



Three new lithobiomorphan centipede specimens from mid-Cretaceous Myanmar amber, a clue on the geological record of Lithobiomorpha

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Abstract

Chilopoda, part of Myriapoda, is a species-rich group of ~3300 formally described species. Yet, the phylogenetic relationship of centipedes is not fully clear, and the scarceness of their fossil record, compared to the closely related Diplopoda, is a major challenge for understanding their evolutionary history. Within Chilopoda, Lithobiomorpha is one of the most problematic concerning its fossil record, so far restricted to the Cenozoic (~40 mya) and with a single lithobiomorphan-like specimen from Kachin amber (~100 mya). Here, we report three new exceptionally well-preserved lithobiomorphan specimens from Myanmar amber (~100 mya). These represent the first report of oldest representatives of Henicopidae from the Cretaceous, and with this the oldest definite record of Lithobiomorpha. Two specimens have ten pairs of walking legs (stage IV), and one has a fully developed trunk. These specimens are similar in many aspects to the extant group of Henicopidae and, more precisely, to *Lamyctes* Meinert, 1868. The specimens seemingly lack ocelli, exhibit ~14 (stage IV) and 24 antenna articles, have 2+2 coxosternite teeth, and present tooth-like setae on their coxosternite margins (=porodont). The fully developed specimen possesses a tibial spinose projection on each tibia of legs 1–11, a blunt projection on the tibia of leg 12, and undivided tarsi on their legs 1–12. With the finding of these specimens, we expand the fossil record of Lithobiomorpha significantly.

Keywords: Kachin amber, Burmese amber, Cretaceous, Henicopidae, *Lamyctes*

Introduction

Myriapoda is a group of soil-dwelling animals with a series of sub-similar appearing trunk segments, each (or most) carrying a pair of walking appendages (Moore 2006). The phylogenetic relationships of Myriapoda with other ingroups of Euarthropoda, as well as the relationships of the major ingroups (Symphyla, Pauropoda, Diplopoda, and Chilopoda) have been debated for a long time (Hwang *et al.* 2001; Harzsch 2006; Harzsch *et al.* 2007; Shear & Edgecombe 2010; Fernández *et al.* 2016; Benavides *et al.* 2023). Representatives of Myriapoda play important ecological roles as detritivores (Pauropoda, Symphyla and Diplopoda), for instance by increasing leaf decomposition rate (Attignon *et al.* 2004), and as predators (Chilopoda; Poser 1988). They can also be used as great bioindicators since they are highly affected by habitat characteristics (Schreiner *et al.* 2012; Madzaric *et al.* 2018; Menta & Remelli 2019).

Despite extensive studies on Myriapoda, the group is still understudied, and its expected biodiversity is higher to what has been previously investigated (Decaëns *et al.* 2006). In general, soil-living animals seem much more diverse than anticipated (“Enigma of soil biodiversity”; Anderson 1975). Also, certain ecosystems, such as soils and caves, remain understudied, and in these ecosystems, little is known concerning the species richness of Myriapoda, each new expedition in caves revealing the presence of novel species (Chagas-Jr & Bichuette 2018;

Stojanović *et al.* 2021; Zagmajster *et al.* 2021; Kos *et al.* 2023).

Chilopoda, or centipedes, is characterised by their first trunk appendages, which are transformed into prehensile venomous claws (“forcipules”, “maxillipeds”; Bonato *et al.* 2010). Chilopoda is a species-rich group (~3300 species; Edgecombe & Giribet 2007; Bonato & Zapparoli 2011) and has five major extant lineages (Scutigermorpha, Lithobiomorpha, *Craterostigmus*, Scolopendromorpha, and Geophilomorpha) and one major fossil group (*Devonobius delta*, Shear & Bonamo 1988), while other fossils are likely representatives of the five major extant lineages. The phylogenetic relationships of these lineages were considered stable and well supported based on morphology, with Scutigermorpha (Notostigmophora) representing the sister-group to all other lineages, grouped into Pleurostigmophora. Within Pleurostigmophora, Lithobiomorpha was considered the sister-group to the remaining lineages. Yet recently, with the development of genome-scale data and phylogenomic methods, this later relationship has been challenged, and two phylogenetic relationships stand out: 1) Lithobiomorpha as sister-group to Phylactometria (*i.e.*, *Craterostigmus* + (Scolopendromorpha + Geophilomorpha)); 2) *Craterostigmus* as sister-group to Amalpighiata (*i.e.*, Lithobiomorpha + (Scolopendromorpha + Geophilomorpha)) (Edgecombe 2007; Edgecombe & Giribet 2007; Edgecombe 2011a; Fernández *et al.* 2014; Wolfe *et al.* 2016; Fernández *et al.* 2018; Benavides *et al.* 2023).

Modern centipedes live in soils (Voigtländer 2011), caverns (Stoev *et al.* 2015; Chagas & Bichuette 2018) and even aquatic habitats (Binyon & Lewis 1963), ranging in size from a few millimeters (*i.e.*, *Dinogeophilus*; Bonato *et al.* 2015) up to 300 mm for *Scolopendra gigantea* (Gonzalez *et al.* 2000). Centipedes are opportunistic and generalist feeders (Günther *et al.* 2014), that can easily switch their prey preferences when detritivores are less available (Klarner *et al.* 2017). Their range of predation is wide: they can prey on spiders, insects and even other centipedes (Juen & Traugott 2007; Voigtländer 2011; Eitzinger *et al.* 2013; Günther *et al.* 2014), as well as small vertebrates such as frogs (Folly *et al.* 2019), lizards (Deimezis-Tsikoutas *et al.* 2020) and bats (Molinari *et al.* 2005). As representatives of Myriapoda play important roles in the modern fauna, we can expect comparable functions in the past.

Within Myriapoda, the number of fossils differs tremendously between the ingroups, with a strong bias towards Diplopoda, and with Pauropoda and Symphyla being extremely rare (Shear & Edgecombe 2010). Yet also, the geological record of Chilopoda, *i.e.*, that of centipedes, is scarce and mostly available in few books and studies (exhaustive references in Perrichot *et al.* 2007;

Penney 2010; Shear & Edgecombe 2010; Edgecombe 2011b; Edgecombe *et al.* 2014; Zhang 2017; Wesener & Moritz 2018; Ross 2019; Edgecombe *et al.* 2023) and are often not studied in detail (Pérez-Gelabert & Edgecombe 2013). A suggested explanation of this rarity of fossils comes from their habitat and unmineralized exoskeleton reducing their fossilisation potential (Shear & Bonamo 1990; Edgecombe & Giribet 2007).

The oldest known fossil of centipedes is a representative of Scutigermorpha (*Crussolum*; Shear *et al.* 1998) from the Silurian (~418 million years ago); the species is mostly known from leg fragments. Another fossil from the Devonian (~385 million years ago), *Devonobius delta*, from Gilboa, roots the minimum divergence of Lithobiomorpha from Phylactometria (being a representative of the latter; Shear & Bonamo 1988).

Until recently, geological records of lithobiomorphan centipedes were thought to be restricted to the Cenozoic Era, when for the other groups older fossils have been described in the past (Shear & Edgecombe 2010). Yet, lithobiomorph-like specimens have been depicted (Zhang 2017), and just recently a new lithobiomorph-like centipede from Kachin amber was reported (~100 million years old; Haug *et al.* 2024). This new description challenged the previous “restriction” to the Cenozoic Era, but it was not possible to identify these specimens as unambiguous representatives of Lithobiomorpha due to many plesiomorphies, with no clear apomorphic characters preserved (*i.e.*, *Lithopendra anjafliessae*, Haug *et al.* 2024).

Here, we investigated three lithobiomorphan centipedes from Myanmar amber (~100 million years ago, Cretaceous Period), including one with a fully developed trunk. They are well preserved and almost complete. We discuss implications of these new findings.

Material and methods

Material

Amber pieces investigated in this study are from the Hukawng Valley (Kachin state, Myanmar). The Hukawng Valley lithology and amber-producing layers have been extensively studied in details, locality map figured (fig. 3 in Cruickshank & Ko 2003; fig. 1 in Yu *et al.* 2019; fig. 1B, C in Xing & Qiu 2020) and sedimentary rocks and fauna have been estimated to be from the Cretaceous Period, precisely Lower Cenomanian (Rasnitsyn 1996; Grimaldi *et al.* 2002; Cruickshank & Ko 2003; Shi *et al.* 2012; Smith & Ross 2018; Mao *et al.* 2018; Yu *et al.* 2019). The first amber piece is part of the Palaeo-Evo-Devo research group collection of arthropods (Ludwig-

Maximilians-Universität München, Germany), stored under the repository number PED 2964. It has been acquired legally on the trading website eBay.com from the seller burmite-researcher. Two centipedes are preserved in this piece, they are referred as PED 2964-1 and PED 2964-2. The second amber piece is from the collection of one of the authors (PM) and is stored under the repository number BUB 4771.

Documentation methods

The studied ambers were placed in a plastic petri dish. In order to reduce optical deformation from curvature of the amber piece, a droplet of glycerol was disposed at the top of the amber piece covered by a glass cover slip. Documentation was performed under a Keyence VHX-6000 digital microscope with coaxial cross-polarized light in front of a white background at different magnifications (300–500x). Sharp images were obtained with the built-in software of the digital microscope: stacks of images in different level of focus were recorded and fused together, the obtained sharp images were then stitched to obtain a panoramic image of each specimen. For better description and highlighting anatomic structures, images are then colour-coded using the software Adobe Photoshop CS2 version 9.0 (9.0x211). Measurements were also done using CS2, with the built-in “rule” tool, rounded to the next 5 µm.

Terminology and taxonomy

For describing the specimens, we followed the terminology of Bonato *et al.* (2010). Where possible, we implemented more neutral terms for better communication in squared brackets, and for a lay audience we implemented additional terms in round brackets. In general, communication within Euarthropoda is often hampered by too highly specialised terminology, which is especially problematic for wider-ranged phylogenetic and functional-ecological comparisons. We therefore see the necessity to provide different terminologies in parallel, allowing non-specialists the access to the information, while also serving specialists. Species identification and description were done based on previous research (Brölemann 1930; Archey 1937; Edgecombe 2001; Edgecombe *et al.* 2002; Stoev 2002; Edgecombe 2011a; Enghoff *et al.* 2013; Iorio *et al.* 2022; GBIF.org 2023). Moreover, as suggested by Minelli and Sombke (2011) for consistency in the description of ontogenetic stages we follow the ontogenetic terminology of Voigtländer (2007).

Results

Description of PED 2964-1

General morphology: Body with a fully developed trunk.

Small individual with a body length of ~4.2 mm (Fig. 1A–C). Trunk with sixteen well-apparent segments, bearing the pair of forcipules [maxillipeds; venom claws] and fifteen pairs of walking legs. Tergite of maxilliped segment slightly visible, 80 µm in length. Longer tergites: t1 (270 µm), t3 (455 µm), t5 (525 µm), t7 (345 µm), t8 (555 µm), t10 (530 µm), t12 (555 µm) and t14 (430 µm). Shorter tergites: t2 (130 µm), t4 (180 µm), t6 (165 µm), t9 (165 µm) and t11 (235 µm). An ultimate tergite (trunk end, te) of 180 µm length located on the intermediate segment. No posterior triangular projections. Tergites are rounded and bordered on their lateral sides. Along the tergites, longitudinal parallel rows of tiny setae are visible: two in the middle and one on each side of the tergites (in total four rows of setae).

Head: Head dorso-ventrally flattened, slightly broader (530 µm) than long (510 µm). Presence of sulci [furrows] at the antero-ventral side of the head. Absence of ocelli (eyes) [lateral eyes] on dorsal and ventral sides as well as the Tömösvary organ (post-antennal organ).

Sensory organs: Two complete antennae [antennulae] of 1.5±0.11 mm length, both comprising 24 antennomeres (antennal articles; Fig. 1B). Antennae are inserted on the antero-lateral ventral side and carry hundreds of sensilla. Antennae are long and thin; reaching until the end of the anterior third of the trunk. The two proximal and distal antennal articles are longer in length, all others sub-similar, consistently small, without alternation of length (in proximo-distal sequence: 2L, 21S, L) [long, short].

Mouth parts: Labrum (clypeolabrum) [hypostome-labrum complex] with four clypeal setae arranged in two parallel straight lines. Mandibles with at least three main teeth, the bristle structure was not available (Fig. 1D, E). Distal parts of second maxillae (“palp”, “endopod”, “telopodite”) visible, long and stout tarsal claw, plumose setae located on the third article (Fig. 1D, E).

Forcipule segment: Two forcipules [maxillipeds; venom claws] made of five elements (Fig. 1D, E). Proximal elements (coxae) [basipods] of the two forcipules are conjoined into a massive coxosternite that presents a median diastema (small gap) and suture. The coxosternite is triangular, broader (425 µm) than long (260 µm). On the coxosternite, teeth are visible, they follow a (1)2+2(1) pattern, including a lateral filiform porodont (tooth-like seta) located on the coxosternite margins. Distal elements forming full rings. Sclerites lateral to the maxilliped continuous with thin sclerotisation posterior to the coxosternite (Fig. 1D, E).

Walking legs: Fifteen fully developed pairs of legs, but the last pair of legs is incompletely preserved, as the further distal elements are outside of the amber (Fig. 1A–C). Legs are incomplete, two are missing: the right leg 2 and left leg 9. Legs 1–12 have seven elements (coxa, trochanter, prefemur, femur, tibia, tarsus and pretarsus), legs 13–14 have eight elements (coxa, trochanter, prefemur,

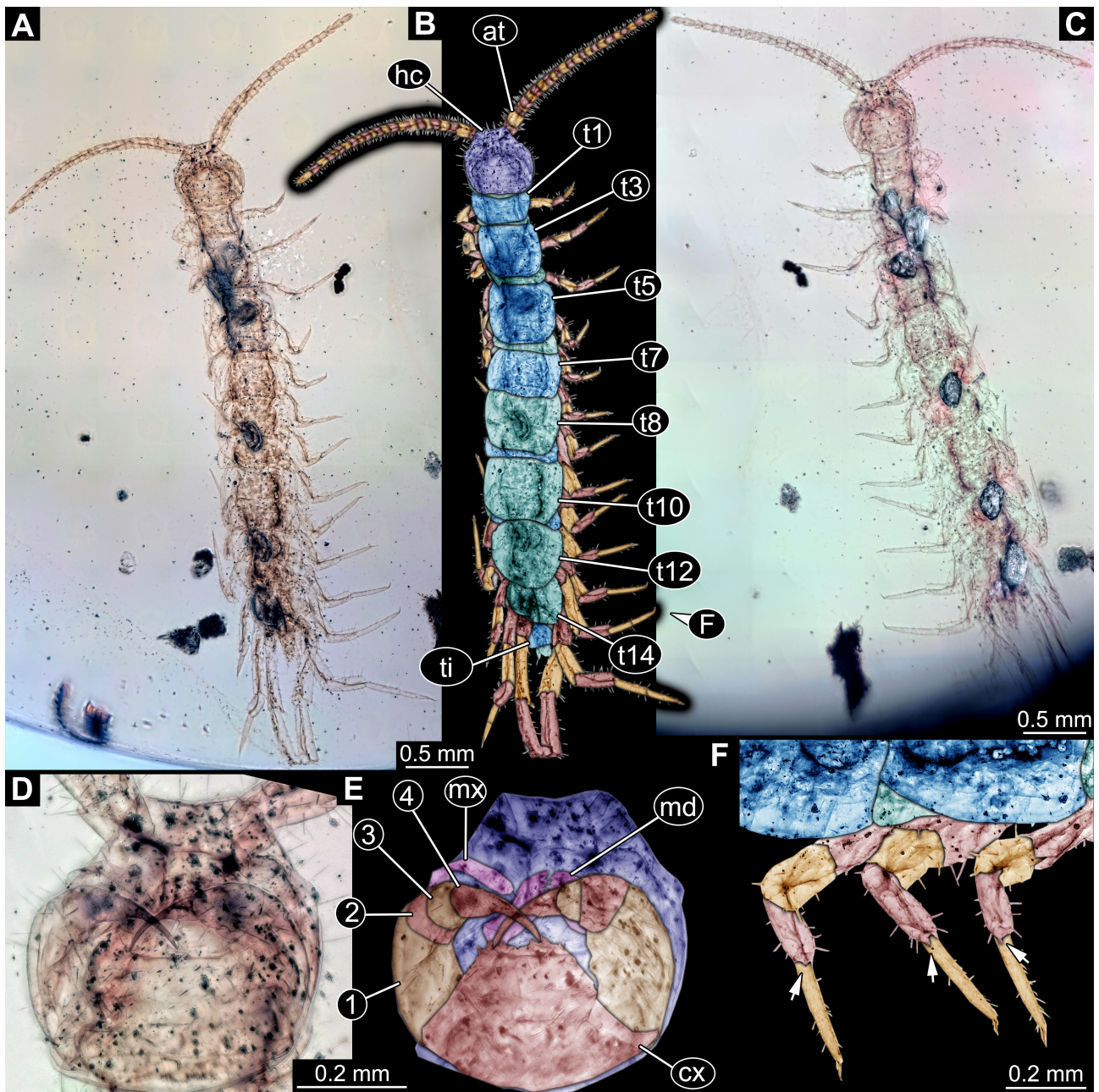


FIGURE 1. PED 2964-1, lithobiomorphan centipede. **A**, Overview of the dorsal side. **B**, Colour-marked version of **A**. **C**, Overview of the ventral side. **D**, Close-up of head in ventral view. **E**, Ventral view of mouth parts with colour-marked structures; 1 to 4 correspond to the elements of the forcipules. **F**, From right to left, leg pairs 10–12, arrows indicate the tibial projection. Abbreviations: at = antenna, cx = coxosternite, hc = head capsule, md = mandible, mx = second maxilla, t1–t14 = segments with walking legs 1–14, ti = intermediate segment.

femur, tibia, tarsus 1, tarsus 2 and pretarsus), we expect the same number of elements for legs 15. In legs 1–7, all elements are of about the same length and width. From legs 8–13, increase in length of the femur and tarsus. Tarsi of legs 1–12 undivided, tarsi of legs 13–14 are bipartite (Fig. 1F; leg 13). Tibia is as long as each tarsomere (tarsal elements) of bipartite legs. Leg spurs encircling the legs are absent, but a spinose projection is present on tibiae of legs 1–11, and a blunt-projection on the tibia of leg 12

(Fig. 1F). Legs seem to increase in length along the body segments as well as becoming much larger in size (Fig. 1A–C). Pretarsus with claws, a single main claw and two accessory claws (anterior and posterior).

Description of PED 2964-2

General morphology: Body is not fully developed. Specimen is small, measuring ~1.68 mm in length (Fig. 2A–C). Along the body, eleven tergites are visible, one on

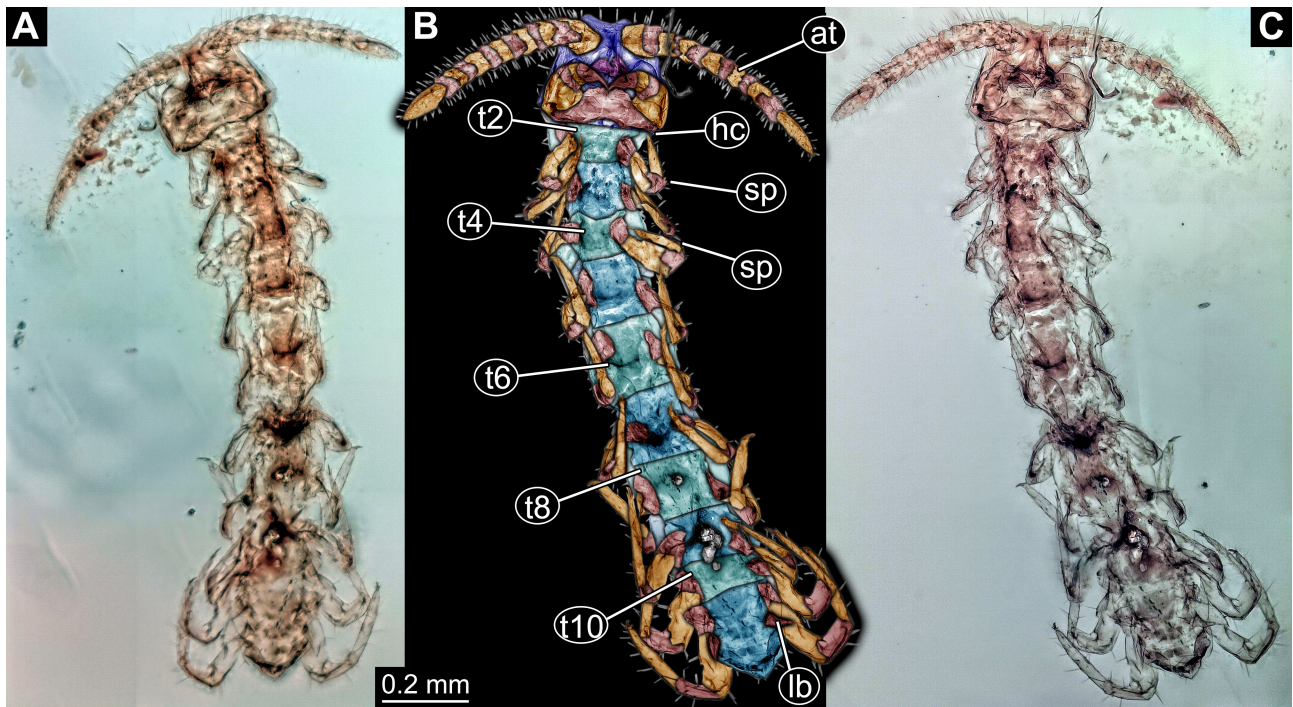


FIGURE 2. PED 2964-2, lithobiomorphan centipede. **A**, Overview of the ventral side. **B**, Colour-marked version of **A**. **C**, Overview of the dorsal side. Abbreviations as follows: at = antenna, hc = head capsule, lb = limb buds, sp = tibial spinose projection, t2–t10 = segments with walking legs 2–11.

the segment bearing the pair of forcipules [maxillipeds; venom claws] and the other ten on the segments bearing the ten pairs of walking legs. They are seemingly rounded and bordered laterally, posterior projections of tergites are absent. A small tergite of 45 μm length is located at the end of the head capsule, dorsal to the forcipules [maxillipeds]. Longer tergites at t1 (140 μm), t3 (235 μm), t5 (505 μm), t7 (210 μm), t8 (220 μm) and t9 (180 μm). Shorter tergites at t2 (140 μm), t4 (100 μm), t6 (70 μm) and t10 (130 μm). Tergites are seemingly rounded and bordered laterally, except for t2 and t6, which are straight.

Head: Head dorso-ventrally flattened, slightly broader (~265 μm) than long (~225 μm). Absence of ocelli on dorsal and ventral sides as well as the Tömösvary organ. Seemingly absence of a median furrow.

Sensory organs: Short pair of antennae [antennulae] of ~520 μm in length, comprising 14 elements, carrying hundreds of sensilla (Fig. 2B). Antennae are reaching until the fourth trunk segment. The two proximal elements and the distal element are longer than the remaining elements. Antennomeres (antennal articles) are seemingly following a pattern of two short elements interspersed by a longer element, at the exception of the proximal antennal article (in proximo-distal sequence: 2L, 3S, L, 2S, L, 2S, L) [long, short].

Mouth parts: Labrum (clypeolabrum) [hypostome-labrum complex] presents four setae that are arranged linearly, parallel to the mouth opening. Mandibles are

unclear, and the bristle structure was not available (Fig. 3F, G). Maxillae visible, only a small fragment of the second maxilla (distal part, “palp”, “endopod”, “telopodite”), the terminal claw (pretarsus) and plumose setae are not visible (Fig. 3F, G).

Forcipule segment: Two forcipules [maxillipeds; venom claws] made of five elements (Fig. 3F). The coxosternite presents a median diastema and suture. It has a trapezoidal shape, broader (~195 μm) than long (~105 μm) with (1)2+2(1) coxosternal teeth, including a filiform porodont on the margins. Distal elements of the forcipules are forming full rings. Sclerites lateral to the maxilliped continuous with thin sclerotisation posterior to the coxosternite (Fig. 3F, G).

Walking legs: Ten fully developed leg pairs, with an additional pair of limb buds on the trunk end (Fig. 2B, C). Legs are tucked under the ventral side. Absence of leg spurs on all legs and presence of a tibial spinose projection on at least right legs 1 and 2 (Figs 2B, 3G). Tarsi of all leg pairs are unipartite. On all legs, pretarsus comprises a main claw with an anterior and posterior accessory claw.

Description of BUB 4771

General morphology: Body is not fully developed. Specimen is small, with an average total body length of ~1.98 mm (Fig. 3A–C). Seemingly one tergite on the first trunk segment, *i.e.* segment bearing the pair of forcipules [maxillipeds; venom claws], followed by

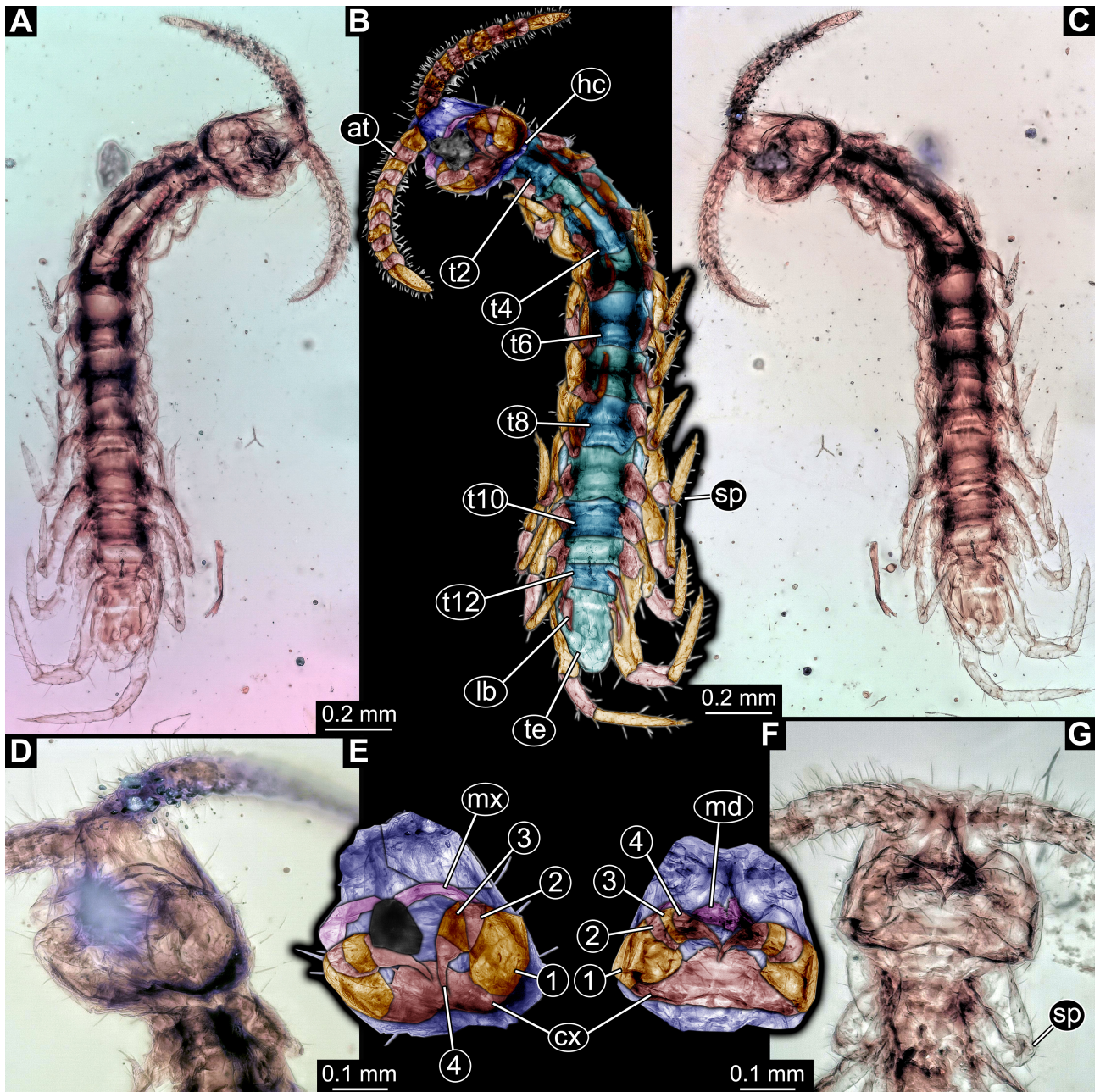


FIGURE 3. Lithobiomorphan centipedes. **A–E**, BUB 4771. **A**, Overview of the dorsal side. **B**, Colour-marked version of **C**. **C**, Overview of the ventral side. **D**, Head capsule and mouth parts, ventral side. **E**, Colour-marked version of **D**; 1–4 correspond to the forcipule elements. **F**, **G**, PED 2964-2, ventral view. **F**, Colour-marked version of **G**; 1–4 correspond to the forcipule elements. **G**, Head capsule and mouth parts, ventral side. Abbreviations: at = antenna, cx = coxosternite, hc = head capsule, lb = limb buds, md = mandibles, mx = 2nd maxillae, sp = tibial spinose projection, te = trunk end, t2–t12 = segments with walking legs 2–12.

twelve tergites indicating twelve segments, but only the anterior ten with pairs of walking legs; the two posterior segments bearing the two pairs of limb buds (Fig. 3B, C). Absence of posterior projections of tergites. Tergite of 45 μm in length formed by the segment bearing the pair of forcipules [maxillipeds; venom claws]. Longer tergites at t1 (137 μm), t3 (237 μm), t5 (275 μm), t7 (285 μm), t8 (235 μm) and t10 (195 μm). Small tergites at t2 (160 μm), t4 (125 μm), t6 (115 μm) and t9 (115 μm) and t11 (90 μm). On the trunk end, a long tergite of 220 μm (t12).

Head: Head dorso-ventrally flattened, slightly longer (~310 μm) than broad (~265 μm ; Fig. 3A–C). Absence of ocelli on dorsal and ventral sides as well as the Tömösvary organ. Seemingly absence of a median furrow.

Sensory organs: Short antennae of ~565 μm in length, comprising 13 articles. Antennae are reaching until the third trunk segment (Fig. 3B). The two proximal articles and the distal article are longer than the remaining ones. Antennomeres (antennal articles) seemingly do not follow any pattern, similar length of the articles, at the

exception of the proximal antennal article (in proximo-distal sequence: 2L, 10S, L) [long, short].

Mouth parts: A piece of dirt blocks access to the mandibles and anterior part of the coxosternite (Fig. 3D, E). Labrum (clypeolabrum) [hypostome-labrum complex] presents four setae that are arranged linearly, parallel to the mouth opening (Fig. 3E). Maxillae are visible but a piece of dirt is blocking the access to more details.

Forciple segment: Two forcipules [maxillipeds; venom claws] made of four elements, that are forming full rings (Fig. 3E). It is trapezoidal, broader (~195 µm) than long (~95 µm). The coxosternites present teeth following (1)2+2(1) pattern, including a lateral filiform porodont at its margins.

Walking legs: Ten fully developed pairs of legs, tucked under the ventral side, with an additional number of two pairs of limb buds (Fig. 3C, D) Leg spurs are absent, but seemingly presence of a spinose projection on at least the left leg 7 (Fig. 3B). Tarsi of all legs are unipartite. On each leg, pretarsus composed of a main claw and two accessory claws (anterior and posterior).

Discussion

General information and preservation

The two amber pieces are well preserved, with only a small breakage point near the inclusion of PED 2964-1. Out of the three specimens investigated, PED 2964-1 is the most exceptionally preserved one. It does not seem to be crushed or flattened and presents almost all of its legs. Both amber pieces show a relatively low amount of dirt, allowing the access of detailed and precise morphological characters.

Representatives of Lithobiomorpha are usually differentiated into two major ingroups: Lithobiidae and Henicopidae. Previous investigations revealed that they share a similar developmental pattern (Andersson 1979), however Lithobiidae has been more heavily studied compared to Henicopidae (Minelli & Sombke 2011). Usually, after hatching they are going through five post-embryonic stages (instars) in which segments are added (anamorphic phase), followed by multiple stages without segment addition (post-anamorphic phase, epimorphic phase). Notably, the number of post-anamorphic stages is not similar, and the number varies between species (Andersson 1979; Andersson 1984; Minelli & Sombke 2011).

An important feature that can be used to infer the developmental stage is the presence of coxal pores (coxal organs) on legs 12–15. The role of the coxal pores is multifunctional (*i.e.*, water intake, exchange of “ions”; Littlewood 1983). Their number is used for describing

post-anamorphic stages of centipedes (Andersson 1984) as well as for species description. This character is particularly difficult to assess in fossils of lithobiomorphan centipedes, and even more in late-stage immatures; coxal pores start to appear at stage V, and they usually possess at that stage a single coxal pore on each coxa (Andersson 1976; Andersson 1981; Andersson 1984). Similar to what has been found in previous studies on centipedes, accessing such a character proves to be too difficult (Haug *et al.* 2013; 2024). An additional important point about the three specimens: They are lying in a flat position within their respective amber pieces, which is good for accessing a lot of characters. However, due to the inaccessibility of the lateral side, identifying features such as the presence of eyes or the Tömösvary organ is impossible. We can therefore not clearly show if these specimens are blind with certainty. It could well be possible, as bulges, indicating eye structures, are not visible in any of them.

General identity of PED 2964-1

When looking back at the phylogenetic tree of centipedes, the first branch is that of Scutigermorpha. Their habitus (seven visible tergites), antennal structure (*i.e.*, long filiform flagellum), faceted eyes, slender forcipule elements are all very distinct from the remaining group of Pleurostigmophora (*i.e.*, Lithobiomorpha, *Craterostigmus*, Scolopendromorpha, and Geophilomorpha). In the case of PED 2964-1, we were not able to find any of these character states.

Continuing within Pleurostigmophora, the forcipule elements of PED 2964-1 are very distinct from those found in the group Epimorpha (Scolopendromorpha + Geophilomorpha). In the latter group, distal part of the venom claws (without the coxa) is made of four elements, but the proximal and distal elements form a joint, leading to elements 2 and 3 not forming continuous rings (*i.e.*, fig. 3.6 in Minelli & Koch 2011; Haug *et al.* 2014). This structure of four elements forming continuous rings is present in the two remaining groups Lithobiomorpha and *Craterostigmus*. These two groups are rather similar, but they are distinct in terms of 1) number of tergites (21 in post-anamorphic *Craterostigmus* and 15 in Lithobiomorpha); 2) 18 antennal articles in *Craterostigmus* and 3) representatives of *Craterostigmus* are presenting a process on the proximal forcipule elements. Overall, PED 2964-1 does not share similar characteristics found in *Craterostigmus*.

Moreover, one of the most important characteristic available in PED 2964-1 is its number of legs (*i.e.*, 15 pairs of legs), indicating an anamorphic development instead of an epimorphic development. Epimorphan centipedes hatch with their final set of legs already developed (Minelli & Fusco 2013) and in higher number

(>15 pairs of legs). Since PED 2964-1 is presenting less than 21 tergites, it is very likely that this is a representative of Lithobiomorpha. When compared to previous studies from Andersson (1979, 1984), PED 2964-1 has a fully developed trunk, thus it could be at least a subadult (post-anamorphic stage). Despite our best efforts, we are not able to precisely identify which post-anamorphic stage it is, since the coxal pores are not available. As stated previously, only two descriptions of lithobiomorph-like centipedes from the Cretaceous Period are available (Zhang 2017; *i.e.*, *Lithopendra anjafliessae*, Haug *et al.* 2024), and only *Lithopendra anjafliessae* has been investigated in detail. *Lithopendra anjafliessae* and PED 2964-1 both share a lithobiomorphan habitus, but their lengths differ, *L. anjafliessae* being longer than PED 2964-1 (respectively 6.75 mm and 4.2 mm). The number of antenna articles is higher in PED 2964-1, but this feature could not be used as a precise character as antennae are incomplete in *L. anjafliessae* (≥ 19 antennal articles). Yet, they both share similar characters, first is the absence of spurs encircling their legs and their structure: articles are decreasing in length from the proximal to the distal article. Nonetheless, due to the last pair of legs in PED 2964-1 being truncated, we are not able to draw a final conclusion about their relatedness, it seems still very likely that PED 2964-1 is not another representative of *L. anjafliessae*.

Representatives of Lithobiidae and Henicopidae are living in same habitats (Decker *et al.* 2014), but representatives of Lithobiidae are more abundant in the northern hemisphere compared to Henicopidae, that are more abundant in the southern hemisphere (Bonato & Zapparoli 2011; Enghoff *et al.* 2013). Many morphological features have been used to differentiate representatives of Lithobiidae from those of Henicopidae: the latter are characterised by the absence of spurs on the legs, only a single pair of ocelli or being blind, continuous

lateral sclerites of the maxilliped segment (Edgecombe *et al.* 2002) and a distal spinose projection that is at least present on the tibia of legs 1–11 in Henicopidae (Zapparoli & Edgecombe 2011). Out of the two ingroups, PED 2964-1 shares more similarities with representatives of Henicopidae and more precisely with the extant representatives of *Lamyctes* Meinert, 1868.

Representatives of *Lamyctes* occur all over the world (Enghoff *et al.* 2013). As they are an ingroup of Henicopidae, they present a distal spinose projection on the tibia of their legs 1–11(12), unipartite tarsi on legs 1–12 and bipartite tarsi on legs 13–15 (Edgecombe 2001; Zapparoli & Edgecombe 2011; Shear 2018). The number of antennal articles in PED 2964-1 is also similar to extant representatives of *Lamyctes*, usually being at around 25 antennal articles (24 in *Lamyctes coeculus* Brölemann, 1889; up to 29 in *Lamyctes africanus* Porath, 1871). In addition, both share a coxosternite with 2+2 teeth, accompanied with one porodont on each margin of the coxosternite. A character that is often used to describe *Lamyctes*, and more generally Henicopinae, an ingroup of Henicopidae, is the absence of posterior projections of the tergites.

It is very likely that PED 2964-1 is an early representative of *Lamyctes*, but further reaching conclusions are difficult as *Lamyctes* is a group with high intraspecific variation (*i.e.*, *Lamyctes emarginatus* Newport, 1844; Edgecombe & Giribet 2003). An interpretation of PED 2964-1 as an early representative of *Lamyctes* Meinert, 1868, is congruent with molecular dating with an estimated divergence between *L. coeculus* and (*L. africanus* + *L. emarginatus*) at around 132 mya, and the divergence of some representatives of Henicopidae around 190 mya (Muriénne *et al.* 2010). Its interpretation as an early representative of *Lamyctes* makes it the first formal and earliest description of a lithobiomorphan centipede, but also that they retained very similar morphological features for ~100 million years.

TABLE 1. Development of legs in the post-embryonic instars of *Lamyctes emarginatus* from Andersson (1979, Table 2) including the three new lithobiomorphans from Myanmar amber.

Instars	Pairs of legs	Half-developed legs	Limb buds
I	7	-	1 large
II	7	1	2 small
III	8	-	2
IV	10	-	2
V	12	-	3
Post-anamorphic	15	-	-
PED 2964-1	15	-	-
PED 2964-2	10	-	1
BUB 4771	10	-	2

Two post-embryonic instars—PED 2964-2 and BUB 4771

The two smaller specimens are relatively well-preserved but seem to be flattened due to the fossilisation. Furthermore, their legs are tucked under their ventral side, making it more difficult to access ventral features and leg features. First of all, it is clear that they both are post-embryonic stages of centipedes, but what are their developmental stages? Both are post-embryonic stages with ten pairs of legs, and the presence of respectively one and two limb buds in PED 2964-2 and BUB 4771. A number of leg pairs below 15 is a clear indication that they are anamorphic centipedes (Edgecombe & Giribet 2007). Yet, in the case of PED 2964-2 and BUB 4771, they both possess ten pairs of legs, which is not present in any larval instars of *Craterostigmus* as they hatch with already twelve pairs (Edgecombe & Giribet 2007; Minelli & Sombke 2011), nor is it present in Scutigermorpha (Verhoeff 1905; Minelli & Sombke 2011). A few apomorphic characters have been listed in the past for Lithobiomorpha (Edgecombe 2011a), consistent features that we identified are: four clypeal setae in front of the labrum and the presence of porodonts on the coxosternite. For BUB 4771, there is no ambiguity concerning its post-embryonic stage as it shares similar features with stage IV lithobiomorphans: 1) ten fully developed leg pairs, and 2) two pairs of limb buds (Table 1; Andersson 1979; Andersson 1984). However, we only found one pair of limb buds for PED 2964-2. It could still be a stage IV immature, as a single pair of limb buds is probably an artifact from low resolution due to the small size (~1.68 mm) and its legs being tucked over the ventral side. Concerning the number of eleven tergites (on segments of walking legs) found in PED 2964-2, the number is odd. At stage IV, a number of twelve tergites should be found, formed by the twelve trunk segments bearing walking legs (Bortolin 2010). Similar to the problem with the limb buds, the visibility of each trunk segment separation was tricky and unclear for PED 2964-2, this is also probably an artifact due to its small size.

PED 2964-2 and BUB 4771 are very similar in length and morphologies, they share a relatively similar number of antennal articles (*i.e.*, 14 and 13; Figs 2B, 3B). The antennae of these two specimens seem to have pairs of shortened articles interspersed by longer ones, a characteristic formally described in a few groups of Henicopinae: *Lamyctes*, *Analamyctes*, and *Henicops* (Edgecombe 2001; Edgecombe *et al.* 2002). Nonetheless, the odd number of antennal articles found in BUB 4771 is peculiar from previous study in extant species. Usually, stage IV lithobiomorphans possess 14 antennal articles (Andersson 1979), due to the small size of this individual and the ambiguity on the precise subdivision

of its antennae it is possible that it is an artefact. Due to the one immature being preserved in the same piece with the larger specimen, a conspecificity of all three specimens seems quite likely.

Scarcity of lithobiomorphans in the geological record

The scarcity of the fossil record of Myriapoda is an ongoing problem since now a few decades (Kraus 1974). To this day, it is still surprising that lithobiomorphan centipedes are absent in the Palaeozoic Era and understudied in the Mesozoic Era (Shear & Edgecombe 2010; Edgecombe 2011b; Fernández *et al.* 2014). Few fossils of Lithobiidae have been formally described in the past; fossil records are mostly confined to the Eocene (*i.e.*, Baltic amber; Haug *et al.* 2013; Fernández *et al.* 2014), with a few specimens that were depicted, but not described in detail from the Mesozoic Era. This was the case until recently, when a new lithobiomorphan-like centipede from Kachin amber, Myanmar has been described (~100 million years old; Haug *et al.* 2024). Yet, this new specimen showed plesiomorphic characteristics from Pleurostigmophora and suggested convergent characters of Scolopendromorpha, due to this ambiguity it was not possible to clearly relate it to Lithobiomorpha. Here, in this study, PED 2964-1 is very likely related to the extant genus of *Lamyctes*, and also PED 2964-2 and BUB 4771 could be related to Henicopidae. Altogether, they represent the first unambiguous record of the group of Henicopidae and Lithobiomorpha from the Cretaceous period. Such report should not be surprising; in fact, fossils seem readily available in numbers from Myanmar amber (numerous specimens in the Palaeo-Evo-Devo collection; see also Zhang 2017).

With the development of new phylogenomic tools, the previously “resolved” phylogeny of Chilopoda from earlier molecular and morphological characters has been questioned concerning the position of *Craterostigmus*. Morphologically, *Craterostigmus* is part of Phylactometria as they share similarities such as lateral eye structure (Müller & Meyer-Rochow 2006), rigidity of the forcipules, coxal organs (Fernández *et al.* 2014); new molecular data indicate a sister-group position to Amalpighiata (Lithobiomorpha, Scolopendromorpha, and Geophilomorpha; Fernández *et al.* 2014).

In the light of novel molecular phylogeny of Chilopoda, descriptions of new unambiguous lithobiomorphans from Myanmar amber are very important. Better molecular clock analyses require good fossil calibration (Near & Sanderson 2004; Hug & Roger 2007), something that cannot be properly performed without early Mesozoic fossils and Palaeozoic fossils of Lithobiomorpha.

Another aspect of the new fossils is exceptional: Two specimens occur in a single amber piece, *i.e.*, are preserved in close proximity. So far, finds of fossil

centipedes were single finds, indicating low densities in the original habitat, which might have partially explained the scarcity. With the piece at hand, we can expect higher densities in Myanmar amber, and we should expect more finds from this deposit.

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