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# The history of short-tailed whip scorpions: changes in body size and flagellum shape in Schizomida

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**Abstract**

Representatives of Schizomida, known as short-tailed whip scorpions, are an understudied group within Megoperculata. They are found subterraneanly in tropical and sub-tropical regions. They lack eyes, have superior mobility, and possess a flagellum which is relevant to their mating, but in general little is known about their general biology. Fossil representatives of Schizomida from a variety of time periods are available for study. Using 23 fossil specimens (14 of which are described here for the first time) and 86 extant individuals from the literature, changes in both body size and flagella shape in Schizomida were compared over time. Measurements of prosoma length and leg length were used as a proxy for body size, and a comparative size analysis was carried out. Individuals from the Cretaceous period were found to be significantly smaller than extant individuals, contrary to our expectations. For flagellum shape, images were used to create reconstructions, which were then analysed using an elliptic Fourier analysis followed by a principal component analysis. The morphological diversity of the male flagellum shape was found to have decreased between the Cretaceous and modern fauna. We discuss potential explanations for our findings, although a greater understanding of the general biology of Schizomida is required to properly interpret our results.

**Keywords** Amber, Body size, Geometric morphometrics, Miniaturization, Myanmar

## Introduction

The size and shape of an organism causes it to perceive and move within a given habitat in a specific way (Jensen & Holm-Jensen, 1980). For example, a walking surface can be discerned as smoother for larger animals, or more rugged for animals of a smaller size (Kaspari & Weiser, 1999; Levin, 1992; Morse et al., 1985). Thus, changes in size can have profound effects on the ecological and biological functions of an organism (Hanken & Wake, 1993). Size may therefore even be used as a proxy for ecological aspects within a certain evolutionary lineage (Mizumoto & Bourguignon, 2021).

Miniaturization, the unidirectional size decrease in a given lineage over its history, seems a widespread phenomenon among representatives of Euarthropoda, and is also well documented in other lineages such as Annelida

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and Tetrapoda (Hanken & Wake, 1993; Polilov, 2015). This common evolutionary trajectory of size decrease has led to the modification of many morphological structures and is therefore seen as a major driver of diversification, e.g. in groups such as Chelicerata *s. str.* (Dunlop, 2019). Miniaturization has dramatic effects on an organism, affecting its ecology, behaviour, and life history (Hanken & Wake, 1993). While it has been acknowledged that size changes such as miniaturization have occurred in many euarthropodan lineages, the exact timeline of such changes is still largely unknown (Dunlop, 2019).

Within Arachnida, the group including, e.g., spiders, scorpions, and mites, several lineages have been suggested to have been affected by miniaturization. Common examples from the literature include the groups Acari (mites; Propistsova et al., 2023), Ricinulei (hooded tickspiders; Dunlop, 2019; Howard et al., 2020), Palpigradi (micro-whip scorpions; Dunlop, 2019), Cyphophthalmi (mite harvestmen; Clouse et al., 2010), and Schizomida (short-tailed whip scorpions, more rarely dwarf whip scorpions; Dunlop, 2019).

Schizomida is an ingroup within Megoperculata (≈ Tetrapulmonata; Clouse et al., 2017). The group is often resolved as the sister group to Thelyphonida (true whip scorpions, vinegaroons; Dunlop et al., 2014). The group including both is often referred to as Uropygi, although this name has also been used for true whip scorpions alone (Clouse et al., 2017).

The first representative of Schizomida was formally described in 1872 by Octavius Pickard-Cambridge; currently around 350 extant formally described species have been recognised (Clouse et al., 2017; Monjaraz-Ruedas & Francke, 2015). Fossils of the group Schizomida are available from the Cretaceous (about 100 Ma), Miocene (ca. 15 Ma), and Pliocene (5.3–1.8 Ma), which provide a view from a variety of time points throughout the history of the group. In addition, Dunlop and Horrocks (1995) reported an early representative of the lineage towards Schizomida (possibly sister species to the group, with Thelyphonida as sister group to both), *Proschizomus petrunkevitchi* (Dunlop & Horrocks, 1995) from the Late Carboniferous (ca. 315 Ma).

In general, research on Schizomida is scarce, often focused on taxonomic aspects and, hence, little is known about their biology. Short-tailed whip scorpions are generally small- to medium-sized representatives of Arachnida, with extant representatives ranging in body length from 3 to 15 mm, with an average of 4–7 mm (Dunlop, 2019). Species of this group have small geographical ranges and low dispersion rates, leading to narrow and localised distributions. Short-tailed whip scorpions are usually found in subterranean environments of tropical and sub-tropical regions (Harvey, 2002; Sturm, 1973), which is consistent with their characteristic lack of eyes (McLean et al., 2018). They are recognised for their outstanding agility, covering distances both forwards and backwards with the same speed, and for exceeding the general maximum running speed expected for their body mass (Humphreys et al., 1989; Sturm, 1973).

The shield of the anterior body region (prosomal shield) is subdivided into three distinct sclerites (pro-, meso-, metapeltidium). The segments forming the propeltidium carry a pair of chelicerae, a pair of vertically acting sub-chelate pedipalps, a pair of feeler-type appendages (modified from the first pair of legs), and the first pair of functional ambulatory appendages. Segments dorsally forming the meso- and metapeltidium each carry a pair of locomotory (=ambulatory) appendages. The posterior body region (opisthosoma) lacks appendages; the terminal end carries a short flagellum (McLean et al., 2018; Rowland, 1975; Sturm, 1973).

There is sexual dimorphism in Schizomida, for example in the pedipalps (McLean et al., 2018) and some qualitative characters, like setal length, can be misleading about the ontogenetic state of a specimen. The flagellum is therefore the main character that allows the identification of reproductive males and is generally used for taxonomic identification. Their flagella tend to be larger and wider and are often more complex in structure, while those of females and immatures are smaller, narrower, and simpler (Rowland, 1972).

Here we explore two aspects of the morphology of short-tailed whip scorpions. First, we compare the shape diversity of male flagella in fossils and in modern-day representatives. This comparison will help to estimate whether the diversification of short-tailed whip scorpions was already well underway in the Cretaceous or occurred afterwards. Second, we compare the body size of fossil and extant short-tailed whip scorpions. As multiple ingroups of Arachnida are used as common examples for miniaturization, we expect that fossil specimens of short-tailed whip scorpions were larger than extant organisms as well, and that the animals became smaller over geological time.

## Materials and methods

### Materials

Material for this study originated from literature (Briggs & Hom, 1972, 1988; Brignoli, 1974; Cokendolpher & Reddell, 1984, 1992; Cokendolpher et al., 2010; de Armas, 1989, 2010; de Armas & Delgado-Santa, 2012; de Armas et al., 2009; De Francesco Magnussen et al., 2022; Dumitresco, 1977; Framenau et al., 2018; Gertsch, 1940; Giupponi et al., 2016; Gröhn, 2015; Harms et al., 2018; Harvey & Humphreys, 1995; Harvey, 1988, 1992, 2000a, 2000b, 2001; Krüger & Dunlop, 2010; Monjaraz-Ruedas, 2013; Monjaraz-Ruedas & Francke, 2015, 2017, 2018; Monjaraz-Ruedas et al., 2016; Pinto-da-Rocha, 1996; Reddell & Cokendolpher, 1986, 1991; Rowland, 1971a, 1971b; Ruiz & Valente, 2019; Santos et al., 2013; Sissom, 1980; Teruel, 2007, 2012, 2013, 2018; Teruel & de Armas, 2012; Yamasaki & Shimojana, 1974) and from the Palaeo-Evo-Devo Research Group Collection of Arthropods at the Ludwig-Maximilians-Universität, München (PED 0183, PED 0370, PED 0398, PED 0504, PED 0528, PED 0646, PED 0693, PED 0705, PED 1035, PED 1067, PED 1118, PED 1163, PED 1193 and PED 1222). These were legally purchased on the trading platform ebay.com from various traders (burmite-miner, burmitefossil, cretaceous-burmite, macro-cretaceous). The newly documented specimens are from Kachin amber, Myanmar (ca. 100 Ma; possibly 99 Ma; Cruickshank & Ko, 2003; Shi et al., 2012; Yu et al., 2019). To exclude ontogenetic variation, only specimens that could reliably be identified as adult males, which have reached their terminal size, were used for both body size and flagella shape analysis. Since there is always some uncertainty, especially when working with fossil material, we were highly conservative in excluding any specimens which could have been mistaken for females or immatures.

For the analysis of body size in Schizomida, we used a total of 23 fossil specimens (both new specimens and specimens adapted from literature) of which only 19 had available prosoma measurements, and 46 extant specimens (Supplementary Table 1). We differentiated fossil specimens into two sub-groups based on the geological periods from which they originated. The first group comprises fossils from Cretaceous Kachin amber, including fourteen new fossils and eight fossils from De Francesco Magnussen et al. (2022). The second fossil group is comprised of one specimen from the Miocene period, which we adapted from the literature. The specimen is preserved in Dominican amber, dating to circa 15 Ma.

For the shape analysis of the flagella (see details below), we used 84 extant specimens adapted from literature and 24 fossil specimens divided in two groups (Supplementary Table 2). The first group is comprised of 23 Cretaceous fossils from Kachin amber, Myanmar. The second group is comprised of one specimen from the Miocene period, adapted from the literature. The shape analysis has a larger sample size than the size analysis, due to often missing scales in the literature. While scales are not needed for shape analysis, their unfortunate lack impedes other analyses like size analysis.

In this study, we used amber pieces originating from Myanmar. Trading with this amber has been suggested to play a role in the military conflict in the country (e.g., Dunne et al., 2022) and that working with it should be paused for now, especially in the context of vertebrate palaeontology (Haug et al., 2023a; Rayfield et al., 2020). Other palaeontologists have provided different views on the topic (e.g., Haug et al., 2020a; Peretti, 2021; Shi et al., 2021). Furthermore, it has been questioned whether Myanmar amber has an actual influence on the conflict e.g., by providing monetary funds (Dunne et al., 2022; Haug et al., 2023a; Poinar & Ellenberger, 2020). In the light of this uncertainty, new documentation protocols for the export process have been suggested (Theodor et al., 2021) but according to trader information and own experiences, amber pieces often sold for a few dollars will not receive separate export papers. In our publications, we are providing all information available to us about the provenance of the specimens for maximum of transparency.

Another issue discussed in recent time is that of involving local people into research (to avoid the so-called "helicopter science" or "parachute science"; e.g., Stefanoudis et al., 2021; Zin-Maung-Maung-Thein & Zaw, 2021; Haug et al., 2023a). We have successfully established a collaboration with biologists from the University of Yangon, Myanmar, to improve in this aspect (Haug et al., 2023b, 2023c).

### Documentation methods

The new specimens in amber were documented by the authors on a Keyence VHX-6000 digital microscope equipped with a ZST 20–2000×objective. All specimens were documented with different backgrounds and light settings to achieve the best contrast (black and white background, unpolarised low-angle ring illumination, cross-polarised coaxial illumination; Haug et al., 2013a). A stack of images with shifting levels of focus was recorded and fused to a sharp image with the built-in software to overcome limitations of depth of field. To overcome limitation of field of view, several adjacent image details were recorded and stitched with the built-in software, resulting in a composite image (Haug et al., 2011, 2018). Additionally, each image was recorded with several different exposure times to avoid overexposed or underexposed areas (HDR; Haug et al., 2013b). The final processing of the images was performed with Adobe Photoshop CS2.

Measurements from those fossil specimens documented on the Keyence VHX-6000 digital microscope were performed using the 3D measurement function of the microscope. This method accounted for estimated differences of depth within the amber between two measured points. Measurements from the remaining specimens were performed in 2D using the software ImageJ (Schneider et al., 2012).

### Proxy for body size

We examined body size in Schizomida over geological time, using leg and prosoma lengths as proxy. Fossil specimens from the Cretaceous and Miocene, as well as extant specimens gathered from the literature, were measured. For literature specimens, numerical size measurements were taken directly from the text when reported, or otherwise measured from images using ImageJ when a scale was included.

We measured the entire length of the prosoma as an approximation of the total body length since the prosoma was typically the clearest and best-preserved body region in the fossil specimens (Fig. 1). As a proxy for leg length, we measured the length of the longest element ("femur") of the second functional walking leg, since it was the leg element best preserved in all fossil specimens (Fig. 1). In fossil specimens, bubbles, debris, and the texture of the amber sometimes overlapped with the specimen, making it more difficult to measure lengths accurately, which may cause less precise measurements in fossil specimens than in extant ones.

### Flagellum shape

For the comparison of flagellum shapes (Fig. 1) we focused on adult males, which can be easily identified by flagellum shape in both fossil and extant specimens. In this way we could exclude ontogenetic variation of the structure. Images of both the fossil and extant specimens were used to create reconstruction drawings of the flagella. Source images of specimens were loaded into Inkscape version 1.0 (https://www.inkscape.org). Flagellum outlines were then redrawn using a mirroring method to achieve symmetry. Measurement scales were included in the drawings. For fossil specimens, flagellum shapes sometimes had to be approximated as the structures were obstructed by bubbles, debris, and the texture of the amber itself.

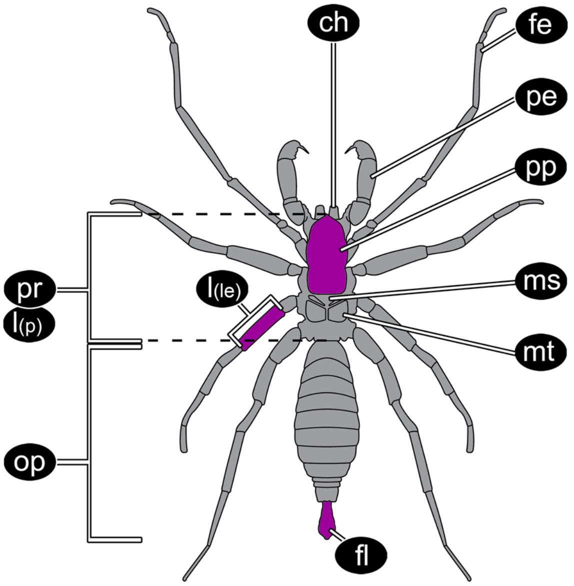

**Fig. 1** Measurements and structures relevant for the here performed analyses of Schizomida, exemplified on the male holotype of *Protoschizomus francki* (reconstruction after Monjaraz-Ruedas, 2013, their Fig. 1). Purple coloured element mark body parts used for the analysis. *Ch* chelicera, *fe* feeler-type appendage, *fl* flagellum, *l(le)* length of leg element measured, *l(p)* length of prosoma measured, *ms* mesopeltidium, *mt* metapeltidium; *op* opisthosoma, *pe* pedipalp, *pp* propeltidium, *pr* prosoma

### Shape analysis

We compared the flagellum shapes by elliptic Fourier outline analysis using the software package SHAPE (© National Agricultural Research Organization of Japan; Iwata & Ukai, 2002). Elliptic Fourier analysis uses the principle of Fourier transformation to decompose a complex two-dimensional shape into a harmonic sum of trigonometric functions weighted with harmonic coefficients describing the original shape (Bonhomme et al., 2014; Braig et al., 2023a). Using the SHAPE pipeline, the outlines are first transformed into vectorised objects (chain codes) represented by numeric values, which are then transformed into normalized elliptic Fourier descriptors. We used 12 harmonics to describe the shape and aligned all shapes along their anterior–posterior axis. These are then analysed using principal component analysis (PCA). The entire procedure including the PCA was applied following Iwata and Ukai (2002; see also Braig et al., 2023b).

### Note on taxonomy

Flagellum shape in adult males is heavily coupled to species differentiation. It is therefore expected that the fossil specimens investigated here represent various species. So far, a single species of Schizomida has been formally described from Kachin amber, Myanmar. We refrain here from erecting new species for our specimens at hand as: (1) the focus of the study is not directed towards taxonomy, and (2) De Francesco Magnussen et al. (2022) have treated this topic. To avoid producing unnecessary synonyms, we therefore will not refer the new specimens to any species.

### Data analysis

Statistical analysis and graphical interpretation of the body size and flagella shape analyses were performed in the R-statistics environment (ver. 4.1.0; R Core Team, 2021). The fossil sub-group "Miocene" was included in graphical interpretation but excluded from quantitative comparison due to its small sample size ($n=1$ for both flagella shape and body size analyses). Graphical interpretation of flagellum shape was achieved using morphospaces (Mitteroecker & Huttegger, 2009), i.e., plotting different axes of the PCA.

Quantitative analysis was achieved using the package dispRity (ver. 1.6.0; Guillerme, 2018). We extracted the first nine PCs from the PCA, as together they amounted to over 99% of variation, and used them as data matrix for the analysis. To estimate the morphological diversity, we calculated the sum of variances across all PCs for every age group (Guillerme et al., 2020; Braig et al., 2023a). We bootstrapped the data (n = 10,000) and performed sample size correction based on rarefaction, using the smaller sample (n = 23). We tested for significant differences between groups using Welch's two-sample t-test. The code is provided in the zenodo repository.

To test for differences in mean lengths of the leg and prosoma between the geological times, we first tested for normality and homoscedasticity (i.e. equal variance of data values, Zuur et. al., 2007) in the data and found the leg lengths to be log-normal and the prosoma lengths to be normally distributed, both heteroscedastic. We then performed Welch's two-sample t-tests for the prosoma lengths and log-transformed leg-lengths.

## Results

### New specimens

All 14 new specimens of male short-tailed whip scorpions are preserved in an orientation that allowed measuring of prosoma and leg elements. All specimens possess the prominent flagellum morphology known from extant adult males: PED 0183 (Fig. 2A, B), PED 0705 (Fig. 2C, D), PED 0370 (Fig. 2E, F), PED 0398 (Fig. 2G, H), PED 0504 (Fig. 3A, B), PED 0528 (Fig. 3C, D), PED 0646 (Fig. 4A–C), PED 0693 (Fig. 4D–F), PED 1035 (Fig. 5A–C), PED

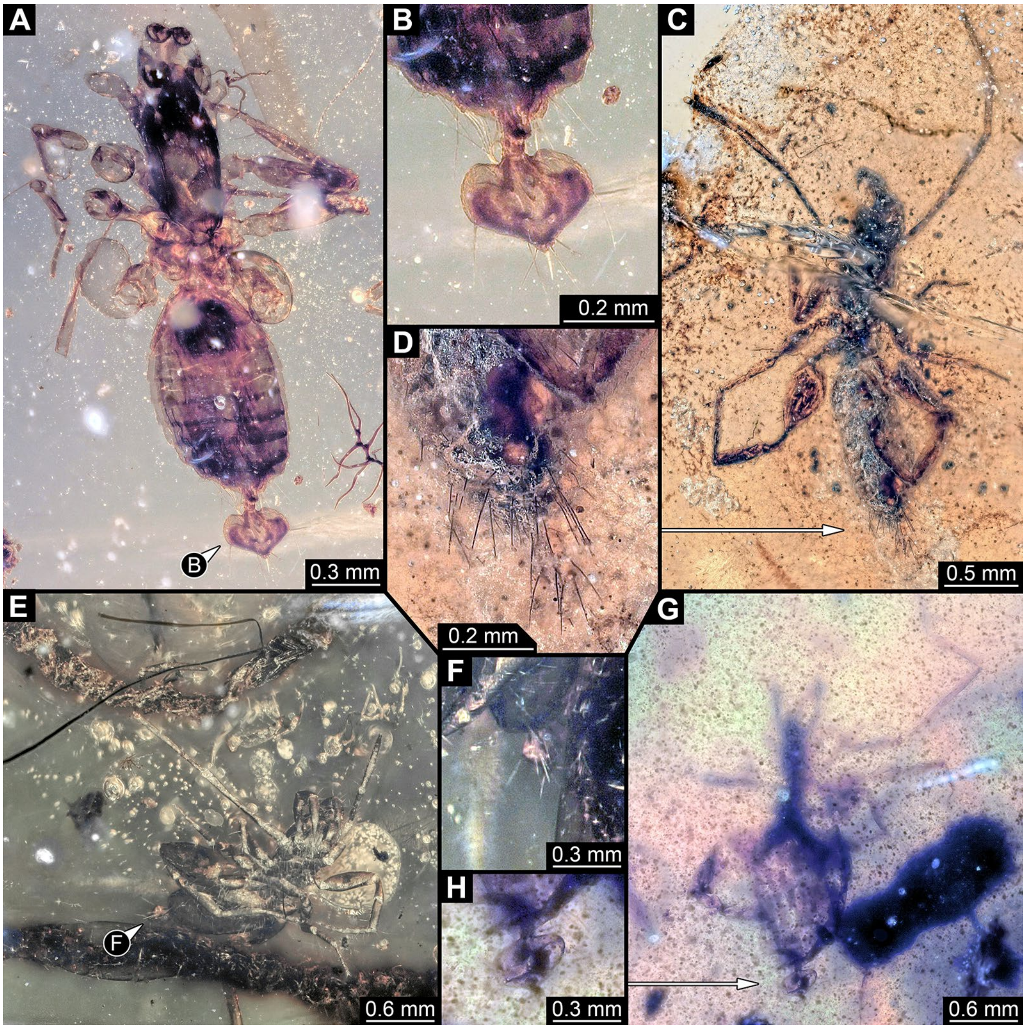

**Fig. 2** New specimens of Schizomida from Cretaceous Kachin amber, Myanmar. **A**, **B**. PED 0183. **C**, **D**. PED 0705. **E**, **F**. PED 0370. **G**, **H**. PED 0398. **A**, **C**, **E**, **G**. Overviews. **B**, **D**, **F**, **H**. Close-ups of flagella

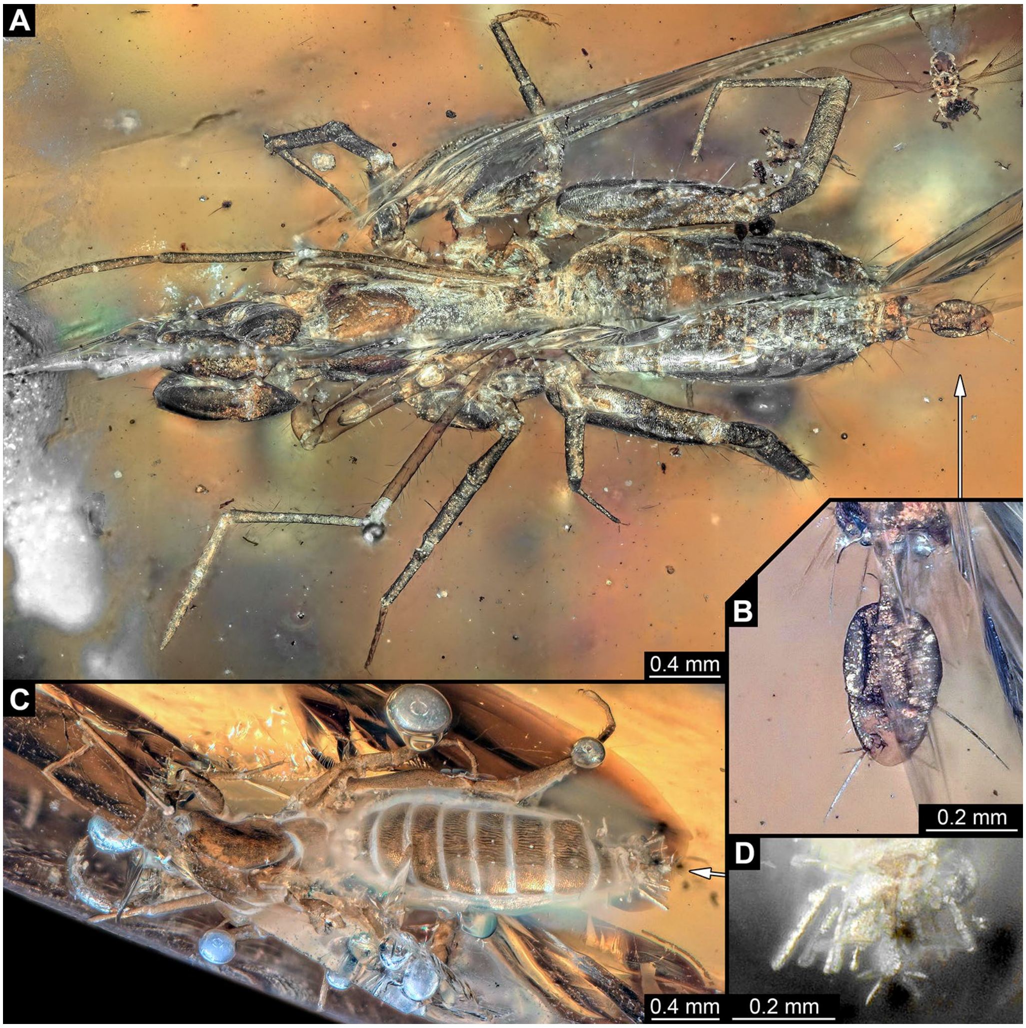

**Fig. 3** New specimens of Schizomida from Cretaceous Kachin amber, Myanmar. **A**, **B**. PED 0504. **C**, **D**. PED 0528. **A**, **C**. Overviews. **B**, **D**. Close-ups of flagella

1193 (Fig. 5D, E), PED 1067 (Fig. 6), PED 1118 (Fig. 7A, B), PED 1163 (Fig. 7C, D), PED 1222 (Fig. 8).

### Comparative flagellum shape analysis

The shape analysis of the flagella resulted in nine principal components (PCs) explaining over 99% of variation (PC1 = 76.4%; PC2 = 10.4%; PC3 = 7.3%; PC4 = 2.1%; PC5 = 1.3%; PC6 = 0.6%; PC7 = 0.5%; PC8 = 0.3%; PC9 = 0.2%; Supplementary Fig. 1).

PC1 predominantly describes the width of the flagellum (Fig. 9A). Positive values indicate thin flagella, while negative values indicate broad flagella. PC2 predominantly describes whether the flagellum trends toward a more triangular shape for negative values or elliptic shape for positive values (Fig. 9A). It also explains the width of the protrusion connecting the flagellum with the opisthosoma. Negative values indicate slim and elongated protrusions, while positive values indicate wide protrusions. The mean flagellum shape of PC1 is almond-like, almost ellipsoid, with the tip at the posterior end and a wide protrusion at the anterior end. This protrusion is the attachment region which connects the flagellum with the last opisthosomal segment.

Fossil representatives of Schizomida plot around the centre of the morphospace, forming an ellipse along the PC1 axis from bottom-left to top-right of the morphospace, indicating that most variation is found between wide and thin flagella (Fig. 9A). The Miocene representative hereby plots in the center of the morphospace, indicating a median morphology. Similarly, extant specimens occupy the centre of the morphospace, with a couple of specimens having triangular flagella with thin and elongated attachment points. Yet, extant specimens also extend the range of possible shapes further, plotting far

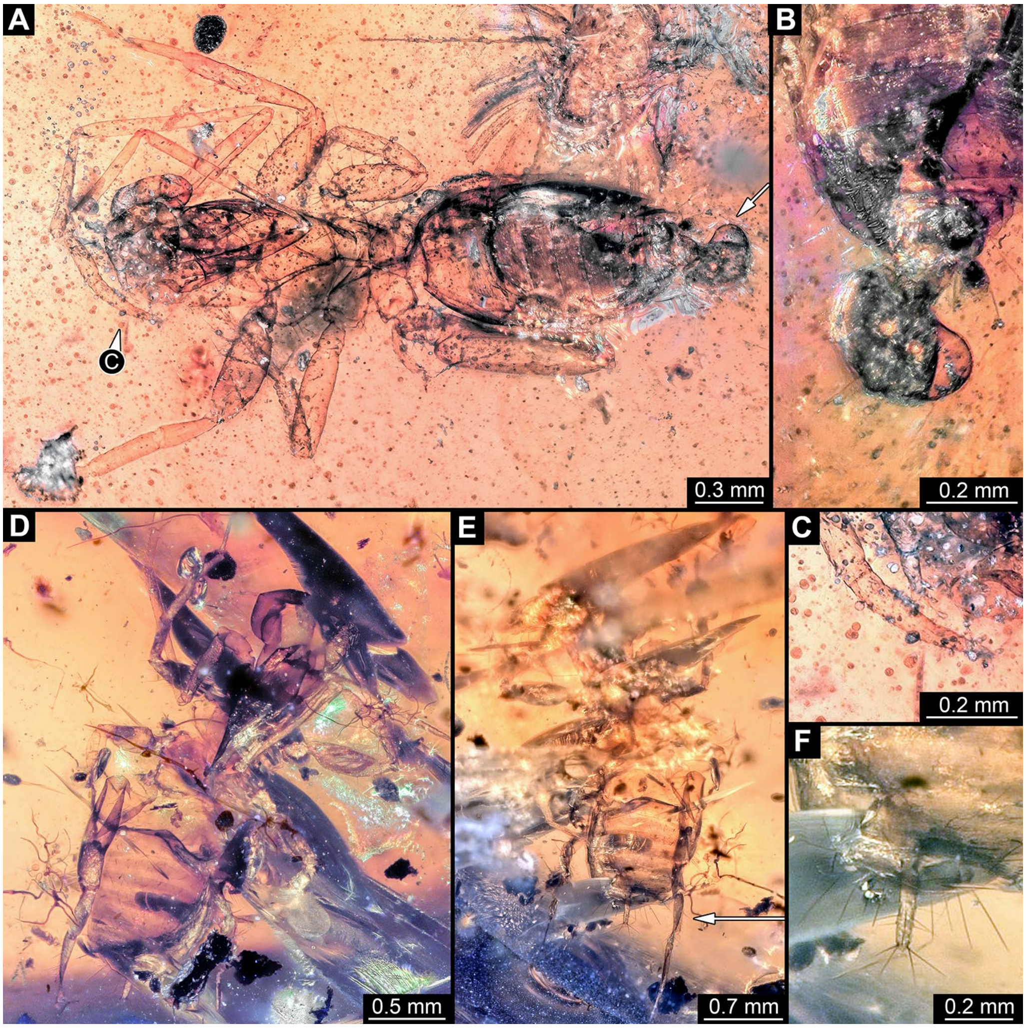

**Fig. 4** New specimens of Schizomida from Cretaceous Kachin amber, Myanmar. **A**–**C**. PED 0646. **A**. Overview. **B**. Close-up of flagellum. **C**. Close-up on distal part of feeler-type appendage. **D**–**F**. PED 0693. **D**. Overview in dorsal view. **E**. Overview in ventral view. F. Close-up of flagellum

towards the top left of the morphospace which indicates wide and elliptical flagella.

The quantitative analysis performed on the morphospace shows that the Cretaceous specimens occupy a larger area of the morphospace, after bootstrapping and sample size correction of the groups (Table 1). However, the difference in size is not significant (Welch's two-sample t-test, p-value > 0.001).

### Comparative size analysis

Body size differed between the Cretaceous and extant specimens. We performed comparative size analysis between extant specimens and fossils from the Cretaceous only. We excluded the specimen from the Miocene due to small sample size (n = 1).

The comparative size analysis yielded a significant difference in mean leg lengths between the two groups (Welch's Two Sample t-test; p-value < 0.001). Testing the prosoma lengths also resulted in a significant difference in the mean values between the two groups (Welch's Two Sample t-test; p-value < 0.001). These results indicate that the fossil representatives of Schizomida originating from the Cretaceous period had significantly smaller body size than the extant ones (Fig. 9B).

## Discussion

### Comparative size analysis

Contrary to our expectation of a decrease in size over time, the mean leg and prosoma lengths of representatives of Schizomida increased significantly between the Cretaceous and extant fauna (Fig. 10; Table 1). We initially expected body lengths of representatives of Schizomida to decrease between the Cretaceous and today, based on the assumed general trend of miniaturization

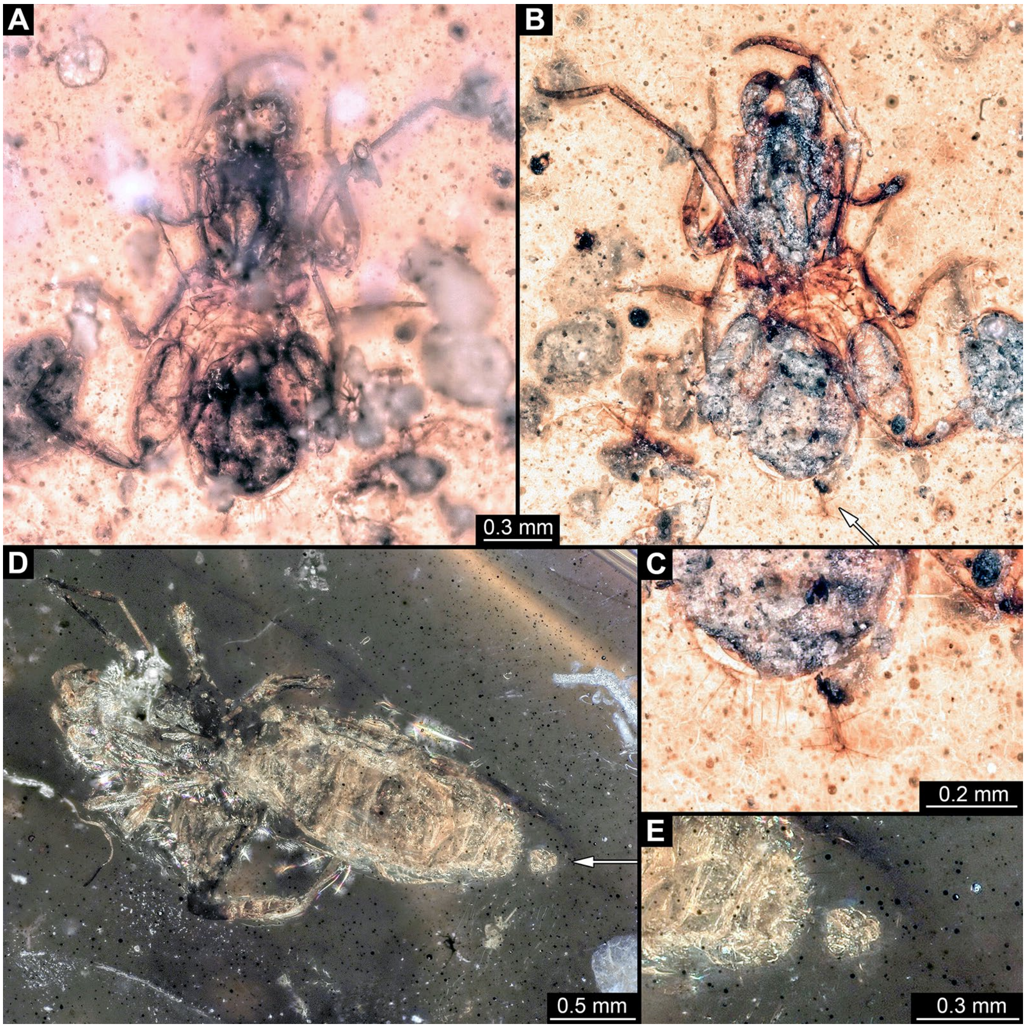

**Fig. 5** New specimens of Schizomida from Cretaceous Kachin amber, Myanmar. **A**–**C**. PED 1035. **A**. Overview in ventral view. **B**. Overview in dorsal view. **C**. Close-up of flagellum. **D**, **E**. PED 1193. **D**. Overview. **E**. Close-up of flagellum

throughout the history of Euarthropoda (e.g., Dunlop, 2019; Polilov, 2015). Furthermore, *Proschizomus petrunkevitchi*, the presumed sister species to Schizomida, is significantly larger than modern short-tailed whip scorpions (Fig. 10; e.g. Dunlop & Horrocks, 1995). In addition, fossil and extant representatives of Thelyphonida, the sistergroup to Schizomida + *Proschizomus*, are larger, well in the centimetre range (Fig. 10). Hence, a larger size of Cretaceous short-tailed whip scorpions would have fit the reasonable assumption of a size reduction in this lineage towards the modern fauna. It should be noted that although *Proschizomus petrunkevitchi* fits well into this scenario, it in fact remains unclear whether it is an adult specimen or possibly an immature which simply had not yet reached its final size.

In his review of miniaturization within Euchelicerata, Dunlop (2019) described some supposedly common trends that may be relevant for short-tailed whip scorpions. For example, a simplification of the overall body organisation and subdivision of body regions for better manoeuvrability, as seen also in Schizomida, is commonly coupled to miniaturization within Euchelicerata (Dunlop, 2019). Both the loss of eyes and the division of the prosomal shield into three sclerites are prominent features of representatives of Schizomida, and though both traits are also undoubtedly linked with the ecology of the animals, they could also indicate evolutionary adaptations to a smaller size (Dunlop, 2019).

Also, though gigantism was common in insects through the Jurassic, an overall size decrease has been observed for insects from the Permian until today (Clapham & Karr, 2012). This decrease is thought to be partly due to the evolution and radiation of aerial predators in the early Cretaceous, which caused predation to overrule

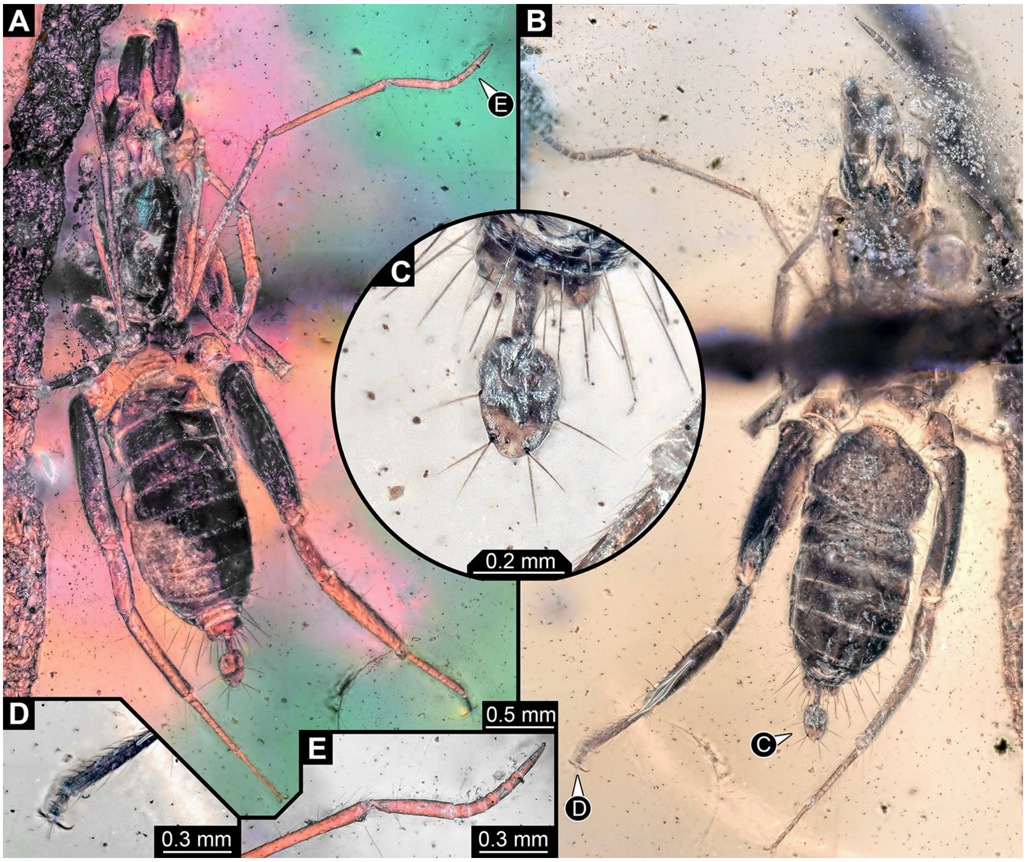

**Fig. 6** New specimen of Schizomida from Cretaceous Kachin amber, Myanmar, PED 1067. **A**. Overview in dorsal view. **B**. Overview in ventral view. **C**. Close-up of flagellum. **D**. Close-up on distal part of walking-type appendage. **E**. Close-up on distal part of feeler-type appendage

atmospheric oxygen availability as the most important constraint on insect body size (Clapham & Karr, 2012). However, we did observe an increase of size for the group Schizomida, not a decrease. It is possible that aerial predation was not a relevant selective pressure for representatives of Schizomida, as they do not fly and are therefore less likely to be targeted by aerial predators. The lack of this predation pressure therefore may have allowed for the here observed size increase in Schizomida.

Despite the general trends towards miniaturization described above, it has also been suggested to be quite common for organisms to become progressively larger throughout the course of the geological history of the overall group (Rensch, 1948). Dubbed as “Cope’s rule,” this principle was indiscriminately explained by some internalized, almost teleological drive of the organisms to become “bigger and better” (Damuth, 1993; Rensch, 1948). This view is, of course, highly outdated (e.g. Gould, 1997; Jablonski, 1997; Nagler et al., 2017), though it is still sometimes implicitly accepted (Benson et al., 2018; Stanley, 1973). A more likely explanation of “Cope’s rule” lies in the way in which many groups of organisms diversified after mass extinctions. Starting up in newly devastated and simplified ecosystems, which are unable to support larger animals, representatives of the groups subsequently grew larger as climacteric ecosystems were able to support large-bodied organisms (Hone et al., 2005; Roopnarine & Angielczyk, 2015).

It has been well-documented that a body size increase can bear multiple advantages (e.g. increased prey capturing ability and wider range of available prey; Dickerson, 1978; Knouft & Page, 2003). For example, a larger overall body size in extant specimens might improve their locomotion in their current habitat, leading to faster and more agile movements through the rugose and harsh environment (Kaspari & Weiser, 1999).

A multitude of factors can drive an evolutionary increase in body size, with most explanations rooted in the physiological control of growth and development (Baranov et al., 2021; Chown & Gaston, 2010). We conjecture that increased environmental stressors, specifically decreasing temperatures after the Cretaceous, could have fostered the body size increase in representatives of Schizomida. Arachnida is a group of ectothermic

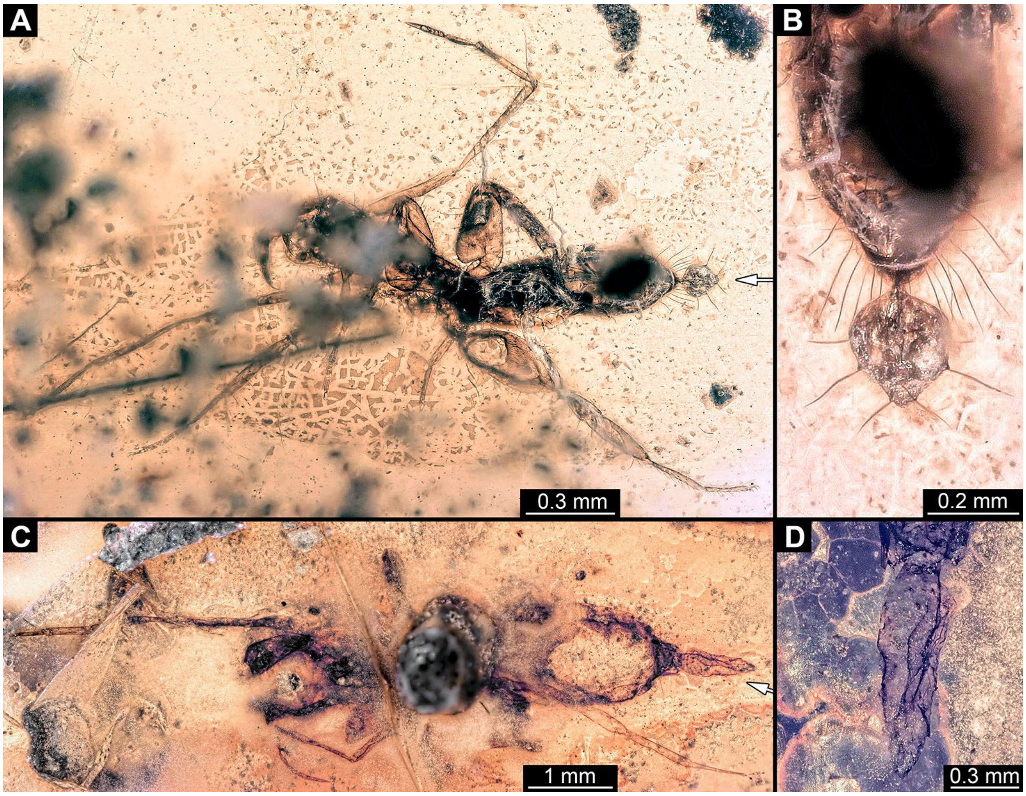

**Fig. 7** New specimens of Schizomida from Cretaceous Kachin amber, Myanmar. **A**, **B**. PED 1118. **C**, **D**. PED 1163. **A**, **C**. Overviews. **B**, **D**. Close-ups of flagella

animals, and therefore their body temperature is dependent on their environment (Huey & Stevenson, 1979; Sinclair et al., 2016). Lower body temperatures result in lower metabolic rates and activity levels. The evolution of a larger body size could facilitate the maintenance of body temperature due to a decreased ratio of surface area to volume (Bergmann, 1847; but see Shelomi, 2012 for challenges of the theory). With this increased body size, they could maintain a metabolic rate in temperatures that are lower than those during the Cretaceous period.

The Cretaceous period (146–66 Ma) has been suggested to have been one of the warmest time periods on Earth, with ocean temperatures of 35 °C and no ice at the poles (Herrle et al., 2015). The following geological period, the Paleogene, had average temperatures of 25 °C, again much higher than current average temperature (Naafs et al., 2018). During the Paleogene, there was a gradual warming event that resulted in the Eocene thermal optimum, which was punctuated by the Paleocene–Eocene Thermal Maximum (PETM). The PETM occurred around 55.5 million years ago, where temperatures rose by a further 5–8 °C (Bowen et al., 2014), with a subsequent decrease.

### Flagellum shape

Male flagellum shape diversity did not differ significantly between fossil and extant specimens, but fossils occupied a larger area within the morphospace after bootstrapping and sample size correction (Table 1). Changes in flagellum shape were not necessarily expected, as it has a practical use as an anchoring mechanism during copulation. The tactile courtship phase of reproduction in this group is called the "Paarungsmarsch," from the German term for "mating march." The male presents his flagellum to the female, who encircles it with her pedipalps and chelicerae, fitting the tips of her chelicerae into special "coupling pockets." The male pulls the female forward while laying a spermatophore on the ground, and the female lowers her genital pore onto the spermatophore while the male pushes her downwards to facilitate the sperm transfer (Ruiz & Valente, 2019; Sturm, 1958). It is therefore apparent that flagellum shape underlies sexual selection pressures and contains some species-specific information (Ruiz & Valente, 2019).

We speculate that the importance of flagellum shape to reproduction may have hampered the evolution of major changes between the Cretaceous period and today. Any changes in the flagellum shape might have distorted the

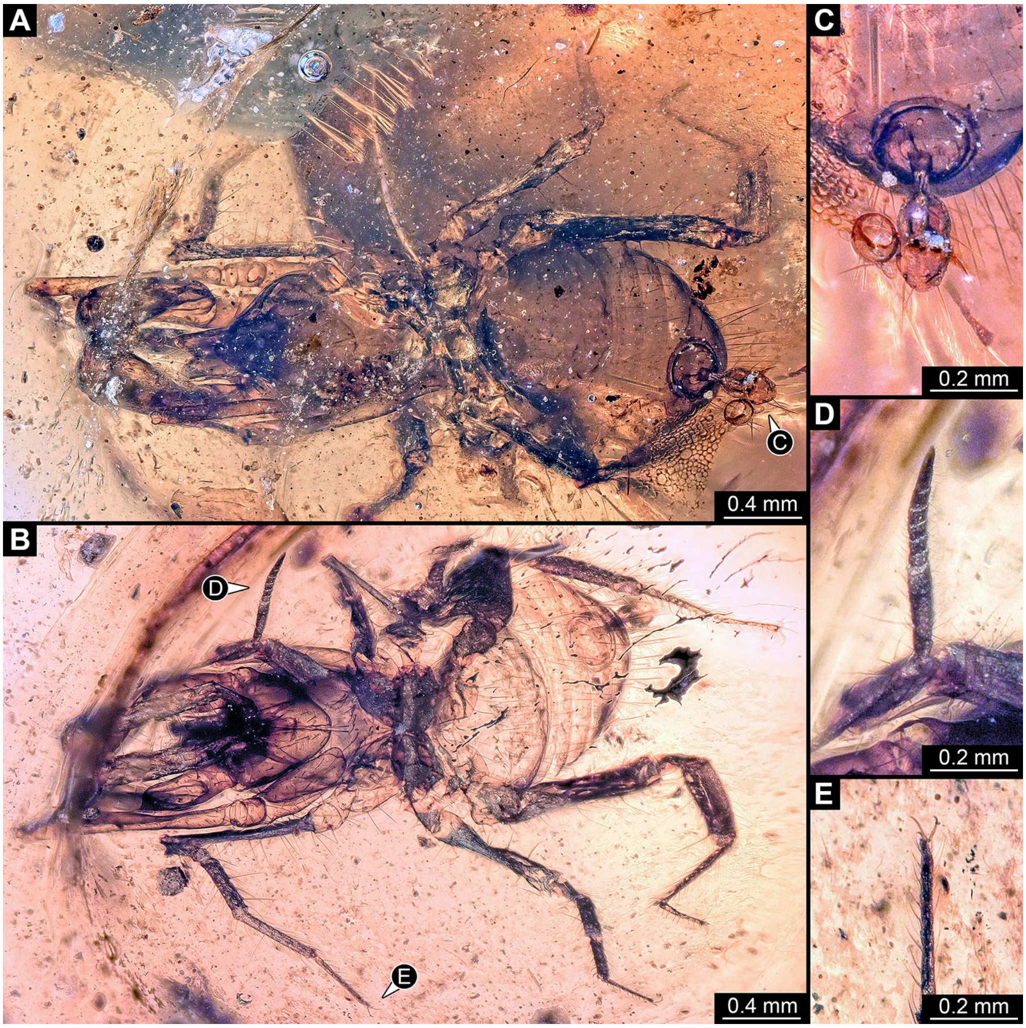

**Fig. 8** New specimen of Schizomida from Cretaceous Kachin amber, Myanmar, PED 1222. **A**, **B**. Overviews. **C**–**E**. Close-ups. **C**. Flagellum. **D**. Distal part of feeler-type appendage. **E**. Distal part of walking-type appendage

position of the coupling pockets and therefore hindered the ability of the female to lock her chelicerae in and successfully reproduce.

Another explanation includes the importance of the chelicerae for feeding. The mechanical coupling of the chelicerae and flagellum could be a driver of speciation, with the shape of the female chelicerae necessarily correlating to the shape of the male flagellum. However, the chelicerae have an additional functional significance in that they are instrumental for the capture and consumption of prey. Therefore, the significance of the chelicerae in the everyday survival of representatives of Schizomida may serve as an opposing selective pressure to the diversification of the male flagellum.

The observation also strongly indicates that the major diversification events of Schizomida happened sometime before the Cretaceous. Molecular clock estimates and fossil specimens suggest the earliest representatives of the group to originate from the Late Carboniferous (Dunlop & Harrock, 1995; Clouse et al., 2017). The diversification therefore likely happened between the Late Carboniferous and the Cretaceous. Even in a challenging taxonomic situation it is therefore possible to use morphological diversity measures to make such estimates.

## Size and shape diversity in Myanmar amber in general

Other organisms in Myanmar amber are known to differ from their extant counterparts in shape. Heads of larvae of certain lacewings are known to have been more diverse in the past (Haug et al., 2020b, 2023c), while in others the modern fauna seems to have a larger diversity (Haug et al., 2021a, 2021b, 2021c). Raptorial appendages

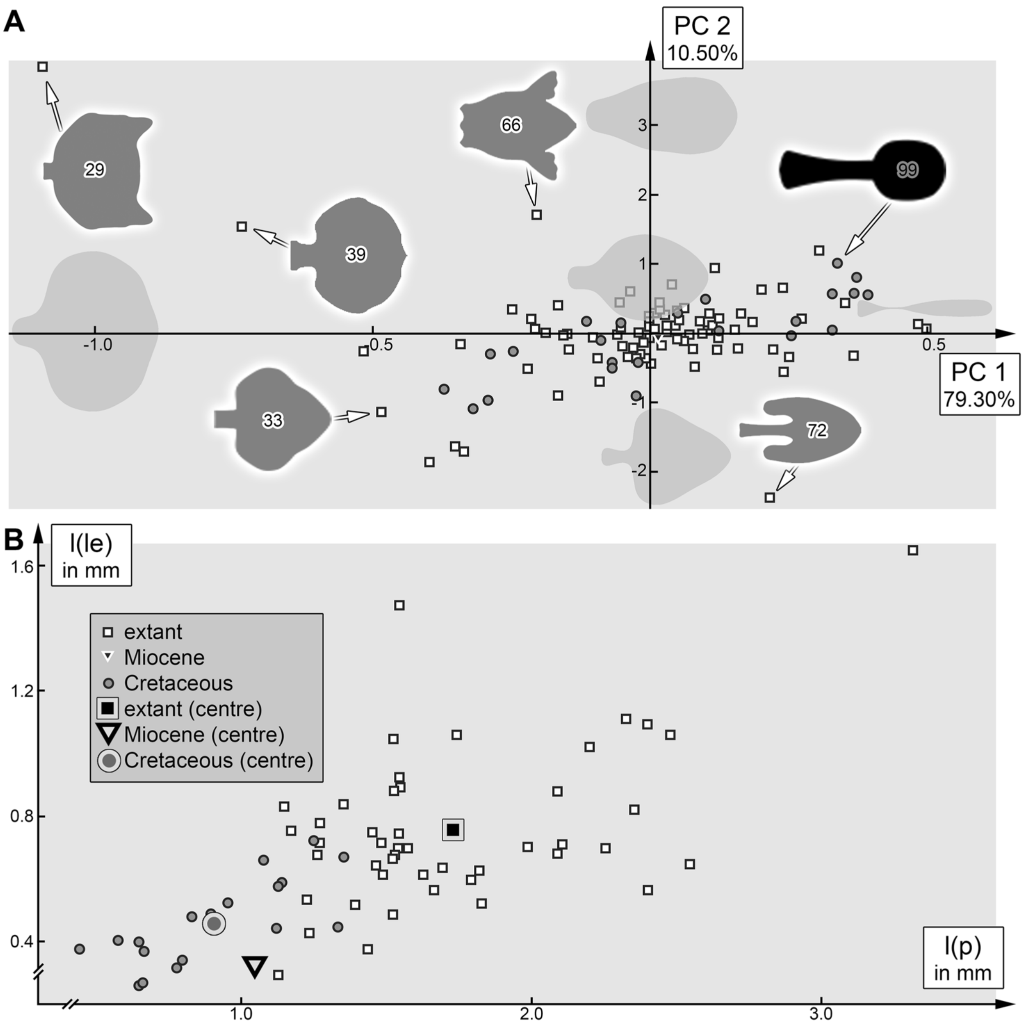

**Fig. 9** Scatter plots of quantitative analyses performed in this study. **A**. PC 2 over PC 1 of principal component analysis of the flagellum shape of extant and fossil representatives of Schizomida. Some extreme flagellum shapes are shown, with extant specimens in grey and fossil specimens in black. On the axes, the average and extreme shapes are shown (− 2 and + 2 standard deviation). **B**. Body size of fossil and extant specimens, described by the relationship between prosoma length (l(p)) and length of leg element (l(le)). Larger symbols represent the mean values for each group (centre)

of adult mantis lacewings were also significantly more diverse back in the Cretaceous, as seen mainly in fossils from Myanmar amber (Baranov et al., 2022). Furthermore, there are also cases within lacewings where no significant change in diversity appears to have occurred between the Cretaceous and today (Haug et al., 2021c). All these different cases of diversity changes (or non-changes) indicate that there are certain restrictions in the morphology of the flagellum that hampered evolutionary changes as discussed above.

**Table 1** Table summarizing the output of the quantitative statistical analysis of flagellum shape and body size comparison

| | Sum var. | Leg mean (mm) | Pro. mean (mm) |
|---|---|---|---|
| Cretaceous | 0.072 | 0.47 | 0.9 |
| extant | 0.062 | 0.76 | 1.73 |

*pro.* Prosoma, *sum var.* sum of variances

Concerning size, there are so far no quantitative data for many other lineages of Euarthropoda. Yet, there have been qualitative statements, for example, for caddisflies (Trichoptera), that these have been smaller in Myanmar amber (Wichard, 2021). One could speculate that this is a filtering effect of preservation in amber, as amber seems to favour the preservation of smaller organisms (e.g., Labandeira, 2014; Penney, 2002). Then again, adult representatives of Schizomida are already quite small, making it uncertain whether a preservation bias would have an effect.

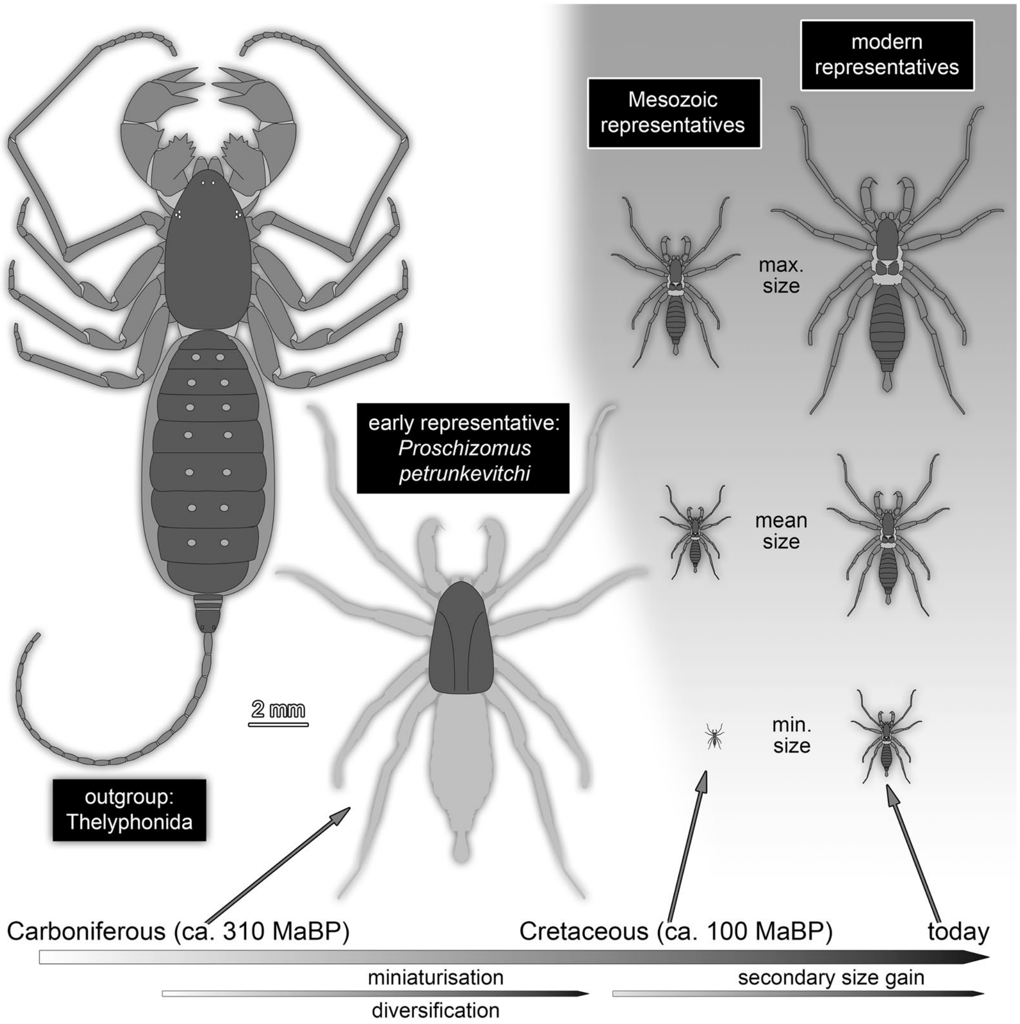

**Fig. 10** Graphical summary of size changes in the evolutionary lineage of Schizomida with reference to its sister group Thelyphonida. All drawings to the same scale. Representative of Thelyphonida drawn after undetermined specimen. Drawing of *Proschizomus petrunkevitchi* mainly based on prosomal shield, further structures (light grey) based on comparison to extant specimens of Schizomida. Other drawings of Schizomida are size modifications of drawing in Fig. 1 to illustrate maximum, mean, and minimum sizes

A size increase between the Cretaceous of Myanmar and the extant fauna has also been observed in lepidopteran caterpillars (Gauweiler et al., 2022). If we generalize the increase of size in these groups for the whole Cretaceous period, then we could conclude that any supposed miniaturization processes in Euarthropoda would have happened before the Cretaceous. Regardless, for further resolving the question of miniaturization in Schizomida and the evolution of the group, we need older fossils, which we so far lack.

## Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13358-024-00321-w.

Supplementary Material 1: Table 1. Containing data of all specimens used for the body size analysis.

Supplementary Material 2: Table 2. Containing data of all specimens used for the flagellum shape analysis.

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JB, MSM, MMO, CH, JTH conceptualization and data acquisition; JB, MSM, MMO work design; JB, FB data analysis; JB, MSM, MMO, FB, CH, JTH data interpretation; JB, MSM, MMO drafts and final versions; CH, JTH, FB manuscript revision.

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**Availability of data and materials**

All data generated or analysed during this study are included in this published article, its figures and its supplementary files. The reconstructed shapes and custom scripts for the R-statistics environment can be downloaded at https://doi.org/10.5281/zenodo.10450567. All data will also be shared by the corresponding author upon request (florian.braig@palaeo-evo-devo.info).

## Declarations

**Competing interests**

The authors declare no competing interests.

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