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A modern type of ant-like stone beetle larva preserved in 99-million-year-old Kachin amber (Coleoptera: Staphylinidae, Scydmaeninae)

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Abstract
Scydmaeninae, the group of ant-like stone beetles, was previously named "Scydmaenidae", but is today recognized as an ingroup of Staphylinidae. The group has a more or less global distribution and includes some 4,900 formally described species. The fossil record of the group seems well studied with almost 40 formally described species so far. However, all the described fossil specimens are adults, which once again demonstrates the rarity of reports of larvae. This fact also applies for the extant counterparts: even the larvae of some modern lineages of Scydmaeninae have not been identified yet. Here we contribute to the fossil record of ant-like stone beetles with the first report of a relatively modern-appearing fossil larva. In the center of the study is a single specimen preserved in 99-million-year-old Kachin amber, Myanmar. The fossil shares multiple characteristics (for example, long and slender antennae, maxillary palps, and walking legs) with modern representatives of second stage larvae of the species *Stenomastigus longicornis.* This similarity indicates a closer relationship to this species, and the fossil is therefore likely a representative of the group Mastigini. In the light of the new find, we discuss phylogenetic implications and the evolution of developmental patterns within Scydmaeninae.

Key words: Scydmaeninae; Cretaceous; Myanmar amber; Burmese amber; metamorphosis.

Introduction

Beetles are important components of many terrestrial ecosystems. Many diverse beetle groups are well-known also to the broader public, such as ladybirds or rove beetles. Yet, there are also numerous less well-known beetle groups comprising quite a number of species.

Scydmaeninae, the group of ant-like stone beetles, includes about 4,900 formally described species (Grebennikov & Newton 2009). The group has a more or less global distribution, with the exception of Antarctica (O'Keefe 2005 p. 280). As the name suggests, adult ant-like stone beetles are, to a certain degree, myrmecoform; at least, they have a more slender appearance and a certain mid-body constriction in dorsal view. Together with their rather small body size, this indeed leads to a certain resemblance to ants (cf. recent discussion of ant mimicry in Haug et al. 2020a).

The larvae of ant-like stone beetles show a certain diversity of body shapes (Jałoszyński 2018), reaching from slender, spindle-shaped, long-legged campodeiform larvae (Jałoszyński & Kilian 2016; Jałoszyński 2018 fig. 14.1C p. 323), over campodeiform larvae with prominent heads (Vit & De Marzo 1989 fig. 1 p. 570), to more onisciform ones (Jałoszyński & Beutel 2012 fig. 1B p. 594; Jałoszyński 2018 fig. 14.1A p. 323). However, the larvae of several lineages of Scydmaeninae have not yet been identified (O'Keefe 2005 p. 280), and in general the larvae must be considered poorly studied (Jałoszyński 2018 p. 331). Despite the morphological differentiation of the larvae, all of these seem to be predators, many of oribatidan mites, but also of other small components of the soil fauna.

For a long time, the group had been named "Scydmaenidae", but it was recognised as an ingroup of Staphylinidae (Grebennikov & Newton 2009; demonstrating that taxonomic ranks do not provide stable group names; see discussion in Béthoux 2007a, b, c, 2010). Hence, ant-like stone beetles are in fact part of the diversification of rove beetles.

The group Scydmaeninae has an astonishing fossil record. Jałoszyński et al. (2016 p. 59) already counted about 20 fossil species, all of these preserved in ambers, including Miocene Dominican amber (Franz 1983), Eocene Baltic amber, (Franz 1983; Jałoszyński 2012), and different Cretaceous ambers from Canada (O'Keefe et al. 1997), Myanmar (Poinar & Brown 2004; Chatzimanolis et al. 2010; Jałoszyński & Peris 2016; Jałoszyński et al. 2016), Spain (Jałoszyński & Peris 2016), and France (Kirejtshuk et al. 2015). Since the counting of species by Jałoszyński et al. (2016), three more species from Eocene Baltic amber (Jałoszyński et al. 2018; Yin & Cai 2018), two more species from Cretaceous Taimyr amber (Jałoszyński & Perkovsky 2016, 2019), and significant 14 new species from Myanmar (Kachin) amber (Cai & Huang 2016; Yin et al. 2017a, b, 2018a, b, 2019a, b; Jałoszyński et al. 2017, 2020; Yin & Cai 2019; Jałoszyński 2020; Yin 2020; Yin & Zhou 2020) have been formally described. Although some species have been differently interpreted after their original description (see e.g. Jałoszyński et al. 2018), this makes almost 40 formally described fossil species of ant-like stone beetles, with an exceptional large species diversity in Kachin amber. All of the known fossils are adults, many are clear males, others can be recognised as females (e.g. Yin 2020). However, despite the quite numerous fossils, so far no larva of an ant-like stone beetle has been reported in the fossil record.

We here fill this gap by reporting a fossil larva of Scydmaeninae, with a very modern type of appearance. We discuss implications of this find for understanding the evolution of development within Scydmaeninae.

Material and Methods

Material

In the center of this study is a single fossil specimen, originating from 99-million-year-old Kachin Myanmar amber, Hukawng Valley, Myanmar (Cruickshank & Ko 2003; Shi et al. 2012; Yu et al. 2019). It comes from the collection of one of the authors (PM, original collection number BUB 4251) and was legally exported from Myanmar before 2017 (see discussion in Haug et al. 2020b). The specimen is now deposited in the collections of the Staatliches Naturhistorisches Museum Braunschweig under repository number SNHMB.G 8109. Within the piece of amber next to the specimen there are multiple small detritus inclusions and small bubbles discernible. Large part of the body of the insect is concealed with white film (also known as "Verlumung").

Documentation methods

The fossil specimen was documented on a Keyence VHX-6000 digital microscope in front of white and black background under different illumination settings (cross-polarized co-axial light and low-angle ring light) (Haug et al. 2013a, 2018). All images were recorded as composite images (Haug et al. 2011), combining several images of varying focus and several adjacent image details as well as different exposure times (HDR, cf. Haug et al. 2013b). Images were further processed and colour-marked with Adobe Photoshop CS2. Schematic restorations were drawn in Adobe Illustrator CS2.

Description of specimen

General

Elongate and slightly flattened body (Figs 1A, B, 2A, 3A), without appendages approximately 2.3 mm long. Body with 20 segments (not all externally visible) differentiated into an anterior head region and posterior trunk region (Fig. 1B). Trunk further differentiated into anterior trunk region (thorax) and a posterior trunk region (abdomen; Fig. 1B).

Head

Head moderately inclined, forwards-orientated mouthparts (sub-prognathous; Fig. 2B, C); sub-hexagonal in dorsal view (Fig. 1B), shorter than wide at its widest point, 1.4x (~0.22 mm long, ~0.3 mm wide).

No stemmata discernible. Labrum (derivative of appendages of ocular segment) wider than long, anterior edge bears multiple setae (Fig. 2C).

Antennae (appendages of post-ocular segment 1) prominent, very long. Each with a small proximal region (membrane?) and two prominent distal elements (Fig. 2B). Antenna longer than head, 3.6x (~0.78 mm). Proximal of the two distal elements 0.19 mm long, in the middle ~0.06 mm wide, but widest proximally (~0.07 mm wide). Distal element longer than proximal element, 2.8x (~0.54 mm) and ~0.05 mm wide, bears numerous setae of different lengths (0.06 mm–0.23 mm long). Post-ocular segment 2 without externally visible structures.

Mandibles (appendages of post-ocular segment 3) symmetrical, sickle-like, with no setae discernible (Fig. 2C), ~0.1 mm long.

Maxillae (appendages of post-ocular segment 4) with several parts discernible: proximal part (stipes) trapezoid in ventral view, wider than long, about 1.4x (~0.07 long, ~0.1 mm wide); distinct median enditic protrusion ("stipital projection", Jałoszyński & Killian 2012 fig. 18 p. 592) with possible galea (Fig. 2C); distally long slender palp with two prominent elements discernible (unclear whether a small proximal element present), both elements of approximately same length (~0.17 mm), proximal element bears setae (Fig. 2B, C).

Labium (conjoined appendages of post-ocular segment 5) with rectangular shape in ventral view (~0.08 mm long and wide). Distally with paired palps, number of elements not discernible (Fig. 2B, C).

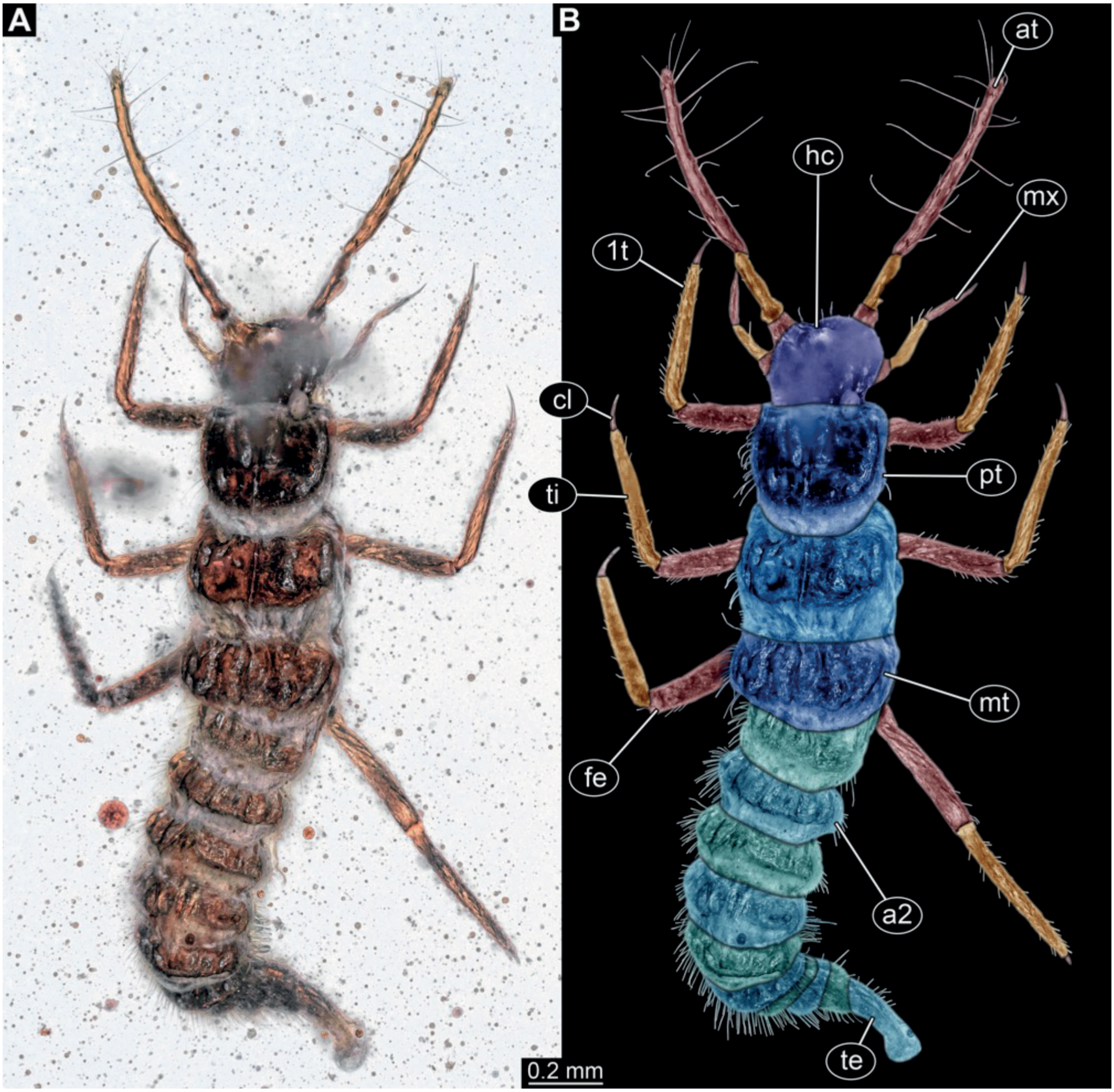

Fig. 1 – Specimen SNHMB.G 8109, Kachin amber. **A** – Dorsal view. **B** – Colour-marked version of A. Abbreviations: 1t = trunk appendage 1 ("front leg"); a2 = abdomen segment 2; at = antenna; cl = claw; fe = femur; hc = head capsule; mt = metathorax; mx = maxilla; pt = prothorax; te = trunk end; ti = tibio-tarsus.

Trunk

Thorax with three segments (pro-, meso-, metathorax; Fig. 1B), all with distinct dorsal and ventral sclerites (tergites, sternites). Prothorax semicircular in dorsal view, longest and narrowest segment of thorax (0.36 mm long, anteriorly 0.32 mm wide). Mesothorax sub-rectangular in dorsal view, as long as prothorax is wide, wider than prothorax, 1.4x. Metathorax semi-circular in dorsal view, shorter than prothorax, about 1.6x; wider than prothorax, 1.3x. All thorax segments bear setae laterally (Fig. 1A, B).

Each thorax segment with a pair of locomotory appendages (legs). Legs long and slender, with four elements (coxa, trochanter, femur, tibiotarsus) and claw (Figs. 1B, 2D). Legs shorter than body, 2.6x (~0.9 mm long), slender (max. width 0.08 mm). Coxa and trochanter short. Femur prominent, elongate (~0.29 mm long), tibiotarsus longer (~0.39 mm long). Both femur and tibiotarsus bear numerous setae (Fig. 1B).

Posterior trunk (abdomen) tapering posteriorly, with ten discernible units, each with dorsal and ventral sclerites (tergites, sternites), bearing numerous setae of different sizes. Abdomen units (segments) 1–9 sub-similar in shape, transverse, abdomen segments 1–4 gradually widening with abdomen segments 3 and 4 being largest of all abdomen

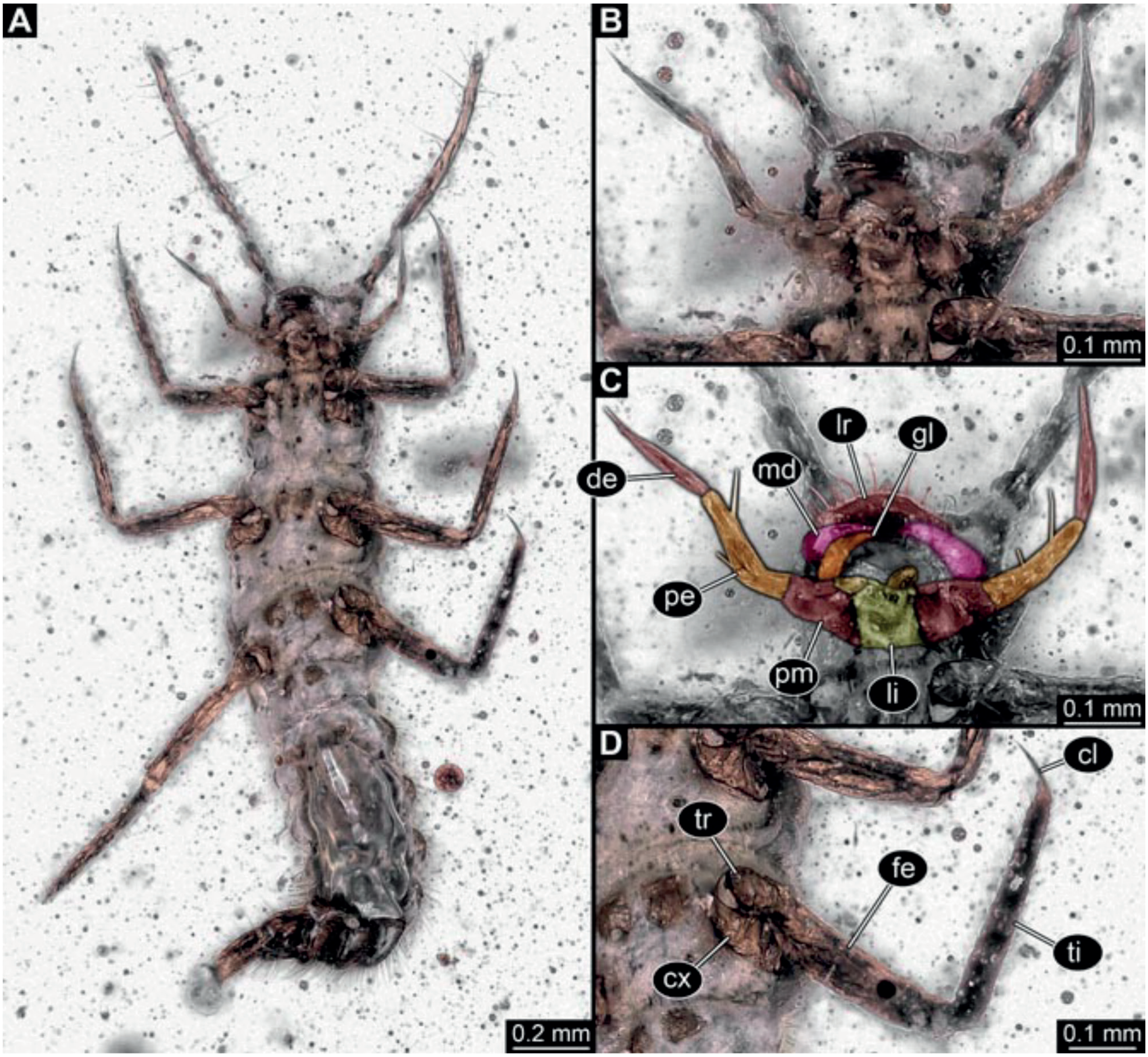

Fig. 2 – Specimen SNHMB.G 8109, Kachin amber. **A** – Ventral view. **B** – Detail of head, ventral. **C** – Colour-marked version of B. **D** – Detail of trunk appendage. Abbreviations: cl = claw; cx = coxa; de = distal visible element of maxillary palp; fe = femur; gl = possible galea; li = labium; lr = labrum; md = mandible; pe = proximal visible element of maxillary palp; pm = proximal region of maxilla (stipes?); ti = tibio-tarsus; tr = trochanter.

segments (~0.16 mm long, ~0.36 mm wide), abdomen segments 5–9 gradually decreasing in size antero-posteriorly. Terminal end of abdomen elongate, ~0.24 mm long and ~0.09 mm wide. Abdomen bears numerous setae. Most posterior unit (terminal end; Fig. 1B) probably undifferentiated compound structure of abdomen segments 10 and 11, elongated, slender.

Discussion

Similarity of the studied fossil to modern counterparts
The here reported fossil has an astonishing similarity to the stage 2 larva of the modern species *Stenomastigus longicornis* (compare Fig. 3A vs. 3B; Jałoszyński & Kilian 2016, p. 153, figs 1–4; Jałoszyński 2018, p. 324, fig.14. 2G). Similarities include the overall body shape, the sclerites on the dorsal side, the prominent antenna with few elements and apparent setae, the very large maxillae with almost leg-like palps with the distal two elements especially elongated, and the trunk appendages (legs). As pointed out, larvae of Scydmaeninae exhibit quite some variation between the different species, hence such a strong similarity of the fossil should be indicative of a close relationship of the fossil to the modern species or at least the larger group.

Stenomastigus longicornis is a representative of Mastigini (Jałoszyński & Kilian 2016). Also other known larvae of Mastigini have a strong similarity to the fossil (e.g.

De Marzo 1984, p. 63, fig. 1; p. 69, fig. 17). Yet, all modern larvae of Mastigini have a subdivision of the distal large antenna element ("antenomere II"; Jałoszyński 2018) into three sections, at least in larval stage 3.

Such a differentiation has not been indicated in all stage 2 larvae (De Marzo 1984, p. 69, fig. 17), and even in cases in which it has been reported in such larvae (Jałoszyński & Kilian 2016), it is indeed difficult to recognise (Jałoszyński & Kilian 2016, p. 5, fig. 5; p. 7, fig. 10), hence possibly less pronounced developed. Still, it seems unlikely that such a subdivision is present in the fossil and just not well apparent; it seems truly absent. We therefore interpret the fossil larva as a representative of Mastigini, possibly a stage 2 larva, that plesiomorphically (ancestrally) lacks the subdivision of the distal prominent antenna element. The fossil represents a possible sister lineage to all extant species of Mastigini that are united by the presence of a distinct subdivision of the distal antenna element. This subdivision could provide a uniting character (apomorphy) for the extant lineages, which so far were resolved in a polytomy with the fossil representatives (Jałoszyński et al. 2018, p. 628, fig. 3; Yin et al. 2019b, p. 8, fig. 6).

The fossil record of Mastigini

Three species of Mastigini have been formally described, all based on adult specimens preserved in Myanmar amber: *Clidicostigus arachnipes* (Jałoszyński et al. 2017), *Cascomastigus monstrabilis* (Yin et al. 2017b), and *Cascomastigus minor* (Yin et al. 2018b). At a first glance, all these can be recognised as quite similar with very long legs, prominent maxillary palps and very prominent antennae of which two pronounced proximal elements with long setae form a special joint allowing to fold them against each other. The three species differ in certain relative lengths as well as their overall size (Fig. 3C–E).

Reliably associating fossil larvae of holometabolans with their corresponding adults is often very challenging and mostly possible when pupa stages are available, ideally preserved together with either larval cuticle remains or pharate or even emerging adults (see examples in Baranov et al. 2019). In the case here, we can at least use size for giving a hint of which of the three known species the larva could more likely be a representative.

We assume that the new larva (Fig. 3F) is a stage 2 specimen (due to the similarity of extant counterparts, see also discussion in Jałoszyński & Kilian 2016). Based on this interpretation, we can further assume, at least roughly, the size of a not preserved stage 3 larva (Fig. 3G) being about twice the size of a stage 2 larva.

Comparing the sizes of the assumed stage 3 larva with that of the adults shows that only a moderate overall size gain would be necessary to reach the size of the adult of *Cascomastigus minor*, still involving quite a significant size gain in the appendages. During the last-larva-to-adult transition, many holometabolans even decrease in overall size (Haug et al. 2020c), hence a more drastic size gain to reach the sizes of the other two species seems unlikely. It is therefore likely that the new larva is a larva of *Cascomastigus minor*. It can, of course, also not be fully excluded that the larva represents a new, so far not formally described species (see discussion in Haug & Haug 2016, 2017). Yet, given the realistic possibility that the larva is indeed the immature of an already formally described species, we refrain from erecting a new species for the larva as this would quite likely create a junior synonym.

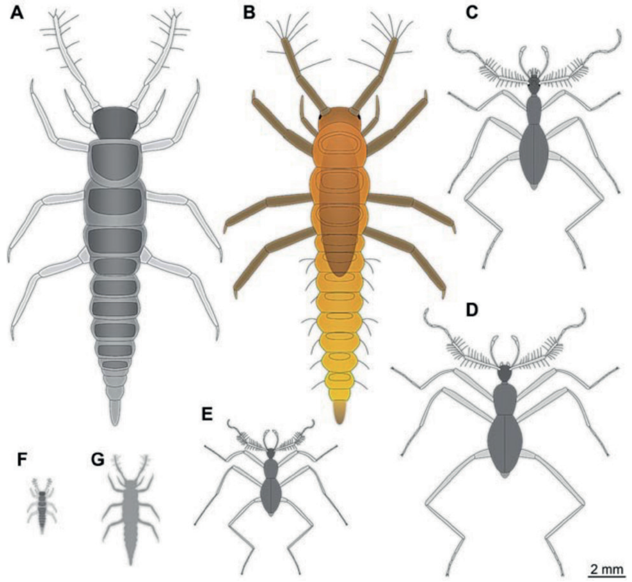

Fig. 3 – Schematic restorations of ant-like stone beetles. **A** – The new fossil (based on Fig. 1); not to scale. **B** – Stage 2 larva of the extant species *Stenomastigus longicornis* (based on Jałoszyński & Kilian 2016 figs 1–4 p. 153); not to scale; note the similarities to the fossil larva. **C–G** – Restorations of different fossils, all to the same scale for size comparison. **C–E** – Fossils of adult ant-like stone beetles. **C**) *Clidicostigus arachnipes* (based on Jałoszyński et al. 2017 fig. 3A p. 114). **D**) *Cascomastigus monstrabilis* (based on Yin et al. 2017b fig. 1a p. 2). **E**) *Cascomastigus minor* (based on Yin et al. 2018b fig. 2A; width of body estimated based on the other species). **F**) The new fossil (same as A), but to scale. **G**) Estimated size of a possible stage 3 larva following the stage 2 larva which the new fossil presumably represents (by simply resizing the latter to 200%).

The metamorphic changes in the lineage of Mastigini

It was noted by Jałoszyński & Kilian (2016 p. 181) that the group Mastigitae (=Masticini+(Clidicini+(*Papusus*+(Leptochromini+(Baltostigini+Mastigini)))); Yin et al. 2019b) is characterized by larvae that already resemble their corresponding adults in many aspects. For Mastigini, it was pointed out that especially the antenna morphology was already strongly similar and that the larvae have already relatively longer legs than in other larvae of Scydmaeninae. As a further point, also the prominent maxillary palps are already present in the larvae, yet the club-shaped tip of the adults is not yet developed.

This is also the case in the fossil larva. It also has already relatively long legs, yet the legs of the possible corresponding adult are even much more elongated. It can be speculated that there is a certain coupling between the two states. Developing strongly elongated structures in adults is mechanically challenging when the corresponding structures in the immatures are very short (see discussions in Saltin et al. 2016; Hörnig et al. 2018; Kiesmüller et al. 2019; Haug 2020). Hence, it is possible that long legs were originally an advantage for the adults and shifted (via heterochrony) to earlier stages (see discussion in Haug et al. 2010); or the other way round, that it was advantageous for the larvae and retained in the adults. As the fossils already show a similar condition as in the modern representatives, they are not informative of a possible order of evolutionary events.

Similarly, it must remain unclear whether the geniculate strongly setose antenna is originally an adult or larval feature, as also here the fossils already have this feature in both stages. It is indeed quite astonishing how similar the larval and adult morphology of the antenna is, in the adult only “amended” by a distal flagellum. It seems unlikely that the fossil larva used this structure in a similar way as it was assumed for the adults, i.e. for trapping collembolans (Yin et al. 2017b, 2018b). The antenna of the larva would most probably not be feasible for catching collembolans due to its smaller size in comparison to that of the adults. It seems more likely that the antenna was used in this stage in a more similar way to modern larvae of Mastigini for sensorial purposes (Jałoszyński & Kilian 2016). This interpretation is also compatible with the absence of the distal flagellum in the larvae, which will take over the sensory function in the adults. This observation indicates that the same structure may have quite different functions depending on the size of the structure.

For holometabolans it is generally assumed to be quite unusual that adults and larvae have a stronger resemblance. In the case of Mastigini, this is clearly a derived state, a less metamorphic condition (see Haug 2020 for extensive discussion) than in other representatives of Scydmaeninae. The fossils demonstrate that this specific type of developmental pattern was already present some 100 million years ago.

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