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MORPHOLOGICAL VARIATION OF LONG-LEGGED VELVET MITE LARVAE IN DEEP TIME

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Abstract. Parasitengona, an ingroup of Trombidiformes, is characterised by a complex life cycle, in which the larval stage is parasitic on animals. Larvae of erythraeoideans or long-legged velvet mites, one ingroup of Parasitengona, parasitise euarthropodan hosts and have extremely long legs that confer them the ability to walk fast. Representatives of Parasitengona in general, and Erythraeoidea in particular, are relatively abundant in the fossil record. Nonetheless, their studies have remained scarce, since, like in most mites, the characters needed for taxonomical identification are hidden within the amber piece. Here, we report 41 new erythraeoidean larvae from the Cretaceous Kachin amber and three specimens from Eocene Baltic amber. We also compare the shape of their habitus between extant and fossil specimens by applying elliptical Fourier analysis (EFA) to their redrawn outlines. According to the shape analysis, there is a certain level of overlap in the morphospace between extant and fossil specimens, but the difference in morphology was statistically significant, pointing to a separation between the two. This is supported by the fact that some morphological characteristics of fossil specimens are not present in extant representatives. Fossil erythraeoideans occupy the area of the morphospace with more elongated legs, which could be related to variations in the availability of their hosts or changes in microhabitat occupied by the mites, although bias in the fossil record cannot be ignored. Although preliminary, our findings demonstrate that quantitative morphological analysis can be applied to specimens of mites not preserved in the best of conditions that may not be of interest for taxonomic studies.

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INTRODUCTION

Mites are common elements of almost every continental ecosystem and represent a not to be underestimated biomass. Mites are, and seem to have always been, fairly small (Sidorchuk 2018), a characteristic that despite their broad morphological diversity, unites the group. This small size has facilitated their entrapment in tree resin, leading to them being abundant in amber pieces when compared to other euarthropodans. Sedimentary fossils reveal that the Acariformes lineage of mites was already present in the Lower Devonian (ca. 410 mya), and as amber inclusions show, mites were already rich and diversified during the Mesozoic (ca. 230 mya) (Krantz 2009; Schmidt et al. 2012).

One particularly abundant group of mites in amber inclusions is Parasitengona, an ingroup of Trombidiformes. This group of mites is characterised by a complex life cycle (Walter et al. 2009) during which inactive (calyptostatic) instars are alternated by active stages. As soon as a parasitengonan mite hatches from its egg, it stays inactive (calyptostatic) as a prelarva. This is followed by the six-legged heteromorphic larva (for a discussion on the term, see Haug 2020), which is generally an ectoparasite of numerous eurarthoropodan and vertebrate hosts (e.g. Martin & Gerecke 2009; Mąkol et al. 2012; Moniuszko & Mąkol 2014; Felska et al. 2018; Haarder & Mąkol 2022), with very few exceptions (Smith 1998). The nymphal stages that follow consist of an inactive protonymph, an active deutonymph that is predatory on other euarthropodans, and, again, an inactive tritonymph. Lastly, the adult shares feeding habits with the deutonymph.

The ingroup of Parasitengona most frequently found in amber inclusions is Erythraeoidea, the group of long-legged velvet mites; more precisely: most common are erythraeoidean larvae (Bartel et al. 2015). The possible reason behind this common occurrence is that, at least in modern representatives, they are mostly associated with debris and tree surfaces, closer to the resin produced by trees, unlike other terrestrial parasitengonan mites that are edaphic (soil associated) (Wohltmann 2001). Erythraeoidean larvae parasitise a long list of euarthropodan hosts, from insects to arachnidans and even other mites and ticks (Welbourn 1983; Wohltmann 2000; Stroiński et al. 2013; Bernard et al. 2019; Haarder & Mąkol 2022), and with varying degrees of specificity (Southcott 1992; Wohltmann 2000). In the fossil record, they are often found still attached to their host, since they have a strong grip to their host's cuticle through a salivary secretion (Åbro 1988). There is one exception to the parasitic lifestyle: representatives of Balaustiinae or sidewalk mites have larvae that are predatory and pollen-feeders (Yoder et al. 2012). Larvae of Erythraeoidea are characterised by their extremely long legs (walking appendages), which often are twice the length of the idiosoma (trunk region in mites) (Wohltmann 2001), and confers them the name of "long-legged velvet mites".

Despite their abundance in the fossil record, given their small size, the difficulties in accessing taxonomically relevant characters have hampered studying these fossil mites in detail. Therefore, fossilised specimens of mites have often been overlooked in amber pieces (Dunlop et al. 2008). In general, with some exceptions (e.g. Grünemaier 2017; Konikiewicz & Mąkol 2018), only very well-preserved specimens have been reported for taxonomical studies (e.g. Kuznetsov et al. 2010; Sidorchuk & Bertrand 2013; Bartel et al. 2015; Sidorchuk et al. 2019), to which time-consuming techniques like amber grinding and polishing have been applied (e.g. Konikiewicz & Mąkol 2018; Sidorchuk et al. 2019). Quantitative morphological analysis has not yet been applied to fossilised mite specimens. This type of analysis has proven to be useful for investigating the biological diversity of other euarthropodan ingroups in deep time (Haug et al. 2024, e.g. Baranov et al. 2020; Haug et al. 2021a; Haug et al. 2023) even in cases when details of morphological structures that are taxonomically relevant are not accessible. In particular, the abundance of erythraeoidean mites enables working with such quantitative methods applied to specimens embedded in amber. In this study we report several new specimens of larvae of long-legged velvet mites from Cretaceous Kachin amber from Myanmar and Eocene Baltic amber. We compare the shape of their habitus between extant and fossil specimens to discuss its implications concerning their diversity and palaeoecology.

MATERIAL AND METHODS

Material

A total of 66 extant specimens were considered from the literature (Southcott 1961; 1988; 1992;

1999; Zhang & Lafuente 1996; Fain & Çobanoğlu 1998; Haitlinger 1999; 2004; 2011; Zhang 2000; Saboori et al. 2007; 2009; Wohltmann et al. 2007; Saboori & Begheri 2011; Salarzehi et al. 2012; Kamran & Alatawi 2014; 2015; 2016; Xu et al. 2019; 2020; Dos Santos Costa et al. 2021; 2022; Bassini-Silva et al. 2022). Additionally, three extant specimens were documented from material deposited at the Zoologische Staatssammlung München, Arthropoda varia.

We documented a total of 44 new fossil specimens embedded in amber (Supplementary materials, File 1). An additional specimen has already been reported and described (Arce et al. 2024). Three additional fossil specimens were considered from the literature (Chiangwu 1996; Kobbert 2013). In total the study considered 69 extant specimens and 48 fossil ones, 117 specimens all together. For the shape analysis (see below), five of the documented fossil specimens were not considered due to incompleteness of their habitus or their position in the amber piece.

Seven of the documented specimens in amber came from the collection of one of the authors (PM; BUB). One specimen is part of the Senckenberg Forschungsinstitut und Naturmuseum in Frankfurt/Main, Palaeozoology I – Amber research (SMF Be 2108a). Thirty-seven specimens are deposited in the Palaeo-Evo-Devo Research Group Collection of Arthropods, Ludwig-Maximilians-Universität München (LMU Munich; PED). They were legally purchased directly from the seller burmite-miner at the trading platform ebay.com; one specimen was purchased from Artur Michalski via the trading platform etsy.com; one specimen was purchased from Jonas Damzen (amberinclusions.eu). Most fossil specimens come from Cretaceous Kachin amber from Myanmar (ca. 100 mya), except for three specimens from Eocene Baltic amber (ca. 35-40 mya), one of these deposited at Senckenberg Forschungsinstitut und Naturmuseum and two at Palaeo-Evo-Devo Research Group Collection of Arthropods, Ludwig-Maximilians-Universität München. Two of the specimens are from Miocene Dominican amber (15-20 mya) and were documented from the literature (Supplementary materials, File 1).

Documentation methods

To document specimens, a Keyence VHX 6000 microscope was used. When accessible, we documented the specimens from both sides, and used different illumination methods (coaxial cross-polarised light, ring light, transmitted light) and background (black, white, glass) to achieve the best result possible, i.e. the best contrast and sharpness. The function HDR (high dynamic range) was applied when necessary. Adjacent frames were obtained and stacked with the built-in software. Final figure plates were made using Photoshop CS2.

Drawing of outlines

For the shape analysis, we used simplified outlines of 112 specimens, 43 fossil and 69 extant (see outline dataset in Supplementary materials, File 2). To get symmetrical outlines, half the body shape was drawn, then mirrored and stitched together. Setae, chelicerae, and claws were not included in the outline, since it is not always possible to see such details in the specimens (in particular the fossils). Pedipalps were included when possible and an additional shape analysis was performed to compare the influence of the pedipalps on the resulting morphospace. This showed that the signal including the specimens without pedipalps is the same as not including them, therefore the final shape analysis was performed with the whole dataset. Legs were artificially straightened (see Haug et al. 2021b for a similar procedure) and oriented. The first leg was displayed at a 45° angle, the second leg at a 0°, and the third leg at -45°, to correct for artefacts of varying leg position The shape of the legs was simplified to a straight line using the average width of the leg, and only the trochanter and tarsus were drawn following the specimen's shape.

Statistical and morphometrical analysis

We used elliptical Fourier analysis (EFA) to interpret the morphological variation of mite body outlines, using the free and open Momocs package (ver. 1.3.2; Bonhomme et al. 2014) in the R-statistics environment (ver. 4.1.0; R Core Team 2021). The code used is provided in Supplementary materials, File 3. For this purpose, 112 of the specimens were used (see Supplementary materials, File 1).

Using the principle of the Fourier transformation, a complex two-dimensional shape is decomposed into a harmonic sum of trigonometric functions, weighted with harmonic coefficients describing the shape (Kuhl & Giardina 1982; Bonhomme et al. 2014; Braig et al. 2024). This process allows for analysis of the shapes using multivariate tools (Bonhomme et al. 2014; Braig et al. 2023). The body outlines are registered with 3850 +/- 293 coordinates, centred and scaled, controlling for the influence of scale difference in the source material. We then used a function of the Momocs package (calibrate_harmonics) to identify the number of harmonics that would best represent the variation in our data set, in this case 16 harmonics (Braig et al. 2023, 2024). We aligned the body shapes according to a homologous starting point, the median posterior point of the idiosoma. The harmonic coefficients are then analysed with a principal component analysis (PCA; Bonhomme et al. 2014; Braig et al. 2023). Of the resulting principal components (PCs), we chose to retain the first 13 PCs, as they accumulated to more than 99% of the variation in the data set, as input data for the following statistical analysis. The cut-off was chosen due to the scree-test being subjective and the computational approach not being feasible (Joliffe 2002; Braig et al. 2023).

Specimens were classified according to their age in only two groups (fossil and modern representatives) since most of them belong to the Cretaceous, and to their lifestyle (parasitic, non-parasitic, and unknown lifestyle). Specimens from literature whose hosts are unknown (e.g. *Curteria southcotti*, *Hauptmannia viticola*), but where there are no records of the ingroup being non-parasitic, were considered parasitic. For a quantitative comparison of fossil and modern representatives we used different metrics for measuring morphological diversity (also called “disparity”; Guillerme et al. 2020). First, differences in sample size between fossil and modern representatives were corrected by rarefaction and bootstrapping (10000 times). We calculated the sum of variances for all principal components for the groups, retrieved from the PCA on the whole data set, as a measure for morphological diversity. The average distance of each group member to its group centroid in relation to the distance of the group centroid to the morphospace centre was used as a measure of position within the morphospace, informing about the difference in morphology (Guillerme et al. 2020; Braig et al. 2023).

Measurements

Linear measurements of the length of the idiosoma and legs were made with ImageJ. For the leg measurements, the length of the right leg is reported, or of the better accessible one. In order to counter any bias, all the measurements have been repeated three times and the mean values was calculated.

RESULTS

Brief description of specimens

General description: The body of all the specimens is organised into gnathosoma and idiosoma; the idiosoma bears three pairs of legs, hence representing a larva. Unless stated otherwise (see below), basipods (coxae) are separated from each other and leg femur is divided into two elements on all three pair of legs. All specimens are from the Cretaceous, except for PED 3462; PED 3425 and SMF Be 2108a, which are from the Eocene. Measurements of idiosoma and legs are reported on Supplementary materials, File 1.

Specimen SMF Be 2108a (Fig. 1A): Specimen accessible in dorsal view. Gnathosoma shape elongated, with at least two stout setae, one on femur and one on tarsus. Scutum (dorsal shield) possibly accessible, with triangular shape and very rounded distal angle. Numerous long setae on posterior area of the idiosoma. Legs with at least some barbed setae; first and third leg approximately twice the length of the idiosoma; with third leg slightly longer than first; second leg slightly less than twice the length of the idiosoma.

Specimen BUB 3150 (Fig. 1B): Specimen (apparently) accessible in dorsal view. Gnathosoma slightly tilted laterally, not very well accessible. Long seta on the tarsus of each leg; legs more than three times the length of the idiosoma; third pair of legs longer than the rest, more than four times the length of the idiosoma; second leg the shortest.

Specimen BUB 3159 (Fig. 1C) Specimen accessible in dorsal view. Legs more than three times the length of the idiosoma; third pair of legs slightly longer than the rest, more than four times the length of the idiosoma; second leg the shortest.

Specimen PED 3492_1 (Fig. 1D): Specimen accessible in dorsal view, with gnathosoma tilted laterally. Two long setae on distal part (tibia or tarsus)

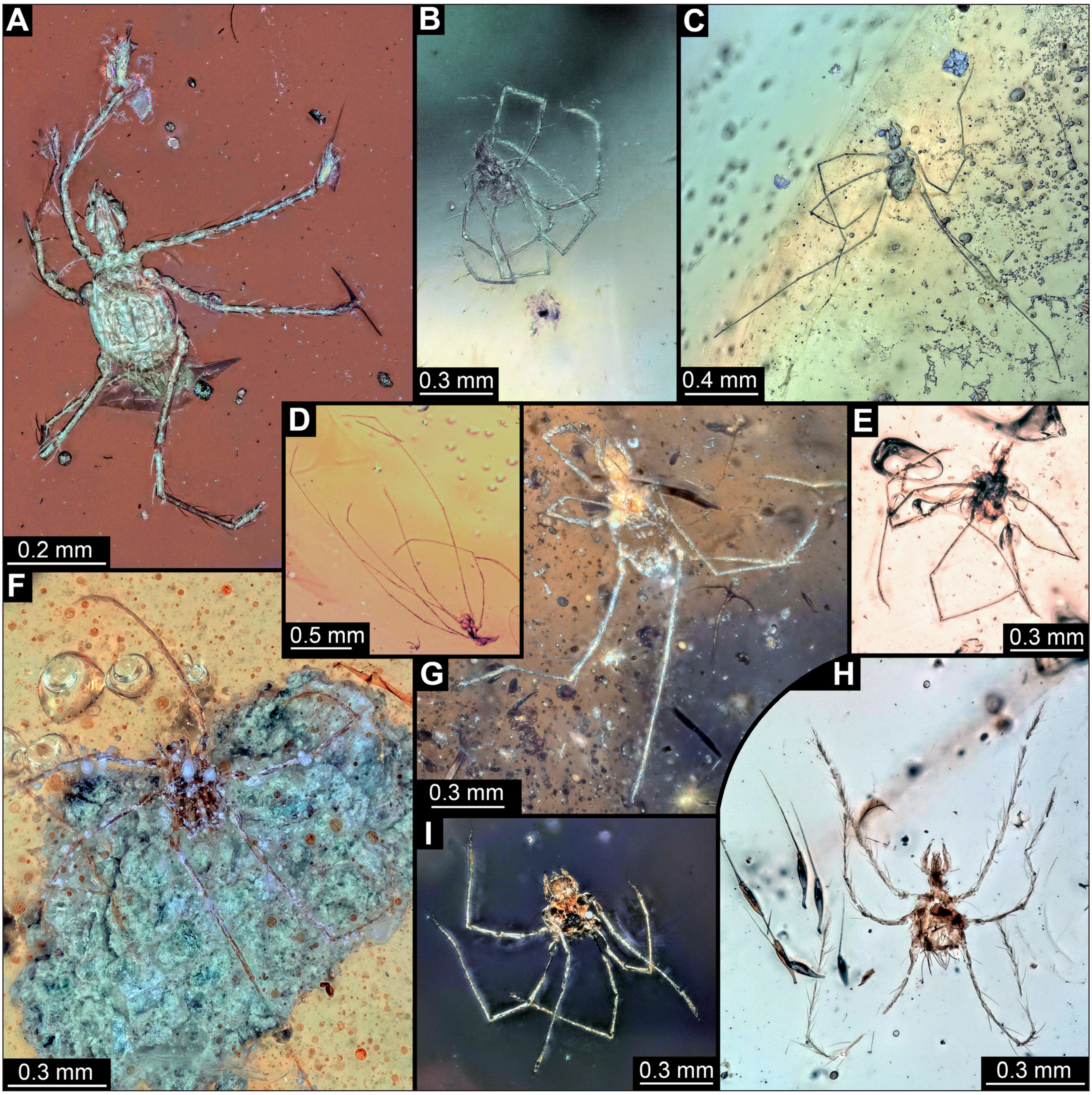

Fig. 1 - Fossil larvae of Erythraeoidea in amber. A) Specimen SMF Be 2108a. B) Specimen BUB 3150. C) Specimen BUB 3159. D) Specimen PED 3492_1. E) Specimen BUB 4778. F) Specimen BUB 4179. G) Specimen BUB 3378_2. H) BUB 3736. I) BUB 3196.

of pedipalps. Legs at least five times the length of the idiosoma, with very long femur and, especially, tibia; third leg much longer than the rest, nine times the length of the idiosoma.

Specimen BUB 3378_2 (Fig. 1G): Specimen accessible in (possibly) ventral view. Pedipalp claws (apparently) bifurcate. First leg the shortest, slightly more than twice the length of the idiosoma; second leg slightly longer; third leg almost five times the length of the idiosoma; femur and tibia longer than the rest of the elements; long femur and tibia, especially on third pair of legs; legs bearing long setae.

Specimen BUB 4778 (Fig. 1E): Specimen accessible in (possibly) ventral view; not well preserved, with amber artifacts on top of the mite body. Pedipalps not accessible. Small process resembling a spine on the trochanter of the third leg; first and second leg subequal in length, three times the length of the idiosoma; third leg slightly longer, four times the length of the idiosoma.

Specimen BUB 4179 (Fig. 1F): Specimen accessible in (possibly) ventral view; not well preserved. Pedipalps with a long seta on tibia (or tarsus?) and prominent terminal claw on pedipalp tibia. First and third pair of legs subequal in length; second pair of legs shorter, almost twice the length of the idiosoma.

Specimen BUB 3736 (Fig. 1H): Specimen accessible in ventral view. Posterior region of gnathosoma narrow; with a prominent terminal claw on pedipalp tibia; pedipalp femur bearing a long seta (no other setae visible on pedipalps). Apparent hypertrichy on idiosoma and legs (higher number of setae); posterior region of idiosoma bearing numerous long setae. Legs with numerous long setae; one particularly long seta on the trochanter of the first pair of legs; legs more than three times the length of the idiosoma; first and second pair of legs subequal in length; third pair of legs slightly longer than the rest, more than four times the length of the idiosoma.

Specimen BUB 3196 (Fig. 1I): Specimen accessible in (possibly) dorsal view. Wide gnathosoma, with a long and thin seta on femur. A long seta on trochanter of the three pairs of legs; legs at least four times the length of the idiosoma; first and second pair of legs subequal in length; third pair of legs longer than the rest, more than five times the length of the idiosoma.

General description of amber piece PED 0776 (Fig. 2A): Eleven mite specimens close to a dermapteran (Fig. 2F).

Specimen PED 0776_9 (Fig. 2B, D): Specimen accessible (apparently) in ventral view. Idiosoma round (Fig. 2D). Gnathosoma with at least one long setae on femur and one long seta on tibia; apparent bifurcate tibial claw; at least two setae on tarsus (Fig. 2B). At least the femur on the third pair of legs divided into two elements. Legs five times the length of the idiosoma; first and third legs subequal in length; second leg slightly shorter; femur divided into two sub-elements; first and second legs bearing one long seta on (apparently) the trochanter.

Specimen PED 0776_4 (Fig. 2C): Specimen accessible (possibly) in dorsal view, not very well preserved. Gnathosoma with visible thumb-like process. Division of femur absent or not visible. Legs more than three times the length of the idiosoma; first and third legs subequal in length; second leg slightly shorter than the rest.

Specimen PED 0776_11 (Fig. 2E): Specimen accessible (apparently) in ventral view. Specimen not very well preserved, idiosoma slightly tilted laterally and broken legs, hence not included in the analysis. Legs around three times the length of the idiosoma; third pair of legs slightly longer.

Specimen PED 0776_12 (Fig. 2F): Shape of idiosoma altered by an artifact in the amber piece, hence not included in the analysis. Gnathosoma not accessible. Division of femur absent or not visible; legs around three times the length of the idiosoma; third pair of legs slightly longer than the rest, more than four times the length of the idiosoma.

Specimen PED 0776_10 (Fig. 2G): Specimen accessible in dorsal view. Division of femur absent or not visible; legs at least three times the length of the idiosoma.

Specimen PED 1236_3 (Fig. 3A): Specimen accessible in dorsal view. Very long femur and tibia; legs at least four times the length of the idiosoma; length of first and third pair subequal to the second pair of legs, more than five times the length of the idiosoma.

Specimen PED 1236_2 (Fig. 3B): Specimen accessible in dorsal view. Long and stout seta on (possibly) femur of pedipalp, and possibly a second one on patella (genu). At least the femur on the third and second pair of legs divided into two elements; legs at least five times the length of the idiosoma; first pair of legs longer than the rest, almost six times the length of the idiosoma.

Specimen PED 1236_1 (Fig. 3C): Specimen accessible in dorsal view, not so well preserved. Longer femur and tibia than the rest of the leg elements; first pair of legs broken, therefore it was not included in the analysis; second pair of legs three times the length of the idiosoma; third pair longer, five times the length of the idiosoma.

Specimen PED 1236_5 (Fig. 3D): Specimen accessible in dorsal view. Long seta on (possibly) fe-

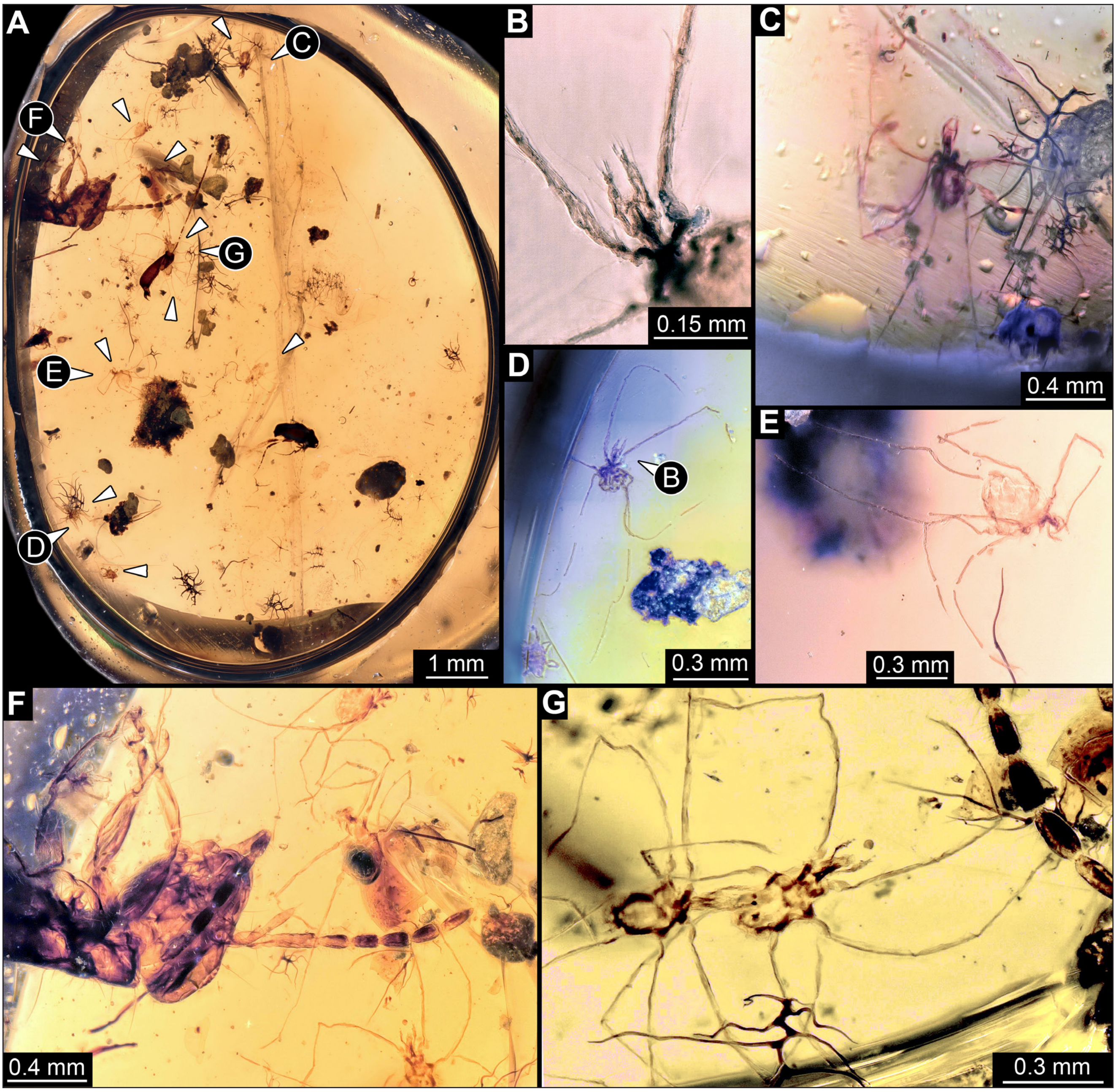

Fig. 2 - Fossil larvae of Erythraeoidea in amber piece PED 0776. A) Overview of amber piece, each points to a mite. B) Closeup to gnathosoma of specimen PED 0776_9. C) Specimen PED 0776_4. D) Specimen PED 0776_9. E) Specimen PED 0776_11. F) Closeup to dermapteran and mite PED 0776_12. G) Specimen PED 0776_10.

mur of pedipalp. Length of first and third pair of legs almost seven times the length of the idiosoma; second pair of legs shorter than the rest, five times the length of the idiosoma.

Specimen PED 1236_4 (Fig. 3E): Specimen accessible in ventral view. Long seta on gnathosoma, similar to length and disposition on specimen in PED 2615_1. Pedipalps only partially visible. Length of first and third legs more than seven times the length of the idiosoma; second leg slightly shorter, six times the length of the idiosoma; long setae on femur and tibia, similar to length and disposition on specimen in PED 2615_1.

Specimen PED 1268_2 (Fig. 3F): Specimen accessible in dorsal view. Apparent dorsal scutum (shield) visible, of triangular shape, and a pair of (possible) bothridia anteriorly. Legs twice the size of the idiosoma, third leg longer than the other two.

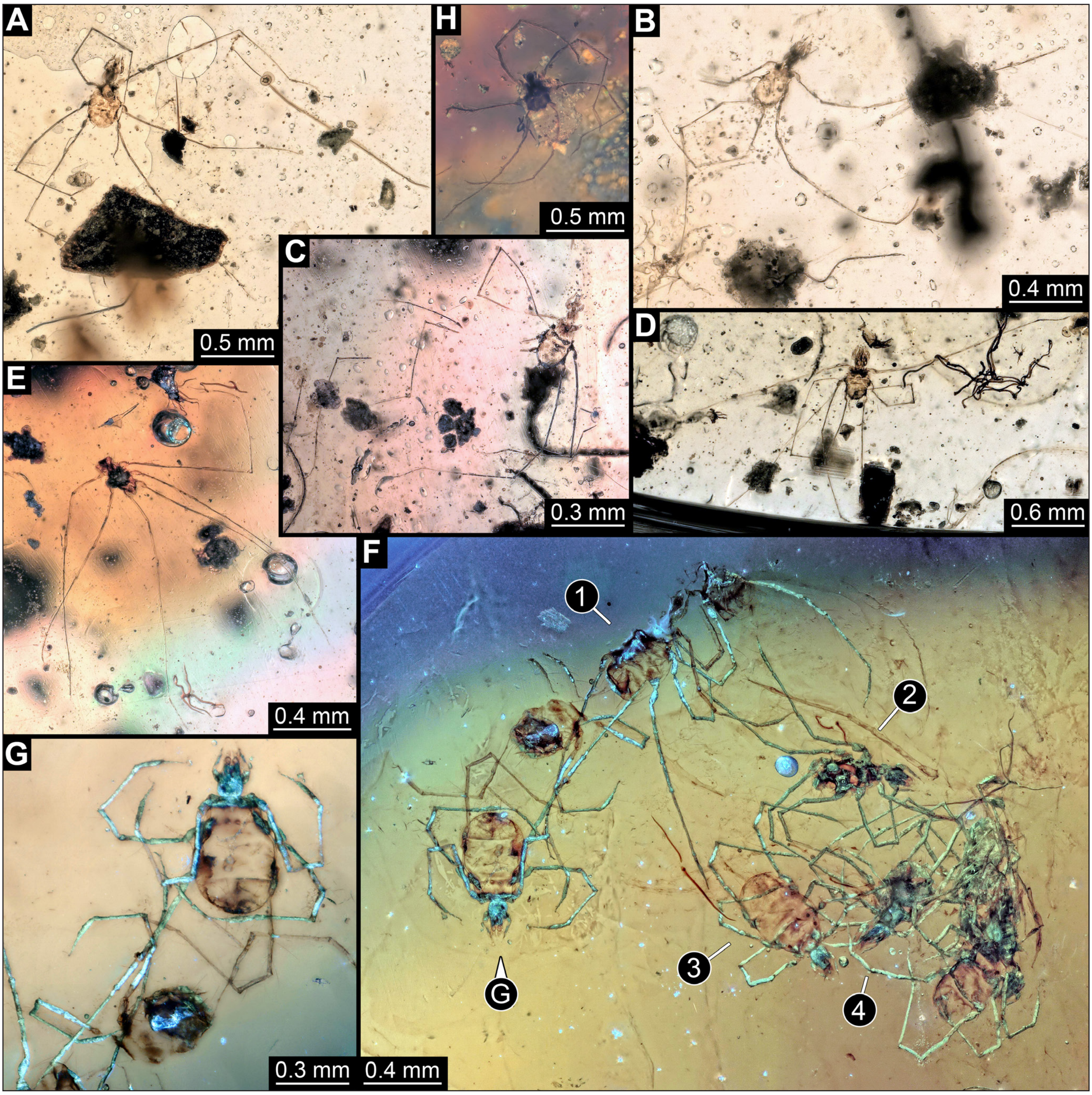

Fig 3 - Fossil larvae of Erythraeoidea in amber. A) Specimen PED 1236_3. B) Specimen PED 1236_2. C) Specimen PED 1236_1. D) Specimen PED 1236_5. E) Specimen PED 1236_4. F) Overview of specimens in amber piece PED 1268: PED 1268_2 (1); PED 1268_3 (2); PED 1268_5 (3); PED 1268_4 (4). G) Specimen PED 1268_1. H) Specimen 2615_1.

Specimen PED 1268_3 (Fig. 3F): Specimen accessible in dorsal view. Similar to specimen PED 1268_2. Legs twice the length of the idiosoma, third leg slightly longer than the other two.

Specimen PED 1268_4 (Fig. 3F): Specimen accessible in dorsal view. Femur al least on first and third pair of legs divided into two elements. Legs twice the length of the idiosoma, third leg slightly longer than the rest.

Specimen PED 1268_5 (Fig. 3F): Specimen preserved in dorsal view. Shape of idiosoma indicates possible physogastry (engorgement). Femur at least on first and third pair of legs divided into two elements. First and second leg 1.5x the length of the idiosoma, third leg longer than the other two, twice the size of the idiosoma; long setae on femur, patella (genu) and tibia of the three pairs of legs, similar to the ones present in specimen PED 1236_4.

Specimen PED 1268_1 (Fig. 3G): Specimen accessible in dorsal view. Shape of idiosoma indicates possible physogastry (engorgement). Femur at least on first and third pair of legs divided into two elements. Legs twice the size of the idiosoma, third leg longer than the other two.

Specimen PED 2615_1 (Fig. 3H): Specimen preserved in dorsal view. Pedipalps bearing a long and stout seta (shape not accessible), possibly located on patella (genu); terminal elements of the pedipalps not accessible. Length of legs subequal, five times the length of the idiosoma; long setae on trochanter, femur, genu and tibia of the three pair of legs, with numerous setae on tarsus.

Specimen PED 3419_2 (Fig. 4A): Habitus similar to specimen PED 3419_1. Specimen accessible in ventral view. Gnathosoma slightly larger than in other specimens. Division of femur absent or not visible. Legs more than three times the length of the idiosoma; third leg longer than the rest, more than four times the length of the idiosoma.

Specimen PED 3419_1 (Fig. 4B): Habitus similar to specimen PED 3419_2. Specimen accessible in ventral view. Gnathosoma larger than in other specimens. Shape of idiosoma indicates slight possible physogastry (engorgement). Femur al least on first pair of legs divided into two elements. Legs more than three times the length of the idiosoma; third leg slightly longer than the rest.

Specimen PED 3214 (Fig. 4C): Specimen accessible in ventral view. First and second leg 1.5x longer than the idiosoma, third leg more than twice the length of the idiosoma.

Specimen PED 3163 (Fig. 4D): Specimen accessible possibly in dorsal view, attached to a host. Shape of idiosoma indicates possible physogastry (engorgement). Gnathosoma not accessible due to its attachment to the host. Division of femur absent or not visible; legs shorter than in other specimens here described, slightly shorter than the idiosoma.

Specimen PED 3403_2 (Fig. 4E): Specimen accessible in ventral view. At least two setae on pedipalps, one on femur, one on genu or tibia. Femur al least on first pair of legs divided into two elements; numerous long setae on legs; one long and stout seta on the trochanter; first leg four times the length of the idiosoma; second leg shorter, almost three times the length of the idiosoma; third leg not accessible, hence not included in the analysis.

Specimen PED 3403_1 (Fig. 4F): Habitus similar to specimen in PED 3411. Specimen accessible in (apparent) ventral view. Gnathosoma with visible thumb like process. Idiosoma rounded shape. No apparent division on femur; legs thicker than in other specimens; all legs more than double the length of the idiosoma; third leg longer than the rest.

Specimen PED 3122 (Fig. 4G): Specimen preserved in ventral view. Attached to a host through the gnathosoma. Shape of idiosoma indicates possible physogastry (engorgement). Femur on three pair of legs divided into two elements; legs at least double the length of the idiosoma; third leg longer than the rest, more than three times the length of the idiosoma.

Specimen PED 3462 (Fig. 4H): Specimen accessible in dorsal view. Pedipalps not completely accessible. Separation of basipods (coxae) not accessible due to position of legs. Long setae on pedipalps, idiosoma and legs; leg tarsus with numerous setae in three pairs of legs; legs more than four times the length of the idiosoma; third leg slightly longer than the rest; tarsus of all legs with two claws and a claw-like empodia (attachment structures).

Specimen PED 3411 (Fig. 4I): Habitus similar to specimen in PED 3403_1. Specimen accessible in (apparent) ventral view. Legs thicker than in other specimens, similar to legs in PED 3403_1; division of femur absent or not visible; long seta on femur of at least the first pair of legs; abundant setae on tarsus; all legs more than twice the length of the idiosoma; third leg longer than the rest.

Specimen PED 3490 (Fig. 4J): Specimen accessible (possibly) in ventral view. Division of femur absent or not visible; legs at least three times the length of the idiosoma; first leg slightly longer than the rest.

Specimen PED 3492_2 (Fig. 4K): Specimen accessible in lateral view, hence not included in the

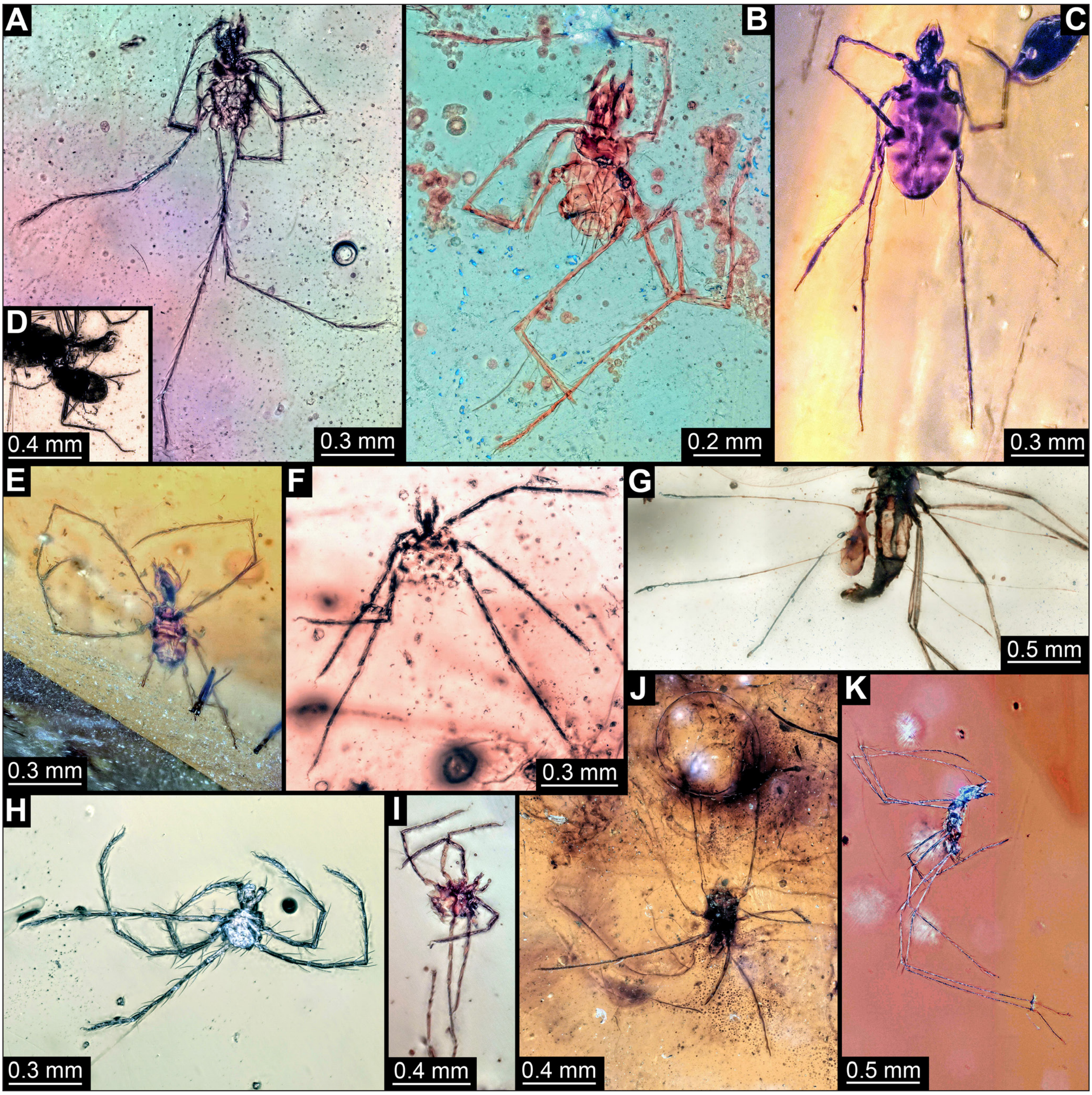

Fig 4 - Fossil larvae of Erythraeoidea in amber. A) Specimen PED 3419_2. B) Specimen PED 3419_1. C) Specimen PED 3214. D) Specimen PED 3163. E) Specimen PED 3403_2. F) Specimen PED 3403_1. G) Specimen PED 3122. H) Specimen PED 3462. I) Specimen PED 3411. J) Specimen PED 3490. K) Specimen PED 3492_2.

analysis. Gnathosoma large compared to other specimens. Femur al least on first pair of legs divided into two elements; legs at least three times the length of the idiosoma, with very long femur and, especially, tibia; third leg extremely longer than the rest, more than five times the length of the idiosoma.

Specimen PED 3425 (Fig. 5A): Specimen accessible in ventral view. Pedipalps with at least three bushy setae with strong setules, one on the pedipalp femur, one on the patella (genu) and one either on patella (genu) or tarsus (undistinguishable). Two stout setae on first and third leg trochanter; legs around twice the length of the idiosoma; third leg slightly longer than the rest.

Specimen PED 3549 (Fig. 5B): Specimen accessible in ventral view. Pedipalps with two setae, the most proximal one (possibly on the patella (genu)

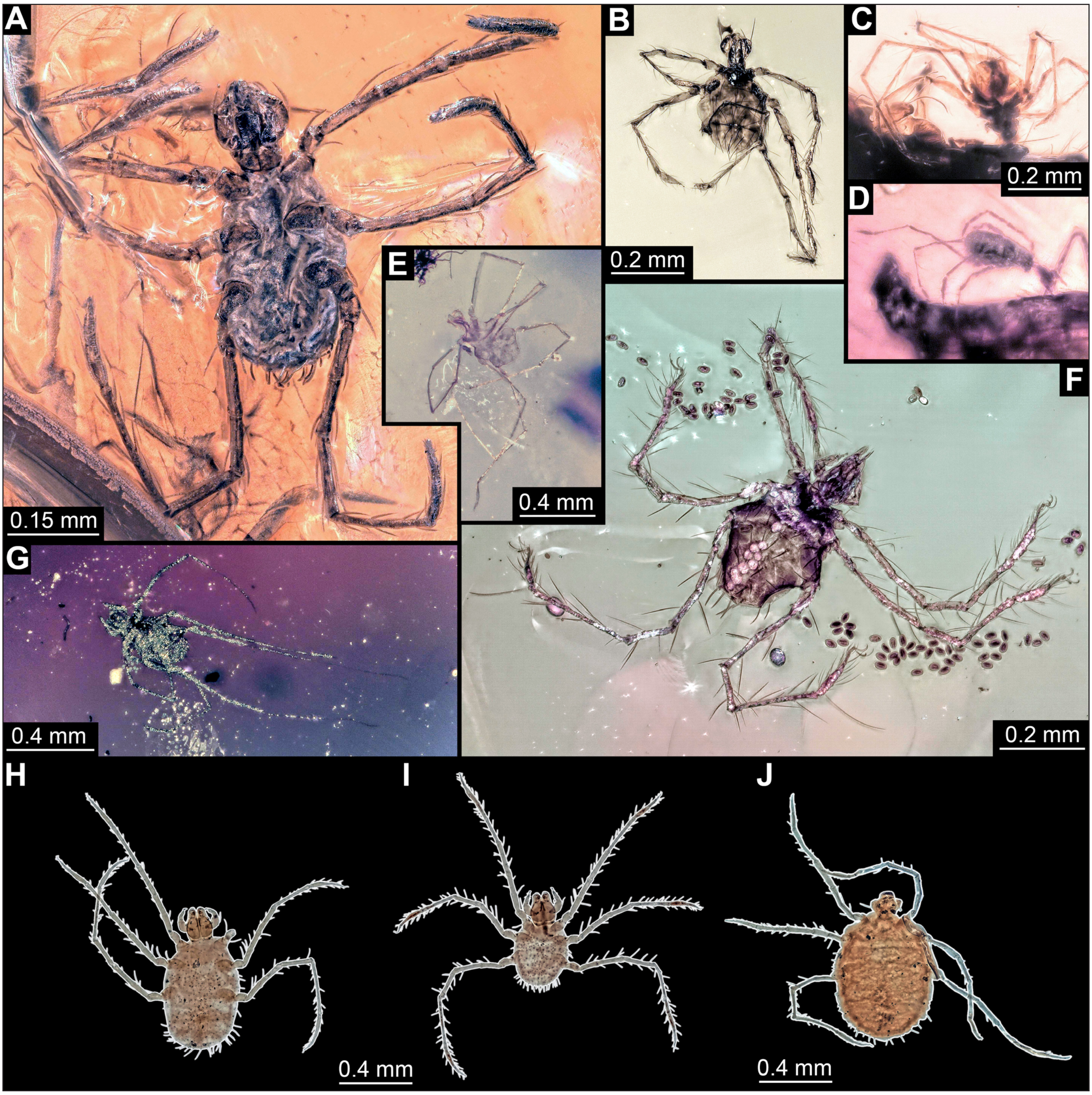

Fig 5 - Fossil larvae of Erythraeoidea in amber (A–G) and extant specimens (H–J). A) Specimen PED 3425. B) Specimen PED 3549. C) Specimen PED 3506. D) Specimen PED 3511. E) Specimen PED 3209_1. F) Specimen PED 3503. G) Specimen PED 3585. H, I, J) Extant specimens of *Erythraeus phalangioides* deposited at Zoologische Staatssammlung München, Arthropoda varia.

longer than the most distal one (on the tarsus?). Femur at least on first pair of legs divided into two elements; first and second legs twice the length of the idiosoma; first leg slightly longer than the rest; third leg slightly shorter than the rest.

Specimen PED 3506 (Fig. 5C): Specimen accessible in ventral view, attached to a host. Gnathosoma not accessible due to its attachment to the host. Femur at least on second and third pair of legs divided into two elements; legs at least twice the length of the idiosoma; third pair of legs longer than the rest, almost three times the length of the idiosoma.

Specimen PED 3511 (Fig. 5D): Specimen accessible in dorsal view, attached to a host. Shape of idiosoma indicates possible physogastry (engorgement). Division of femur absent or not visible; legs shorter than in other specimens here described, at least 1.2x the length of the idiosoma, third pair of legs longer than the rest, almost three four times the length of the idiosoma.

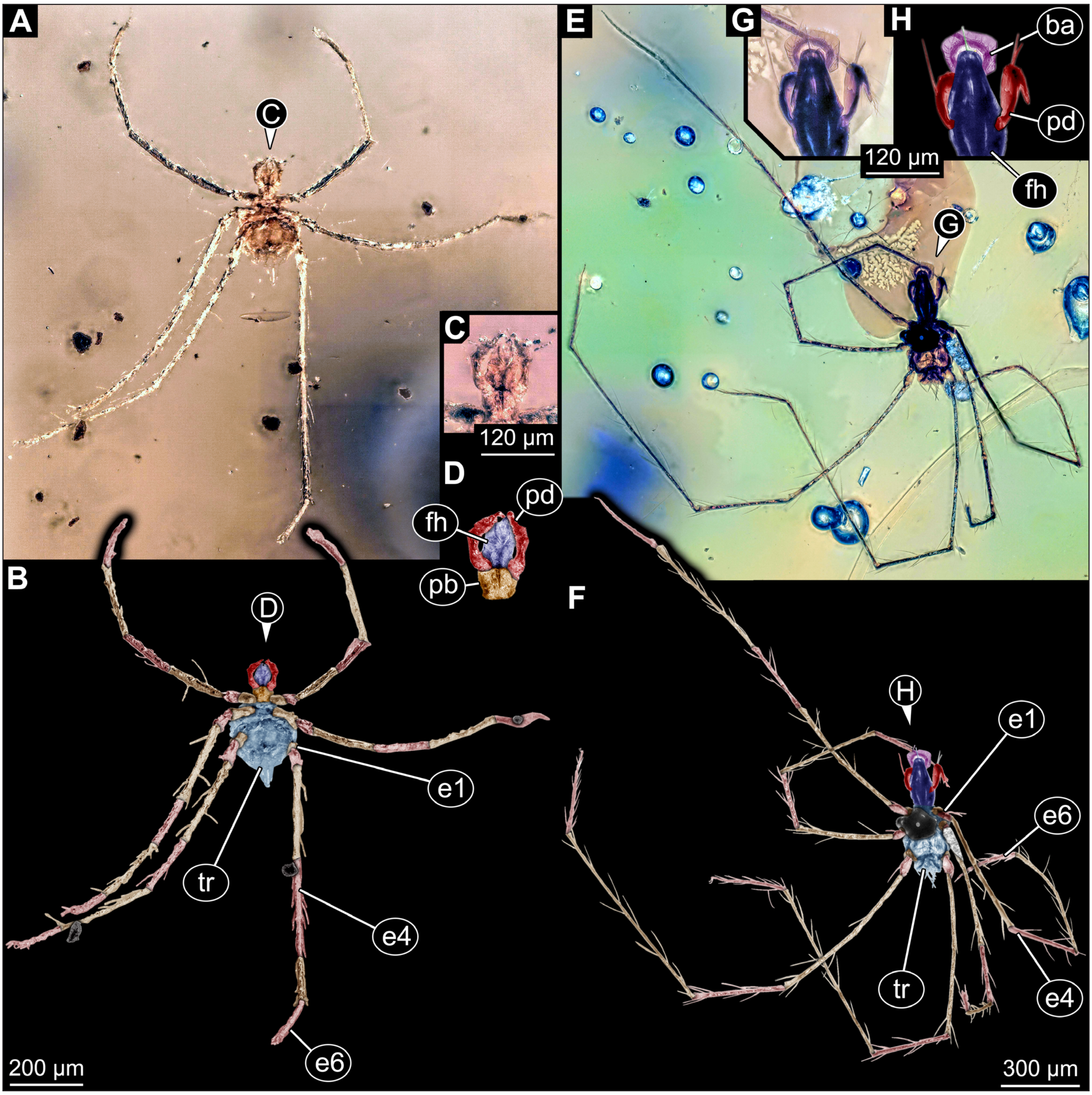

Fig 6 - Fossil larva of Erythraeoidea in amber. A) Habitus of specimen PED 2615_2. B) Habitus of specimen PED 2615_2 coloured marked. C) Gnathosoma of specimen PED 2615_2. D) Gnathosoma of specimen PED 2615_2 colour marked. E) Habitus of specimen PED 3134. F) Habitus of specimen PED 3134 coloured marked. G) Gnathosoma of specimen PED 3134. H) Gnathosoma of specimen PED 3134 colour marked. ba= buccal aperture; fh= functional head; pd= pedipalps; pb= pedipalp basipods; tr= trunk; e1, e4, e6= leg element number.

Specimen PED 3209_1 (Fig. 5E): Specimen accessible in dorsal view. Division of femur absent or not visible; legs more than three times the length of the idiosoma; third pair of legs slightly longer than the rest, almost four times the length of the idiosoma.

Specimen PED 3503 (Fig. 5F): Specimen accessible in ventral view. Chelicerae protruding from the buccal aperture. At least two moderately long setae on pedipalps. Long setae on legs and idiosoma, with one very long seta on tarsus of legs, longer on the third leg. Basipods (coxae) separated from each other, although less separation between first and second basipod than in other specimens here described; legs more than twice the length of the idiosoma; third leg slightly longer.

Specimen PED 3585 (Fig. 5G): Specimen accessible (possibly) in dorsal view, not very well preserved. Division of femur absent or not visible; legs length at least 2.5x the length of the idiosoma; third leg longer than the rest, more than three times the length of the idiosoma.

Specimen PED 2615_2 (Fig. 6A, B): Specimen accessible in ventral view. Gnathosoma small and short pedipalps compared to other specimens (Fig. 6C, D). Rounded idiosoma; with six long setae on the distal area of the idiosoma. Long and stout setae on legs, particularly one long setae on femur of three pair of legs; first and second pair of legs three times the length of the idiosoma, with second pair of legs slightly longer than the first; third pair of legs the longest, more than four times the length of the idiosoma.

Specimen PED 3134 (Fig. 6E, F): Specimen accessible in ventral view. Gnathosoma extremely large compared to other specimens (Fig. 6G, H); one long and stout seta on pedipalp femur; possibly a seta on pedipalp patella (genu); numerous setae on pedipalp tibia; pedipalp claw absent or not visible. Numerous setae on the distal area of the idiosoma. Femur and tibia extremely long, tarsus also long compared to other specimens; apparent processes resembling spines on trochanter of three pairs of legs; first pair of legs six times the length of the idiosoma, second pair of legs the shortest, almost five times the length of the idiosoma, third pair of legs eight times the length of the idiosoma.

Shape analysis

The PCA resulted in 13 principal components explaining over 99% of the shape variation (see Supplementary materials, File 4 for a PCA analysis showing the different age of each specimen, see Supplementary materials, File 5 for results of the PCA analysis and Supplementary materials, File 6 for the graphical component loadings). PC1 explains 39.9% of the shape variation and is dominated by the length of the legs and the size of the idiosoma. Negative values indicate long legs, with the three pairs of legs being subequal in length, and a small idiosoma; positive values indicate shorter legs, with the first pair of legs shorter than the rest, and a larger and longer idiosoma. PC2 explains 30.9% of the shape variation, and is dominated by the length of the legs and the gnathosoma. Negative values indicate shorter legs, with the first pair of legs longer than the rest, a larger and broader idiosoma, and a more prominent gnathosoma, positive values indicate longer legs with the first pair being longer than the third. PC3 explains 10.4% of the shape variation and is dominated by the size of the body and the leg length. Negative values indicate shorter legs, with the first pair of legs longer than the rest, and a large idiosoma; positive values indicate longer legs, with the third pair of legs slightly longer than the rest, and a more prominent gnathosoma at higher values. PC4 explains 5.8% of the shape variation and is dominated by the width and length of the idiosoma. Negative values indicate a longer idiosoma and prominent gnathosoma; positive values indicate a shorter but wider idiosoma, longer legs, and the third pair of legs longer than the rest.

Plotting PC1 versus PC2 showed some level of overlap between extant and fossil specimens, although most fossil specimens occupied the area of higher PC2 values and relatively low PC1 values (Fig. 7). The resulting plot of PC3 versus PC4 shows great overlap between fossil and extant specimens, with most extant specimens occupying the lower right area of the plot (high PC3 values and low PC4 values; Fig. 8). Two fossil specimens from the Cretaceous plotted outside the area of where most specimens grouped together, one at low PC4 values, and one opposite to it, at high PC4 values. One extant specimen plotted at extremely low PC3 values.

When considering all dimensions of the morphospace, we found significant differences in the size of the occupied morphospace between the fossil and extant representatives (Welch's two sample t-test; p-value < 0.001). Additionally, we found that extant and fossil representatives were significantly different in their position within the morphospace (Welch's two sample t-test; p-value < 0.001).

Discussion

Identity of the specimens

The oldest known erythraeoidean is an adult from a non-amber deposit, the Crato Formation (Brazil), a Lower Cretaceous deposit (113.0–125.0 mya; Dunlop 2007). From Cretaceous amber inclusions, there were 19 fossil erythraeoidean mites described to date, one from Canadian amber (72.1–83.6 mya, Vercammen-Grandjean 1973), and 18 from Kachin amber (Kobbert 2013; Konikiewicz & Mąkol 2018; Arce et al. 2024a, Fig. 4G; Arce et al. 2024b). From Kachin amber, nine correspond to the larval stage (Vercammen-Grandjean 1973; Kobbert 2013; Konikiewicz & Mąkol 2018; Arce et al. 2024a; Arce et al. 2024b). There are eight more reports of larvae attached to their hosts that have not been further described in detail, five from Lebanese amber (ca. 130 mya, Poinar et al. 1994; Poinar & Milki 2001; Azar 2007; Azar et al. 2010; Boucot & Poinar 2010), one from Raritan New Jersey amber (89–94 mya, Grimaldi 2000), and two from Canadian amber (ca. 70–80 mya, Poinar et al. 1993; Poinar et al. 1997). Here we report 41 new erythraeoidean larvae from the Cretaceous Kachin amber, expanding the reports from Cretaceous amber to more than doubling the record. We also report three erythraeoidean larvae from Eocene Baltic amber. The record of erythraeoidean mites in Eocene amber is better known than the Cretaceous one. To date, 30 erythraeoidean fossil mites (Koch & Berendt 1854, Vitzthum 1943; Eichmann 2002; Bartel et al. 2015; Sidorchuk et al. 2019) have been described from Baltic amber, from which 5 are larvae attached to hosts (Eichmann 2002). Additionally, eight more adult erythraeoidean specimens have been reported from the Eocene Bitterfeld (Saxonian) amber (38–47.8 mya) (Bartel et al. 2015). According to Bartel et al. (2015), there are many inclusions of erythraeoidean mites still to be described from Baltic and Bitterfeld amber.

All specimens reported here can be identified as larvae of mites since their body is divided into gnathosoma and idiosoma, and they have three pairs of legs instead of four (as in post-larval mites). The length of the legs more than twice the length of the idiosoma in most specimens, the separation between the first pair of basipods, and their habitus makes it possible to identify the mites here described as larvae of erythraeoidean mites. In well-preserved specimens accessible in ventral view, the urstigmata (structure between coxae of two anterior legs) and anus seem to be absent. These features are present in larvae of most other ingroups of Parasitengona but not found in Erythraeoidea (Southcott 1961). Although there are a few exceptions (specimens in PED 1268, PED 3503, PED 3134 and PED 2615_2), most specimens here described have a leg length more than twice the idiosoma length. This is a typical character of long-legged velvet mites (Wohltmann 2001), although exceptions exist among some ingroups, such as *Abrolophus* (Wohltmann et al. 2001), *Balaustium* (Southcott 1961) or *Ramsayella* (Zhang 2000). However, in the specimens in which the length of the legs is less than twice the length of the idiosoma, their habitus is compatible with Erythraeoidea. It is remarkable that the legs in erythraeoideans seem to differ in length between each other, and in most, the longest one is generally the third pair, followed by the first pair, and the shortest is the second pair. Although there were exceptions, this was observed in both fossils here described and extant specimens (e.g. *Erythraeus phalangioides*, Fig. 5H—J; *Leptus holgeri*, Haitlinger 1999; *Nagoricanella salehi*, Kamran & Alatawi 2015; *Trichosmaris dispar*, Dos Santos Costa et al. 2021).

Further identification of the here reported specimens to ingroups of Erythraeoidea is hampered by the fact that most characters are concealed, as it happens with most mite specimens in amber. Nevertheless, it is highly probable that all mites in PED 1268, given their similarities, are representatives of the same taxonomic group. The same applies to the specimens in PED 0776, although relative measurements of their legs are not as uniform. Specimens in PED 1236 also seem to be representatives of the same taxonomic group. Additionally, PED 1236_4 seems to be closely related to the specimen PED 2615_1. Also, PED 3403_1 and PED 3411 share the same characteristic thick legs and seem to be closely related.

The protruding gnathosoma of larva PED 3134 could potentially be correlated with their feeding behaviour. It resembles that of the larva of *Hydrachna magniscutata*, a representative of Hydrachnidia (water mites), although the rest of their body shape does not look alike. Although this species is considered parasitic (Davids 1972), according to Mitchell (1957) it has been discussed that the large capitulum could be related to them being also phytophagous, although there are no detailed observations on this type of feeding behaviour. However, representatives of the non-parasitic ingroup within Erythraeoidea, Balaustiinae, also have a prominent gnathosoma, which has been suggested to be linked to their phytophagous feeding habits as pollen feeders (Southcott 1961).

The relatively large gnathosoma of PED 3419_1, PED 3419_2, PED 3492_1 and PED 3492_2 compared to other specimens, resembles that of *Proterythraeus southcotti* (Vercammen-Grandjean 1973), a representative of Erythraeidae from Cretaceous Canadian amber. Furthermore, PED 3492_2 is also similar to this species with respect to its habitus and general chaetotaxy (setae disposition), although legs are longer in the mite here reported.

The separation of basipods (coxae) in some specimens (PED 3503, PED 3134) is not as prominent as in other specimens. This is visible also in specimens of Balaustiinae and some representatives of *Abrolophus* (Southcott 1961; Wohltmann et al. 2001), therefore it is still possible to interpret these specimens as representatives of Erythraeoidea. The legs of these specimens are also not as long as in the rest, but still twice the length of the idiosoma. As already mentioned, legs in Balaustiinae and *Abrolophus* are also quite short (even shorter than the idiosoma). Adult specimens identified as Balaustiinae have been found in amber from the Eocene (Koch & Berendt 1854; Vitzthum 1943), although there are no described larvae of these ingroups. Unfortunately, other characters are not accessible in PED 3503 and PED 3134, such as the dorsal shield (scutum), and therefore further identification is not possible.

As a general rule, in fossil specimens here described, elongation of the legs seems to be correlated with both the elongation of the femur and tibia elements. This can also be seen in modern representatives that occupy the same area in the morphospace as the fossil ones, like in *Erythraeus bibadakiensis* (e.g. Haitlinger 2011, fig. 6-11), in *Erythraeus uhadi* (Kamran & Alatawi 2014, fig. 5-13) and in *Trichosmaris dispar* (Dos Santos Costa et al. 2021, fig. 6, 7). On the contrary, modern specimens that plot outside the overlapping area with fossil ones, such as *Curteria southcotti* (Wohltmann et al. 2007), tend to have subequal length of the leg elements. Studies on leg usage and biodynamics would enlighten how these morphological differences affect the movement of their walking appendages.

Morphospace analysis

Despite at least a certain level of overlap in the morphospace between extant and fossil groups, the difference in morphology was statistically significant, pointing to a separation between the two groups. According to our analysis, fossil larvae of Erythraeoidea group together at lower PC1 and higher PC2 values, the area of the morphospace with body shapes dominated by longer legs and a smaller idiosoma (Fig. 7). There is an overlap in the central part of this area of the morphospace, where also some of the extant representatives are located. Nevertheless, the extant fauna of erythraeoidean larvae seems to be more widespread on the morphospace, pointing to a higher diversity of shapes. This result is even more remarkable when considering that fossils cover a larger time span than extant representatives and that differences in sample size were corrected in the analysis to make the data robust against outliers. Possibly some of the morphological diversity that exists today was not yet present in the past. However, fossilised representatives must have lived on or near the bark surface to be entrapped in the tree resin. In consequence, biases in the fossil record have to be considered when comparing it to extant representatives. There are no clear differences between fossils from different ages (Supplementary materials, File 4). Nevertheless, a possible bias linked to the imbalance in sample size cannot be ruled out since most fossils included in the analysis are from Cretaceous Kachin amber origin (38 specimens from Cretaceous Kachin amber against three species from Eocene Baltic amber and two from Miocene Dominican amber).

On the other hand, part of the morphospace occupied by fossils is not occupied by modern representatives, which suggests that some of the diversity of the group was lost over time. This pattern is further supported by characteristics found in some specimens here described (see above) that, to the best of our knowledge, have not been reported from extant erythraeoidean mites. These characteristics include the extremely long legs of PED 3492_1 and PED 3134 (up to nine and eight times the length of the idiosoma, respectively), the spine-like process in BUB 4778 and PED 3134, the thick legs of PED 3403_1 and PED 3411, and the large gnathosoma of PED 3134. Lower values of PC2 are also linked to a more prominent gnathosoma, an area of the morphospace only occupied by the extant fauna. Yet, the overlap between extant and fossil specimens is much more pronounced in the PC4 versus PC3 (Fig. 8), where groups are mostly indistinguishable.

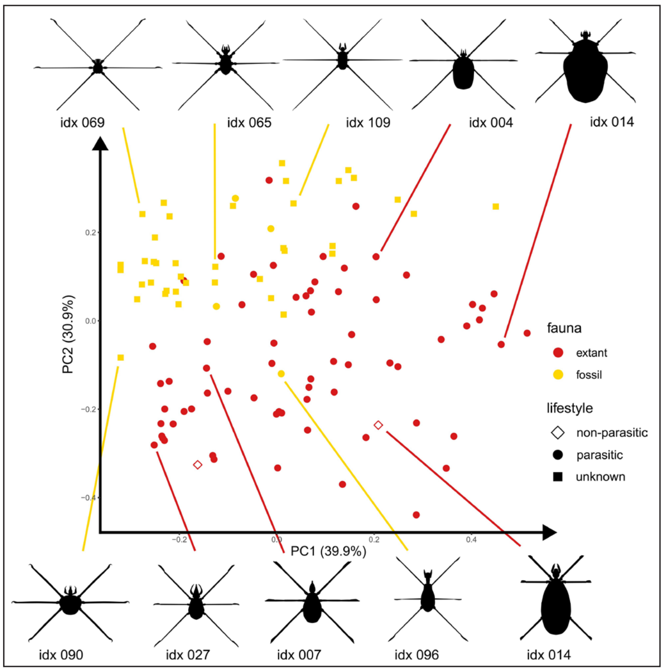

Fig. 7 - Plot of Principal Component Analysis of PC1 versus PC2 as partial representation of the morphospace. Idx number refers to the number associated to each specimen in Supplementary materials, File 1.

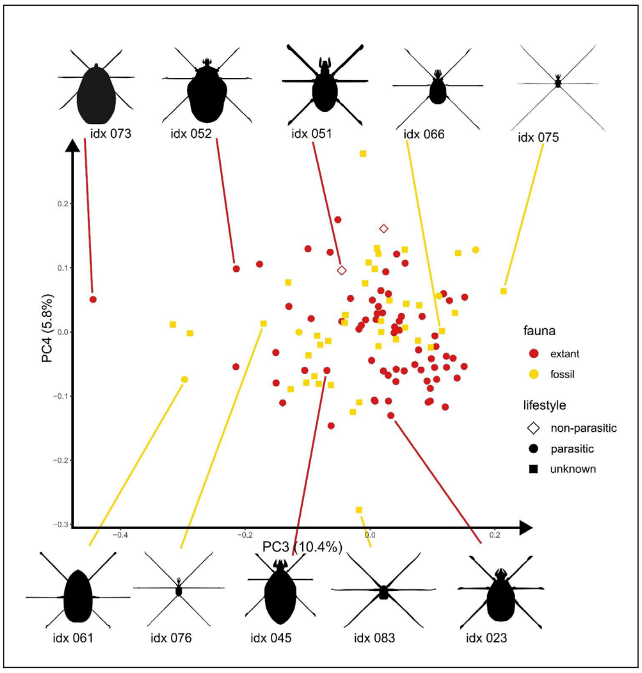

Fig. 8 - Plot of Principal Component Analysis of PC3 versus PC4 as partial representation of the morphospace. Idx number refers to the number associated to each specimen in Supplementary materials, File 1.

Leg length

Leg length seems to be the most prominent difference between extant and fossil long-legged velvet mite specimens. Long legs are often linked to faster locomotion not only in diverse euarthropodan ingroups (e.g. crustaceans, Kralj-Fišer et al. 2020; ants, Feener et al. 1988; beetles, Forsythe 1981), but also in vertebrates (Losos & Sinervo 1989, Trochet et al. 2019). Longer legs confer longer strides, hence reducing the cost of locomotion. The long legs of erythraeoidean mites compared to other terrestrial representatives of Parasitengona indeed seem to be related to their faster movement when walking on a surface. Although erythraeoidean mites, like the rest of parasitengonan larvae, depend on their host for long distance dispersion (Treat 1975; Seeman & Walter 2023), erythraeoidean larvae can walk as fast as 6.67 E-3 m/s (Wohltman 2000). This is quite impressive when compared to the speed of larvae of other terrestrial lineages of Parasitengona (3.17 E-4–4.17 E-4 m/s for Microtrombidiidae, 2.17 E-3–2.50 E-3 m/s in other representatives of Trombidioidea, 9.17 E-4 m/s for Calyptostomatidae; Wohltman 2000).

But why do fossil mites group in the area of the morphospace dominated by body shapes with longer legs? One possibility is that their hosts were more scattered or less abundant in past times, which would have prompted them to move faster to achieve longer distances in less time, and minimise the energy spent while searching for a host. As a second possibility, this could be linked to a change of the microhabitat used by erythraeoideans. It has been suggested that erythraeioideans may have gone through a process of host switch from more aquatic hosts to more xerous ones, maybe having been dispersed from one type of environment to a new one by certain dipteran hosts during the Cretaceous (Konekowikz & Mąkol 2018). Although there are some erythraeoidean ingroups that inhabit humid areas and even transient biotopes (Wohltmann 2006), compared to other terrestrial parasitengonans, extant erythraeoideans are more resistant to desiccation and their eggs can hatch in dryer experimental conditions (Wohltman 2006). This could have had an influence in achieving a higher morphological diversity. The Kachin amber habitat is deemed as a tropical forest (Grimaldi et al. 2002). Since the microhabitat surrounding erythraeoideans was probably highly humid, in search of their hosts, mites may have had to wander on temporary ponds on leaves and tree surfaces. In such cases, it is possible to hypothesise that their long legs would have allowed them to have their idiosoma and head further away from the water surface, as in water striders (Gerridae). However, this does not completely explain the long legs of these mites, since water mites whose larvae are aerial and are linked to shallow water surfaces before encountering their hosts, such as larvae of Thyasidae or Hydrovolziidae, have comparatively shorter legs than long-legged velvet mites (Mitchell 1957).

Long-legged velvet mites have abundant sensory setae of different types located on their legs (Southcott 1961). An alternative explanation for longer legs in fossil specimens could be linked not to movement and locomotion, but to the fact that legs can also be considered sensory organs, which in turn could be explained by variations in habitat use. For example, cavity living has been proposed as a strong selection force for long legs in euarthropodans, possibly due to the need of a higher sensory capacity where light is not available (Langecker 2000).

Opposing observations

Even though shape analysis is valuable to measure morphological diversity, it does not come without its limitations. The shape of the mites can be influenced by the level of engorgement (physogastry), making the idiosoma appear bigger. Also in extant fauna, mites are preserved in slides where they are pressed between the slide and the coverslip. This storage may distort their appearance by expanding the idiosoma. Likewise, as mentioned above, the sampling bias of the fossil record in amber cannot be ignored (Solórzano-Kraemer et al. 2015; 2018). Amber comes from tree resin, and therefore will most likely preserve specimens that were found on the tree bark or close to it. Modern specimens here analysed belong to different habitats. Therefore, the fact that fossil representatives do not occupy the same morphospace as extant ones does not necessarily mean that in former times modern body shapes were not present, but certain body shapes may not have been preserved depending on their microhabitat (see discussion in Haug et al. 2021b). However, it does point to an extinction of fossil morphologies in the group Erythraeoidea.

In relation to this, the fact that fossil representatives do not match the body shape of non-parasitic representatives (specimens of Balaustiinae) may be related to the fact that Balaustiinae may simply be difficult to identify as erythraeoidean larvae as in the fossil record not all characters are accessible. As mentioned above, representatives of Balaustiinae and *Abrolophus* have their first two basipods closer to each other than in the rest of erythraeoidean mites, and additionally, larvae of Balalustiinae also tend to have shorter legs. However, their habitus and general chaetotaxy are similar to other species of Erythraeoidea. The specimen from PED 3503 bears a distance between basipod 1 and 2 similar to the ones in Balaustiinae, but recognisable as a representative of Erythraeoidea through other characteristics. The morphospace shows that non-parasitic specimens, all representatives of Balaustiinae, plot relatively far from the fossil ones.

Outlook

The analysis demonstrates that erythraeoidean larvae in the Kachin amber forest had more elongated legs than their modern counterparts. Comparable observations of more elongated structures than in modern forms have been made for larvae of snakeflies (Haug et al. 2020, 2022) and lacewings (Haug et al. 2019a, b, 2021b). For the two insect groups, the more extreme morphologies can be understood as a result of the overall larger diversity of their larval forms (Haug et al. 2022, 2023). For the erythraeoidean larvae it appears more like a directed shift over time. Still, given the biases discussed above, observations on erythraeoideans remain preliminary. As demonstrated here the quantitative morphological analysis can make use of specimens that may not be of interest for taxonomic studies.

Supplementary Material

Supplementary materials can be accessed through the following DOI: 10.5281/zenodo.11093740

Supplementary materials, File 1: Detailed information of specimens included in this study.

Supplementary materials, File 2: Outline dataset used in the elliptical Fourier analysis.

Supplementary materials, File 3: R code of the statistical analysis.

Supplementary materials, File 4: Plot of Principal Component Analysis (PC1 versus PC2 and PC3 versus PC4) with specimens differentiated by age.

Supplementary materials, File 5: PC scores of each specimen from the PCA analysis.

Supplementary materials, File 6: Graphical component loadings from the PCA analysis.

Data Availability Statement

The data supporting the results of this research are available upon request. Interested researchers may contact the corresponding Author to obtain access.

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References

Arce S.I., Haug C., Haug J.T. & Amaral A. (2024a) - Driven apart: fossil parasitic long-legged velvet mite larvae on gall midges represent a long lost parasitic association between mites and dipterans. *Palaeoentomology*, 7(2): 254-264. https://doi.org/10.11646/palaeoentomology.7.2.9

Arce S.I., Haug C., Müller P., Haug J.T. & Fu Y.-Z. (2024b) - Oldest record of a larva of long-legged velvet mite (Erythraeoidea) parasitising an immature planthopper. *Palaeoentomology*, 7(4): 461-464. https://doi.org/10.11646/palaeoentomology.7.4.3

Azar D. (2007) - Preservation and accumulation of biological inclusions in Lebanese amber and their significance. *Comptes Rendus - Palevol*, 6(1-2): 151-156. https://doi.org/10.1016/j.crpv.2006.10.004

Azar D., Gèze R. & Acra F. (2010) - Lebanese Amber. In: Penney D. (Ed.) - Biodiversity of fossils in amber from the major world deposits: 271-298. Siri Scientific Press, Manchester.

Åbro A. (1988) - The mode of attachment of mite larvae (*Leptus* spp.) to harvestmen (Opiliones). *Journal of Natural History*, 22(1): 123-130. https://doi.org/10.1080/00222938800770091

Bartel C., Konikiewicz M., Mąkol J., Wohltmann A. & Dunlop J.A. (2015) - Smaridid mites in Baltic and Bitterfeld amber, with notes on the fossil record of terrestrial Parasitengona (Trombidiformes: Prostigmata). *Annales Zoologici*, 65(4): 641-659. https://doi.org/10.3161/00034541ANZ2015.65.4.009

Bassini-Silva R., Scopel W., Lima E.F.B., Silva-Neto A.M., Flechtmann C.H.W., Welbourn C., Ochoa R., Brescovit A. D., Barros-Battesti D. M. & Jacinavicius F. C. (2022) - *Charletonia rocciai* Treat and Flechtmann, 1979 (Trombidiformes: Erythraeidae): Larval redescription and new records for Brazil. *International Journal of Acarology*, 48(6): 433-441. https://doi.org/10.1080/01647954.2022.2092650

Baranov V., Wang Y., Wedmann S. & Haug J.T. (2020) - Eco-morphological diversity of larvae of soldier flies and their closest relatives in deep time. *PeerJ*, 8: e10356. https://doi.org/10.7717/peerj.10356

Bernard R., Felska M. & Mąkol J. (2019) - Erythraeid larvae parasitizing dragonflies in Zambia-description of *Leptus* (*Leptus*) *chingombensis* sp. nov. with data on biology and ecology of host-parasite interactions. *Systematic and Applied Acarology*, 24(5): 790-813. https://doi.org/10.11158/saa.24.5.6

Boucot A.J. & Poinar G.O. (2010) - Fossil behavior compendium. CRC Press, 363 pp.

Bonhomme V., Picq S., Gaucherel C. & Claude J. (2014) - Momocs: Outline Analysis – Using R. *Journal of Statistical Software*, 56(13): 1-24. https://doi.org/10.18637/jss.v056.i13

Braig F., Haug C. & Haug J.T. (2023) - Diversification events of the shield morphology in shore crabs and their relatives through development and time. *Palaeontologia Electronica*, 26(3): a53. https://doi.org/10.26879/1305

Braig F., Giménez L., Torres G. & Haug J.T. (2024) - Outline analysis as a new method for investigating development in fossil crabs. *Palaeontologia Electronica*, 27(1): a24. https://doi.org/10.26879/1207

Davids C. (1972) - The water mite *Hydrachna conjecta* Koenike, 1895 (Acari, Hydrachnellae), bionomics and relation to species of Corixidae (Hemiptera). *Netherlands Journal of Zoology*, 23(4): 363-429.

Dos Santos Costa S.G, Gomes-Almeida B.K. & Pepato A.R. (2022) - A new larval species of the genus *Smaris* (Smarididae, Parasitengona) from a Brazilian cave. *Acarina*, 30(2): 219-224. https://doi.org/10.21684/0132-8077-2022-30-2-219-224

Dos Santos Costa S.G., Welbourn C., Klimov P. & Pepato A.R. (2021) - Integrating phylogeny, ontogeny and systematics of the mite family Smarididae (Prostigmata, Parasitengona): Classification, identification key, and description of new taxa. *Systematic and Applied Acarology*, 26(1): 85-123. https://doi.org/10.11158/saa.26.1.6

Dunlop J.A. (2007) - A large parasitengonid mite (Acari, Erythraeoidea) from the Early Cretaceous Crato Formation of Brazil. *Fossil Record*, 10(2): 91-98. https://doi.org/10.1002/mmng.200700001

Dunlop J.A., Penney D., Tetlie O.E. & Anderson L.I. (2008) - How many species of fossil arachnids are there. *Journal of Arachnology*, 36(2): 267-272. https://doi.org/10.1636/CH07-89.1

Eichmann F. (2002) - Paläosymbiose in Bernstein. *Arbeitskreis Paläontologie Hannover*, 30: 1-28.

Fain A. & Çobanoğlu S. (1998) - Two new larval Erythraeidae (Acari) of the genus *Hauptmannia* Oudemans, 1910 from Turkey. *Entomologie*, 68: 63-69.

Feener D.H.J., Lighton J.R.B., Bartholomew G. (1988) - Curvilinear allometry, energetics and foraging ecology: a comparison of leaf-cutting ants and army ants. *Functional Ecology*, 2(4): 509-520.

Felska M., Wohltmann A. & Mąkol J. (2018) - A synopsis of host-parasite associations between Trombidioidea (Trombidiformes: Prostigmata, Parasitengona) and arthropod hosts. *Systematic and Applied Acarology*, 23(7): 1375-1479. https://doi.org/10.11158/saa.23.7.14

Forsythe T.G. (1981) - Running and pushing in relationship to hind leg structure in some Carabidae (Coleoptera) - *The Coleopterists Bulletin*, 35(4): 353-378. http://www.jstor.org/stable/4007954

Grimaldi D. (2000) - Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey. Backhuys Publishers, Leiden, 498 pp.

Grimaldi D.A., Engel M.S. & Nascimbene P.C. (2002) - Fossiliferous cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates*, 3361: 1-71. https://doi.org/10.1206/0003-0082(2002)361<0001:FCAFMB>2.0.CO;2

Grünemaier M. (2017) - Not just hyphae—The amber mite *Glaesacarus rhombeus* as a forager on hardened resin surfaces and a potential scavenger on trapped insects. *Palaeodiversity*, 10(1): 129-134. https://doi.org/10.18476/pale.v10.a9

Guillerme T., Puttick M.N., Marcy A.E. & Weisbecker V. (2020) - Shifting spaces: Which disparity or dissimilarity measurement best summarize occupancy in multidimensional spaces? *Ecology and Evolution*, 10: 7261-7275. https://doi.org/10.1002/ece3.6452

Haarder S. & Mąkol J. (2022) - Terrestrial Parasitengona mites (Trombidiformes) of Denmark – new data on parasite-host associations and new country records. *Acarologia*, 62(2): 508-520. https://doi.org/10.24349/yglc-mnck.

Haitlinger R. (1999) - Six new species of *Leptus* Latreille, 1796 (Acari, Prostigmata, Erythraeidae) from South-East Asia. *Miscellania Zoologica*, 22(2): 51-68.

Haitlinger R. (2004) - New records of mites (Acari: Prostigmata: Erythraeidae, Trombidiidae, Eutrombidiidae) from Croatia, with descriptions of three new species. *Natura Croatica*, 13(2): 143-160.

Haitlinger R. (2011) - A new genus and four new species of erythraeid mites from Indonesia , with new records of the family (Acari: Prostigmata: Erythraeidae) - *Revista Iberica de Aracnología*, 19: 47-54.

Haug J.T. (2020) - Why the term "larva" is ambiguous, or what makes a larva? *Acta Zoologica*, 101: 167-188. https://doi.org/10.1111/azo.12283

Haug C., Braig F. & Haug J.T. (2023) - Quantitative analysis of lacewing larvae over more than 100 million years reveals a complex pattern of loss of morphological diversity. *Scientific Reports*, 13: 6127. https://doi.org/10.1038/s41598-023-32103-8

Haug G.T., Haug C., van der Wal S., Müller P. & Haug J.T. (2022) - Split-footed lacewings declined over time: indications from the morphological diversity of their antlion-like larvae. *PalZ*, 96: 29-50. https://doi.org/10.1007/s12542-021-00550-1

Haug J.T., Haug G.T., Zippel A., van der Wal S., Müller P., Gröhn C., Wunderlich J., Hoffeins C., Hoffeins H.-W. & Haug C. (2021a) - Changes in the morphological diversity of larvae of lance lacewings, mantis lacewings, and their closer relatives over 100 million years. *Insects*, 12: 860. https://doi.org/10.3390/insects12100860

Haug J.T., Baranov V., Braig F. & Haug C. (2024) - Morphoecospaces, or how to measure biodiversity in a different way. *Acta Zoologica*, 105(4): 496-513. https://doi.org/10.1111/azo.12486

Haug J.T., Baranov V., Müller P. & Haug C. (2021b) - New extreme morphologies as exemplified by 100 million-year-old lacewing larvae. *Scientific Reports*, 11: 20432. https://doi.org/10.1038/s41598-021-99480-w

Haug J.T., Müller P. & Haug C. (2019a) - A 100-million-year old slim insectan predator with massive venom-injecting stylets-a new type of neuropteran larva from Burmese amber. *Bulletin of Geosciences*, 94(4): 431-440. https://doi.org/10.3140/bull.geosci.1753

Haug J.T., Müller P. & Haug C. (2019b) - A 100-million-year old predator: a fossil neuropteran larva with unusually elongated mouthparts. *Zoological Letters*, 5: 29. https://doi.org/10.1186/s40851-019-0144-0

Haug J.T., Müller P. & Haug C. (2020) - A 100 million-year-old snake-fly larva with an unusually large antenna. *Bulletin of Geosciences,* 95: 167-177. https://doi.org/10.3140/bull.geosci.1757

Joliffe I.T. (2002) - Choosing a subset of principal components or variables, pp. 111-149. In: Joliffe I.T. (Ed.) - Principal component analysis. Springer Series in Statistics. Springer, New York, NY. https://doi.org/10.1007/0-387-22440-8_6

Kamran M. & Alatawi F.J. (2014) - Erythraeid mites (Prostigmata, Erythraeidae) from Saudi Arabia, description of three new species and a new record. *ZooKeys*, 95(445): 77-95. https://doi.org/10.3897/zookeys.445.7861

Kamran M. & Alatawi F.J. (2015) - New species and new records of subfamily Abrolophinae (Acari: Erythraeidae) from Saudi Arabia. *Systematic and Applied Acarology*, 20(2): 195-202. https://doi.org/10.11158/saa.20.2.6

Kamran M. & Alatawi F.J. (2016) - A new genus of the subfamily Balaustiinae (Acari: Prostigmata: Erythraeidae) from Saudi Arabia. *Systematic and Applied Acarology*, 21(1): 79-84. https://doi.org/10.11158/saa.21.1.6

Kobbert M.J. (2013) - Wunderwelt Bernstein: Faszinierende Fossilien in 3-D. WBG (Wissenschaftliche Buchgesellschaft), Darmstadt, 96 pp.

Koch C.L. & Berendt G.C. (1854) - Die im Bernstein befindlichen Crustaceen, Myriapoden, Arachniden und Apteren der Vorwelt. Edwin Groening, Berlin, 124 pp.

Konikiewicz M. & Mąkol J. (2018) - Insight into fossil fauna of terrestrial *Parasitengona mites* (Trombidiformes: Prostigmata) – The first representatives of Erythraeina Welbourn, 1991 and Trombidiina Welbourn, 1991 in Burmese amber. *Cretaceous Research*, 89: 60-74. https://doi.org/10.1016/j.cretres.2018.02.017

Kralj-Fišer S., Premate E., Copilaş-Ciocianu D., Volk T., Fišer Ž., Balázs G., Herczeg G., Delić T. & Fišer C. (2020) - The interplay between habitat use, morphology and locomotion in subterranean crustaceans of the genus *Niphargus*. *Zoology*, 139: 125742. https://doi.org/10.1016/j.zool.2020.125742

Krantz G.W. (2009) - Origins and phylogenetic relationships. In: Krantz G.W. & Walter D.E. (Eds.) - A Manual of Acarology, 3rd edition, pp. 3-4. Texas Tech University Press, Lubbock, Texas.

Kuhl F.P. & Giardina C.R. (1982) - Elliptic Fourier features of a closed contour. Computer Graphics and Image *Processsing*, 18: 236-258. https://doi.org/10.1016/0146-664X(82)90034-X

Kuznetsov N., Khaustov A. & Perkovsky E. (2010) - First record of mites of the family Stigmaeidae (Acari, Raphignathoidea) from Rovno Amber with description of a new species of the genus *Mediolata*. *Vestnik Zoologii*, 44(6): e-49-e-51.

Langecker T.G. (2000) - The effects of continuous darkness on cave ecology and cavernicolous evolution. In: Wilkens H., Humphreys W.F. & Culver D.C. (Eds.) - Ecosystems of the World 30: Subterranean Ecosystems: 135-157. Elsevier, Amsterdam.

Losos J.B. & Sinervo B. (1989) - The effects of morphology and perch diameter on sprint performance of Anolis lizards. *Journal of Experimental Biology*, 145(1): 23-30. https://doi.org/10.1242/jeb.145.1.23

Mąkol J., Kłosińska A. & Łaydanowicz J. (2012) - Host–parasite interactions within terrestrial Parasitengona (Acari, Trombidiformes, Prostigmata), *International Journal of Acarology*, 38(1): 18-22. https://doi.org/10.1080/01647954.2011.583276

Moniuszko H. & Mąkol J. (2014) - Chigger mites (Actinotrichida: Parasitengona, Trombiculidae) of Poland. An updated distribution and hosts. *Annals of Parasitology*, 60(2): 103-117.

Martin P. & Gerecke R. (2009) - Diptera as hosts of water mite larvae - an interesting relationship with many open questions. *Lauterbornia*, 68: 95-103.

Mitchell R. (1957) - Major evolutionary lines in water mites. *Systematic Zoology*, 6(3): 137-148. https://doi.org/10.2307/2411752

Poinar G.O., Acra A. & Acra F. (1994) - Animal-animal parasitism in Lebanese amber. *Medical Sciences Research* 22: 159.

Poinar G., Krantz G.W., Boucot A.J. & Pike T.M. (1997) - A unique Mesozoic parasitic association. *Naturwissenschaften*, 84(7): 321-322. https://doi.org/10.1007/

s001140050405

Poinar G.O., Treat A.E. & Southcott R.V. (1991) - Mite parasitism of moths: Examples of paleosymbiosis in Dominican amber. *Experientia*, 47(2): 210-212. https://doi.org/10.1007/BF01945430

Poinar G.O., Pike E.M. & Krantz G.W. (1993) - Animal-animal parasitism. *Nature,* 361: 307-308. https://doi.org/10.1038/361307b0

Poinar Jr. G.O. & Milki R. (2001) - Lebanese amber. The oldest insect ecosystem in fossilized amber. Oregon State University Press, 96 pp.

R Core Team (2021) - R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Saboori A. & Begheri M. (2011) - A new species of *Smaris* Latreille, 1796 from Iran. *Zoology in the Middle East*, 52(1): 105-110. https://doi.org/10.1080/09397140.2011.10638484

Saboori A., Hajiqanbar H. & Kamali K. (2007) - First record of the little known genus *Andrevella* Southcott, 1961 (Acari: Erythraeidae) from Iran, with a description of a new species. *Systematic and Applied Acarology*, 12(1): 47. https://doi.org/10.11158/saa.12.1.7

Saboori A., Khaustov A.A., Hakimitabar M. & Hajiqanbar H. (2009) - A new genus and species of larval Erythraeinae (Acari: Prostigmata: Erythraeidae) from Ukraine and the taxonomic state of *Zhangiella*. *Zootaxa*, 2203(1): 22-30. https://doi.org/10.11646/zootaxa.2203.1.2

Salarzehi S., Hajiqanbar H., Torshiz A.O. & Noei J. (2012) - Description of a new species of the genus *Fessonia* (Acari: Prostigmata: Smarididae) from Iran. *Revue Suisse de Zoologie*, 119(4): 409-415. https://doi.org/10.5962/bhl.part.150200

Schmidt A.R., Jancke S., Lindquist E.E., Ragazzi E., Roghi G., Nascimbene P.C., Schmidt K., Wappler T. & Grimaldi D.A. (2012) - Arthropods in amber from the Triassic Period. *Proceedings of the National Academy of Sciences*, 109(37): 14796-14801. https://doi.org/10.1073/pnas.1208464109

Seeman O.D. & Walter D.E. (2023) - Phoresy and mites: more than just a free ride. *Annual Review of Entomology*, 68(1): 69-88. https://doi.org/10.1146/annurev-ento-120220-013329

Shatrov A.B. & Soldatenko E.V. (2021) - Larvae of the fresh-water mite *Limnochares aquatica* (L., 1758) (Acariformes: Hydrachnidia: Limnocharidae) and their stylostome evolving during feeding on *Gerris lacustris* (L., 1758) (Hemiptera: Gerridae). *Journal of Natural History*, 55(29-30): 1895-1916. https://doi.org/10.1080/00222933.2021.1974112

Sidorchuk E.A. (2018) - Mites as fossils: Forever small? *International Journal of Acarology*, 44(8): 349-359. https://doi.org/10.1080/01647954.2018.1497085

Sidorchuk E. & Bertrand M. (2013) - New fossil labidostomatids (Acari: Labidostomatidae) from Eocene amber and presence of an Apustulate species in Europe. *Acarologia*, 53(1): 25-39. https://doi.org/10.1051/acarologia/20132079

Sidorchuk E.A., Konikiewicz M., Welbourn W.C. & Mąkol J. (2019) - Active postlarval forms of plume-footed *Eatoniana* (Trombidiformes: Parasitengona, Erythraeidae) in the Eocene Baltic amber. *Zootaxa*, 4647(1): 44-53. https://doi.org/10.11646/zootaxa.4647.1.6

Smith B.P. (1998) - Loss of larval parasitism in parasitengonine mites. *Experimental & Applied Acarology,* 22: 187-199. https://doi.org/10.1023/A:1006010230247

Solórzano-Kraemer M.M., Delclòs X., Clapham M.E., Arillo A., Peris D., Jäger P., Stebner F. & Peñalver E. (2018) - Arthropods in modern resins reveal if amber accurately recorded forest arthropod communities. *Proceedings of the National Academy of Sciences*, 115(26): 6739-6744. https://doi.org/10.1073/pnas.1802138115

Solórzano-Kraemer M.M., Kraemer A.S., Stebner F., Bickel D.J. & Rust J. (2015) - Entrapment bias of arthropods in Miocene amber revealed by trapping experiments in a tropical forest in Chiapas, Mexico. *PLoS ONE*, 10(3): e0118820. https://doi.org/10.1371/journal.pone.0118820

Southcott R.V. (1961) - Studies on the systematics and biology of the Erythraeoidea (Acarina), with critical revision of the genera and subfamilies. *Australian Journal of Zoology*, 9(3): 367-610.

Southcott R.V. (1988) - Two new larval Erythraeinae (Acarina: Erythraeidae) from New Zealand, and the larval Erythraeinae revised. *New Zealand Journal of Zoology,* 15(2): 223-233. https://doi.org/10.1080/03014223.1988.10422617

Southcott R.V. (1992) - Revision of the larvae of *Leptus* Latreille (Acarina: Erythraeidae) of Europe and North America, with descriptions of post-larval instars. *Zoological Journal of the Linnean Society*, 105(1): 1-153. https://doi.org/10.1111/j.1096-3642.1992.tb01228.x

Southcott R.V. (1999) - Larvae of *Leptus* (Acarina: Erythraeidae), free-living or ectoparasitic on arachnids and lower insects of Australia and Papua New Guinea, with descriptions of reared post-larval instars. *Zoological Journal of the Linnean Society*, 127(2): 113-276. https://doi.org/10.1111/j.1096-3642.1999.tb00677.x

Stroiński A., Felska M. & Mąkol J. (2013) - A review of host-parasite associations between terrestrial Parasitengona (Actinotrichida: Prostigmata) and bugs (Hemiptera) - *Annales Zoologici*, 63(2): 195-221. https://doi.org/10.3161/000345413X669522

Treat A.E. (1975) - Mites of moths and butterflies. Cornell University Press lthaka, NY, 362 pp.

Trochet A., Le Chevalier H., Calvez O., Ribéron A., Bertrand R. & Blanchet S. (2019) - Influence of substrate types and morphological traits on movement behavior in a toad and newt species. *PeerJ* 6: e6053. https://doi.org/10.7717/peerj.6053

Vercammen-Grandjean P.H. (1973) - Study of the "Erythraeidae, R.O.M. No. 8" of Ewing, 1937. In: Daniel M., Rosický B. (Eds.) - *Proceedings of the 3rd International Congress of Acarology*: 329e335. Academia, Prague.

Vitzthum H. (1943) - Acarina. In: Bronns H.G. (Ed.) - Klassen und Ordnung des Tierreichs. Vol 5 (IV, 5) - Akademische Verlagsgesellschaft, Leipzig, 1011 pp.

Walter D.E., Lindquist E.E., Smith I.M., Cook D.R. & Krantz G.W. (2009) - Order Trombidiformes. In: Krantz G.W. & Walter D.E. (Eds.) - A Manual of Acarology, 3rd edition: 233-420. Texas Tech University Press, Lubbock, Texas.

Welbourn W.C. (1983) - Potential use of trombidioid and erythraeoid mites as biological control agents of insect pests. In: Hoy M.A., Cunningham G.L. & Knutson L. (Eds.) - Biological control of pests by mites. Agricultural Experiment Station, Division of Agriculture and Natural Resources, Special Publication, 3304: 103-140.

University of California, Berkeley.

Wohltmann A. (2000) - The evolution of life histories in Parasitengona (Acari: Prostigmata) - *Acarologia*, 41(1-2): 145-204.

Wohltmann A. (2001) - Closely related species of Parasitengonae (Acari: Prostigmata) inhabiting the same area: Patterns facilitating coexistence. In: Halliday R.B., Walter D.E., Proctor H.C., Norton R.A. & Colloff M.J. (Eds.) - Acarology: Proceedings of the 10th International Congress of Acarology: 121-135. CSIRO Publishing, Melbourne.

Wohltmann A., Gabryś G. & Mąkol J. (2006) - Acari: Terrestrial Parasitengona inhabiting transient biotopes. In: Gerecke R. (Ed.) - Süßwasserfauna von Mitteleuropa. Chelicerata: Araneae/Acari I. 7(2-1): 168-240. Springer Spektrum, Berlin, Heidelberg. https://doi.org/10.1007/978-3-662-55958-1_6

Wohltmann A., Mąkol J. & Gabryś G. (2007) - Description of the larva of *Curteria* Southcott, 1961 (Acari, Parasitengona, Erythraeidae) with notes on biology and life cycle. *Biologia*, 62(5): 573-580. https://doi.org/10.2478/s11756-007-0114-4

Wu R.J.C. (1996) - Secrets of a lost world: Dominican amber and its inclusions; Privately Published, Santo Domingo, Dominican Republic, 222 pp.

Xu S.Y., Yi T.C., Guo J.J. & Jin D.C. (2019) - First record of the genus *Dambullaeus* (Trombidiformes: Erythraeidae: Callidosomatinae) in China with description of a new species and a revised generic diagnosis. *International Journal of Acarology*, 45(8): 456-462. https://doi.org/10.1080/01647954.2019.1682663

Xu S.Y., Yi T.C., Guo J.J. & Jin D.C. (2020) - Four new species of larval Callidosomatinae (Acari: Prostigmata: Erythraeidae) and a newly recorded genus *Iguatonia* from China with notes on generic concept. *Systematic and Applied Acarology*, 25(2): 285-326. https://doi.org/10.11158/saa.25.2.9

Yoder A., Jajack A.J., Tomko P.M., Rosselot A.E., Gribbins K.M. & Benoit J.B. (2012) - Pollen feeding in *Balaustium murorum* (Acari: Erythraeidae): visualization and behaviour. *International Journal of Acarology*, 38: 641-647. https://doi.org/10.1080/01647954.2012.733024

Zhang Z.-Q. (2000) - *Ramsayella*, new genus of Erythraeinae (acari: Erythraeidae) parasitic on grasshoppers in New Zealand. *International Journal of Acarology*, 26(1): 33-40. https://doi.org/10.1080/01647950008683633

Zhang Z.-Q. & Lafuente A.G. (1996) - *Abrolophus* and *Grandjeanella* larvae (Acari: Erythraeidae) ectoparasitic on thrips (Thysanoptera: Thripidae). *Systematic and Applied Acarology*, 1: 127-144.