



Convergent evolution of defensive appendages – a lithobiomorph-like centipede with a scolopendromorph-type ultimate leg from about 100 million-year-old amber

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Abstract

Centipedes are predatory representatives of the group Myriapoda and important components of the soil and leaf-litter fauna. The first pair of trunk appendages is modified into venom-injecting maxillipeds in all centipedes. The number of trunk appendage pairs varies between the different groups of centipedes, from 15 pairs as apparently ancestral (plesiomorphic) condition, up to 191 pairs. The last pair of trunk legs can be used for different tasks in centipedes, e.g. mechano-sensation, defense, or stridulation. Many morphological details are also known from fossil centipedes, but especially the oldest fossils are often fragmentary and the fossil record in general is rather scarce. Especially the late appearance of lithobiomorphans in Cenozoic ambers is notable, though some not formally described lithobiomorph-like specimens from Cretaceous amber from Myanmar have been published. We present here a new specimen from Cretaceous Kachin amber, Myanmar with a lithobiomorph-type of morphology, *Lithopendra anjafliessae* gen. et sp. nov. The very large ultimate leg appears to have been used for defence and is, in relative proportions, larger than in any known lithobiomorph, only comparable to that in scolopendromorphans. With this, the specimen presents a mixture of characters, which are in the modern fauna only known from two different centipede groups. We discuss the implications of this new fossil, also concerning events of convergence in this lineage.

Keywords Chilopoda · Lithobiomorpha · Scolopendromorpha · Myanmar amber · Burmese amber · Convergence

Introduction

Chilopoda, the group of centipedes, is an ingroup of Euarthropoda (the latter also including shrimps, beetles, spiders and all their closer relatives; Edgecombe and Giribet 2007). Chilopoda has about 3,100 formally described species (Minelli 2011). All centipedes are terrestrial predators and as such ecologically important components especially of the soil and leaf-litter fauna (Voigtländer 2011).

Chilopoda is generally considered to include five major ingroups, branching off consecutively: Scutigromorpha

including about 60 formally described species (Minelli 2011), Lithobiomorpha with about 1,120 formally described species (Minelli 2011), *Craterostigmus* including two species (Edgecombe and Giribet 2008), and the two sistergroups Geophilomorpha with more than 1,250 formally described species (Minelli 2011; Bonato et al. 2014) and Scolopendromorpha including more than 670 formally described species (Edgecombe 2011a; Minelli 2011) (for an alternative phylogenetic interpretation, see e.g. Fernández et al., 2014 and discussion below). The five major ingroups can be rather easily differentiated already by a rough view, for example by the number of their walking legs (at least in adults) and sclerotised plates on their back (tergites). Scutigromorphans have 15 pairs of very long walking legs. Also representatives of Lithobiomorpha and *Craterostigmus* have 15 pairs of walking legs, but shorter ones. Lithobiomorphans have 15 tergites, yet some are shorter and not always visible; individuals of *Craterostigmus* have 21 tergites (Edgecombe and Giribet 2008). Scolopendromorphans have 21–23 pairs of legs (with the exception of a single species with 25 leg pairs and another one with 39–43 leg pairs; Chagas-Junior

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et al. 2008, 2022), and geophilomorphans have at least 27 pairs of legs, but up to 191 (Kenning et al. 2017).

The most striking feature of all centipedes (and autapomorphy of Chilopoda) is the morphology of their first pair of trunk appendages, which evolved into a pair of venom-injecting claws (Haug et al. 2014 and references therein). The exact morphology differs in the five groups and allows the reconstruction of distinct evolutionary events further specialising certain mechanical aspects (Haug et al. 2014 and references therein). All trunk legs posterior to the venom claw, besides the very last one (and in certain cases also the penultimate one), are walking-type appendages.

The last pair, or pair of ultimate legs can be used (and be morphologically specialised) in many ways (recently reviewed in Kenning et al. 2017). To list just some:

- 1) It can be formed as a very elongated, possibly mechano-sensorial structure in some lithobiomorphans (Edgecombe 2001 fig. 2 p. 205) and as a clear mechano-sensorial feeler-like structure in scutigermorphans (Kenning et al. 2017 fig. 2 p. 5) and some scolopendromorphans (Schileyko 2009 fig. 3e p. 522; Chagas-Junior 2011; Schileyko 2013 fig. 8 p. 43; De Azara and Ferreira 2014; Schileyko 2014 fig. 44 p. 172).
- 2) It can be formed as a defensive structure (Verhoeff 1902–1925) for performing strikes in some lithobiomorphans (Edgecombe 2001 fig. 17 p. 226; Voigtländer et al. 2017 fig. 12A p. 26), appearing similar in *Crateostigmus* (Edgecombe and Giribet 2008 fig. 2 p. 3) and even stronger expressed in some scolopendromorphans (Chagas-Junior et al. 2008 figs. 8–11 p. 42; Schileyko 2009 fig. 3b p. 521; Di et al. 2010 fig. 3 p. 57; Muadsub et al. 2012 fig. 7F, G p. 44; Kronmüller and Lewis 2015 fig. 1B p. 271; Siriwut et al. 2016).
- 3) It can be formed as a leaf-like structure for stridulation in some scolopendromorphans (Schileyko 2009 fig. 3f p. 522; Kronmüller and Lewis 2015 fig. 1C p. 271; Kenning et al. 2017 fig. 6 p. 12)
- 4) It can be formed as a sensorial structure in (some?) geophilomorphans (Sombke and Müller 2021), but appears rather unspecialised on a less magnified view.

The fossil record of Chilopoda is scarce in certain aspects (Shear and Edgecombe 2010; Edgecombe 2011b), but many details are known well enough to include fossils into evolutionary reconstructions (e.g. Haug et al. 2014). The oldest remains of fossil centipedes are fragments of legs of scutigermorphans from the Silurian (Shear et al. 1998), other fragments are known from the Devonian (Shear et al. 1998; Anderson and Trewin 2003; Haug and Haug 2017). More complete, but still fragmented pieces, are known from the Devonian as cuticle remains of *Devonobius delta*, which shares some characters with *Crateostigmus* (Shear and Bonamo 1988). In the Carboniferous, scutigermorphans

and scolopendromorphans are known from more or less complete body fossils (Mundel 1979; Haug et al. 2014). Geophilomorphans make their appearance in the Jurassic (Schweigert and Diel 1997; Haug et al. 2014). Only lithobiomorphans are unusual in their time of appearance: besides their relatively early branching off and their rather plesiomorphic morphology (most likely strongly resembling the ground pattern of Pleurostigmophora, which includes all centipedes besides Scutigermorphans), the oldest formally described fossils are from Cenozoic ambers (Edgecombe 2011b).

Yet, some lithobiomorph-like, not formally described specimens preserved in about 100 million-year-old Kachin amber from Myanmar were shown in Zhang (2017; see also Wesener and Moritz 2018). We here report a new specimen with a lithobiomorph-type of morphology from Cretaceous Kachin amber, Myanmar. The ultimate leg is very large, especially in comparison to the penultimate leg, and appears to represent a defensive appendage. It is in fact larger, in relative proportions, than in any known lithobiomorph, in this way only comparable to that in scolopendromorphans. We discuss implications of this find concerning the fossil record of Chilopoda and convergent evolution in this lineage.

Material and methods

Material

In the centre of this study is a single fossil centipede, preserved in 100 million-year-old Kachin amber, Myanmar. It was legally purchased via the internet platform [ebay.com](https://www.ebay.com) from the trader burmite-miner. The specimen is now deposited in the Palaeo-Evo-Devo research group collection of arthropods, Ludwig-Maximilians-Universität München, Germany under repository number PED 1818.

Documentation methods

We documented the fossil centipede under a Keyence VHX-6000 digital microscope with cross-polarised coaxial light and unpolarised low-angle ring light in front of a black and a white background at a magnification of 200x. Each part of the specimen was documented with a stack of images (frames) in different levels of focus. Sharp images were fused from these stacks. Several adjacent sharp images were automatically stitched together to a panorama image with the built-in software (for details, see Haug et al. 2013, 2018). The resulting image of the fossil centipede was colour-marked in Adobe Photoshop CS2.

Measurements and comparisons

For a comparison between the new specimen and other centipedes, we used quantitative morphology, applying ratios of

linear measurements on specific morphological structures. Due to certain similarities of the new fossil specimen with lithobiomorphans and scolopendromorphans, only these two groups were considered for the comparison. Representatives of these groups were exclusively studied based on illustrations in the literature that provided sufficient details and the appropriate angle of view to perform the measurements in the same way as on the images of the fossil specimen. Measurements were performed with a calliper (precision 0.1 mm, which is higher than the pixel size) on the images on the computer screen. Measured dimensions include the maximum width and length of the third most distal element (presumably the tibia) of one ultimate leg and one penultimate leg per specimen (Suppl. Table 1). All possible ratios of the widths and lengths were analysed with a principal component analysis using the program PAST (for results of the analysis, see Suppl. Tables 1, 2). The most influential ratios (i.e. the most contributing variables in the first principal components) were then plotted in a scatter plot.

For comparison, some specimens were reconstructed and symmetrized in the vector-based graphic program Adobe Illustrator CS2 and assembled in Adobe Photoshop CS2.

Terminology

Using a terminology that is understandable to a broad audience, while at the same time having distinct and precise meaning is crucial for science communication. Within the group Euarthropoda, many different terminologies have been established, often using the same term for different structures (“antenna” in Insecta and Malacostraca is not the same structure) or the same structure has been addressed to with different names (“hypopharynx” in Insecta is “paragnathus” in Malacostraca). We therefore add cross-referencing to our description by adding terms for Euarthropoda in square brackets and alternative terms in round brackets to enhance understandability for non-centipede-specialists.

Results

Systematic palaeontology

Myriapoda Latreille, 1802

Chilopoda Latreille, 1817

Pleurostigmophora Verhoeff, 1901

Lithopendra gen. nov.

Etymology: Reference to the similarities with lithobiomorph centipedes, “litho”, and similarities to scolopendromorph centipedes, “pendra”.

Type species: *Lithopendra anjafliessae*

Diagnosis: as for the species.

Lithopendra anjafliessae sp. nov.

(Figs. 1 and 4)

Etymology: In honour of Dr. Anja Fließ as a representative of the Volkswagen Foundation for continuous support of science, research, and science communication by her and the entire team of the foundation.

Holotype: PED 1818

Diagnosis: Centipede with an overall lithobiomorph habitus and with a very large ultimate leg, longer than penultimate one, c. 1.6 times.

Type locality: Kachin amber, Myanmar

Description of the specimen: Body with 22 inferable segments plus a trunk end, ocular segment and 21 post-ocular segments (Fig. 1a–c), total length without appendages c. 6.75 mm, maximum width c. 0.8 mm. Ocular segment and post-ocular segments 1–5 forming distinct capsulate head. Further posterior segments are trunk segments.

Ocular segment without apparent structures (eyes, upper lip) [hypostome-labrum-complex]. Post-ocular segment 1 with a pair of prominent appendages, antennae [antennulae]. Antenna elongated, feeler-like, length c. 1.85 mm and maximum width c. 0.2 mm, subdivided into at least 19 elements. Each element wider than long. Elements consecutively decreasing in size from proximal to distal. Post-ocular segment 2 without apparent structures.

Post-ocular segment 3 and 4 without visible prominent structures (mandibles, maxillae 1) [maxillulae]. Post-ocular segment 5 with a pair of prominent appendages, maxillae 2 [maxillae]. Only distal part of maxilla apparent (palp) [endopod], geniculate to sub-chelate in shape, subdivided into at least four elements.

Post-ocular segment 6 (trunk segment 1) with a pair of prominent appendages, maxillipeds (Fig. 1d). Proximal part (coxosternum) [basipod] difficult to discern; distal part of maxilliped (telopod) [endopod] sub-chelate, subdivided into four elements. The most proximal element is sub-rectangular in shape, longer than wide, length of lateral edge c. 0.4 mm, maximum width c. 0.25 mm. The following two elements are both rectangular, shorter than wide, smaller than the most proximal element and similar to each other. The most distal element is claw-like in shape, longer than wide.

Post-ocular segment 7 (trunk segment 2) with a pair of prominent appendages, walking appendages. Segment wider than long, tergite not accessible. Walking appendages subdivided into at least four elements, all wider than long.

Post-ocular segments 8–21 (trunk segments 3–16) sub-similar. Post-ocular segment 8 with slightly longer walking appendages. Post-ocular segment 9 similar to preceding segment. Post-ocular segment 10 slightly longer. Post-ocular segment 11 slightly shorter. Post-ocular segment 12 slightly longer. Post-ocular segment 13 slightly wider. Post-ocular segment 14 slightly shorter, with slightly longer walking appendages. Post-ocular segment 15 slightly longer, with

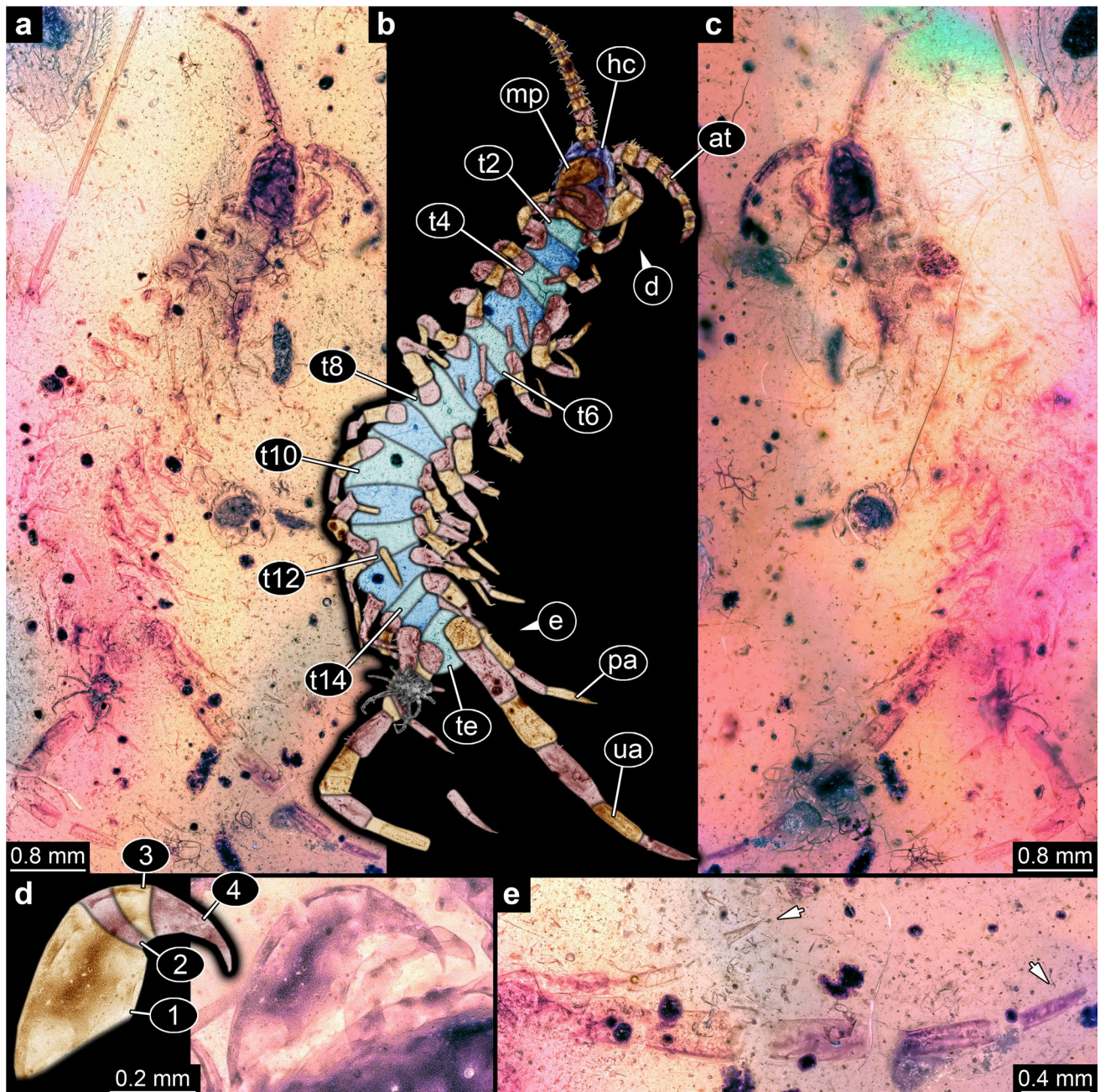


Fig. 1 Holotype of *Lithopendra anjafiessae* gen. et sp. nov., PED 1818. **a–c** Overview. **a** Ventral view. **b** Colour-marked version of **a**. **c** Dorsal view. **d** Left maxilliped as colour-marked (left) and regular version (right). **e** Left penultimate and part of ultimate appendage;

arrows point to tips. Abbreviations: 1–4 elements of maxilliped; at antenna; hc head capsule; mp maxilliped; pa penultimate appendage; t2–t14 trunk segments 2–14; te trunk end; ua ultimate appendage

slightly longer walking appendages. Post-ocular segment 16 slightly shorter. Post-ocular segment 17 slightly shorter and narrower. Post-ocular segment 18 slightly wider. Post-ocular segment 19 slightly shorter. Post-ocular segment 20 slightly longer; appendages of this segment, penultimate appendages, about 2.4 mm long, significantly longer than those of

the preceding segments (Fig. 1b, e). Post-ocular segment 21 slightly longer, with a pair of very prominent appendages, ultimate appendages. Ultimate appendages about 3.8 mm long, significantly longer and wider than penultimate appendages, subdivided into at least six elements (Fig. 1b, e). Further posterior structures of the trunk not apparent.

Morphometric comparison

The principal component analysis resulted in six principal components (PCs). Of these, PC1–PC3 already explain about 99% of the overall variation, with PC1 explaining 81.9%, PC2 11.0%, and PC3 6.1% (Suppl. Tab. 2).

When plotting the ratio (length of the ultimate leg / width of the ultimate leg) over the ratio (length of the ultimate leg / length of the penultimate leg), the area occupied by scolopendromorphans almost fully includes the area occupied by lithobiomorphans, as well as the new specimen (Fig. 2a). The area occupied by scolopendromorphans is about twice as large as the area occupied by lithobiomorphans. It extends more along the x-axis, which represents the ratio between the lengths of ultimate and penultimate legs. The new specimen does not plot in the area occupied by lithobiomorphans, but very close to it, well within the area occupied by scolopendromorphans (Fig. 2a).

When plotting the ratio (width of the ultimate leg / width of the penultimate leg) over the ratio (length of the ultimate leg / length of the penultimate leg), the area occupied by scolopendromorphans likewise includes a large part of the area occupied by lithobiomorphans, as well as the new specimen (Fig. 2b). Again the occupied area of scolopendromorphans is several times as large as the area occupied by lithobiomorphans. The area occupied by lithobiomorphans is concentrated close to the origin. The part of this area not overlapping with the area occupied by scolopendromorphans plots even closer to the origin. The new specimen does not plot in the area occupied by lithobiomorphans, but very close to it, well within the area occupied by scolopendromorphans (Fig. 2b).

When plotting principal component 2 (PC2) over principal component 1 (PC1), the area occupied by scolopendromorphans is larger than the area occupied by lithobiomorphans, about two times (Fig. 2c). The area occupied by scolopendromorphans overlaps with the area occupied by lithobiomorphans, as well as the new specimen. It especially spreads more in the positive direction of the PC2 axis. The area occupied by lithobiomorphans is largely located on the negative side of the PC2 axis. The new specimen plots outside the area occupied by lithobiomorphans, due to PC2 values, but within the area occupied by scolopendromorphans (Fig. 2c, d).

Discussion

Possible identity of the new specimen

For evaluating the relationships of the new specimen, we need to consider the observable details in a comparative frame (see, e.g. Edgecombe 2011a for phylogeny of Chilopoda). There are alternative interpretations of the phylogeny within Chilopoda

(see also Introduction). The position of *Craterostigmus* in recent analyses has been questioned (see Fernández et al. 2014). Concerning character evolution of important structures (also of the new specimen) such as the venom claw, this aspect is only little affected by this newer phylogenetic interpretation. Furthermore, for comparing fossils we can only rely on morphological characters, and these make a sister-group position of *Craterostigmus* to Epimorpha more likely.

As already mentioned, the first ingroup branching off within Chilopoda is Scutigermorpha. Representatives of this group have 15 pairs of very long walking appendages. Scutigermorpha is the sistergroup to Pleurostigmophora. Pleurostigmophora is characterised by several autapomorphies; most important for our study is a change in the morphology of the venom claw (maxilliped; forcipule): the endopod is rotated so that both are in the same plane of movement, the insertion area of the endopod is further median, and elements 2 and 3 of the endopod are shorter. This morphology is also seen in our fossil, indicating that the fossil is a representative of Pleurostigmophora. This interpretation is further supported by the fact that the distal element is a single continuous entity (tarsungulum), another feature of Pleurostigmophora.

The next group branching off is Lithobiomorpha. Representatives of this group also bear 15 pairs of walking appendages. Also the fossil has this number of walking appendages, yet as apparent by scutigermorphans, this is a plesiomorphic character. Further features characterising the group Lithobiomorpha are coxal pores arranged in a single row on walking leg pairs 12–15. and the female gonopod with spurs on its most proximal element and a broad, scalloped claw terminally. The specimen does not appear to show such a type of gonopods, which may point to it being a male or, if it is a female, not being a representative of Lithobiomorpha. While both interpretations are possible, none of them can be further supported. As the amber is full of dirt particles and small bubbles, identifying pores (such as coxal pores) with confidence is not possible.

Lithobiomorpha is the sistergroup to Phylactometria. Representatives of Phylactometria are characterised by several apomorphies, yet an important one that is in principle possible to observe in a fossil is the reduced mobility between the proximal elements of the maxilliped (Edgecombe and Giribet 2007 p. 161). Unfortunately, this very detail is not well accessible and can in fact not be evaluated.

The next group branching off is *Craterostigmus*. Representatives of *Craterostigmus* also bear 15 pairs of walking appendages, but have several trunk segments with two tergites, bearing 21 tergites in total. Also this detail is not accessible in our fossil.

Craterostigmus is the sistergroup to Epimorpha including Scolopendromorpha and Geophilomorpha. Representatives of Epimorpha can be characterised by several apomorphies, but the most important one for our study is the increased number of body segments. The new specimen has only 15

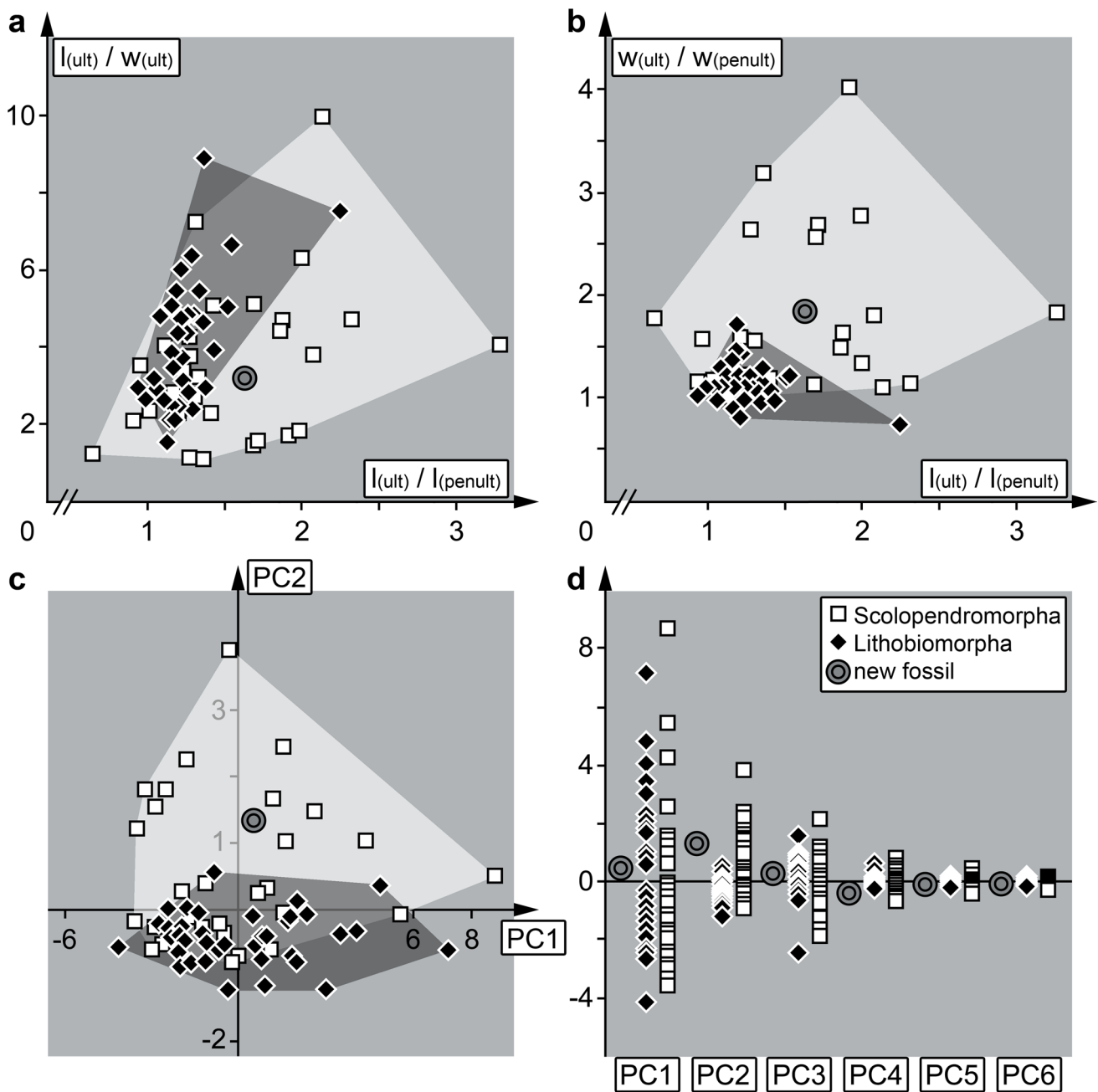


Fig. 2 Visualization of the measured dimensions and principal components of the posterior legs of different centipedes. **a** Ratio (length of the ultimate leg / width of the ultimate leg) over the ratio (length of the ultimate leg / length of the penultimate leg). **b** Ratio (width of the ultimate leg / width of the penultimate leg) over the ratio (length

of the ultimate leg / length of the penultimate leg). **c** Principal component 2 over principal component 1. **d** Ranges of the values for principal components 1–6. Abbreviations: $l(penult)$ length of penultimate leg; $l(ult)$ length of ultimate leg; PC principal component; $w(penult)$ width of penultimate leg; $w(ult)$ width of ultimate leg

body segments and is therefore unlikely a representative of Epimorpha. Although the fossil shares most characters with Lithobiomorpha, most of these similarities are plesiomorphies. Many important details are unfortunately not available in the fossil. It could represent the sistergroup to all remaining pleurostigmophorans, the sistergroup to Lithobiomorpha, but also the sistergroup to Phylactometria,

Craterostigmus, or even Epimorpha. Yet, also an ingroup position within Lithobiomorpha is well possible. The fossil, together with two specimens reported in Zhang (2017, see also Wesener and Moritz 2018), represents the oldest occurrences of a lithobiomorph-type morphology.

It cannot be easily excluded that the new specimen is conspecific with (at least one of) the two lithobiomorph-like

specimens from Zhang (2017, depicted together with two other, non-lithobiomorphan centipedes; Fig. 3b, c). The one specimen (Zhang 2017 p. 132 upper image) is only incompletely shown and does not provide access to the ultimate legs. The other specimen (Fig. 3a; Zhang 2017 p. 132 lower image) is an immature not yet possessing all segments, therefore not possessing these appendages.

The ultimate legs of the new specimen

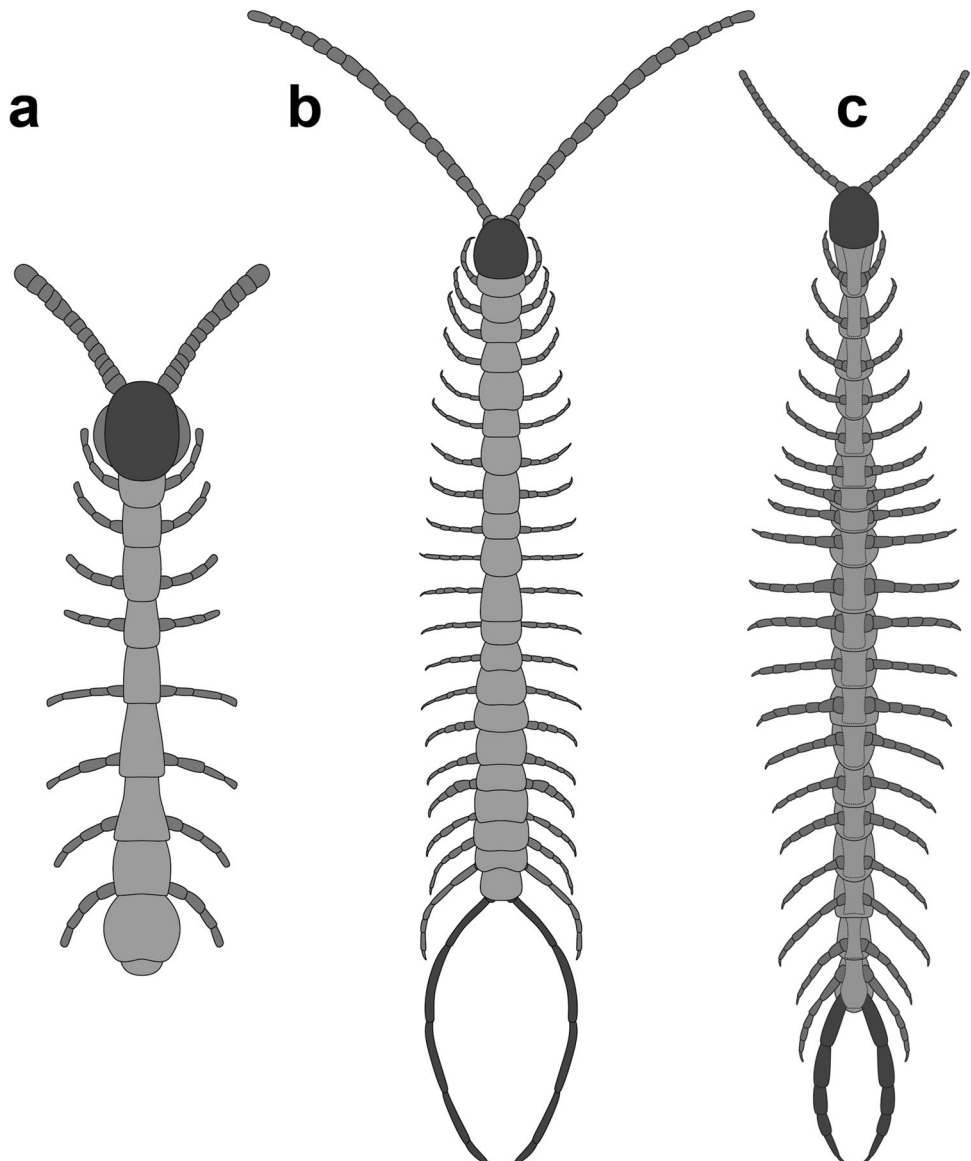
The most prominent morphological structures of the new fossil are the ultimate legs. These are much larger in relative proportions than in any modern lithobiomorphan. To be more precise, there are some lithobiomorphans with relatively longer ultimate appendages, but these are much more slender than those in the fossil (compare Fig. 4a, b with Fig. 4c).

Similar prominent sizes of ultimate appendages, not only concerning length but also width, only occur in scolopendromorphans (Fig. 4d, e). These prominent appendages are usually used as defensive structures. We therefore assume the same function also for the fossil. Hence, although the fossil has an overall lithobiomorph-like morphology, its ultimate appendages are much more of a scolopendromorph-type. As the new fossil is not an ingroup of Scolopendromorpha (not even Epimorpha), the supposed defensive appendages must have evolved convergently to those in scolopendromorphans.

Convergent evolution in Chilopoda

There are several other examples of convergent evolution in Chilopoda. One of them is the evolution of feeler-like ultimate appendages in Scutigermorpha, Scolopendromorpha

Fig. 3 Centipedes from Cretaceous Myanmar amber, modified after Zhang (2017). **a** Lithobiomorpha sp. (p. 132 lower image). **b** Scolopendriidae sp. (p. 128 upper image). **c** Cryptopidae sp. (p. 128 lower image). Images not to scale



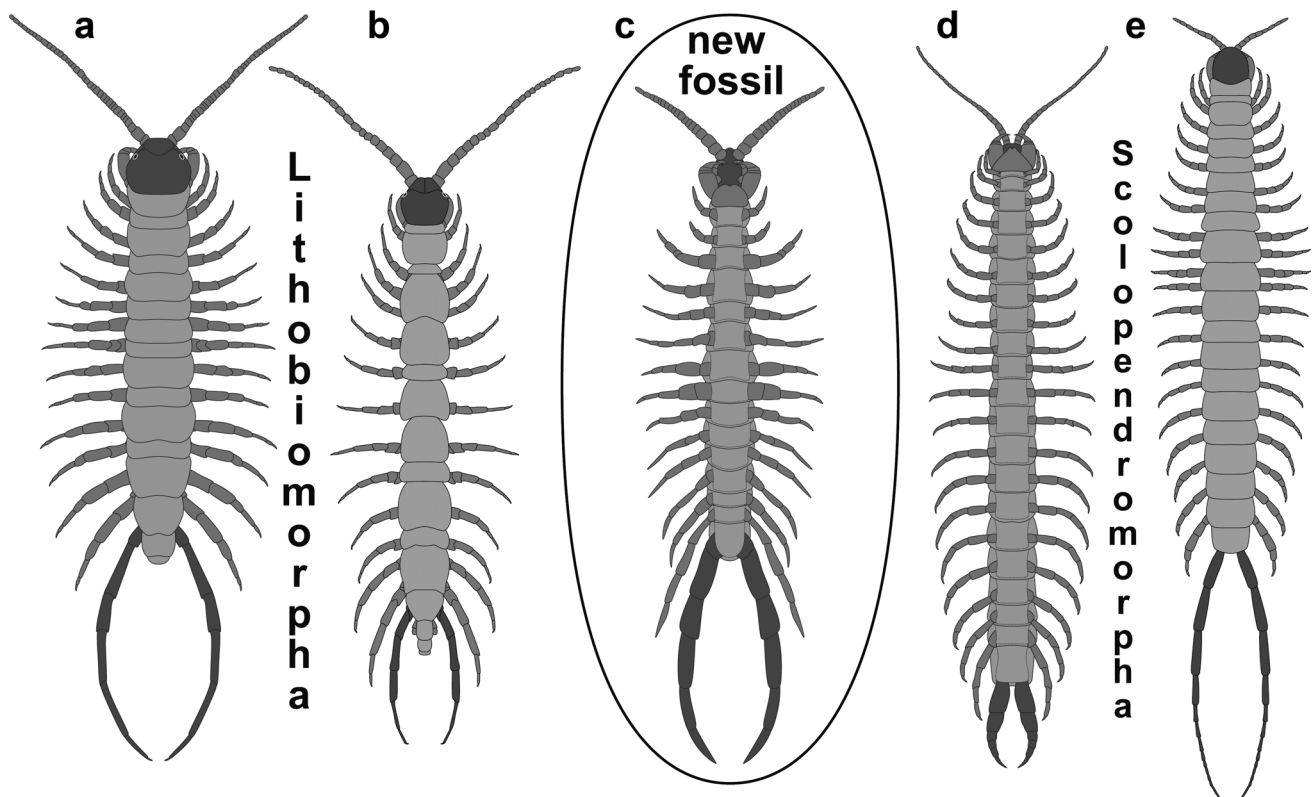


Fig. 4 Comparison of the new fossil (c) with representatives of Lithobiomorpha (a, b) and Scolopendromorpha (d, e) modified from different literature sources. **a** *Analamyctes tucumanus* (Edgecombe 2001 fig. 2). **b** *Paralamyctes* (*Thingathinga*)

hornerae (Edgecombe 2001 fig. 17). **c** New fossil, *Lithopendra anjafliessae* gen. et sp. nov. **d** *Theatops chuanensis* (Di et al. 2010 fig. 3). **e** *Newportia monticola* (Schileyko 2014 fig. 45). Images not to scale

and to a certain extent also Lithobiomorpha. Also the drastic increase of segment number within Geophilomorpha, with up to a total of 191 pairs of legs (Kenning et al. 2017), is found in one species of Scolopendromorpha, which bears between 39 and 43 pairs of legs (Chagas-Junior et al. 2008) instead of between 21 and 23 or rarely 25 pairs of legs (Chagas-Junior et al. 2022).

Usually we can assume that similar selective pressure leads to similar solutions in the form of convergent evolution. Such similarities can be understood in different contexts. Often very similar-appearing morphologies may lead to competition and ultimately lead to exclusion, at least in a specific habitat. We could therefore speculate that a lithobiomorph-like centipede with scolopendromorph-type ultimate leg may not have co-occurred with scolopendromorphans with large ultimate legs. Yet, in Kachin amber such scolopendromorphans are in fact known (Fig. 3b, c; Zhang 2017 p. 128). The presence of defensive structures in both centipedes may therefore be coupled to a high pressure by predators.

Also co-occurrence of similar morphologies in different lineages can be positively selected in cases of mimicry. Mimicry seems to have been rarely, if at all, investigated for centipedes, and it remains unclear whether this could play a role here. One aspect of mimicry could play a role in at least in some centipedes, self-mimicry. The phenomenon refers to cases in which one part of an organism resembles another part of the same organism, e.g. the anterior and posterior part of the same individual resemble each other (in snakes: Gehlbach 1972; Grobman 1978; in caterpillars: Leong 2010). A possible predator therefore has problems in identifying the head and instead attacks the trunk end. So far, this phenomenon has not been explicitly reported for centipedes, yet the overall shape of some centipedes clearly causes this effect. The feeler-like ultimate appendages in scutigermorphans and their antennae cause this effect quite well, but also the ultimate appendages of scolopendromorphans, lithobiomorphans, and the new fossil *Lithopendra anjafliessae* cause this effect to a certain degree.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12549-023-00581-3>.

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Conflict of interest The authors declare that they have no conflict of interest.

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