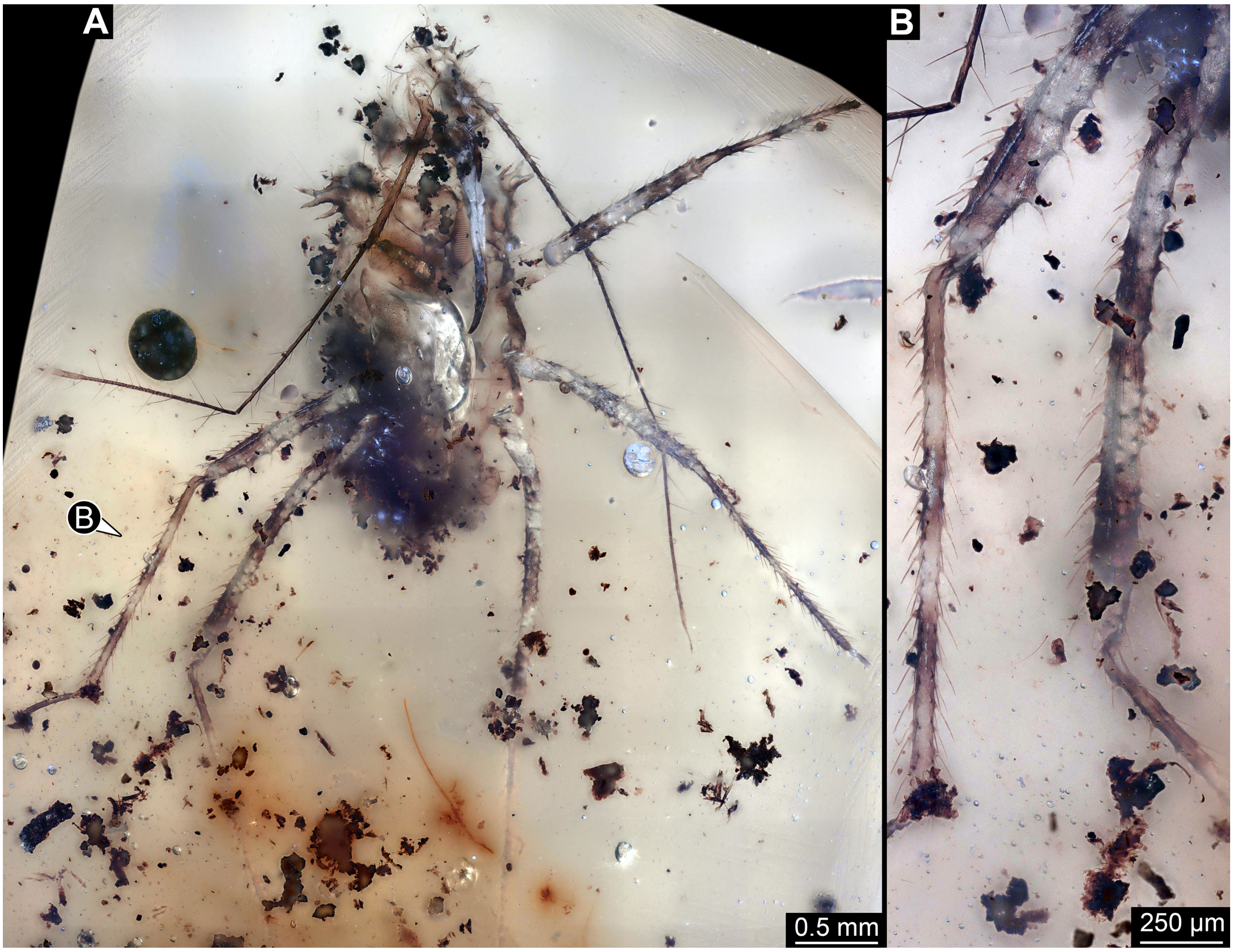

FIGURE 5. New specimen of true bug with stripes on legs, PED 4269. **A**, Ventral view. **B**, Detail of legs.

and bright regions) on head and thorax tergites (Fig. 4B). Colour patterns are also apparent on different appendages. Maxilla palps distally with a dark tip (Fig. 4B).

Thorax appendages (legs) sub-similar, colour pattern clearer at the two anterior pairs. No details on proximal leg elements. Pattern on femur weak, it appears that there are two dark stripes flanked by three bright stripes (Fig. 4B). Tibia with six stripes, from proximal to distal: bright, dark, bright, dark, bright, dark (Fig. 4C). Tarsus with three elements. Proximal element longest, with a very short dark stripe, a long bright one, and distally again with a narrow dark stripe (Fig. 4B). Distal elements entirely dark.

Cercus not subdivided, with four bright and four dark stripes, proximally bright, distally dark (Fig. 4D). Bright stripes shorter than dark ones (Fig. 4D).

Heteropteran specimen PED 4269

Small heteropteran immature (Fig. 5A). Dorsal side of the specimen with numerous dirt particles, likely parts of a camouflaging cloak (Fig. 5A). Numerous spine-like protrusions on head and thorax tergites. Those on prothorax forked. Antennae very long, longer than central body. Mouthparts forming prominent beak (Fig. 5A). Appendages of thorax (legs) with apparent colour pattern (Fig. 5B).

Foreleg and midleg sub-similar in pattern. Femur with five stripes, three bright and two dark ones. Distal bright stripe quite short. Tibia with six stripes, three dark and three bright ones, proximally dark, distally bright (Fig. 5B). Tarsus not or incompletely preserved. Hindleg femur with five stripes, three dark, two bright ones (Fig. 5B). Tibia incompletely accessible (two deep in the amber), but appears also striped.

Fulgoromorphan specimen PED 4197

Small fulgoromorphan immature (Fig. 6A, B). Well preserved. Entire body with colour preservation (Fig. 6A, C). Head capsule with a clear dark anterior region, a bright stripe further posterior at the level of the compound eyes (Fig. 6D). Further posterior with a dark stripe, at the level of the antennae.

Proximal two elements of antennae (scapus, pedicellus) apparent, distal parts thin, filiform (arista).

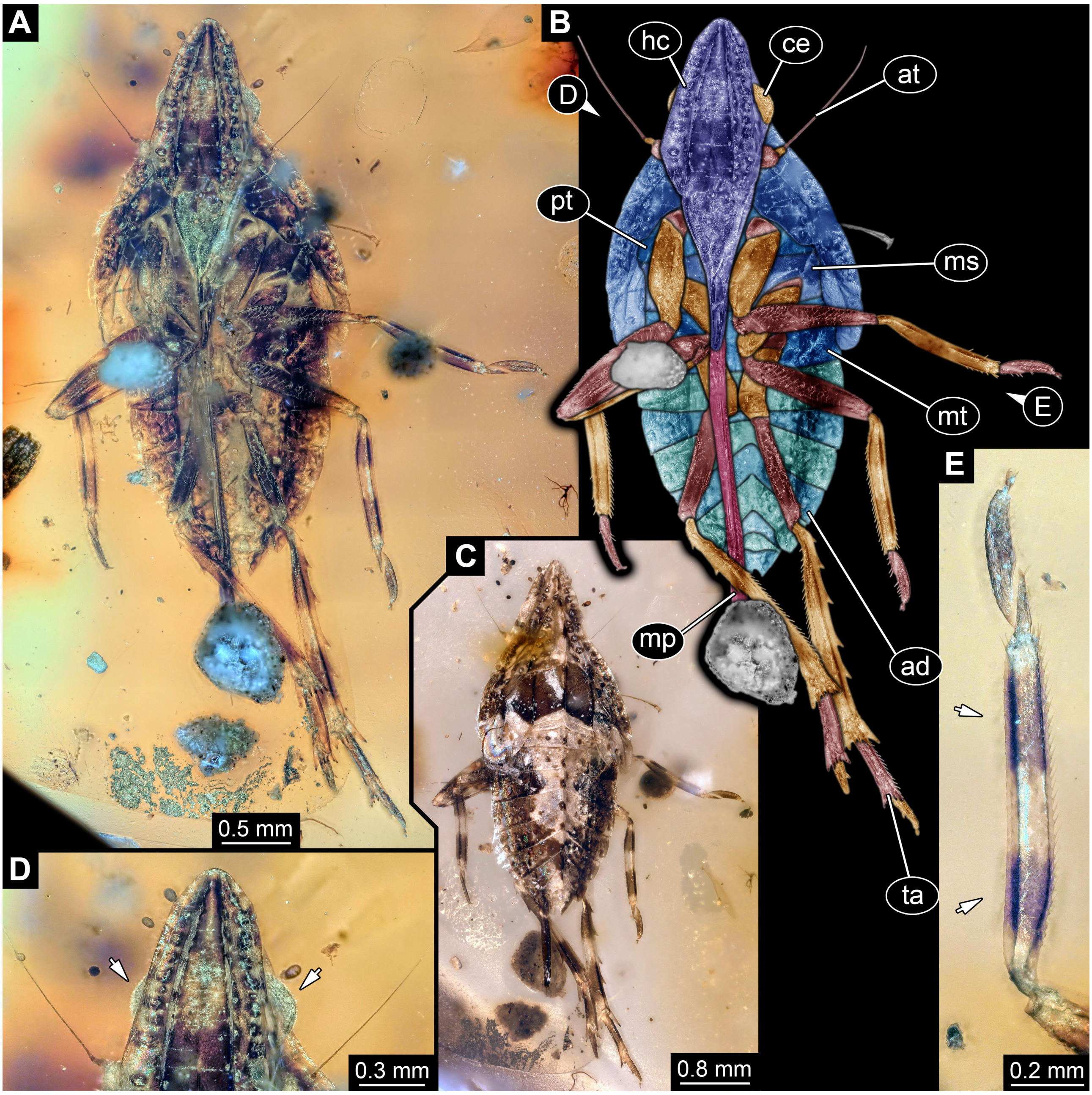

FIGURE 6. New specimen of planthopper with stripes on legs, PED 4197. **A**, Ventral view. **B**, Colour-marked version of **A**. **C**, Dorsal view. **D**, Detail of head with compound eyes (arrows). **E**, Detail of legs with two dark stripes on tibia (arrows). Abbreviations: ad = abdomen; at = antenna; ce = compound eye; hc = head capsule; mp = mouthparts; ms = mesothorax; mt = metathorax; pt = prothorax; ta = tarsus.

Mouthparts forming distinct beak, long, extending beyond the posterior end of the main body (Fig. 6A, B).

Thorax appendages (legs) all sub-similar, with proximal parts dark. Femur proximally dark, very distally bright. Tibia with five stripes, three bright, two dark ones (Fig. 6E). Tarsus with two elements, both dark, not as dark as dark stripes on other leg elements.

Fulgoromorphan specimen PED 4304

Small fulgoromorphan immature. Relatively well preserved, accessible in ventral view (Fig. 7A). Main body with indications of colour preservation. Thorax tergites with more complex pattern not well reconstructible. Abdomen tergites varying to a certain degree, but several of them with a dark stripe posteriorly and a dark spot laterally in the middle along the anterior-posterior axis.

Foreleg tibia with indistinct colour pattern, appears sub-similar to better preserved pattern on midleg. Midleg tibia with nine stripes, five bright, four dark ones (Fig. 7B, C). Proximal bright stripe short, first dark stripe longer, four stripes (bright and dark) similar in length, next bright stripe about twice the length of previous stripe, next dark

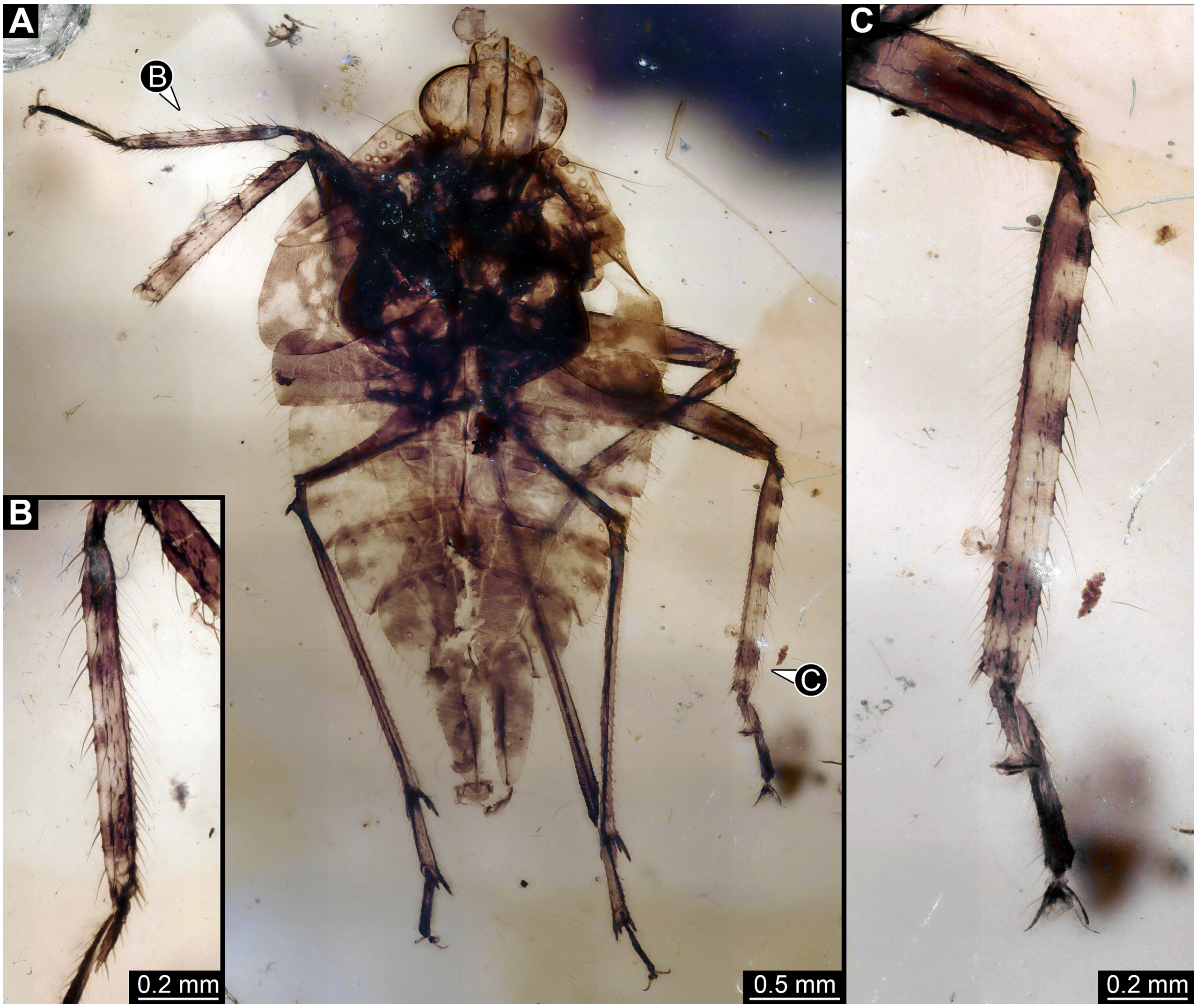

FIGURE 7. New specimen of planthopper with stripes on legs, PED 4304. **A**, Ventral view. **B**, **C**, Detail of legs. **B**, Foreleg. **C**, Midleg.

stripe again shorter, about as long as the last dark one, distal bright stripe slightly shorter. The proximal two dark stripes are medially connected by a dark region. The tarsus appears overall dark, but even darker distally. Hindlegs without indications of stripes (Fig. 7A).

Neuropteran specimen PED 4279

Small lacewing larva. Anterior part of body incompletely preserved, mouthparts and part of head missing, outside of the amber (Fig. 8A, B). Neck region strongly elongate.

Legs with well apparent stripes pattern. Tibia with five stripes, three dark, two bright; tarsus with bright stripe proximal, dark one distally (Fig. 8C, D).

Discussion

Identity of the specimens

All specimens described here are immatures. This makes species-level identification difficult to impossible, but identification to a coarser degree is achievable.

PED 2590, 2666, 4207, 4266: These specimens share all the prominent foreleg with spines/setae on femur and tibia (Figs 1A, 2A–C). With the specific arrangement these can all be identified as representatives of Mantodea. Although mostly incomplete, the overall arrangement of spines and setae is very similar to that in species of *Burmantis* (Grimaldi, 2003: fig. 3, p. 9; Delclòs *et al*., 2016: fig. 4 left, p. 99; Izquierdo-López *et al*., 2025: fig. 2, p. 8). This makes it likely that all four specimens are also representatives of this group or at least closely related to it.

PED 0261, 1075, 4302: The specimens are incomplete and have an overall roach-like appearance and are therefore interpreted as representatives of Dictyoptera, but lack characters of the ingroup Mantodea (Figs 2D, 3). Further informative characters are not preserved, prohibiting further-reaching identification of these specimens.

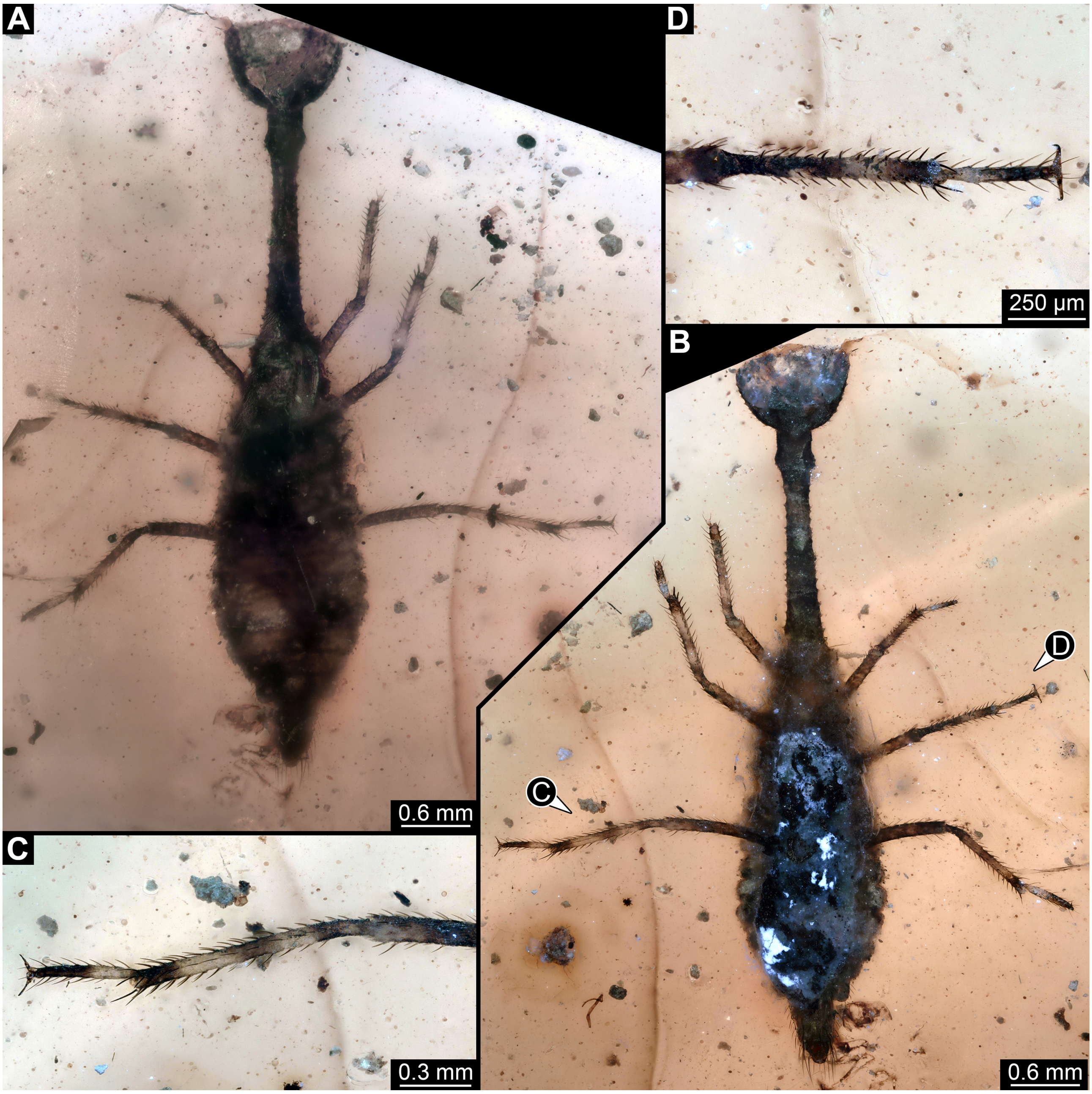

FIGURE 8. New specimen of long-necked antlion with stripes on legs, PED 4279. **A**, Dorsal view. **B**, Ventral view. **C**, **D**, Details of legs. **C**, Hindleg. **D**, Midleg.

PED 4305: The undivided cerci indicate that this specimen is a representative of Orthoptera, the long antennae indicate that it is furthermore a representative of Ensifera (Fig. 4). The specific arrangement of spines and setae on the maxilla palp, foreleg, midleg and cerci identify this animal as a representative of *Gryllobencain patrickmuelleri* (Haug *et al*., 2022).

PED 4269: The specimen is likely a late stage immature and has mouthparts forming a distinct beak that arises from the head rather anteriorly (Fig. 5A). This indicates that the specimen is a representative of Heteroptera. With the long antennae and legs and the possible camouflaging cloak, the specimen resembles immature heteropterans reported by Wang *et al*. (2016: fig. 4B, C, p. 4). These were interpreted as representatives of Reduviidae. We therefore tentatively also identify the new specimen as a representative of Reduviidae.

PED 4197: The specimen can be interpreted as a representative of Fulgoromorpha based on the antennae being ventrally positioned under the eyes (Fig. 6D) and the presence of numerous prominent sensory pits on the head (Wilson, 2005; Bräunig *et al*., 2012). It represents a later stage immature, as indicated by the rather large and prominent developing wings (Fig. 6C). Furthermore,

FIGURE 9. Palaeoartistic interpretation of the different fossil specimens with disruptive colouration described in this study; drawings by one of the authors (GTH).

the developing forewings do not reach the tip of the hindwings, and the hindtarsi have two elements, which excludes that it is a last stage immature (Zenner *et al*., 2005).

PED 4304: Also this specimen is a fulgoromorphan based on the antennae and sensory pits on the head (Fig. 7A; Wilson, 2005; Bräunig *et al*., 2012). It shows strong similarity to known specimens of Neazoniidae and Mimarachnidae, especially concerning the dorso-ventrally flattened body and elliptical outline in dorsal view (note that the relation of the two groups to each other is currently unclear; Kiesmüller *et al*., 2024). Neazoniidae is only known from immatures preserved in Lebanese and French amber, characterised by sensory pits on the abdomen tergites arranged in groups of 3–4 (Szwedo, 2007, 2009). Mimarachnidae is mostly known from adults, with few species known as immatures (Liu *et al*., 2024). The new specimen is more similar to the known immatures of Mimarachnidae by having displaced pairs of sensory pits on the abdomen tergites. Moreover, the hindtibia possesses a single proximal spine, which is also known in representatives of *Jaculistilus*, an ingroup of Mimarachnidae (Zhang *et al*., 2018). The specimen is likely an immature stage 2–3 as indicated by small developing forewings with minimal overlap with the developing hindwings, and hindtarsi with two elements (Zenner *et al*., 2005).

PED 4279: Although parts of the head are missing, the overall habitus and especially the long neck region (Fig. 8A, B) immediately identify the specimen as a long-necked antlion larva, *i.e*., a representative of Crocinae and ingroup of Neuroptera. Fossil larvae with similarly long necks have been reported repeatedly (Xia *et al*., 2015; Zhang, 2017; Haug *et al*., 2019, 2021, 2024).

True preservation of colour pattern or artefact?

Distinguishing genuine colour preservation from artefacts can be challenging, but in these specimens the assessment is straightforward: the same stripe patterns occur on left and right legs, which are preserved in different orientations within the amber. This makes a preservational artefact highly unlikely. We therefore interpret the alternating bright and dark leg stripes as original colour patterns of the living animals.

Aposematism or disruptive colouration?

There appears to be a general tendency to interpret striped patterns in amber fossils as aposematic. Such conclusions, however, require careful evaluation (see *e.g*., discussion in Hinkelman, 2023). In several cases, the patterns have not been documented in sufficient detail—or at least not presented in a way that allows confident assessment. Preservation quality plays a major role here: older Lebanese amber is often more challenging, and the available material is limited. This makes it difficult to examine fine details such as leg stripes (Sendi & Azar, 2017: fig. 2A, p. 15; interpreted as aposematic), which may have contributed to some interpretations of aposematism.

As noted earlier, stripes can serve two distinct functions: deterring predators (aposematism) or preventing detection (disruptive colouration). Suggested cases of aposematism typically involve bright colours, especially red or yellow (*e.g*., Xu *et al*., 2022 for orthopterans). When bright colours are absent, small white patches may occur on otherwise dark legs, as in a heteropteran with dark legs and small white areas (Fabrikant & Novoselska, 2024: fig. 6). The new fossils differ markedly: their stripes form alternating dark and lighter bands, with no indication that the lighter areas were originally bright or strongly white.

Combined aposematic-camouflage patterns are also known (Barnett *et al*., 2023), but these usually involve bright colours—particularly yellow—and a higher number of densely spaced stripes (Barnett *et al*., 2016, 2017, 2018). All the fossils described here lack these features. For all specimens, the alternating leg stripes are therefore more plausibly interpreted as disruptive colouration rather than aposematism.

Patterns on legs

In most discussions of aposematic or disruptive colouration in amber fossils—and in other preservation types—the focus is typically on wing patterns (*e.g*., Chen *et al*., 2019 for Hemiptera; Hinkelman, 2023 for Dictyoptera). All specimens reported here, however, are immatures and therefore lack fully developed wings. The relevant patterns are instead found on the appendages, primarily the legs.

Four of the specimens are mantodeans, so it is unsurprising that similar leg patterns have been documented in mantodean immatures (Grimaldi, 2003: fig. 3, p. 9; Delclòs *et al*., 2016: fig. 4 left, p. 99; Izquierdo-López *et al*., 2025: fig. 2, p. 8), although these patterns have rarely been discussed. For predators, camouflage or crypsis can serve two functions: avoiding detection by larger predators and enabling a stealthier approach toward prey. For disruptive colouration operating against a ground or bark background, the former function is likely the more relevant (Fig. 9). Prey animals, viewing the predator from a different angle, may not experience the same outline-breaking effect. *Gryllobencain patrickmuelleri* independently evolved a predatory lifestyle with grasping forelegs (Haug *et al*., 2022), so its similar stripe pattern is not unexpected. The same applies to the lacewing larva, consistent with the first clear report of disruptive colouration in a comparable larva (Haug *et al*., 2024).

Striped legs also appear frequently in cockroach fossils (*e.g*., Sendi & Azar, 2017: fig. 2A, p. 15; Šmídová & Lei, 2017: fig. 3B, p. 192), which aligns with the fact that many extant cockroaches show similar patterns (Vršanský *et al*., 2019: fig. 5c, p. 78). For true bugs, striped legs have already been reported in predatory immatures (Wang *et al*., 2016: fig. 4B, C, p. 4), so the new examples fit well within this pattern. In planthoppers, stripes are not uncommon (Szwedo, 2009: fig. 2A, C, p. 5; Jiang *et al*., 2019: fig. 3b, p. 4; Fu & Huang, 2020: fig. 4c, p. 6), though they have seldom been discussed. A recently described Miocene true bug from Tibet bears stripes on both the rim of the abdomen and the legs (Dai *et al*., 2025: fig. 1a, b, p. 2), superficially resembling the planthopper specimen PED 4304. However, unlike PED 4304, the leg stripes in the Miocene fossil do not match the pattern on the abdomen, suggesting functional differences. This is plausible given that the Miocene species was inferred to have had a semi-aquatic lifestyle, whereas PED 4304 likely lived on bark.

Convergent evolution of stripes

As the examples presented here demonstrate, striped leg patterns evolved repeatedly and independently across multiple lineages. Although the overall appearance of these patterns is broadly similar, the details vary. Many specimens show a comparable number of dark stripes on the distal leg elements (femur, tibia, tarsus), with 5–6 dark bands being particularly common. However, their exact placement differs. Dark cuticle is often mechanically harder than lighter cuticle (well documented in spiders and their relatives, Dalingwater 1987; and also in insects: Dennell, 1944; Hackman & Goldberg, 1971). One might therefore expect dark stripes to coincide with regions experiencing the highest mechanical stress, such as joints. Yet this is not consistently the case; in some specimens, the joints are among the lighter areas.

Not all patterns are closely comparable. The fulgoromorphan specimen PED 4304, for example, shows a distinctly denser arrangement of stripes, with four dark and five bright bands on the tibia. The spacing of these stripes appears to correspond to the spacing of dark spots on the body, potentially blending body, legs, and background into a single visual unit (Fig. 9).

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