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Texas beetle larvae (Brachypsectridae) – the last 100 million years reviewed

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Abstract

Larvae of Brachypsectridae (Texas beetles) have often been considered rare. However, they are known from North America, Asia and Australia in the extant fauna, and from Miocene, Eocene and Cretaceous ambers. We review the overall record of extant and fossil larvae of Brachypsectridae represented in the literature. Furthermore, we present three new specimens, which were all documented via light microscopy. Two of the specimens are from Baltic amber, and the third one is from the Cretaceous amber of Myanmar; the latter was additionally documented via synchrotron radiation micro-computed tomography. The number of known extant specimens, more than 20, is unusually high compared to other small groups of beetles and with respect to the low number of eight formally described species. The number of fossil specimens from the Miocene, Eocene and Cretaceous is low, two to three specimens per time slice. This makes a comparison of morphological diversity difficult. Still such an analysis of overall body shape as well as of the anterior body region revealed no significant quantitatively recognisable changes over time. However, some qualitative changes in the morphology of the antenna and lateral processes from the Cretaceous to younger faunas could be identified.

Keywords: Brachypsectridae; Coleoptera; Myanmar amber; Baltic amber; Dominican amber; synchrotron radiation micro-computed tomography.

1. Introduction

The Coleoptera (beetles) has often been considered the most successful group of animals (the twist in this view was discussed in Haug et al. 2016). Despite the enormous species richness with more than 380,000 formally described species, most adult beetles can be recognised as such even by a layperson. How does the high species diversity go together with a rather recognizable appearance and hence a seemingly low morphological diversity? This "secret" is immediately solved when looking at the life history of beetles. Beetles, like all representatives of Holometabola, develop through discrete larval stages that differ distinctly from their corresponding adults in morphology and ecology. These larvae also differ significantly from each other (Lawrence 1991; Lawrence et al. 2011; Beutel & Leschen 2016), revealing that the true diversity of beetles, in the sense of being morphologically different, appears to be the diversity of beetle larvae.

The group Brachypsectridae is a species-poor lineage of beetles, also known as Texas beetles. Hitherto, there are eight formally described extant species (Lawrence et al. 2020: 8) from North America, India, Malaysia and Australia (Lawrence 1991: 422). Adults of Brachypsectridae are relatively small-sized, lightly sclerotized and inconspicuous beetles that seem to be quite rare and short-lived (Ferris 1927; Crowson 1973; Lawrence 1991: 421). Nevertheless, also here the larvae are very peculiar. When the larvae were first presented to the public (Barber 1905), the corresponding adult was completely unknown and the larvae were considered an 'enigma' (Ferris 1927; Blair 1930) that was finally resolved with the work of Blair (1930).

Even though today both adult and immature stages are well known, the specimens of Brachypsectridae are often only rarely sampled and omitted from many analyses (e.g., molecular analysis of Bocakova et al. 2007; Kundrata et al. 2014). Therefore, the exact phylogenetic relationship of the group remained a contentious issue. Recently, there appears to be strong support for a position of Brachypsectridae within Elateroidea (Bocakova et al. 2007; Lawrence et al. 2011; Kundrata et al. 2014; McKenna et al. 2015). In the results of a morphological analysis performed by Lawrence et al. (2011), Brachypsectridae appear to form a monophyletic group also including Throscidae, Cerophytidae, and Eucnemidae. In the phylogeny of Kundrata et al. (2014, fig. 2) the three latter groups cluster closely together as well, with Throscidae and Cerophytidae being sister groups. Within the phylogeny of McKenna et al. (2015), Brachypsectridae is in a sister-group position to (Throscidae + Cerophytidae + Eucnemidae). There are also similarities to other representatives of Elateroidea, namely Lycidae, Lampyridae, Cantharidae, and Elateridae.

The larvae of Brachypsectridae are dorso-ventrally flattened and have an oval outline in dorsal or ventral view. In this view, the head is roughly rectangular; the antennae are short, stout, and paddle-shaped; the mandibles are sickle-shaped, piercing mouthparts with a closed sucking channel (Beutel 1995). The trunk is divided into an anterior part (thorax) and a posterior part (abdomen). The trunk segments have lateral protrusions with numerous spines, resulting in a comb-like appearance. Two pairs of protrusions arise from each of the thoracic segments and one pair from each of the eight further abdomen segments, summing up to a total of 14 prominent protrusions on each side of the body (however, Blair 1930 pointed out that also the abdomen segments have a second pair of protrusions, but these are tiny and often not easily visible). The trunk end is elongated and triangular.

The larvae of Brachypsectridae are not only "eye-catching" due to their branched protrusions, but also due to modified scales covering their body (Beutel 1995, fig. 11a; Costa et al. 2006, figs. 19–26; Lawrence et al. 2011, figs. 74B, 83C). Another specific characteristic of these larvae is an intermediate condition between a firmly continuous clypeus-labrum complex (which is characteristic for other larvae of Elateroidea) and a free labrum (Beutel 1995).

The piercing-sucking mandibles with internal perforation and opening at the base and tip of the mandibles as seen in larvae of Brachypsectridae are also present in larvae of other ingroups of Elateroidea (e.g., Drilini, Phengodidae, Rhagophthalmidae, Lampyridae; Lawrence et al. 2011). Such mandibles may be derived from mandibles with open inner grooves (Crawson 1972; Beutel 1995). A loss of a specific pre-oral filter is probably also correlated with the mode of feeding of these beetles. It seems that the loss is secondary and the characteristic is shared with other ingroups of Elateroidea (Throscidae, Eucnemidae and Lycidae; Lawrence et al. 2011). The maxillae and labium are joined together into a maxillolabial complex with incomplete sutures (a character also found in Eucnemidae; Lawrence et al. 2011).

The oval body, the protrusions, and the piercing mandibles remind of certain lacewing larvae (Neuroptera; Fleenor & Taber 1999: 360), more specifically larvae of owlflies (Ascalaphidae; Grimaldi & Engel 2005: 384, fig. 10.43; Costa et al. 2006: 415) or those of split-footed lacewings (Nymphidae; see recent review in Haug et al. online first and references therein). Indeed comparably to many lacewing larvae, larvae of Brachypsectridae are sit-and-wait predators, which can starve for quite some time (Barber 1905: 118). Ferris (1927: 281) even reported movements when handling prey that he compared to those of antlion larvae.

There are overall only a few reports of larvae of Brachypsectridae from the extant fauna, and they might seem rare, yet Fleenor & Taber (1999) suggested that they can be locally common. Petrzelkova et al. (2017) pointed out that the rarity might be an artefact. Many aspects of the biology are still unknown, for example the number of larval stages (Costa et al. 2006, p. 415; Klausnitzer 2009: 732). For now, there are at least three larval stages (Costa et al. 2006: 416). Recently, a first instar larva was mentioned, but with only some details shown (Lawrence et al. 2020: 5).

With their distinct morphology, larvae of Brachypsectridae can easily be identified as such. This makes it also possible to recognise such larvae in the fossil record rather easily. All fossil records of these larvae have been found in amber. This includes specimens in about 15–20 million-year-old Miocene Dominican amber (Poinar 1992; Wu 1996; Poinar & Poinar 1999; Woodruff 2002; Scheven 2004; Klausnitzer 2009), in about 40 million-year-old Eocene Baltic amber (Scheven 2004; Klausnitzer 2009) and most recently in 100 million-year-old Myanmar amber (Zhao et al. 2020).

We here review the entire record of larvae of Brachypsectridae, extant and fossil, report additional specimens and compare the morphological diversity of these larvae through time. In our study, diversity is represented by the variation of quantifiable morphology as a proxy.

2. Material and methods

2.1. Material

A single new specimen is reported here from Cretaceous Myanmar amber ("Burmese amber"), about 100 million-year-old deposits of Hukawng Valley, Kachin State, Myanmar (Cruickshank & Ko 2003). The specimen was legally purchased via the internet platform ebay.com, from the trader burmite-miner. The specimen is deposited in the Palaeo-Evo-Devo Research Group Collection of Arthropods, Ludwig-Maximilians-University of Munich, Germany (PED 0435).

Two further new specimens come from the collection of Christel and Hans-Werner Hoffeins (CCHH 1181-2 and 1228-6, to be deposited in the amber collection of Senckenberg Deutsches Entomologisches Institut (SDEI), Müncheberg, Germany).

In addition, all specimens reported and depicted in the literature are complied here. Each specimen was interpreted as a simplified drawing (more details below).

2.2. Documentation methods

Documentation of PED 0435 was performed on a Keyence VHX 6000 digital microscope. We photographed the specimen one time illuminated by coaxial cross-polarised light (Haug et al. 2013b) and one time by unpolarised ring light. Under both illuminations, documentation was performed with a white and a black background. The built-in HDR function was used to optimise the images (cf. Haug et al. 2013a). Image stacks were recorded to overcome limitations in depth of field; several adjacent stacks were recorded to overcome limitations in field of view (Haug et al. 2008, 2011). The images providing the best contrast were used.

Additionally, PED 0435 was imaged at the Imaging Beamline P05 (Greving et al. 2014; Wilde et al. 2016) operated by

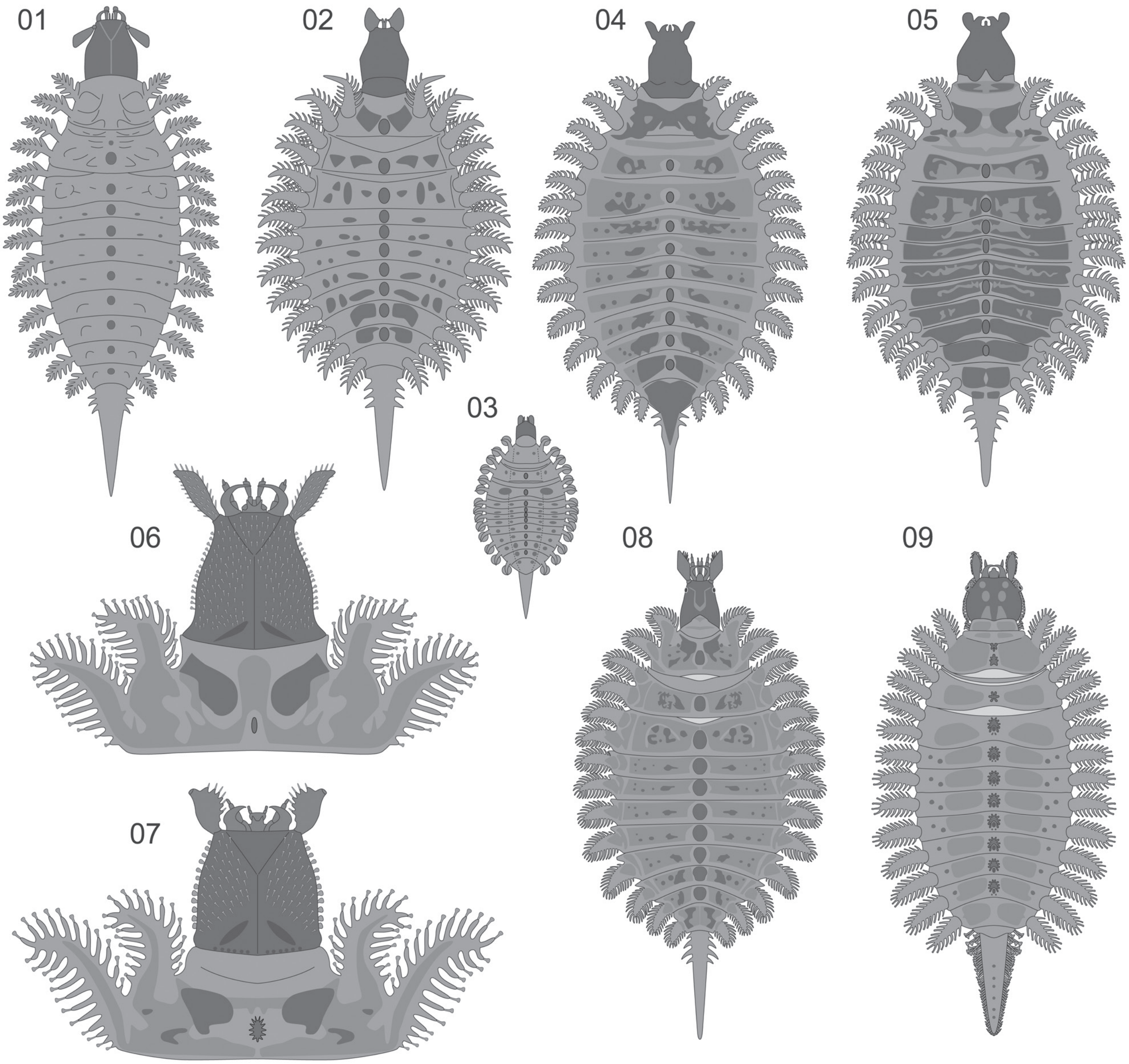

Fig. 1. Interpretations of larvae of Brachypsectridae from the literature; all specimens from the extant fauna; 01: from Barber (1905, fig. 11); 02: from Ferris (1927: 280); 03–07: from Blair (1930); 03: *Brachypsectra fulva* (Blair 1930, pl. 1, fig. 1); 04: *B. fulva* (Blair 1930, pl. 1, fig. 2); 05: *B. lampyroides* (Blair 1930, pl. 1, fig. 3); 06: *B. fulva* (Blair 1930, pl. 1, fig. 4); 07: *B. lampyroides* (Blair 1930, pl. 1, fig. 5); 08: from Lawrence (1991), *B. fulva* (Lawrence 1991: 421, fig. 34.457a); 09: from Lawrence & Britton (1991; redrawn after Lawrence et al. 1995).

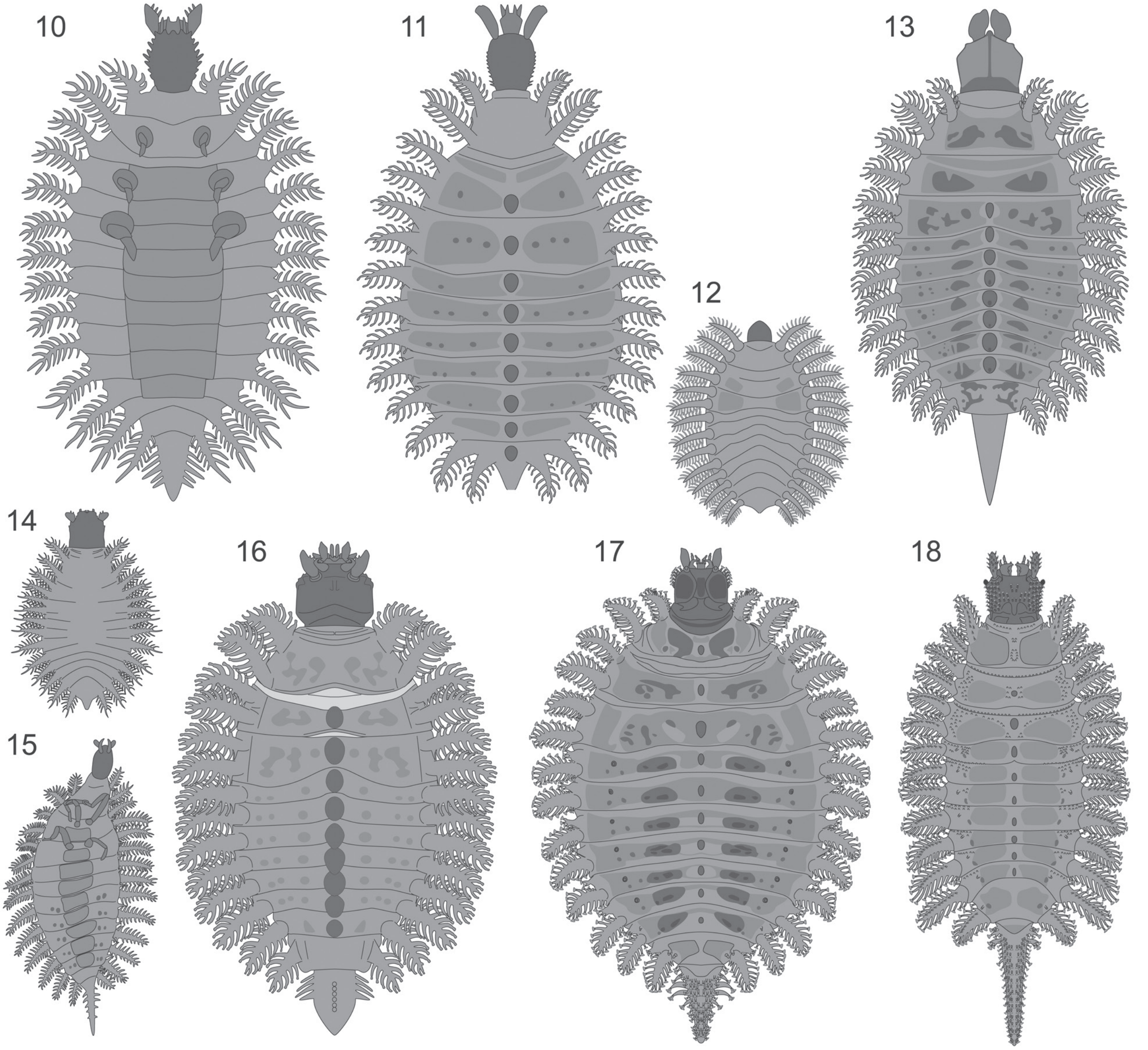

Fig. 2. Interpretations of larvae of Brachypsectridae from the literature, continued; 10–12: larvae from Miocene Dominican amber; 10: from Poinar (1992: 136, fig. 74); 11: from Wu (1996: 131, fig. 198), *Brachypsectra* ? *moronei*; 12: from Wu (1996: 136, fig. 225); 13: larva from extant fauna, *Brachypsectra fulva,* from Fleenor & Taber (1999: 360, fig. 1); 14, 15: from Scheven (2004); 14: larva from Eocene Baltic amber (Scheven 2004: 10); 15: larva from Miocene Dominican Amber (Scheven 2004: 120); 16–18: larvae from extant fauna; from Costa et al. (2006); 16: *B. fulva* (combined from Costa et al. 2006, figs. 20, 24); 17: *B. lampyroides* (Costa et al. 2006, fig. 50); 18: *Brachypsectra* sp. (Costa et al. 2006, fig. 73).

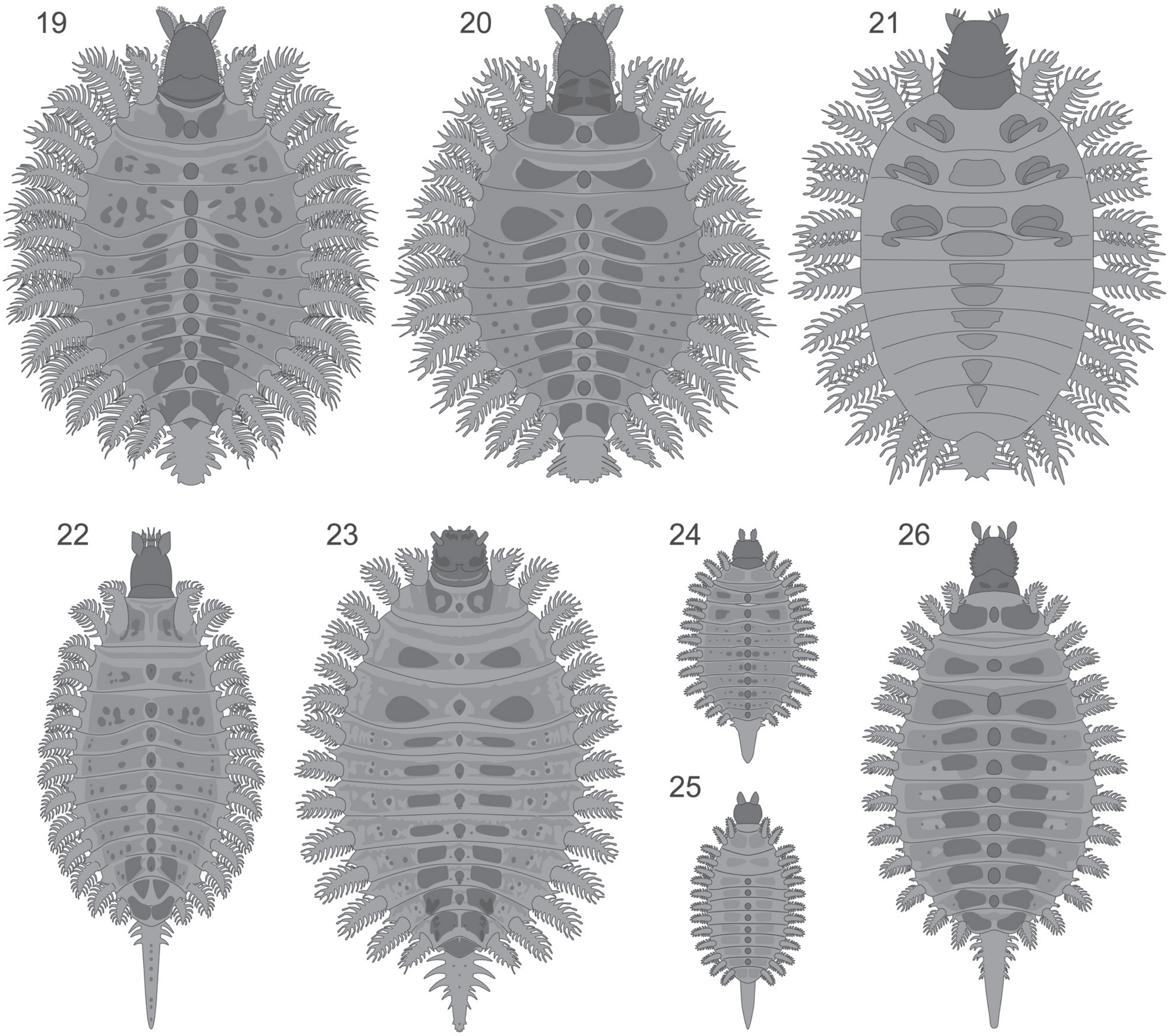

Fig. 3. Interpretations of larvae of Brachypsectridae from the literature, continued; 19–21: from Klausnitzer (2009); 19, 20: larvae from the extant fauna, *Brachypsectra* cf. *lampyroides*; 19: last larval stage (Klausnitzer 2009, fig. 1); 20: penultimate larval stage (Klausnitzer 2009, fig. 3); 21: larva from Eocene Baltic amber (Klausnitzer 2009, fig. 19); 22–26: larvae from the extant fauna; 22: from Lawrence et al. (2011), *B. fulva* (Lawrence et al. 2011, fig. 65D); 23: from Petrzelkova et al. (2017), *Brachypsectra* sp. (Petrzelkova et al. 2017, fig. 2I); 24–26: from Lawrence et al. (2020), *B. cleidecostae*; 24, 25: larvae from Diamantina Lakes National Park; 24: small larva (Lawrence et al. 2020, fig. 5C); 25: large larva (Lawrence et al. 2020, fig. 5C); 26: larva from Stubb's waterhole (Lawrence et al. 2020, fig. 6B).

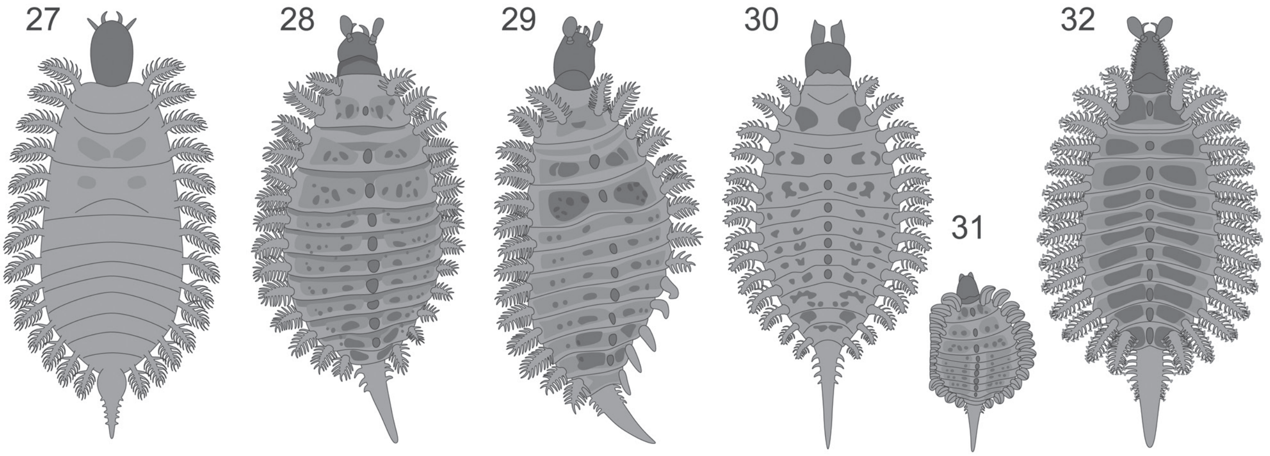

Fig. 4. Interpretations of larvae of Brachypsectridae from the literature, continued, and additional specimen; 27: larva from Cretaceous Myanmar amber; from Zhao et al. (2020, combined from their figs. 1 and 2); 28–31: larvae from the extant fauna, presumably all of *Brachypsectra fulva*; from the database bugguide.com; 28: based on image 114820; 29: based on image 175768; 30: based on image 1601732; 31: based on image 1709093; specimen appears cut off on the left side as it was partly concealed in the original photo; 32: specimen from the Hoffeins collection (based on Fig. 5A, B).

the Helmholtz-Zentrum Hereon at the storage ring PETRA III (Deutsches Elektronen Synchrotron - DESY, Hamburg, Germany), using a photon energy of 18 keV and a sample-to-detector distance of 150 mm. Projections were recorded using a 50 MP Ximea CB500MG-CM camera system with an effective pixel size of 0.92 µm. For the tomographic scan, 2501 projections at equal intervals between 0 and π were recorded. Tomographic reconstruction was done by applying a transport of intensity phase retrieval approach and using the filtered back projection algorithm (FBP) implemented in a custom reconstruction pipeline using Matlab (Math-Works) and the Astra Toolbox (Moosmann et al. 2014; van Aarle et al. 2015, 2016). Raw projections were binned twice for further processing, resulting in an effective pixel size of the reconstructed volume (voxel) of 1.83 µm. SR-µCT scans of PED 230 and AKBS-0030 were performed at the imaging cluster of the KIT light source of Karlsruhe Institute of Technology using a parallel polychromatic x-ray beam produced by a 1.5 T bending magnet. The beam was spectrally filtered by 0.2 mm aluminium to remove low-energy components from the beam. The resulting spectrum had a peak at about 15 keV, with a full width at half-maximum bandwidth of about 10 keV. A fast-indirect detector system was employed, consisting of a 12 µm LSO: Tb scintillator (Cecilia et al. 2011), diffraction limited optical microscope (Optique Peter) coupled with a 12 bit pco.dimax high-speed camera with 2016 x 2016 pixels. Scans were done by taking 3,000 projections at 70 frames per second and optical magnifications of 5× (PED-230 and AKBS-0030) and 10× (AKBS-0030), resulting in an effective pixel size of 2.44 µm and 1.22 µm, respectively. The samples were scanned in several height steps. We used the control system concert (Vogelgesang et al. 2016) for automated data acquisition and online reconstruction of tomographic slices for data quality assurance. Online and final data processing including tomographic reconstruction were performed by the UFO framework (Vogelgesang et al. 2012).

The two specimens from the Hoffeins collection were documented with a Nikon Coolpix 4500 attached to a Wild M3Z microscope.

2.3. Image processing

Images recorded on the Keyence VHX 6000 digital microscope were processed automatically by the built-in software. Adobe Photoshop CS2 was used for optimising all images (histograms, saturation, sharpness). Tiff-stacks resulting from CT-scans were imaged as volume renders in OSIRIX.

2.4. Presentation

All visible structures of PED 0435 were colour-marked to provide an interpretation of the structures. Adobe Illustrator CS2 was used to redraw larvae of Brachypsectridae from the literature. The drawings were slightly simplified; corresponding structures were given similar colours.

2.5. Shape analysis

All accessible specimens (extant and fossil) were redrawn by hand in Adobe Illustrator CS2. The better preserved body half (left or right) was drawn and mirrored. The resulting image was checked against the original to reduce possible artefacts. Dorsal and ventral views were used, as the orientation does not strongly (or not at all) influence the outline. Reconstructed outlines were analysed in SHAPE (see also Braig et al. 2019; Haug et al. 2020a).

Two different datasets were used. Dataset 1 used the outline of the entire body; however, the trunk end was omitted, as it was oriented upwards in some specimens. During chaincoding, the images were simplified using the 'Evo-filter' set to 7–8 (depending on specimen), cutting off most of the protrusions and appendages (otherwise, the chain codes would have been too long and created an error message in later processing). Dataset 2 used the outline of the anterior body (head and prothorax). Some smaller specimens were excluded as the posterior border of the prothorax could not be properly evaluated. Same as for dataset 1, during chaincoding, the images of dataset 2 were simplified by using the 'Evo-filter' set to 3–4, cutting off most of the secondary protrusions and appendages. Harmonics were set to 20 in both datasets.

2.6. Morphospace occupation

We compared the diversity of shape of extant and fossil larvae, the latter further differentiated into Miocene, Eocene and Cretaceous larvae. For each of the four time slices, the ranges of occupation of the dominating assembled dimensions (principal components resulting from the shape analysis) were plotted and compared. Plotting was performed in OpenOffice 4.02.

3. Results

3.1. List of specimens

All occurrences of depictions of larvae of Brachypsectridae are listed chronologically. Cases in which the same specimen has been re-figured are also included chronologically with reference to the original occurrence. While this includes a certain redundancy, it should represent the most complete way of cross-referencing, avoiding to interpret the same specimen as two independent occurrences.

1) Barber (1905, fig. 11) provided a photograph (at least it appears to be a photograph, yet due to the compression of the electronic version available to the authors it cannot be fully excluded that this is a very detailed drawing) in dorsal view of a larva of the group Brachypsectridae (Fig. 1; specimen 1). Size

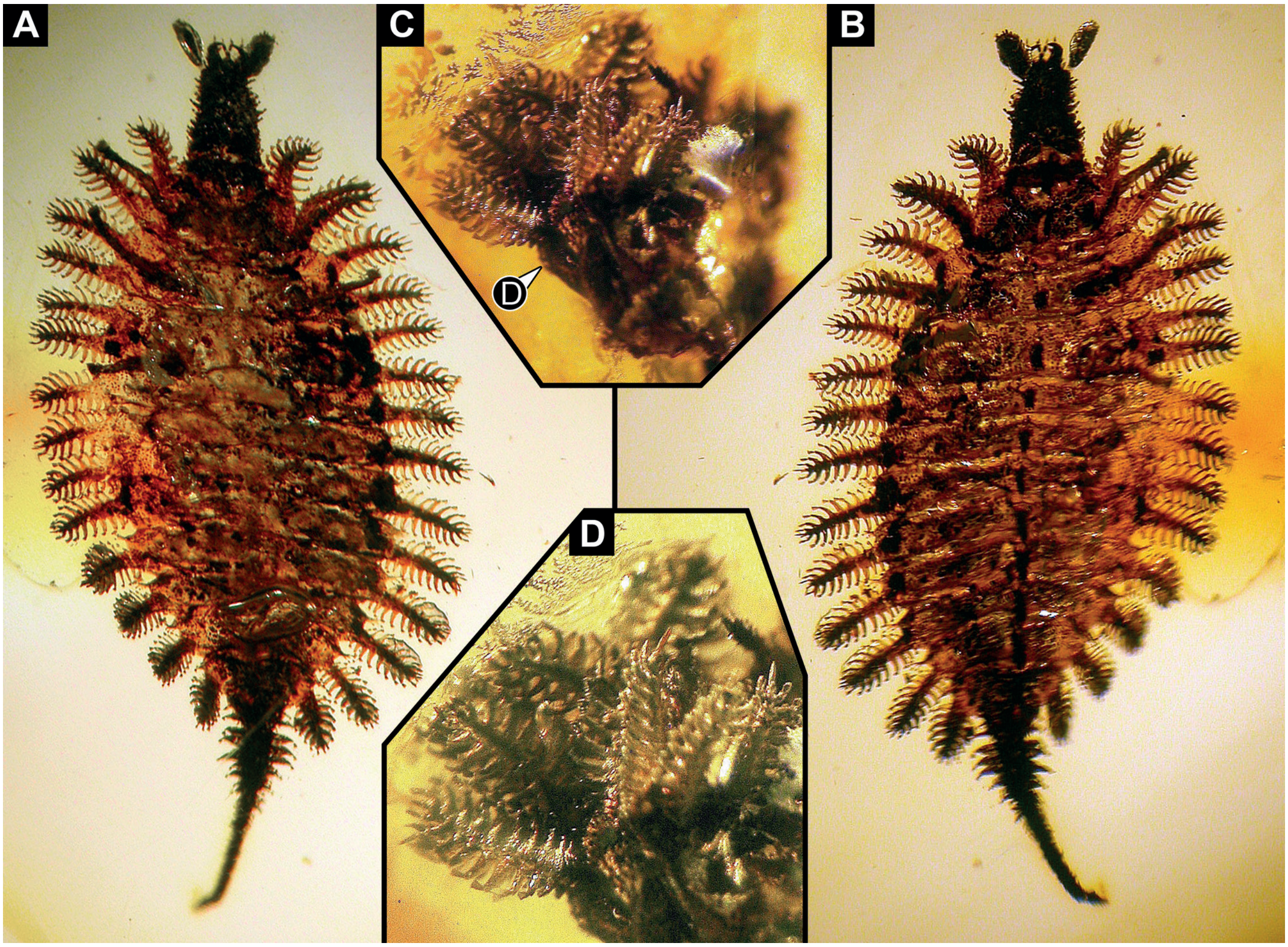

Fig. 5. Larvae of Brachypsectridae preserved in Baltic amber, Hoffeins collection (future part of the amber collection of Senckenberg Deutsches Entomologisches Institut (SDEI), Müncheberg, Germany); **A, B**: specimen 32, CCHH 1118-2; A: dorsal view; B: ventral view; **C, D**: CCHH 1228-6, exuvia, size about 2.6 x 1.5 mm; C: overview; D: detail of branched processes; images not to scale.

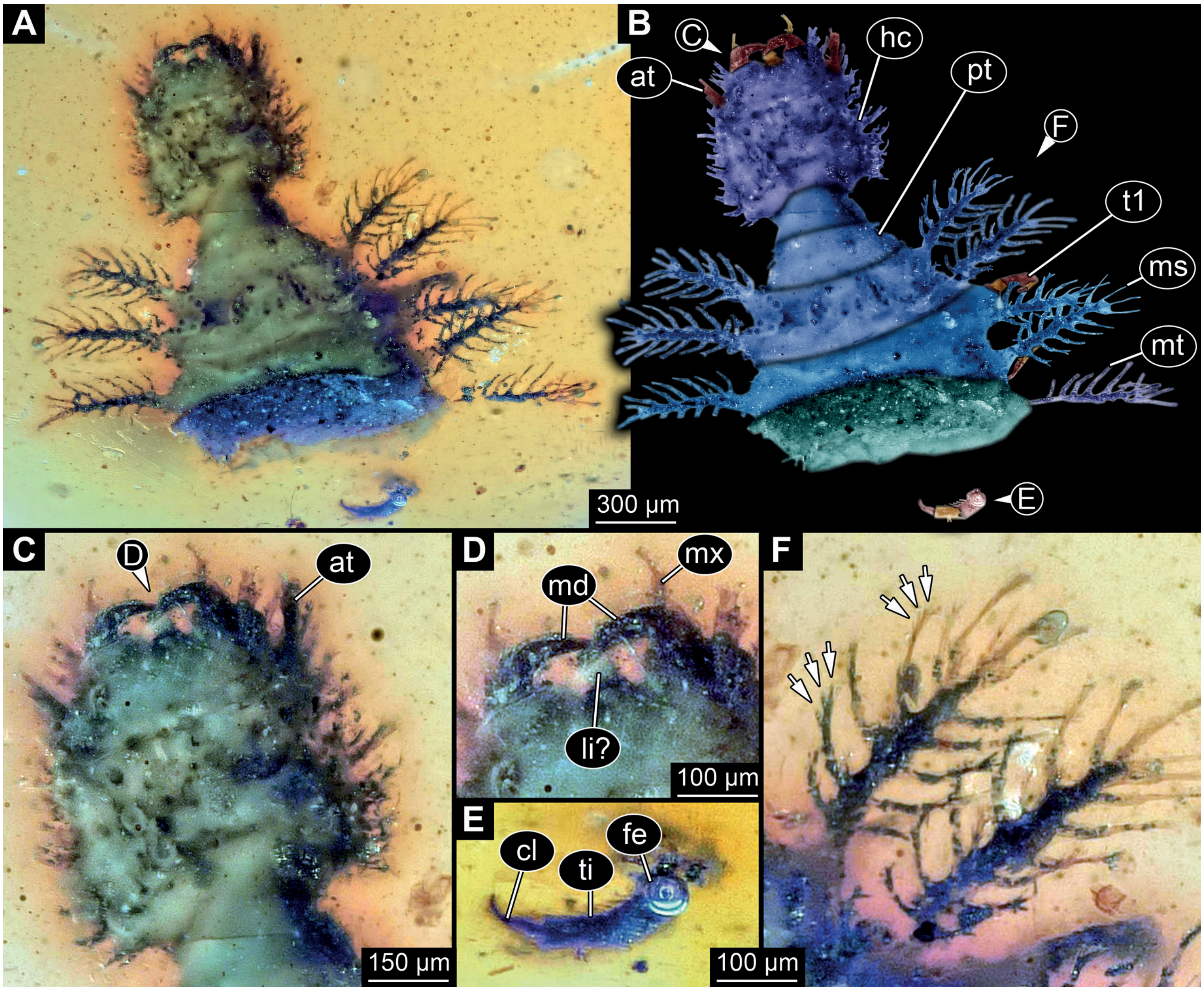

Fig. 6. Larva of Brachypsectridae preserved in Myanmar amber, PED 0435; **A**: overview; **B**: colour-marked version of A; **C**: close-up of head; **D**: close-up of mouthparts; **E**: close-up of distal part of isolated trunk appendage; **F**: close-up of protrusions of prothorax; arrows point to tertiary protrusions arising from secondary protrusions. Abbreviations: at = presumed antenna; cl = claw; fe = femur; hc = head capsule; li? = possible labium; md = mandible; ms = mesothorax; mt = metathorax; mx = maxilla; pt = prothorax; t1 = trunk/thorax appendage 1; ti = tibiotarsus.

was given as a magnification factor, which is not informative for the electronic version available to the authors. Several details were provided including: drawings of different types of spines (Barber 1905, fig. 12), a photo-micrograph of a leg and some of the processes (Barber 1905, fig. 13), and a close-up view of the anterior body with head and prothorax (Barber 1905, fig. 14). According to the text, the author had several specimens available. It seems that the specimen was re-figured in Böving & Craighead (1931) and Chu (1949) (see discussion there).

2) Anonymous (1908: 14) mentioned but did not figure larvae of the group Brachypsectridae. Some of the mentioned specimens have been shown in Barber (1905).

3) Ferris (1927: 280) provided the photograph of a larva of the group Brachypsectridae in dorsal view (Fig. 1; specimen 2) The image was originally provided by Prof. O. E. Essig. No indication of its size was provided.

4) Blair (1930) solved the "enigma" of the larvae in focus here and identified them as immatures of the group Brachypsectridae. He provided three photographs of larvae of the group, including one of an alive larva of *Brachypsectra fulva* (Blair 1930, pl. 1, fig. 1), a fixed specimen of *B. fulva* (Blair 1930, pl. 1, fig. 2), and a fixed specimen of *B. lampyroides* (Blair 1930, pl. 1, fig. 3). Additionally, detailed drawings of the anterior region (head and prothorax) for a larva of *B. fulva* (Blair 1930, pl. 1, fig. 4) and *B. lampyroides* (Blair 1930, pl. 1, fig. 5) were provided. The photo of the alive larva of *B. fulva* does not match the fixed specimen. In addition, the two drawings do not match the photographs. According to the text, Blair had several specimens

available. We therefore assume that five different specimens have been shown (Fig. 1; specimen 3 on his fig. 1; specimen 4 on his fig. 2; specimen 5 on his fig. 3; specimen 6 on his fig. 4; specimen 7 on his fig. 5). Additionally, details of the clypeus and labrum (his [text-]fig. 2a), mandible (his [text-]fig. 2b), as well as maxillae and labium (his [text-]fig. 2c) were provided.

5) Böving & Craighead (1931, pl. 74C) provided a drawing of a larva of the group Brachypsectridae. The outline of the specimen matches that of the larva depicted in Barber (1905), including the orientation of the slightly tilted trunk end. We therefore regard it as a redrawing of specimen 1. In addition, a number of details were provided as drawings (all on their plate 74), including: processes (A, D), a leg (B), setae (E), mouthparts (F). It remains unclear whether these are also based on the data provided by Barber (1905) or whether the authors had additional specimens available.

6) Chu (1949) provided a simplified drawing of a larva of the group Brachypsectridae (Chu (1949: 96, fig. 239). It matches the outlines of specimen 1 quite precisely. We therefore consider it a simplified re-figure of specimen 1.

7) Lawrence (1991: 421, fig. 34.457a) provided a detailed drawing of a larva of *Brachypsectra fulva* in dorsal view. The specimen does not match any of the previously figured ones and is therefore considered a new specimen (Fig. 1; specimen 8). Additionally, SEM images of an isolated head in antero-dorsal (Lawrence 1991, fig. 34.457b) and partially ventral view (Lawrence 1991, fig. 34.457c) were provided, as well as a simplified drawing of the maxillo-labial complex (Lawrence 1991, fig. 34.457d). No direct indications of size were provided. It remains unclear whether all images show the same specimen.

8) Lawrence & Britton (1991) seem to have figured a larva of the group Brachypsectridae (Fig. 1; specimen 9, see discus-

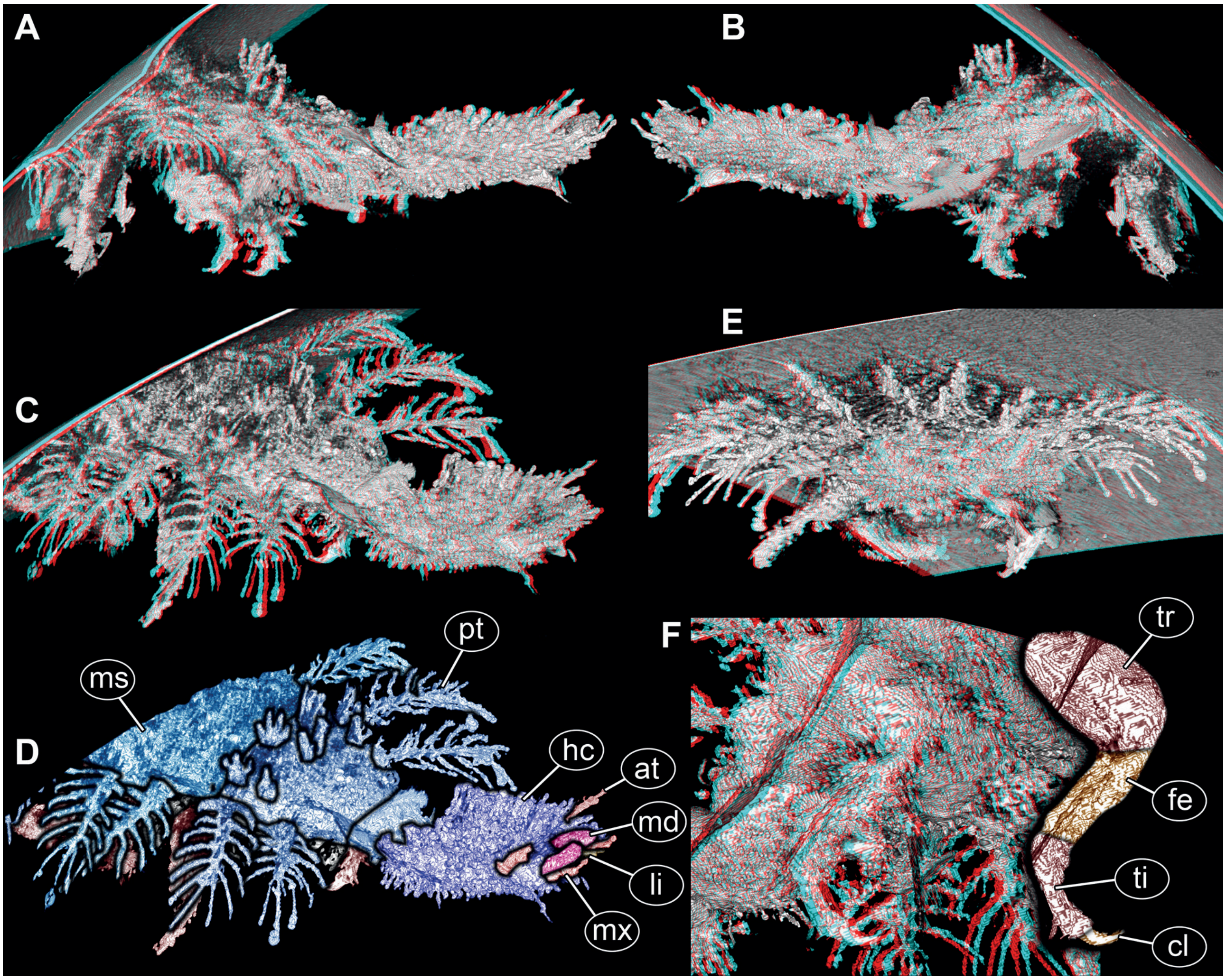

Fig. 7. Red-cyan stereo anaglyphs of synchrotron radiation micro-computed tomography scans of larva of Brachypsectridae in Myanmar amber, PED 0435; use red-cyan glasses to view; **A, B**: overview in lateral views; **C**: overview in dorsal view; **D**: colour-marked version of C; **E**: overview in frontal view (?); **F**: close-up of colour-marked thorax appendage. Abbreviations: at = presumed antenna; cl = claw; fe = femur; hc = head capsule; li = labium; md = mandible; mx = maxilla; pt = prothorax; ti = tibiotarsus; tr = trochanter. Images not to scale.

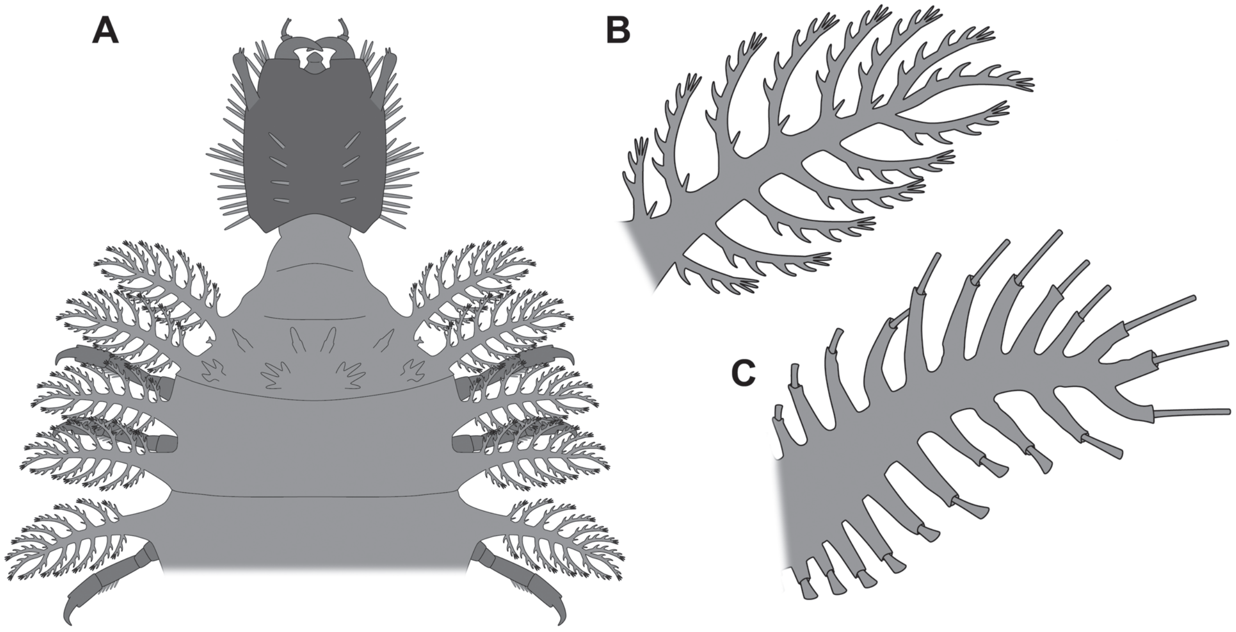

Fig. 8. Larva of Brachypsectridae preserved in Myanmar amber, PED 0435, continued and comparison; **A**: restoration of anterior body; **B**: restoration of single protrusion; **C**: protrusion of extant larva for comparison (based on Klausnitzer 2009, fig. 6; specimen 21).

sion further below). The publication was not available to the authors. The specimen was re-figured by Lawrence et al. (1995).

9) Poinar (1992) provided a photograph of a larva of the group Brachypsectridae (Fig. 2; specimen 10), preserved in Miocene Dominican amber (Poinar 1992: 136, fig. 74), representing the first fossil record of a larva of Brachypsectridae. The specimen was stated to be part of the Cardeon collection, Miami, Florida (according to Woodruff 2002: 164, the collection may be partly based in Chile). The specimen is well accessible in ventral view with only few dirt particles covering certain areas. The corresponding areas on the other side of the body are well accessible. No indication of size was provided. The specimen was re-figured in Poinar & Poinar (1999) and apparently Poinar (2010, see discussion below).

10) Lawrence et al. (1995) re-figured the specimen of Lawrence & Britton (1991; specimen 9; Fig. 1). The specimen was shown as a detailed drawing, yet it appears to be slightly schematized. The specimen does not match any of the previous records and was therefore considered as a new specimen (see above). No indication of its size was provided.

11) Wu (1996) published a book on Miocene Dominican amber, including images of two larvae of Brachypsectridae preserved in this type of amber. According to Woodrufff (2002: 170) the book is a re-published version of an earlier one in Chinese. The first specimen (Wu 1996: 131, fig. 198) is available in dorsal view (Fig. 2; specimen 11), no indication of size was provided; in later publications size was stated to be 5 mm (Grimaldi & Engel 2005). The specimen was re-figured several times (Woodruff 2002; Grimaldi & Engel 2005, see discussion there; Costa et al. 2006). The image of the second specimen in Wu (1996: 136, fig. 225) is smaller and does not provide a lot of details (Fig. 2; specimen 12). It seems accessible in dorsal view.

12) Fleenor & Taber (1999: 360, fig. 1) provided a photograph of a larval specimen of *Brachypsectra fulva* (Fig. 2; specimen 13). The image showed the specimen in its habitat in dorsal view. No indication of size was provided. According to the text, the authors had more than 50 specimens available and indicated that they must be very common in their habitats.

13) Poinar & Poinar (1999: 132 and between pp. 110 and 111, in both cases their fig. 133) re-figured specimen 10, i.e., the larva in Dominican amber from Poinar (1992).

14) Woodruff (2002: 166, fig. 17) re-figured specimen 11, i.e., one specimen from Wu (1996).

15) Scheven (2004) figured two larvae of Brachypsectridae preserved in amber. The first one (Fig. 2; specimen 14) is preserved in Eocene Baltic amber (Scheven 2004: 10). It is well accessible in dorsal view, but partly covered by dirt. The second one (Fig. 2; specimen 15) is preserved in Miocene Dominican amber (Scheven 2004: 120). It is well accessible in slightly oblique dorsal view. For both specimens no indication of size was provided. Both specimens were re-figured by Klausnitzer (2009); he also provided additional details of the specimens (see below).

16) Grimaldi & Engel (2005: 384, fig. 10.43) figured a larva of Brachypsectridae preserved in Miocene Dominican amber. Size was given as 5 mm. Origin was stated to be the Morone Collection, accession number M2198. The specimen shows significant similarities to specimen 11, i.e. a specimen from Wu (1996, re-figured in Woodruff 2002). Similarities include an incision-like impurity on the right side of the specimen and

the dirt particles around it, although the image in GRIMALDI & ENGEL (2005) clearly differs in the exact viewing angle from that shown in WU (1996, re-figured in WOODRUFF 2002). According to WOODRUFF (2002), the specimen from WU (1996) was sold after it was photographed by WU to another collection with the exact whereabouts unknown. Due to the similarities, we see it as likely that the specimen shown in GRIMALDI & ENGEL (2005) is specimen 11, i.e. the specimen originally shown in WU (1996).

17) COSTA et al. (2006) figured several larvae of Brachypsectridae. They presented a micrograph showing a larva of *Brachypsectra fulva* building its cocoon (COSTA et al. 2006, fig. 18). The specimen is only vaguely visible and is not further considered here.

Furthermore, COSTA et al. (2006) provided details of larvae of *B. fulva*, including details of the head, as drawings in dorsal (COSTA et al. 2006, fig. 19) and ventral view (COSTA et al. 2006, fig. 20), as SEM micrographs in ventral (COSTA et al. 2006, fig. 21), in dorsal view (COSTA et al. 2006, fig. 22), and frontal view (COSTA et al. 2006, fig. 23). They also provided an overview of the trunk as an SEM micrograph (COSTA et al. 2006, fig. 24) as well as close-up SEM micrographs (COSTA et al. 2006, figs. 25, 26). Together this provides information on one entire specimen that can be further considered here (Fig. 2; specimen 16). Also more details of the larva were provided as drawings: maxillae and labium (COSTA et al. 2006, figs. 27, 28), mandibles (COSTA et al. 2006, figs. 29, 30), antennae (COSTA et al. 2006, figs. 31, 32), clypeus and labrum (COSTA et al. 2006, fig. 33), anterior locomotory appendage ("leg", COSTA et al. 2006, fig. 34 part), spiracles (COSTA et al. 2006, figs. 34 part, 35) and some of the lateral protrusions of the trunk (COSTA et al. 2006, figs. 36, 37). According to the description, the authors had 25 specimens available (one of it is an exuvia). All specimens originated from North America (Arizona, California, Texas).

The authors also provided a habitus drawing of a larva of *Brachypsectra lampyroides* (Fig. 2; specimen 17) in dorsal view (COSTA et al. 2006, fig. 50). Also more details of the larva were

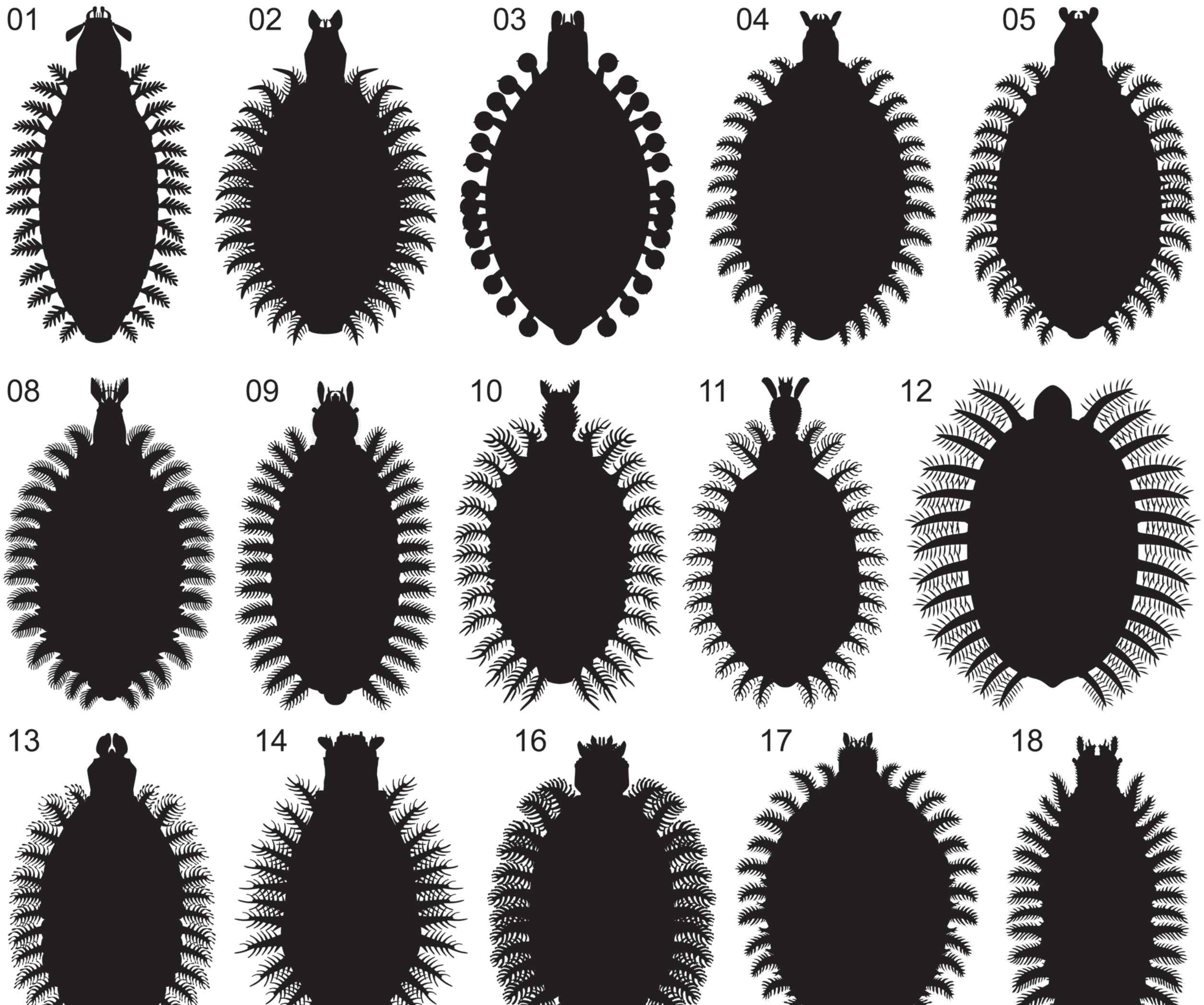

Fig. 9. Data set for shape analysis of entire body outline; note: the trunk end was omitted.

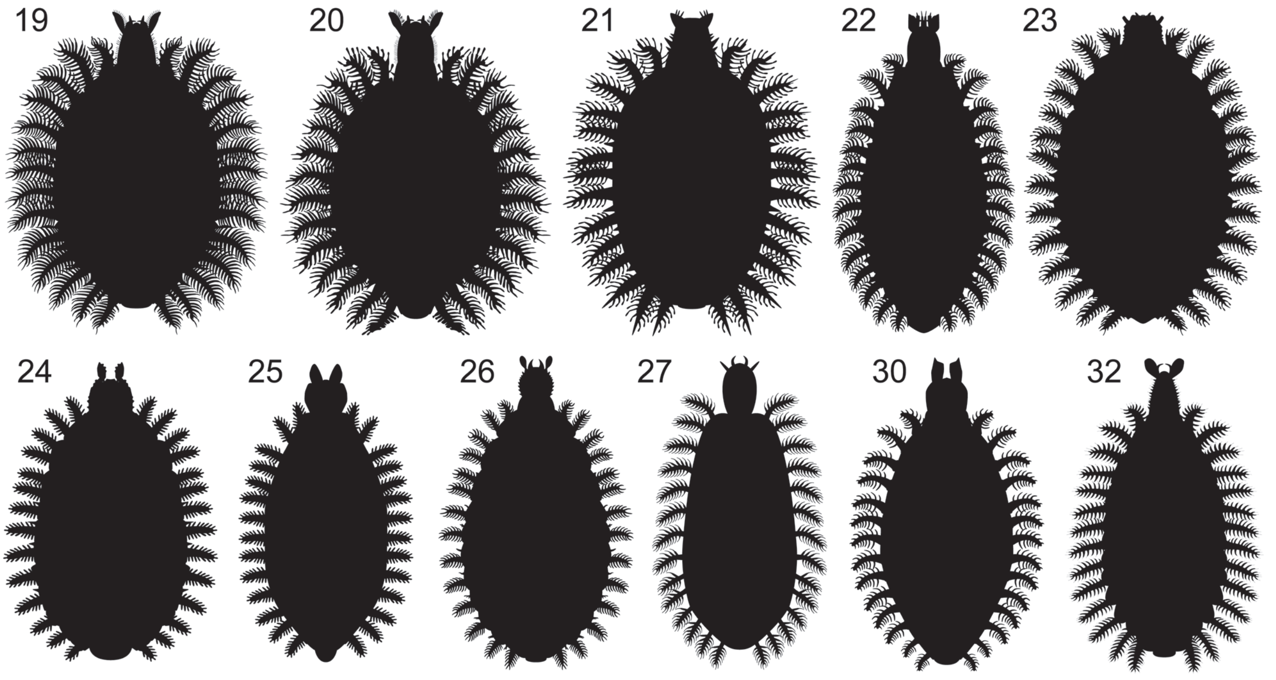

Fig. 10. Data set for shape analysis of entire body outline, continued; note: the trunk end was omitted.

provided as drawings: head (Costa et al. 2006, figs. 51, 52), maxillae and labium (Costa et al. 2006, figs. 53, 54), mandibles (Costa et al. 2006, figs. 55, 56), antennae (Costa et al. 2006, figs. 57, 58), clypeus and labrum (Costa et al. 2006, fig. 59), anterior locomotory appendage ("leg", Costa et al. 2006, fig. 60 part), spiracles (Costa et al. 2006, figs. 60 part, 61) and some of the lateral protrusions of the trunk (Costa et al. 2006, figs. 62, 63). According to the description, a single specimen was the basis for the observations. It originated from South India.

Costa et al. (2006, fig. 70) re-figured specimen 11, i.e. a specimen from Wu (1996; same as in Woodruff 2002 and Grimaldi & Engel 2005) and formally described the new species *Brachypsectra moronei* based on this fossil larva. Additionally, close-up micrographs of the head region were provided (Costa et al. 2006, figs. 71, 72).

The authors also provided a habitus drawing of a larva (Fig. 2; specimen 18) of *Brachypsectra* sp. in dorsal view (Costa et al. 2006, fig. 73). Also more details of the larva were provided as drawings: head (Costa et al. 2006, figs. 74, 75), maxillae and labium (Costa et al. 2006, fig. 78), mandibles (Costa et al. 2006, figs. 80, 81), antennae (Costa et al. 2006, figs. 76, 77), clypeus and labrum (Costa et al. 2006, fig. 82), epipharynx (Costa et al. 2006, fig. 79) anterior locomotory appendage ("leg", Costa et al. 2006, fig. 83 part), spiracles (Costa et al. 2006, figs. 83 part, 84) and some of the lateral protrusions of the trunk (Costa et al. 2006, figs. 85, 86). According to the description, four specimens were the basis for the observations. They all originated from Australia.

18) Klausnitzer (2009) figured several larvae of Brachypsectridae. He provided micrographs of a presumably last larval stage (Fig. 3; specimen 19) of *Brachypsectra* cf. *lampyroides*. This includes a dorsal view (Klausnitzer 2009, fig. 1), a ventral view (Klausnitzer 2009, fig. 2), a close-up of the head in dorsal view (Klausnitzer 2009, fig. 8) and the trunk end in dorsal view (Klausnitzer 2009, fig. 14).

He also provided micrographs of a presumably penultimate larval stage (Fig. 3; specimen 20) of *Brachypsectra* cf. *lampyroides*. This includes a dorsal view (Klausnitzer 2009, fig. 3), a ventral view (Klausnitzer 2009, fig. 4), and close-ups on the surface of the trunk segments (Klausnitzer 2009, fig. 5), some of the lateral protrusions (Klausnitzer 2009, fig. 6), the terminal end (Klausnitzer 2009, fig. 7), the head (Klausnitzer 2009, fig. 8), the antenna (Klausnitzer 2009, fig. 9), mandibles (Klausnitzer 2009, fig. 10), maxillae and labium (Klausnitzer 2009, fig. 11), locomotory appendage 1 (front leg; Klausnitzer 2009, fig. 13), and locomotory appendage 2 (mid leg, Klausnitzer 2009, fig. 12). Furthermore, he reported that the larva was apparently close to moulting and already had the structures of the next instar visible (e.g., front leg; Klausnitzer 2009, fig. 13). He was able to prepare the trunk region free, figuring the not yet folded out lateral protrusions of the trunk (Klausnitzer 2009, fig. 16).

Furthermore, Klausnitzer (2009, figs. 19, 20) figured a fossil larva (Fig. 3; specimen 21) of the group *Brachypsectra* as micrographs in dorsal and ventral view. The specimen is preserved in Eocene Baltic amber. It is part of the collection Gröhn (no. 2514); size was given as 2.68 mm.

Klausnitzer (2009) also re-figured specimens 14 and 15, i.e. the two specimens from Scheven (2004), providing some further details. Specimen 15, the specimen from Dominican amber, was stated to be part of the Velten collection, accession number 316; size was provided as 5.5 mm. The specimen was presented in dorsal view (Klausnitzer 2009: 739, fig. 17, slightly different angle than the image in Scheven 2004) and ventral view (Klausnitzer 2009, fig. 18).

Specimen 14, the specimen from Baltic amber, was stated to be also part of the Velten collection, accession number 12; size was given as 2.03 mm. The specimen is accessible in dorsal view (Klausnitzer 2009, fig. 21).

19) Poinar (2010: 33, fig. 21) depicted a larva of Brachypsectridae in dorsal view, preserved in Dominican amber. It matches the exact outline of specimen 10, i.e. the specimen shown in Poinar (1992) and Poinar & Poinar (1999) in ventral view, including a large piece of dirt on the right "shoulder" of the specimen. We therefore interpret this as a re-illustration of specimen 10. Here, the specimen was stated to be part of the Cardoen collection.

20) Lawrence et al. (2011) provided several images of a larva (Fig. 3; specimen 22) of *Brachypsectra fulva*. This included a habitus micrograph in dorsal view (Lawrence et al. 2011, fig. 65D), and SEM micrographs of the head in dorsal (Lawrence et al. 2011, fig. 83D) and frontal view (Lawrence et al. 2011, fig. 74B).

21) Gröhn (2015: 288, figs. 2564 left and right) depicted a spiny beetle larva. The specimen was labelled 'Brachyspectridae (?)' [sic!]. However, the specimen differs significantly from larvae of Brachypsectridae; the large pronotum entirely conceals the head when seen from dorsal. Hence, we do not further consider it here.

22) Petrzelkova et al. (2017) provided several images of a larva (Fig. 3; specimen 23) of *Brachypsectra* sp. This included habitus micrographs in dorsal (Petrzelkova et al. 2017, fig. 2I) and ventral view (Petrzelkova et al. 2017, fig. 2J), and close-

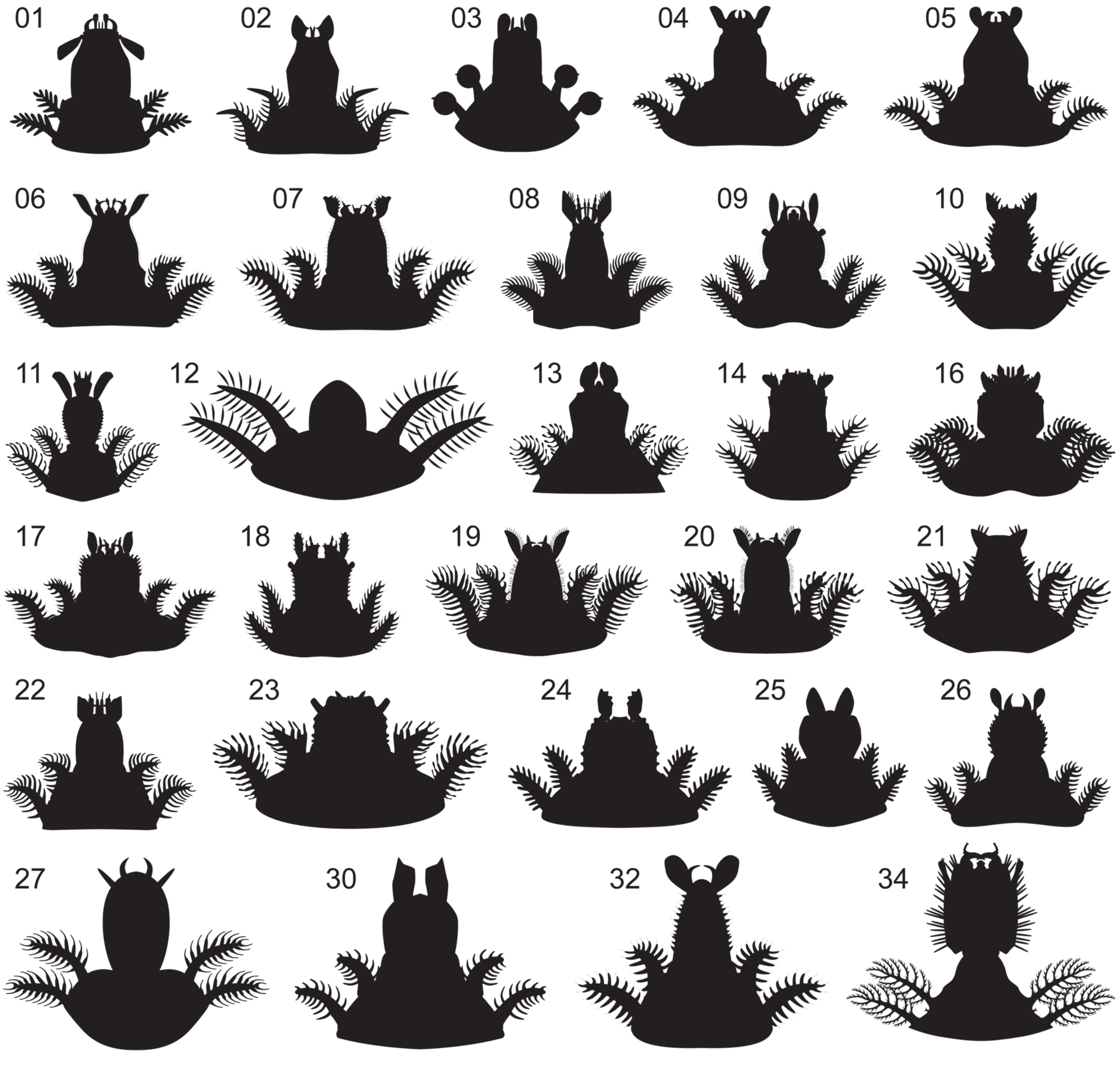

Fig. 11. Data set for shape analysis of anterior body (head and prothorax) outline.

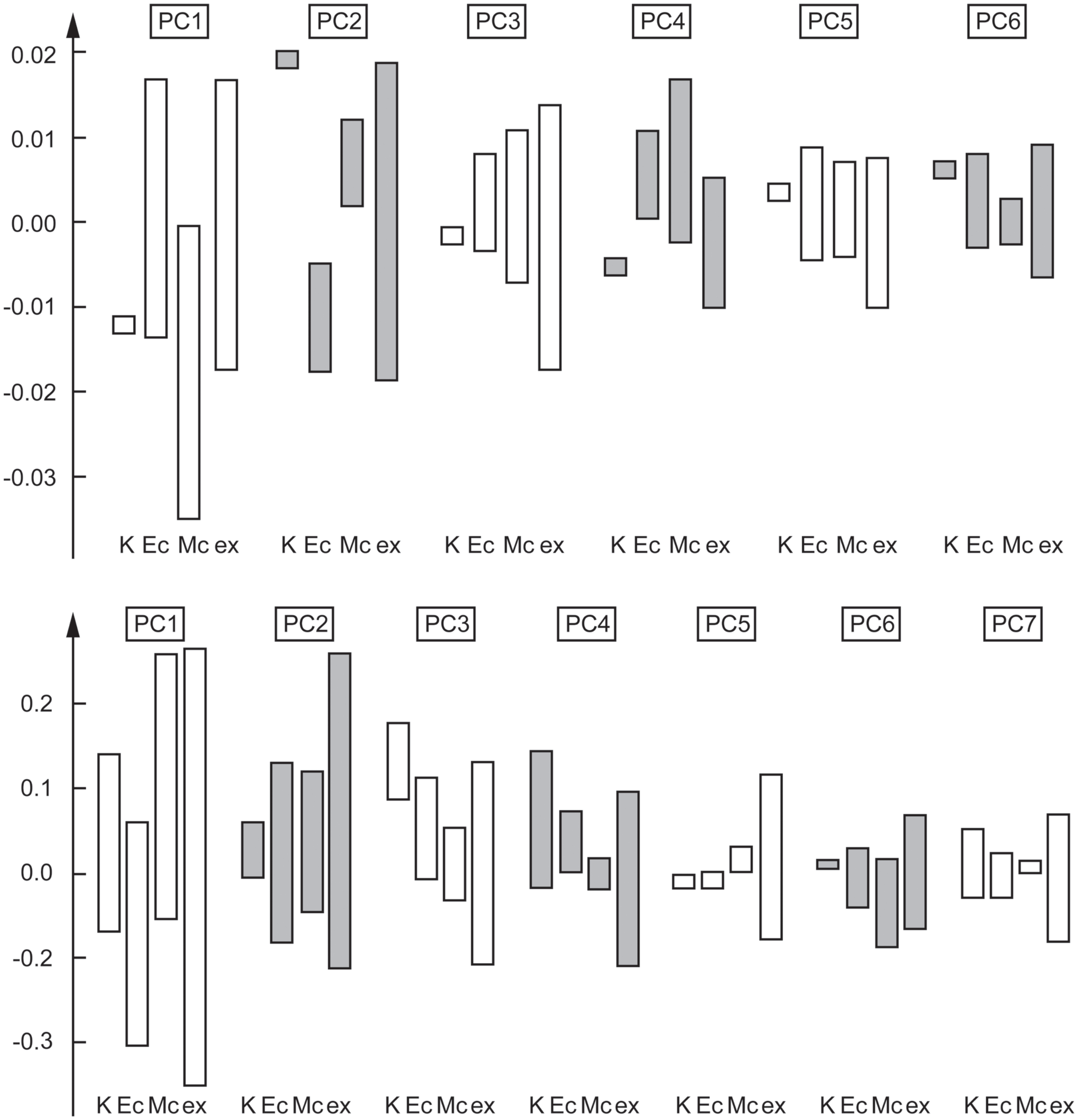

Fig. 12. Plots of ranges of PC values; upper graph showing results of outline of entire body, lower graph of outline of anterior body region (head and prothorax). Abbreviations: Ec = Eocene; ex = extant; K = Cretaceous; Mc = Miocene.

up micrographs of the head in dorsal (Petrzelkova et al. 2017, fig. 2K) and ventral view (Petrzelkova et al. 2017, fig. 2L). According to the text, only a single specimen was available. The specimen originated from Cyprus.

23) Lawrence et al. (2020) provided images of several larvae of the newly formally described species *Brachypsectra cleidecostae*. This includes a larva from Diamantina Lakes, Australia, of which one side of the trunk in dorsal view (Lawrence et al. 2020: 4, fig. 2A) and a ventral view of the head (Lawrence et al. 2020, fig. 2B) were provided as micrographs. The specimen was not presented as a habitus depiction and can therefore not be further considered here.

Another larva was collected in Arkaroola, Australia. The specimen was shown in dorsal view (Lawrence et al. 2020: 5, fig. 3A), yet the specimen is curled and slightly oblique and cannot be further considered here. Further close-up micrographs include anterior body (Lawrence et al. 2020, fig. 3B), trunk end (Lawrence et al. 2020, fig. 3C), prothorax (Lawrence et al. 2020, fig. 3D), dark areas on anterior abdomen (Lawrence et al. 2020, fig. 3E) and on posterior abdomen Lawrence et al. 2020, fig. 3F).

Also details of various larvae were provided as micrographs, including close-ups on the anterior region of isolated labia of a late instar of *B. fulva* (Lawrence et al. 2020, fig. 3G), of a first instar of the same species (Lawrence et al. 2020, fig. 3H) and of a late instar of *B. cleidecostae* (Lawrence et al. 2020, fig. 3I), as well as mandibles of *B. cleidecostae* (Lawrence et al. 2020, fig. 3J) and *B. fulva* (Lawrence et al. 2020, fig. 3K).

Two larvae were collected at the type locality of the new species, Diamantina Lakes National Park. A single photograph (Lawrence et al. 2020, fig. 5C) shows both in more or less dorsal view and demonstrates that one larva (Fig. 3; specimen 24) is significantly larger than the other one (Fig. 3; specimen 25).

Another larva was collected at Stubb's Waterhole, Australia. The larva (Fig. 3; specimen 26) was depicted on a micrograph in dorsal view (Lawrence et al. 2020, fig. 6B).

24) Zhao et al. (2020) reported the first larva of Brachypsectridae preserved in 100 million-year-old amber from the Cretaceous of Myanmar ("Burmese amber"; Fig. 4; specimen 27). The authors provided photographic images in (latero-)dorsal view (Zhao et al. 2020: 2, fig. 1A), in (dorso-)lateral view (Zhao et al. 2020: 2, fig. 1B) and in ventral view (Zhao et al. 2020: 2, fig. 1C). Additionally, close-up micrographs were provided of the head in dorsal view (Zhao et al. 2020: 3, fig. 2A) and in ventral view (Zhao et al. 2020: 3, fig. 2B), the maxilla (Zhao et al. 2020: 3, fig. 2C) and the antenna (Zhao et al. 2020: 3, fig. 2D). Furthermore, the authors provided a restoration drawing of the specimen (Zhao et al. 2020: 4, fig. 3). We here deviate partly from this restoration drawing, orienting our interpretation more on the provided photographs. For example, we had the impression that the angle of the processes of the trunk was in the restoration drawing not arranged as in the photograph.

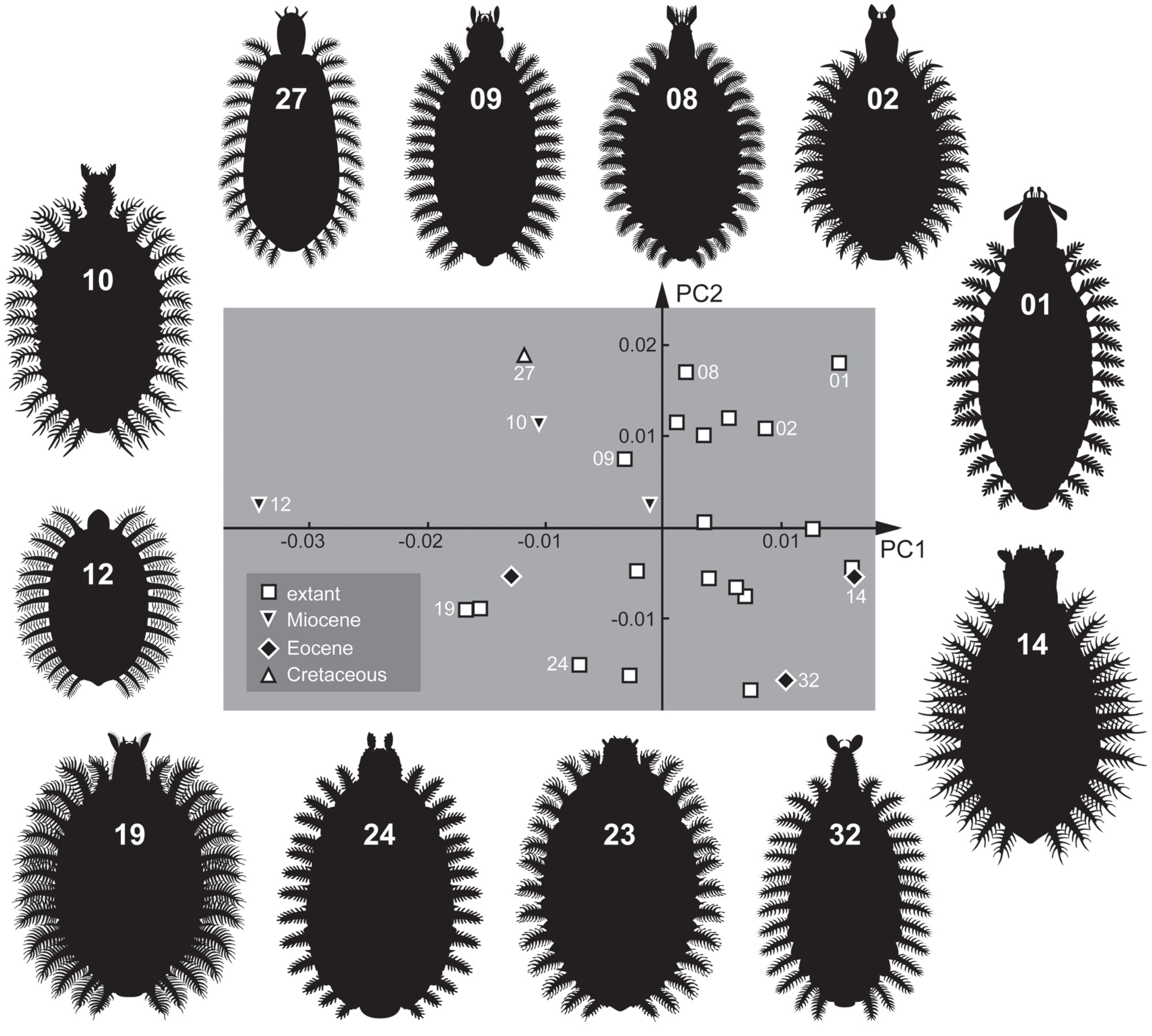

Fig. 13. Scatter plot of PC2 vs. PC 1 of outline of entire body; note that specimen 12 is a pronounced outlier, most likely due to the small size of the original image, allowing only for a rather coarse reconstruction.

25) Websites are often not considered to be “proper” scientific sources. Still, given the relative scarceness of data on larvae of Brachypsectridae, we use them here as additional data source. Especially the community ‘bugguide’ (https://bugguide.net) is very active and well sorted, hosted by Iowa State University, and each entry is given an identifier (see also discussion in Haug & Haug 2019; Haug et al. 2020a, online first):

– Image 114820 (© 2007 Jeff Gruber) is labelled ‘Texas beetle larva – *Brachypsectra fulva*’ and shows a photograph of a larva of Brachypsectridae in slightly oblique dorsal view (Fig. 4; specimen 28).

– Image 175768 (© 2008 Graham Montgomery) is labelled ‘Brachypsectridae? – *Brachypsectra fulva*’ and shows a photograph of a larva of Brachypsectridae in slightly oblique dorsal view (Fig. 4; specimen 29). Additional images of this specimen are available; we used the one that provided most information. The size of the specimen has been stated to be about 10 mm.

– Image 1601732 (© 2018 Britta Nippert) is labelled ‘strange larva – *Brachypsectra fulva*’ and shows a photograph of a larva of Brachypsectridae in rather direct dorsal view (Fig. 4; specimen 30). Additional images of this specimen are available; we used the one that provided most information. The size of the specimen has been stated to be less than 10 mm.

– Image 1709093 (© 2019 Brittneyp10) is labelled ‘Found in bathroom – *Brachypsectra fulva*’ and shows a photograph of a larva of Brachypsectridae in slightly oblique antero-dorsal view (Fig. 4; specimen 31). The size of the specimen has been stated to be the ‘size of my pinky nail’.

26) Two specimens originate from the Hoffeins collection (future part of the amber collection at the Senckenberg Deutsches Entomologisches Institut (SDEI), Müncheberg, Germany). Both specimens are preserved in Eocene Baltic amber.

The first specimen (Figs. 4, 5A, B; CCHH 1181-2; specimen 32) is a rather complete larva of Brachypsectridae, well accessible in dorsal and ventral view. Amber with beetle larva was treated in an autoclave (Hoffeins 2012). The larva shows minor modifications of the head with mouthparts and antennae, as well as the trunk end. Otherwise it is very similar to other specimens known from amber.

The second specimen (Fig. 5C, D; CCHH 1228-6; specimen 33) appears to be an exuvia of a larva of Brachypsectridae. The cuticle is strongly crumpled, but reveals the lateral, branched processes (Fig. 5C). It is even possible to recognise the distal, spatula-like, movable tips known from extant specimens (Fig. 5D).

27) A new specimen is reported here from Cretaceous Myanmar amber (Fig. 6; PED 0435; specimen 34). The specimen is largely covered by white film (“Verlumung”), concealing many details; only accessible from the dorsal side. The specimen is incomplete, only the anterior part of the body is inside of the amber piece, including the head, prothorax, half of the

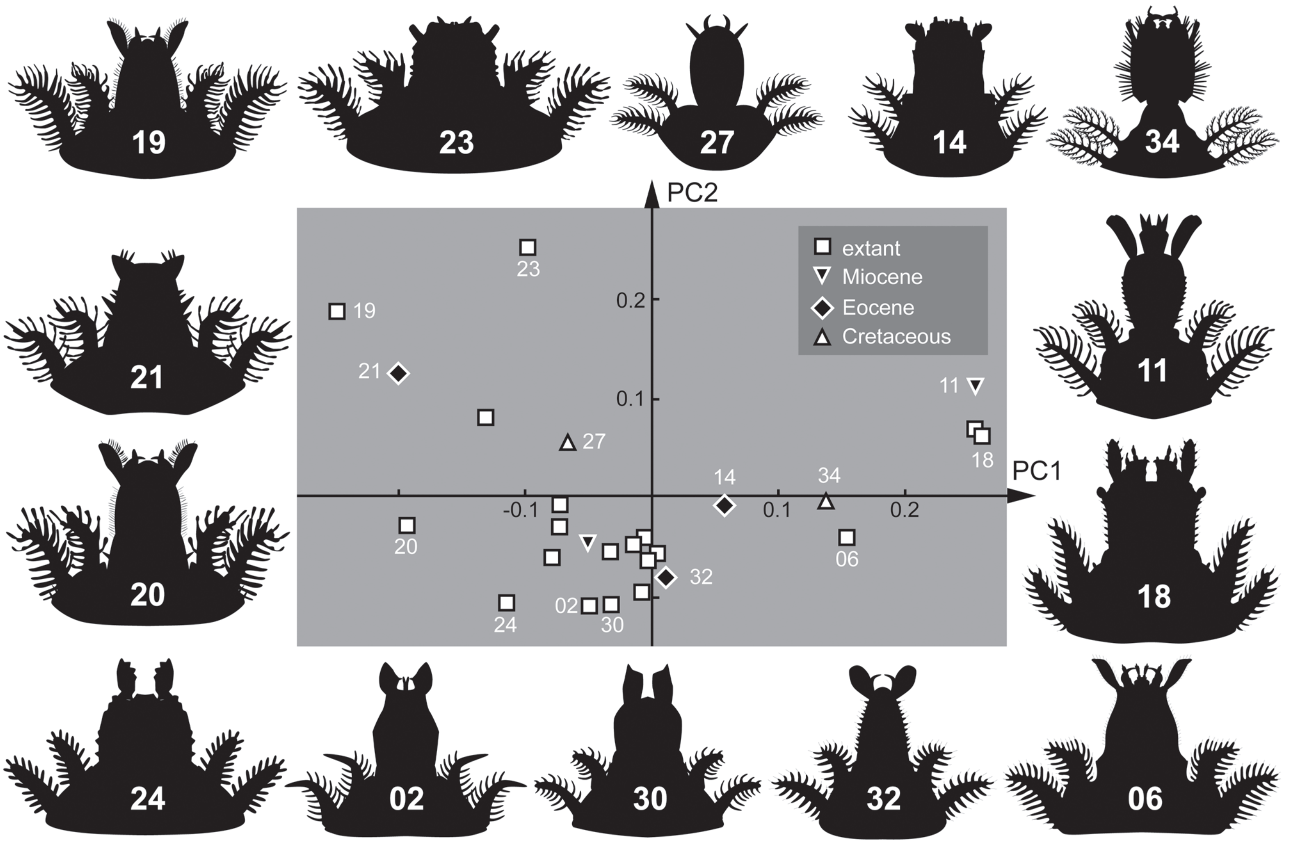

Fig. 14. Scatter plot of PC2 vs. PC 1 of outline of anterior body.

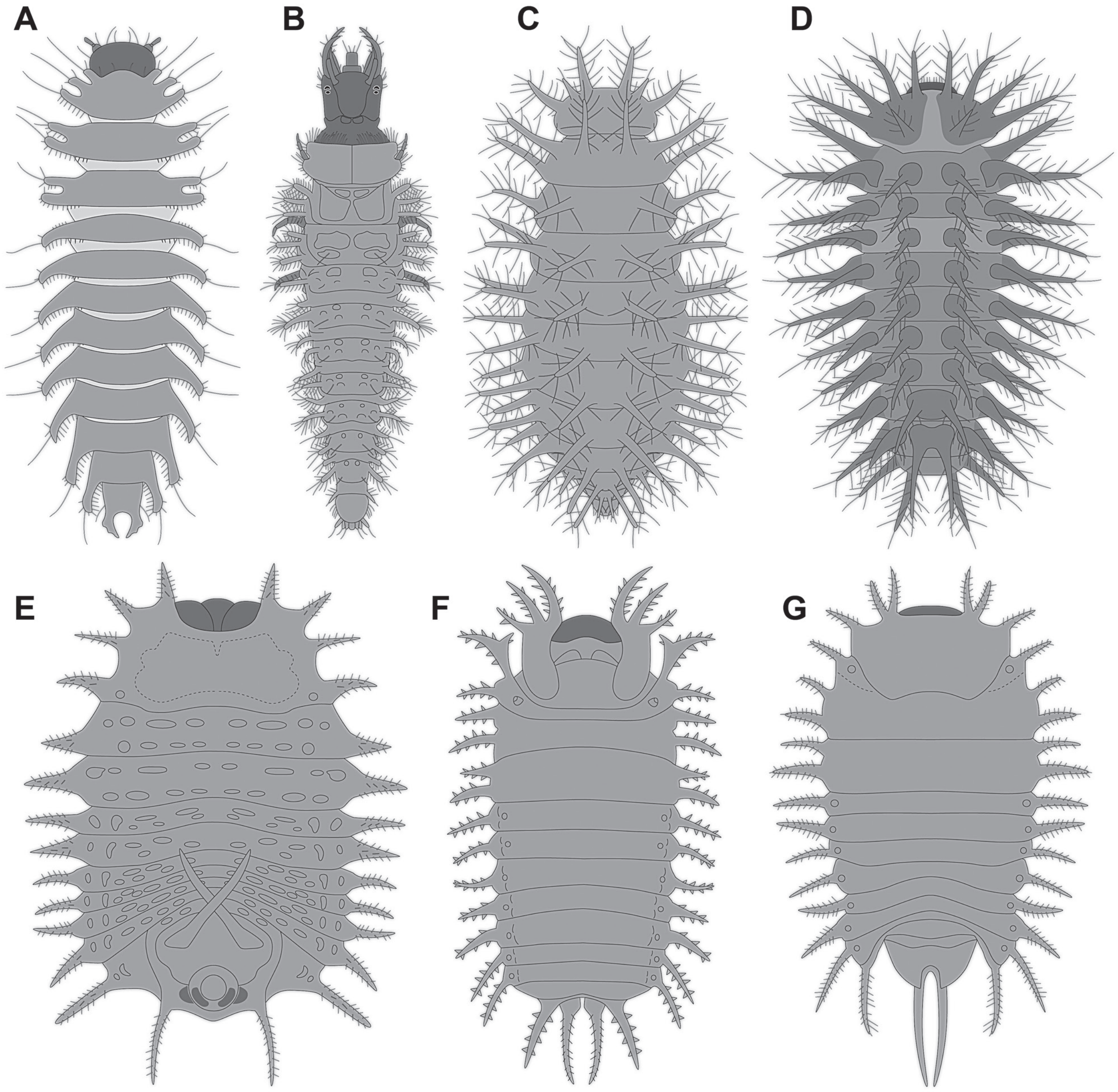

Fig. 15. Other beetle larvae with prominent processes; **A**: Micropeplidae, *Micropeplus neotomae*, (based on NEWTON 1991: 335, fig. 34.168); **B**: Hydrophilidae, *Derallus* sp. (based on SPANGLER 1991: 356, fig. 34.297); **C, D**: Coccinelidae (based on LESAGE 1991: 489); **C**: *Epilachna* sp., LESAGE 1991, fig. 34.570; **D**: *Chilichorus* sp., LESAGE 1991, fig. 34.571; **E–G**: Chrysomelidae (based on LAWSON 1991: 574); **E**: *Chelymorpha cassidea* (LAWSON 1991, fig. 34.802a); **F**: *Johnthonota nigripes* (LAWSON 1991, fig. 34.803a); **G**: *Plagiometriona clavata* (LAWSON 1991, fig. 34.804a).

mesothorax and the far lateral part of one side of the metathorax (Figs. 6A, B, 7A–E, 8A). Head roughly rectangular in dorsal view (Fig. 6C). With numerous spines or setae on the surface. Details partly obscured by impurities of the amber.

3.2. Description of the new specimen PED 0435

Head prognathous, protracted and elevated, rectangular in dorsal view (Figs. 6C, 7A–E), slightly longer (0.58 mm) than wide (0.52 mm). Ocular segment apparent by the elongate labrum. No eyes apparent. Post-ocular 1 segment (i.e., the segment following the ocular one) apparent by its possible pair of appendages, antennae (Fig. 6C). Antenna indistinct, short rod-like, arising antero-laterally from head capsule. Shorter than the head width, 0.25x (0.13 mm). Number of antenna elements not apparent, possibly three. Post-ocular segment 2 (intercalary segment) without externally recognisable structures. Post-ocular segment 3 apparent by its pair of appendages, mandibles (Figs. 6D, 7D). Mandibles arising anteriorly from head capsule, prominent, symmetrical, hook-shaped (strongly inward curved), broader at base, 0.15 mm long. Post-ocular segments 4 and/or 5 indicated by maxillary palps and distal part of labium (Figs. 6D, 7D). Details not apparent.

Trunk with anterior neck-like region (0.17 mm long), widening posteriorly (width anteriorly 0.28 mm, width posteriorly 0.38 mm), connected to prothorax. Prothorax without neck-like region 0.45 mm long, widening posteriorly (width anteriorly 0.38 mm, width posteriorly 0.88mm). Ventrally with a pair of appendages. (Figs. 6B, 7F).

Appendages well developed, four major elements (Fig. 7F). Proximal region (possible coxa) not well accessible; trochanter (element 1) 0.43 mm long, femur (element 2) 0.32 mm long, tibiotarsus (element 3) 0.31 mm long, tarsus (element 4) forms a claw (~0.12 mm long). Dorso-laterally on prothorax a pair of protrusions on each side apparent (0.36–0.46 mm long). Protrusions with seven secondary protrusions on each side (~0.12 mm long). Each secondary protrusion with small, spine-like, tertiary protrusions (~0.02 mm long), exact number unclear due to preservation, at least five or six (Figs. 6F, 8B; for comparison with extant larva, see Fig. 8C).

Posterior part of prothoracic tergite bearing two transverse rows of four protrusions (Fig. 7D). Protrusions in the anterior row with proximal socket-like and distal spine-like region; lateral protrusions in the posterior row with three tips arising from a narrow proximal socket; median protrusions in the posterior with four tips arising from a broad proximal socket (Figs. 7D, 8A).

Mesothorax medially (0.14 mm) shorter than laterally (right side 0.4 mm), 0.35x, and 0.95 mm wide. Appendages and dorso-lateral protrusions on mesothorax apparent. Posterior part of mesothorax missing, especially on the left side. Metathorax largely missing as well, only a part of one similar-appearing protrusion and distal, isolated part of trunk appendage preserved (Fig. 6E).

3.3. Shape differences

Shape analysis of the entire outline (excluding the trunk end) of 26 specimens of sufficient quality (Figs. 9, 10) resulted in six effective principal components (PCs), PC1 explaining 33.9%, PC2 31.0%, PC3 11.5%, PC4 7.5%, PC5 5.8%, and PC6 3.9% of the overall variation (see also Suppl. 1). The shapes are more complex; therefore, it is not simple to verbally express the differences along each dimension (PC; see Suppl. 2).

Shape analysis of the outline of the anterior body region (head and prothorax) of 29 specimens of sufficient quality (Fig. 11) resulted in seven effective principal components, PC1 explaining 47.3%, PC2 18.0%, PC3 13.2%, PC4 6.3%, PC5 4.4%, PC6 2.9%, and PC7 2.4% of the overall variation (see also Suppl. 3). The shapes are also quite complex; still it is possible to identify some aspects of the factor loadings (PC; see Suppl. 4). PC1 is strongly influenced by the length of the processes. PC2 is strongly influenced by the length of the head. PC3 is influenced by the prominence of the antennae. PC4 is influenced by the width of the processes. PC5 and 7 are influenced by asymmetry, which hints to small errors in our dataset that should be fully symmetric. PC6 is influenced by the prominence of the mouth parts.

3.4. Differences through time

The occupation of morphospace is always largest in the modern fauna; only in one case it is as large as that of one of the fossils (Fig. 12; values in Suppl. 5). In most cases, the occupied space of the fossils lies within that of the modern fauna. Only in few aspects, a fossil lies outside the range of the modern fauna. There are more outliers in the outline of the entire shape than in that of only the anterior body region.

When PC2 and PC1 of the outline of the entire body are plotted against each other, the fossil specimens plot in about the same area as the extant specimens (Fig. 13). However, specimen 12 plots relatively far outside, but this is most likely due to the small size of the original image, which led to a rather coarse reconstruction.

Also when PC2 and PC1 of the outline of the anterior body are plotted against each other, fossil and extant specimens occupy about the same area of the morphospace (Fig. 14). The new specimen described here, specimen 34, plots well within the area of the unequivocal larvae of Brachypsectridae.

4. Discussion

4.1. Identity of the new Cretaceous specimen

Unfortunately, the new fossil from the Cretaceous is incomplete. Nevertheless, the preserved part already gives some interesting details. The head is roughly rectangular in dorsal view and armed with numerous spines or setae. The mandibles are prominent, hook-like, and forward-projecting. The prothorax and mesothorax each bear a pair of processes on each side. These processes are long and branching. All these features are characteristic for larvae of Brachypsectridae. While there are other larvae with processes that appear roughly comparable, especially the head is very different in most of these (Fig. 15). Furthermore, the new fossil plots well inside the area of the morphospace occupied by definite larvae of Brachypsectridae, supporting an interpretation of the new fossil as a larva of Brachypsectridae.

Still there are some differences in the new larva that need to be considered. First, the large paddle-shaped antennae known in the extant, Miocene and Eocene larvae are not present in the new fossil. Also the antennae in the Cretaceous larva reported by Zhao et al. (2020) lack the paddle-like antennae (Zhao et al. 2020, fig. 2D). As paddle-like antennae appear to be present in Eocene and Miocene specimens, this might be a character apomorphic for a group including the modern-day forms together with the Miocene and Eocene fossils, but excluding the Cretaceous forms.

Another difference is the detailed structure of the processes. In modern larvae of Brachypsectridae, the processes have branches that end in movable tips (Fig. 8C; hence these should be considered setae) that can be elongate or shovel- to spatula-like. In the new fossil, the branches have secondary branchings and no movable tips (Fig. 8B). This specific character cannot be easily evaluated for many of the other fossils, especially not on the Cretaceous fossil reported by Zhao et al. (2020). The new Cretaceous larvae differs in significant aspects from the larva described by Zhao et al. (2020), thus it is unlikely that these two larvae are conspecific.

The difference might mean that the new fossil is only more distantly related to Brachypsectridae, more specifically it could represent the sister group to Brachypsectridae. Additional and more complete specimens could in the future help to resolve this aspect with more confidence. We decided not to erect a new species based on the new fossil as it might represent the larval stage of an already formally described Cretaceous species of Brachypsectridae (see also further below on this aspect).

4.2. Abundance of larvae of Brachypsectridae

Extant larvae of Brachypsectridae have been considered to be rare (see Introduction), yet some studies have already indicated that they locally occur in quite substantial masses (Fleenor & Taber 1999; Petrzelkova et al. 2017). Also when looking at the numbers, the coverage is in fact not bad; in total, we have 34 specimens: two specimens from the Cretaceous, four from the Eocene, four from the Miocene, and 24 extant ones. If we compare this to some other groups, the ratio of known larval specimens to formally described species is quite high, regardless of the ontogenetic stage they are based on.

Together with various co-authors, we have tried to compile comparable data sets for other lineages, revealing worse ratios. For false flower beetles (Scraptiidae) we can expect that about 200 extant species have larvae with enlarged terminal ends, but only 17 such larvae are available from the extant fauna, 14 more specimens are known from Baltic amber (Haug & Haug 2019; Zippel et al. accepted), and two from Myanmar amber (Zippel et al. accepted). Also for the closer related lacewings, we often have less larval specimens than known species from the modern fauna: for silky lacewings (Psychopsidae), there are 27 species and eleven known extant larvae (long-nosed antlions; Haug et al. 2020a); for split-footed lacewings (Nymphidae), there are 33 species and 25 extant larvae (Haug et al. online first). Only for thread-winged lacewings (Crocinae) there are 47 species and 57 extant larvae (long-necked antlions; Haug et al. 2021a). Still, this ratio is clearly worse than that for Brachypsectridae.

We can assume that long-necked antlions and even more so larvae of Brachypsectridae have a better coverage as these larvae are clearly eye-catchers. This seems to be an important factor for the state of scientific coverage of a group (Kristensen et al. 2007: 700). Therefore, larvae of Brachypsectridae appear proportionally more often not only in the literature, but also in databases than many other larvae. Also the presence of these larvae in so far three types of ambers does not speak for a rarity. Larvae generally are often less taken care of from the scientific side, as it is more challenging to erect species on larval specimens (see also further below). Hence, it is quite likely that there are in fact more of these larvae available, but have not yet made it into the literature.

4.3. Species problems in fossil representatives of Brachypsectridae

It is a common theme that erecting species is considered important in biology. However, this process is in fact not simple, since a concept of what a species is, is often missing, especially when dealing with fossils (Haug & Haug 2017). This may lead to overestimations of species numbers. A good example for such difficulties can also well be found within Brachypsectridae. Zhao et al. (2020) erected a new species based on a single larva they found in

Myanmar amber. This is quite problematic. Already two species of Brachypsectridae had been described from the same locality based on adults (Tihelka et al. 2019; Qu et al. 2019). Thus, it cannot be excluded that the larva reported by Zhao et al. (2020) is conspecific with one of these two species. Despite this fact, the authors did not consider the other two species in the discussion and did not provide a differential diagnosis that allows to distinguish the newly erected species from already existing ones.

For Miocene Dominican amber it has been suggested that it includes specimens indistinguishable from modern-day species (Woodruff 2002: 166; Hörnschemeyer et al. 2010). It might seem natural to interpret specimen 11 as conspecific to an adult beetle described as *B. moronei*. Yet, it is also well possible that the larva is conspecific to the extant species *B. vivafosile*. The interpretation of fossil holometabolan larvae is generally challenging as many, if not most, species are erected and diagnosed based on adult males. We should therefore be more careful when interpreting larvae on species level and also express the uncertainties. We therefore suggest to use *Brachypsectra* ? *moronei* for specimen 11.

4.4. Diversity of larvae of Brachypsectridae through time

In comparable studies of lineages within Neuropteriformia (= Neuropterida + Coleopterida) involving morphometric aspects it was possible to demonstrate that the fossil representatives differed in some cases significantly from their modern relatives (e.g., Haug et al. 2019a, b, 2020a, b, 2021a, online first), while in other lineages extant and fossil larvae showed no significant differences (Haug et al. 2021b). Furthermore, even small data sets of fossil larvae could outweigh a larger extant data set and demonstrate that these larvae were more form-diverse in the past (Haug et al. 2020a, online first). This seems not to be the case for larvae of Brachypsectridae. Here the fossil data sets are indeed too small, with only two to three specimens to be analysed for each fossil time slice but around 20 extant specimens, to show a comparable or even larger morphological diversity.

In some analyses certain fossil larvae appear to plot outside the area of the morphospace occupied by the extant larvae (Figs. 12, 13). However, the specimens in these extraordinary positions were more difficult to interpret for the reconstruction for the shape analysis (e.g., specimen 12 was based on a very small original image, resulting in a rather coarse reconstruction); hence, we consider these as artefacts of our interpretations. Therefore, we cannot detect any decrease of morphological diversity towards the modern fauna.

We also do not see a real "trend" over time for most shape aspects. This does not mean that there are no directed shifts, but that the small sample sizes may very likely conceal such aspects. Yet, there is a certain directed pattern for PC3 and less so for PC4 in the analysis of the anterior body. PC3 is influenced by the prominence of the antenna, and it indeed appears that the antennae become more prominent paddle-shaped over time. PC4 is influenced by the width of the processes, and the ones of the Cretaceous larvae seem indeed to be slimmer. More specimens for the fossil samples will be necessary to detect more such aspects.

Despite the fact that larvae of Brachypsectridae are often considered rare, there are in fact more larvae available than for many other more species-rich groups (see above) and are hence likely to provide a good representation of the modern-day morphological diversity. The very few fossils are unlikely to provide a similarly good coverage of the extinct fauna. Still, also small data sets have the potential to show shifts or certain losses (Haug et al. 2021a). As we find no signal in this direction, it seems that the morphology indeed remained rather unchanged for at least 100 million years. Only some qualitative differences concerning the new fossil, namely the exact branching of the lateral processes, provides a weak indication that there was some more variation in larvae of Brachypsectridae 100 million years ago.

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5. References

Anonymous (1908): Minutes of 218th regular meeting. – Proceedings of the Entomological Society of Washington, **10**: 14.

Barber, H. S. (1905): Illustrations of an undetermined coleopterous larva. – Proceedings of the Entomological Society of Washington, **7**: 117–121.

Beutel, R. G. (1995): Phylogenetic analysis of Elateriformia (Coleoptera: Polyphaga) based on larval characters. – Journal of Zoological Systematics and Evolutionary Research, **33**: 145–171.

Beutel, R. G. & Leschen, R. A. B. (2016): Handbook of Zoology. Arthropoda: Insecta. Coleoptera, Beetles. Morphology and Systematics. Archostemata, Adephaga, Myxophaga, and Polyphaga partim. Volume 1 (2nd Edition). Berlin (de Gruyter).

Blair, K. G. (1930): *Brachypsectra*, Lec. – The solution of an entomological enigma. – Transactions of the Royal Entomological Society of London, **78**: 45–50.

Bocakova, M., Bocak, L., Hunt, T., Teraväinen, M. & Vogler, A. P. (2007): Molecular phylogenetics of Elateriformia (Coleoptera): evolution of bioluminescence and neoteny. – Cladistics, **23**: 477–496.

Böving, A. G. & Craighead, F. C. (1931): An Illustrated Synopsis of the Principal Larval Forms of the Order Coleoptera. Brooklyn, New York (Brooklyn Entomological Society).

Braig, F., Haug, J. T., Schädel, M. & Haug, C. (2019): A new thylacocephalan crustacean from the Upper Jurassic lithographic limestones of southern Germany and the diversity of Thylacocephala. – Palaeodiversity, **12**: 69–87.

Burakowski, B. (1975): Development, distribution, and habits of *Trixagus dermestoides* (L.), with notes on the Throscidae and Lissomidae (Coleoptera, Elateroidea). – Annales Zoologici, **32**: 375–405.

Cecilia, A., Rack, A., Douissard, P. A., Martin, T., dos Santos Rolo, T., Vagovič, P., Hamanna, E., van de Kamp, T., Riedel, A., Fiederle, M. & Baumbach, T. (2011): LPE grown LSO: Tb scintillator films for high resolution x-ray imaging applications at synchrotron light sources. – Nuclear Instruments and Methods in Physics Research, **648** (Supplement 1): 321–323.

Chu, H. F. (1949): How to Know the Immature Insects. Pictured Key Nature Series. Dubuque, Iowa (M. C. Brown Company Publishers).

Costa, C., Vanin, S. A., Lawrence, J. F., Ide, S. & Branham, M. A. (2006): Review of the family Brachypsectridae (Coleoptera: Elateroidea). – Annals of the Entomological Society of America, **99**: 409–432.

Crowson, R. A. (1972): A review of the classification of Cantharoidea (Coleoptera), with the definition of two new families, Cneoglossidae and Omethidae. – Revista de la Universidad de Madrid, **21**: 33–77.

Crowson, R. A. (1973): On a new superfamily Artematopoidea of polyphagan beetles, with the definition of two new fossil genera from the Baltic Amber. – Journal of Natural History, **7**: 225–238.

Cruickshank, R. D. & Ko, K. (2003): Geology of an amber locality in the Hukawng Valley, northern Myanmar. Journal of Asian Earth Sciences, **21**: 441–455.

Ferris, G. F. (1927): Notes on an entomological enigma. – The Canadian Entomologist, **59**: 279–281.

Fleenor, S. B. & Taber, S. W. (1999): Review of *Brachypsectra* LeConte with a new record of the Texas beetle (*B. fulva* LeConte; Coleoptera: Brachypsectridae). – The Coleopterists' Bulletin, **53**: 359–364.

Greving, I., Wilde, F., Ogurreck, M., Herzen, J., Hammel, J. U., Hipp, A., Friedrich, F., Lottermoser, L., Dose, T., Burmester, H., Müller, M. & Beckmann, F. (2014): P05 imaging beamline at PETRA III: first results. In: Stock, S. R. (ed.): Developments in X-Ray Tomography IX. – SPIE Proceedings, **9212**: 92120O–92120O–8.

Grimaldi, D. & Engel, M. S. (2005): Evolution of the Insects. Cambridge (Cambridge University Press).

Haug, C., Mayer, G., Kutschera, V., Waloszek, D., Maas, A. & Haug, J. T. (2011): Imaging and documenting gammarideans. – International Journal of Zoology, **2011**: art. 380829.

Haug, C., Shannon, K. R., Nyborg, T. & Vega, F. J. (2013a): Isolated mantis shrimp dactyli from the Pliocene of North Carolina and their bearing on the history of Stomatopoda. – Bolétin de la Sociedad Geológica Mexicana, **65**: 273–284.

Haug, G. T., Baranov, V., Wizen, G., Pazinato, P. G., Müller, P., Haug, C. & Haug, J. T. (2021a): The morphological diversity of long-necked lacewing larvae (Neuroptera: Myrmeleontiformia). – Bulletin of Geosciences, **96**: 431–457.

Haug, G. T., Haug, C., Pazinato, P. G., Braig, F., Perrichot, V., Gröhn, C., Müller, P. & Haug, J. T. (2020a): The decline of silky lacewings and morphological diversity of long-nosed antlion larvae through time. – Palaeontologia Electronica, **23**(2): a39.

Haug, G. T., Haug, C., van der Wal, S., Müller, P. & Haug, J. T. (online first): Split-footed lacewings declined over time: indications from the morphological diversity of their antlion-like larvae. – PalZ.

Haug, J. T. & Haug, C. (2017): Species, populations and morphotypes through time – challenges and possible concepts. – BSGF, Earth Sciences Bulletin, **188**: 20.

Haug, J. T. & Haug, C. (2019): Beetle larvae with unusually large terminal ends and a fossil that beats them all (Scraptiidae, Coleoptera). – PeerJ, **7**: e7871.

Haug, J. T., Haug, C. & Ehrlich, M. (2008): First fossil stomatopod larva (Arthropoda: Crustacea) and a new way of documenting Solnhofen fossils (Upper Jurassic, Southern Germany). – Palaeodiversity, **1**: 103–109.

Haug, J. T., Haug, C. & Garwood, R. (2016): Evolution of insect wings and development – new details from Palaeozoic nymphs. – Biological Reviews, **91**: 53–69.

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. (2021b): Changes in the morphological diversity of larvae of lance lacewings, mantis lacewings and their closer relatives over 100 million years. – Insects, **12**: 860.

Haug, J. T., Müller, P. & Haug, C. (2019a): A 100-million-year old predator: a fossil neuropteran larva with unusually elongated mouthparts. – Zoological Letters, **5**: 29.

Haug, J. T., Müller, P. & Haug, C. (2019b): 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**: 431–440.

Haug, J. T., Müller, C. H. G. & Sombke, A. (2013b): A centipede nymph in Baltic amber and a new approach to document amber fossils. – Organisms Diversity & Evolution, **13**: 425–432.

Haug, J. T., Pazinato, P. G., Haug, G. T. & Haug, C. (2020b): Yet another unusual new type of lacewing larva preserved in 100-million-year old amber from Myanmar. – Rivista Italiana di Paleontologia e Stratigrafia, **126**: 821–832.

Hoffeins, C. (2012): On Baltic amber inclusions treated in an autoclave. – Polskie Pismo Entomologiczne, **81**: 165–181.

Hörnschemeyer, T., Wedmann, S. & Poinar, G. (2010): How long can insect species exist? Evidence from extant and fossil *Micromalthus* beetles (Insecta: Coleoptera). – Zoological Journal of the Linnean Society, **158**: 300–311.

Klausnitzer, B. (2009): Bemerkungen zu rezenten und fossilen Larven (Bernstein) der Gattung *Brachypsectra* LeConte (Coleoptera, Brachypsectridae). – Contributions to Natural History, **12**: 721–742.

Kristensen, N. P., Scoble, M. J. & Karsholt, O. L. E. (2007): Lepidoptera phylogeny and systematics: the state of inventorying moth and butterfly diversity. – Zootaxa, **1668**: 699–747.

Kundrata, R., Bocakova, M. & Bocak, L. (2014): The comprehensive phylogeny of the superfamily Elateroidea (Coleoptera: Elateriformia). – Molecular Phylogenetics and Evolution, **76**: 162–171.

Lawrence, J. F. (1991): Brachypsectridae (Cantharoidea). In: Stehr, F. W. (ed.): Immature Insects, **2**: 421–422; Dubuque, Iowa (Kendall).

Lawrence, J. F. & Britton, E. B. (1991): Coleoptera (Beetles). In: Naumann, I. D. (ed.) Insects of Australia: a Textbook for Students and Research Workers (2nd Edition): 543–683; Melbourne (Melbourne University Press).

Lawrence, J., Hastings, A., Dallwitz, M. & Paine, T. (1995): Beetle Larvae of the World. Interactive Identification and Information Retrieve for Families and Subfamilies. CD-ROM. Version 1.0 for MS-DOS.

Lawrence, J. F., Monteith, G. B. & Reid, C. A. (2020): A new *Brachypsectra* LeConte from Australia (Coleoptera: Brachypsectridae) with comparative notes on adults and larvae. – Papéis Avulsos de Zoologia, **60** (special issue): e202060(s.i.).02.

Lawrence, J. F., Ślipiński, A., Seago, A. E., Thayer, M. K., Newton, A. F. & Marvaldi, A. E. (2011): Phylogeny of the Coleoptera based on morphological characters of adults and larvae. – Annales Zoologici, **61**(1): 1–217.

Lawson, F. A. (1991): Chrysomelidae (Chrysomeloidea) (= Cassididae, Cryptocephalidae, Megalopodidae, Sagridae, etc.). In: Stehr, F. W. (ed.): Immature Insects, **2**: 568–585; Dubuque, Iowa (Kendall).

LeSage, L. (1991): Coccinellidae (Cucujoidea). In: Stehr, F. W. (ed.): Immature Insects, **2**: 485–494; Dubuque, Iowa (Kendall).

McKenna, D. D., Wild, A. L., Kanda, K., Bellamy, C. L., Beutel, R. G., Caterino, M. S., Farnum, C. W., Hawks, D. C., Ivie, M. S., Jameson, M. L., Leschen, R. A. B., Marvaldi, A. E., McHugh, J. V., Newton, A. F., Robertson, J. A., Thayer, M. K., Whiting, M. F., Lawrence, J. F., Ślipiński, A., Maddison, D. R. & Farrell, B. D. (2015): The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. – Systematic Entomology, **40**: 835–880.

Moosmann, J., Ershov, A., Weinhardt, V., Baumbach, T., Prasad, M. S., LaBonne, C., Xiao, X., Kashef, J. & Hoffmann, R. (2014): Time-lapse X-ray phase-contrast microtomography for in vivo imaging and analysis of morphogenesis. – Nature Protocols, **9**: 294–304.

Newton, A. F. Jr. (1991): Micropeplidae (Staphylinoidea). In: Stehr, F. W. (ed.): Immature Insects, **2**: 334–335; Dubuque, Iowa (Kendall).

Petrzelkova, I., Makris, C. & Kundrata, R. (2017): The genus *Brachypsectra* LeConte, 1874 (Coleoptera: Brachypsectridae) in the Palaearctic Region. – European Journal of Taxonomy, **276**: 1–14.

Poinar, G. Jr. (2010): Palaeoecological perspectives in Dominican amber. – Annales de la Société Entomologique de France, **46**(1–2): 23–52.

Poinar, G. O. (1992): Life in Amber. Redwood City (Stanford University Press).

Poinar, G. O. & Poinar, R. (1999): The amber forest: a reconstruction of a vanished world. Princeton (Princeton University Press).

Qu, T., Yin, Z., Huang, D. & Cai, C. (2019): First Mesozoic brachypsectrid beetles in mid-Cretaceous amber from northern Myanmar (Coleoptera: Elateroidea: Brachypsectridae). – Cretaceous Research, **106**: 104190.

Rosenberg, E. C. (1943): Neue Lyciden-Larven (Beitrag zur Kenntnis der Lebensweise, Entwicklung und Systematik der Käfer. V.). – Entomologiske Meddelser, **24**: 1–42.

Scheven, J. (2004): Bernstein-Einschlüsse: Eine untergegangene Welt bezeugt die Schöpfung. Erinnerungen an die Welt vor der Sintflut. Hofheim a. T. (Kuratorium Lebendige Vorwelt).

Spangler, P. J. (1991): Hydrophilidae (Hydrophiloidea) (including Helophoridae, Hydrochidae, Sphaeridiidae, Spercheidae). In: Stehr, F. W. (ed.): Immature Insects, **2**: 355–358; Dubuque, Iowa (Kendall).

Tihelka, E., Huang, D. & Cai C. (2019): Diverse Texas beetles (Coleoptera: Elateroidea: Brachypsectridae) in mid-Cretaceous Burmese amber: sexual dimorphism and palaeoecology. – Palaeoentomology, **2**: 523–531.

van Aarle, W., Palenstijn, W. J., Cant, J., Janssens, E., Bleichrodt, F., Dabravolski, A., De Beenhouwer, J., Batenburg, K. J. & Sijbers, J. (2016): Fast and flexible X-ray tomography using the ASTRA toolbox. – Optics Express, **24**: 25129–25147.

van Aarle, W., Palenstijn, W. J., De Beenhouwer, J., Altantzis, T., Bals, S., Batenburg, K. J. & Sijbers, J. (2015): The ASTRA Toolbox: A platform for advanced algorithm development in electron tomography. – Ultramicroscopy, **157**: 35–47.

Vogelgesang, M., Chilingaryan, S., dos Santos Rolo, T. & Kopmann, A. (2012): UFO: a scalable GPU-based image processing framework for on-line monitoring. In: 2012 IEEE 14th International Conference on High Performance Computing and Communication & 2012 IEEE 9th International Conference on Embedded Software and Systems, Liverpool: 824–829.

Vogelgesang, M., Farago, T., Morgeneyer, T. F., Helfen, L., dos Santos Rolo, T., Myagotin, A. & Baumbach, T. (2016): Real-time image-content-based beamline control for smart 4D X-ray imaging. – Journal of Synchrotron Radiation, **23**: 1254–1263.

Wilde, F., Ogurreck, M., Greving, I., Hammel, J. U., Beckmann, F., Hipp, A., Lottermoser, L., Khokhriakov, I., Lytaev, P., Dose, T., Burmester, H., Müller, M. & Schreyer, A. (2016): MicroCT at the imaging beamline P05 at PETRA III. – AIP Conference Proceedings, **1741**: 030035.

Woodruff, R. E. (2002): A new species of the beetle genus *Brachypsectra* from the Dominican Republic, with fossil connections (Coleoptera: Brachypsectridae). – Insecta Mundi, **549**: 161–170.

Wu, R. J. C. (1996): Secrets of a Lost World: Dominican Amber and its Inclusions. Santo Domingo (published by the author).

Zhao, X., Zhao, X., Jarzembowski, E., Tian, Y. & Chen, L. (2020): The first record of brachypsectrid larva from mid-Cretaceous Burmese amber (Coleoptera: Polyphaga). – Cretaceous Research, **113**: 104493.

Zippel, A., Haug, C., Hoffeins, C., Hoffeins, H.-W. & Haug, J. T. (accepted). Expanding the record of larvae of false flower beetles with prominent terminal ends. – Rivista Italiana di Paleontologia e Stratigrafia.

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Electronic supplements

The following additional electronic datasets related to this contribution are hosted together with the digital version of this contribution (https://bioone.org/journals/Palaeodiversity/volume-14/issue-1):

Suppl. 1. Results of the principal component analysis of the shape of the entire body.

Suppl. 2. Graphical representation of the factor loadings of the shape analysis of the entire body.

Suppl. 3. Results of the principal component analysis of the shape of the anterior body.

Suppl. 4. Graphical representation of the factor loadings of the shape analysis of the anterior body.

Suppl. 5. Values of the effective principal components (PC) from the analysis of the entire body shape (AN1) and of the anterior body shape (AN2) of each specimen.