

The first adult mantis lacewing from Baltic amber, with an evaluation of the post-Cretaceous loss of morphological diversity of raptorial appendages in Mantispidae

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Abstract

Mantis lacewings (Neuroptera: Mantispidae) are prominent and charismatic predatory representatives of Insecta. Nevertheless, representatives of the group are surprisingly scarce in Paleogene deposits after a relative abundance of specimens known from Cretaceous. Here we present *Mantispa? damzenogedanica* sp. nov., representing the first adult of Mantispidae described from Baltic amber and the only Eocene adult mantispid hitherto preserved in amber. The new fossil species is also among the earliest representatives of Mantispinae, certainly the oldest adult of this group described from amber. Additionally, we discuss the changes through time in the ecological morphospace within Mantispidae based on the morphological diversity (\approx disparity) of the raptorial legs. Possible explanations for the post-Cretaceous decline in the morphological diversity of mantis lacewings are posited.

Key Words

amber, fossil, lacewings, mantid flies, morphology, Neuroptera, shape

1. Introduction

Many of the numerous representatives of Insecta unfortunately invoke revulsion in most people. Nonetheless, some groups can inspire greater collective fascination and even appreciation and affection, such as butterflies and bees. Alongside these are the praying mantises (Mantodea), which are often kept and bred as pets as well as featured in zoological displays and educational programs (McMongile 2013, Green 2014). For non-entomologists, it is generally unknown that several other insect lineages

bear a resemblance to praying mantises and show similar specializations. Adults of Mantispidae resemble many highly-specialized praying mantises not only in the morphology of the raptorial (i.e., grasping) forelegs, but also in the elongation of the prothorax, the often considerably anterior insertion of the forelegs, practically below the head, or the exophthalmic compound eyes on the highly mobile head, aiding in the detection of prey.

Mantis lacewings are representatives of Neuroptera (i.e., lacewings and their relatives). Neuroptera today comprise about 6,000 species worldwide (Engel et al.

2018, Winterton et al. 2018, Snyman et al. 2020, Ardila-Camacho et al. 2021). Mantispidae are classified within the larger group Mantispoidea, which aside from mantis lacewings also includes the groups Rhachiberothidae (thorny lacewings) and Berothidae (beaded lacewings), as well as extinct groups such as Mesoberothidae and Dipteromantispidae (Ardila-Camacho et al. 2021). Relationships of Mantispidae within Neuroptera, as well as its interrelationships within the group, have been recently revised by Ardila-Camacho et al. (2021) based on morphological characters. These authors recovered a single origin of the raptorial appendages within Mantispoidea, with Berothidae as sister group to Rhachiberothidae + Mantispidae (Ardila-Camacho et al. 2021). These authors, however, did not recover a monophyletic Mantispidae, as they recovered Symphrasinae as sister group to Rhachiberothidae, a result congruent with that of Winterton et al. (2018) based on anchored phylogenomics. As a result, Ardila-Camacho et al. (2021) classified Symphrasinae within Rhachiberothidae.

Although diverse by neuropteran standards, mantis lacewings lack the remarkable diversity of other holometabolans, such as beetles, wasps, and flies. The group Neuroptera, and in fact the more inclusive group Neuropterida, which includes the species-poor lineages Megaloptera and Raphidioptera, is likely to have been significantly more diversified and disparate in the Cretaceous (e.g., Aspöck and Aspöck 2007, Liu et al. 2016, 2018, Wang et al. 2016, Badano et al. 2018, Haug et al. 2019a, b, 2020a, b, c, in press, Lu et al. 2020, Zippel et al. 2021). Such a pattern has been observed for several constituent lineages of Neuropterida, for which it seems that the loss of morphological diversity (\approx disparity) was not a one-step event as is often assumed in relation to the end-Cretaceous or other mass extinction events. Instead, the Eocene fauna, at least, has been found to have a kind of transitional diversity between the Cretaceous and modern ones – less diverse than the Cretaceous, but still noticeably differing from the extant fauna (e.g., Haug et al. 2020a), the latter in line with its paratropical climate versus temperate environments today in the same region.

Mantis lacewings seem to have been more dominant, or at least common, in the Cretaceous, as demonstrated by numerous adult mantis lacewings in Cretaceous deposits, especially in amber (Poinar and Buckley 2011, Pérez-de la Fuente and Peñalver 2019, Lu et al. 2020, Shi et al. 2020a, b), although they have also been discovered in sedimentary rocks (Jepson et al. 2013). Some of these mantis lacewings also exhibit a more disparate range of morphologies relative to their modern counterparts, especially in their raptorial forelegs (Lu et al. 2020, Shi et al. 2020b), reinforcing the notion of a loss of morphological diversity in Mantispidae.

The Eocene record of Mantispidae is rather sparse and hampers a further understanding of the evolution of the group. A single adult specimen from British amber, *Whalleya venatrix* Whalley 1983, has hitherto been reported as a putative mantis lacewing (Whalley 1983, Willmann

1994). This species, however, was later reassessed as a representative of Rhachiberothidae (Engel 2004, Markarkin and Kupryjanowicz 2010, Ardila-Camacho et al. 2021). From the otherwise profusely rich Baltic amber only larval stages of mantis lacewings have been reported (Ohl 2011, Wunderlich 2012), and even these have been few in number (namely four larvae in two pieces of amber). This fact is noteworthy given that, although more than a dozen adults are known from Cretaceous ambers (Poinar and Buckley 2011, Pérez-de la Fuente and Peñalver 2019, Lu et al. 2020, Shi et al. 2020a, b), only a few larvae have yet been discovered (Haug et al. 2018, 2021a; Pérez-de la Fuente and Peñalver 2019).

Here we report the first adult of Mantispidae from Baltic amber and place it into a larger framework regarding the quantitative morphology of raptorial forelegs across the lineage in terms of extant and extinct diversity. These morphometric comparisons serve as a proxy for the breadth of ecologies and predatory behaviors within Mantispidae during different episodes of their evolutionary history.

2. Material and methods

2.1. Material

The specimen studied herein corresponds to an adult mantis lacewing preserved in Eocene Baltic amber. The specimen was found at the Yantarny mine, Kaliningrad (Russia), and originally belonged to the personal collection of Jonas Damzen, who acquired it from a commercial source in Yantarny, Kaliningrad District. The specimen is now deposited in the Museum of Gdańsk (Gdańsk, Poland), under the accession number MG/B/1172. The sediments bearing the Baltic amber have sometimes been stratigraphically placed as late Bartonian to earliest Priabonian, with the richer concentrations of amber lower among these, based on lithological and palynological data (Kasiński et al. 2020). However, determining the age of Baltic amber is a complex issue and a matter of ongoing debates (Sadowski et al. 2017, Baranov et al. 2019, Kasiński et al. 2020). The minimal age of Baltic amber appears to be 34 Ma, with recent studies pointing to a late Eocene age (Sadowski et al. 2017, Baranov et al. 2019).

2.2. Documentation methods

The specimen was documented using microscopy and synchrotron radiation-based X-ray computed microtomography (SR- μ CT). First, the specimen was examined under a Keyence VHX-6000 digital microscope under different light settings (Haug et al. 2013a, Hörnig et al. 2016). Stacks of photographs were recorded from the specimen in different views, which were fused into single sharp images. Thus, all photographs presented are composite images. Adjacent image details were merged into

large panorama images. Additionally, the HDR function was used to prevent areas that were excessively dark and too bright to appear on the photographs (cf. Haug et al. 2013a). All processing was done automatically by the built-in software.

The amber specimen was scanned with Imaging Beamline P05 (IBL; Greving et al. 2014, Wilde et al. 2016) operated by the Helmholtz-Zentrum Hereon at the PETRA III storage ring (Deutsches Elektronen Synchrotron – DESY, Hamburg, Germany), using a photon energy of 18 keV and a sample-to-detector distance of 100 mm. Projections were recorded with a custom developed 20 MP CMOS camera system with an effective pixel size of 1.28 μm (Lytaev et al. 2014). For each tomographic scan 3601 projections at equal intervals between 0 and π were recorded. Tomographic reconstruction was conducted by applying a transport of intensity phase retrieval approach and using the filtered back projection algorithm (FBP) carried out 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 2.56 μm . We have reconstructed the scanned volumes using Drishti ver. 2.6.6 (Limaye 2012). To decrease the demands of RAM and video card of the computer used, we have downsampled all the tiff images by 50% and subsequently cropped the empty space around the amber piece using Fiji ‘scale’ and ‘crop’ functions (Schindelin et al. 2012). After that we rendered the 3D volume of the animal in Drishti ver. 2.6.6 (Limaye 2012).

2.3. Morphometric analysis

In order to provide a comparative framework, we considered all fossil representatives of the group Mantispidae from the literature in which the profemur and its inner integumentary processes bearing terminal modified setae (i.e., the often so-called ‘spines’), including the largest of such processes if present (the so-called major ‘spine’), were accessible. Therefore, a total 22 fossil specimens, plus the new species, were included (see Suppl. material 2: Table S1 for sources of the images; table is supplied as online supplement here: https://github.com/chironomus/Mantispidae-shape-analysis/blob/main/_CLEANED_FOR_EOCENE_Raptorial_Neuropterans.xls from here on referred as “Supplement table 1”). We redrew the profemoral functional lateral outline (\approx evolutionary anterior side of appendage) of these fossil species in Adobe Illustrator CS2 or Inkscape. Final outlines were transformed into 24-bit bmp-files (available here <https://github.com/chironomus/Mantispidae-shape-analysis>). The data set was supplemented by 38 extant specimens encompassing all the mantis lacewings ingroups (‘subfamilies’) also redrawn from the literature (see Suppl. material 1 https://github.com/chironomus/Mantispidae-shape-analysis/blob/main/_CLEANED_FOR_EOCENE_Raptorial_Neuropterans.xls), for which images of the femora of the raptorial legs were available in lateral view. Due to preservational limitations, many fossil specimens were omitted from the analysis. See Suppl. material 2: Table S1 (https://github.com/chironomus/Mantispidae-shape-analysis/blob/main/_CLEANED_FOR_EOCENE_Raptorial_Neuropterans.xls) for the complete list of the specimens analysed.

The program package Shape was used for further analysis (Iwata and Ukai 2002). At first, shapes (outlines of the profemora) were translated into numerical enumerators (chain code) via Elliptic Fourier Transformation, while in a second step the outlines were aligned. Finally, the data set was subjected to a Principal Component Analysis (PCA). Ten harmonics were used as a base setting. Scatterplots of the main dimensions (PCs) were plotted in OpenOffice Calc. Final representations were re-drawn in Adobe Illustrator CS2.

2.4. Morphological terminology

Wing venation interpretation and nomenclature follows that of Breitzkreuz et al. (2017), and other terminology follows that used elsewhere for Mantispidae (e.g., Pérez-de la Fuente and Peñalver 2019, Lu et al. 2020).

3. Results

3.1. Systematic palaeontology

Neuroptera Linnaeus, 1758

Mantispidae Leach, 1815

Mantispinae Leach, 1815

***Mantispa* Illiger in Kugelnann, 1798**

***Mantispa? damzenogedanica* sp. nov.**

<http://zoobank.org/8C79CEEC-9800-4EB3-9665-B6FE756F83FF>

Figs 1–4

Derivatio nominis. The specific epithet is a combination of ‘Damzen’, honouring Mr. Jonas Damzen (Vilnius), who found, prepared, and made the specimen available, and ‘gedanicum’, relative to Gedania, one of the Latin names for Gdańsk (Poland), where the specimen will be housed permanently.

Holotype. MG/B/1172, Museum of Gdańsk (Gdańsk, Poland). The specimen is well preserved, albeit missing distal parts of some appendages and heavily covered by white foam (= ‘Verlummung’), particularly thick on the posterior part of the body, namely the abdomen. A single spider and six non-biting midges (Diptera: Chironomidae: Chironominae: Tanytarsini) are present as syninclusions.

Type locality and age. Baltic amber from Yantarny mine in Yantarny, Kaliningrad (formerly Palmnicken, Königsberg), Russia; Eocene (late Bartonian–earliest Priabonian). The precise extraction location within the Yantarny mine remains unknown.

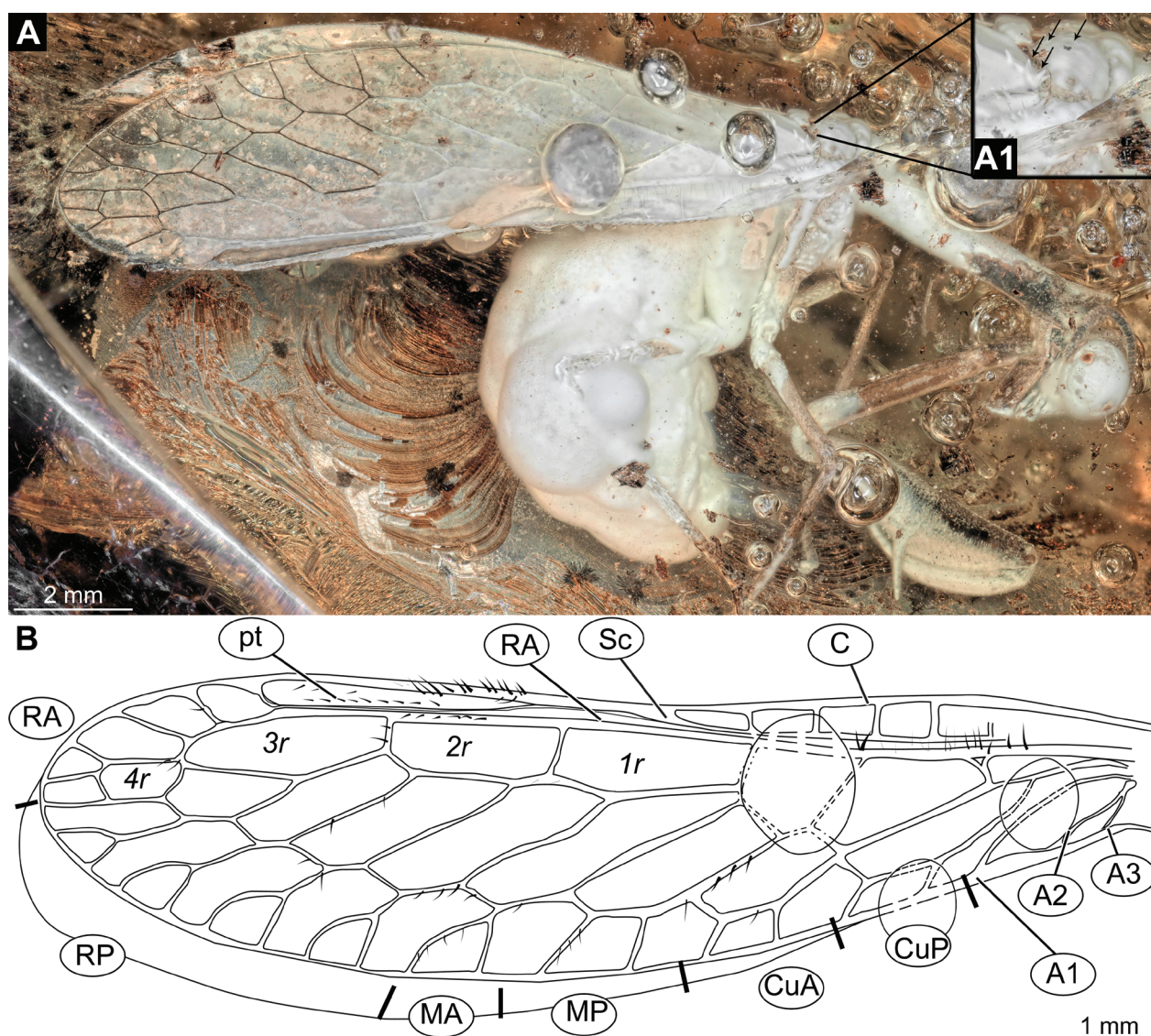


Figure 1. *Mantispa? damzenogedanica* sp. nov., holotype MG/B/1172. **A.** Photograph of the habitus in lateral view; **A1.** Meso-thorax with stout setae visible through the Verlumung, enlarged (arrows); **B.** Drawing of the right forewing. Abbreviations (mostly veins): 1–4r = radial cells; A = anal; CuA = cubitus anterior; CuP = cubitus posterior; C = costa; MA, media anterior; MP, media posterior; pt = pterostigma; RA = radius anterior; RP = radius posterior; Sc = subcosta.

ZooBank. In accordance with the ICZN, the specific epithet is registered in ZooBank (www.zoobank.org) under the following LSID: [8C79CEEC-9800-4EB3-9665-B6FE756F83FF](https://zoobank.org/8C79CEEC-9800-4EB3-9665-B6FE756F83FF).

Diagnosis. The new specimen can be distinguished from all extant and fossil mantis lacewing representatives based on the following combination of characters: Head moderately wider than long; antennae relatively short, with flagellomeres compact and slightly wider than long in profile, last flagellomere gradually tapering distally; distal third of antennae seemingly with a pale band; occiput, pronotum and mesothorax bearing short, stout, erect setae, at least those from the occiput and pronotum not confined to raised bases; pronotum about 4.6× times longer than wide posteriorly, lacking abrupt constrictions throughout, apparently smooth; forewing with pterostigma well sclerotized, elongate, bearing

sparse macrosetae along its entire length, distally ending at the midlength of cell 3r, proximal end tapered; forewing lacking supernumerary radial crossveins, with cell 4r small, proximally closed by a brief 3ra-rp crossvein; profemur with major integumentary process ('spine') smooth, length 0.52× the profemoral length, with ten smaller processes.

Description. Sex unknown. Winged lacewing, total length 13.7 mm as preserved. Head. Broad, short, moderately wider than long, 1.5 mm wide, 0.9 mm long, roughly triangular in anterior view. Ocular segment recognizable by large, ovoid compound eyes, 0.97 mm in diameter, prominent yet not particularly abutting, and trapezoid labrum, about 0.30 mm long. Posterior region of head capsule (occiput) with short, stout, erect setae visible through Verlumung, apparently not confined to raised bases. Antenna long (about 1.9 mm), with at least

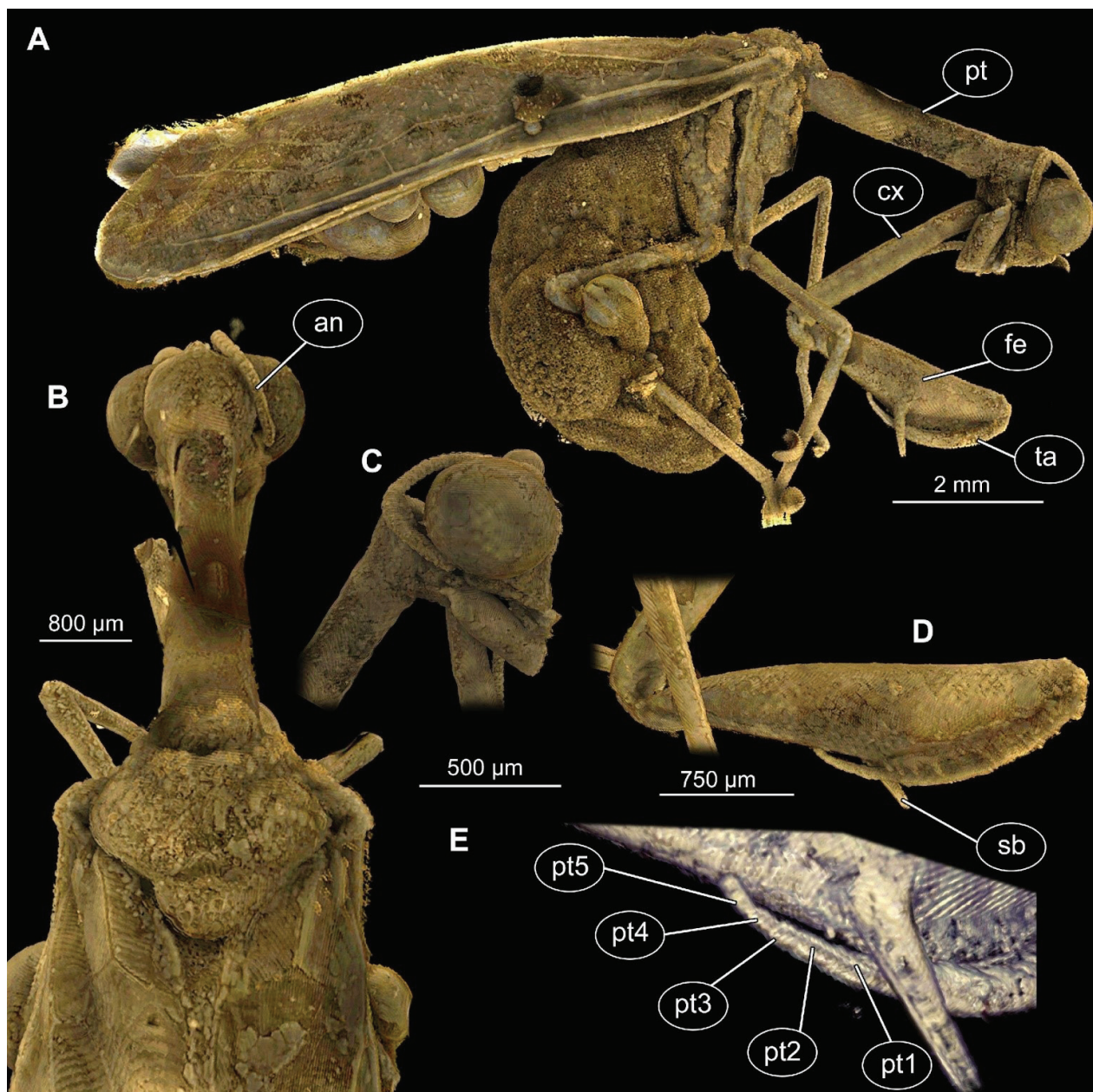


Figure 2. *Mantispa? damzenogedanica* sp. nov., holotype MG/B/1172, all volume renderings based on SRμCT. **A.** Habitus in lateral view; **B.** Head and thorax in dorsal view; **C.** Head and anterior pronotum in lateral view; **D.** Left raptorial foreleg in lateral view; **E.** Detail of the former. Abbreviations: an = antenna; cx = coxa; fe = femur; pt = prothorax; pt1–5 = tarsomeres 1–5; ta = protarsus; sb = submedial ‘spine’.

22 articles (scapus, pedicellus, flagellomeres); distal third of antennae seemingly with a pale band. Flagellomeres rectangular in profile, slightly wider than long, compact, not significantly expanding in width distally. Mandibles 0.32 mm long. No further details accessible. Maxillae elongate, with proximal part, stipes (with two endites, galea and stipes), and distal part, palp, visible. Lacinia elongate, with eight strong distal teeth, 0.40 mm long. Galea about 0.14 mm long. Maxillary palp arising latero-distally from stipes, cylindrical, with three visible palpomeres. Total length of the palpomeres 0.50 mm long.

Labium oval in general shape. Details challenging to discern due to partial concealing by structures of thorax.

Thorax. Prothorax elongate, with pronotum tubular (fully fused ventrally), cylindrical, slightly decreasing in diameter distally, then expanding from its distal 2/3 onwards, 3× longer than wide (maximum width), 3.2 mm long, 1.1 mm wide basally, 0.6 mm wide medially, 0.8 mm wide distally. Prothorax densely covered with microtrochia, with smooth dorsal surface. Maculae (i.e., paired anteriodorsal areas of the pronotum distinctive in colour and/or shape, if apparent) with inconspicuous acute cusps. Pronotum very elongate, about 4.6× longer than wide posteriorly, lacking transversal ridges or corrugations (exact texture unknown due to Verlumung covering); pronotal prozone gently raised in lateral view,

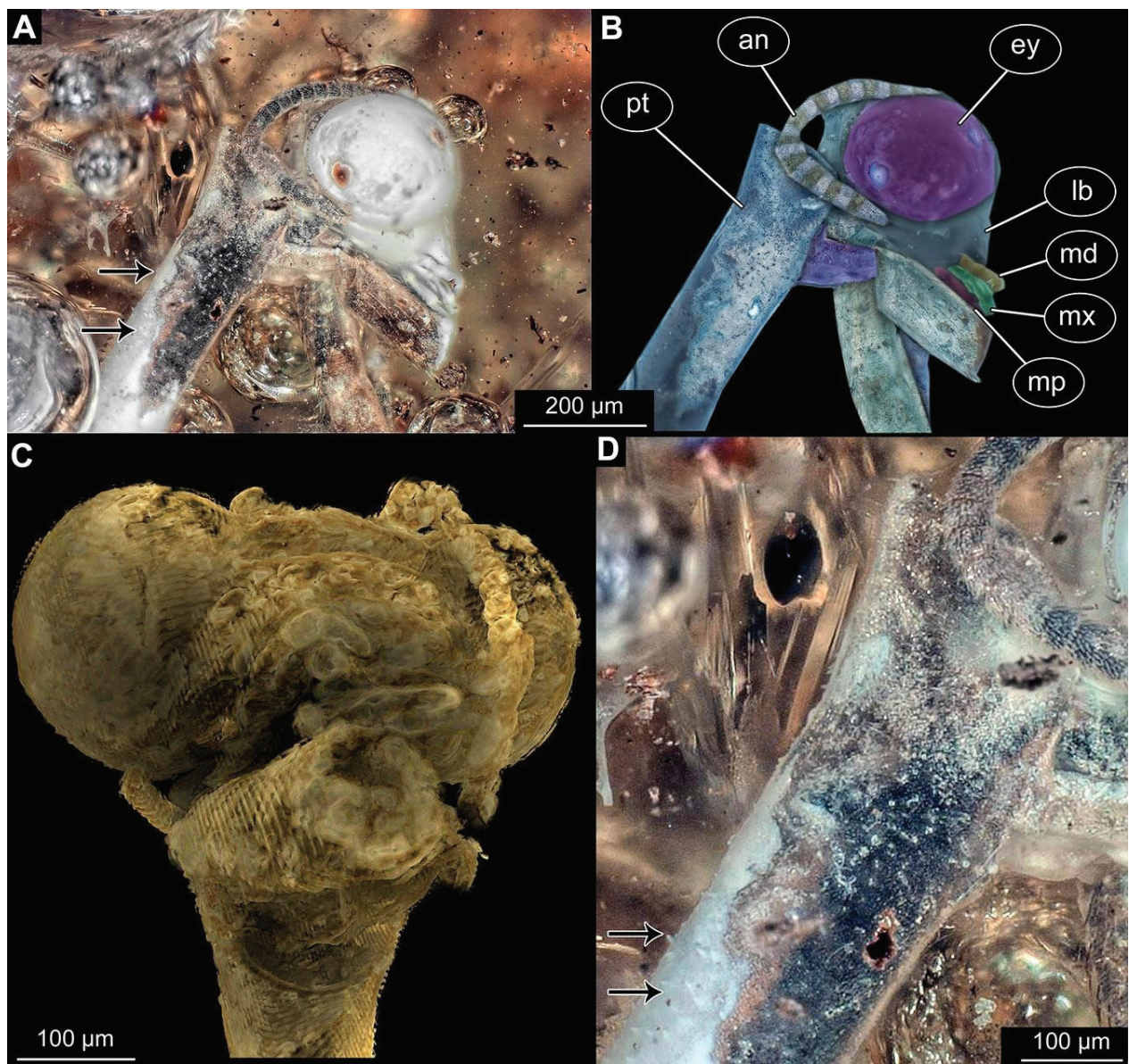


Figure 3. *Mantispa? damzenogedanica* sp. nov., holotype MG/B/1172. **A.** Photograph of the head and anterior pronotum in lateral view; **B.** Same, tagged and colour-marked; **C.** Head in ventral view, volume rendering based on SRµCT, showing visible mouthparts; **D.** Detail of the anterior pronotum in lateral view; note the stout setae (arrows). Abbreviations: an = antenna; ey = eyes; lb = labrum; md = mandible; mp = maxillary palp; mx = maxilla, proximal part; pt = prothorax.

anterior edge with two lateral rounded invaginations and a median, rather acute protrusion in dorsal view. Pronotum with short, stout, erect setae visible through *Verlummung*, not confined to raised bases. Prothorax bearing a pair of prominent appendages in far anterior position, i.e., the raptorial forelegs (only one preserved more completely). Coxa 3.40 mm long; trochanter, ca. 0.60 mm long; femur prominent, 3.30 mm long; tibia 2.48 mm long; tarsus 0.25 mm long; pretarsus not visible. Femur compressed, with prominent integumentary processes ('spines') originating medially; most prominent 'spine' submedial in position, located at 0.85 mm from proximal edge; at least ten additional, less-developed 'spines' present; exact armature hard to discern due to *Verlummung*. Stitz organs (terminal, sensory chitinous

cones on integumentary processes) not discernible. Combined length of tibia and tarsus much shorter than that of femur. Tarsus composed of five tarsomeres. Tarsomere 1 not distally extended, longer than remaining tarsomeres. Pretarsal claw not visible; possible arolium not discernible.

Mesothorax trapezoid in dorsal view, 0.80 mm long. Dorsal surface with several setae visible through *Verlummung*. Femur 2.20 mm long; tibia 1.70 mm long; basitarsus 2.20 mm long; pretarsal claws simple.

Forewing 9.9 mm long, 2.7 mm wide, relatively narrow in shape; membrane apparently hyaline, with no visible infuscations (i.e., darkened areas) other than that of the pterostigma. Venation dark in colour; trichosors (i.e., veinlet-like structures between proper wing veins present



Figure 4. *Mantispidae damzenogedanica* sp. nov., holotype MG/B/1172, volume renderings based on SRμCT. **A.** Pronotum, dorso-oblique view; **B.** Pronotum, lateral view.

at the wing margin, often highly setose) absent along all costal margin; all veins sparsely setose, with R bearing particularly long setae; humeral vein not visible; five costal veinlets present; Sc apparently meeting C half the length of 1rp cell; no sc-r or sc-ra crossveins visible, if present; pterostigma well-sclerotised, apparently tapered basally, gently expanding distally, bearing sparse setae, beginning distally of 1ra-rp crossvein, ending midway of cell 3r; distal edge of pterostigma sub-perpendicular to costal margin (not markedly oblique/subparallel); space between C and RA relatively broad throughout; radial triangle distinct, relatively small; four radial cells (1r–4r) between RA and main branch of RP, the distalmost (4r) distinctly small, subtrapezoid, closed proximally by a very brief 3ra-rp crossvein; RP with five posterior branch-

es; media simple, reaching wing margin right below cell 1r; CuA and CuP simple, forking not visible (blocked by a bubble), but likely proximal to radial triangle; cup-a1 crossvein not visible (blocked by a bubble); all anal veins simple, A1 concave; A2 sinuous, A3 slightly convex, these two fused proximally with a thick common stem; a1-a2 crossvein not visible.

Metathorax difficult to observe both on optical and 3d images. Femur 1.80 mm long; tibia 2.30 mm long; basitarsus 3.50 mm long, further distal tarsomeres not preserved. Hind wings almost entirely covered by the forewings and hence venation not discernible.

Abdomen. Abdomen largely concealed by Verlumung. Individual segments not discernible. Tergites appear simple, not keeled. Genitalia not visible.

3.2. Morphometric analysis

The final data set included three species of Mantispidae from the Jurassic, 14 from the Cretaceous, two from the Eocene, three from the Miocene, and 38 extant specimens. These encompass a wide diversity of the group, including representatives from all major ingroups ('sub-families'), both extinct and extant. The shape analysis resulted in five effective principal components (PCs). For the graphical representation of the PC's correspondence to morphology, see Suppl. material 1: Fig. S1.

PC1 explains 43.08% of the overall variation. It is dominated by overall stoutness of the profemur and the size of the major, sub-medial integumentary process (= 'spine'), if present. A low value indicates an overall stout shape and a poorly developed major 'spine'. A high value indicates a more elongate shape and a well-differentiated major 'spine'.

PC2 explains 27.84% of the overall variation. It is dominated by overall stoutness of the profemur and the size of the major 'spine', if present. A low value indicates that this structure is more differentiated and elongate in shape, whereas a high value indicates that it is less developed, has a stouter shape, and the major 'spine' is less well set off.

PC3 explains 11.15% of the overall variation. It is dominated by the position of the major 'spine' (if present) along the proximal distal axis. A low value indicates a more distal position, whereas a high value indicates a more proximal position.

PC4 explains 5.22% of the overall variation. It is dominated by the shape of the proximal part of the profemur. A low value indicates a more pointed shape, while a high value indicates a more rounded shape.

PC5 explains 3.78% of the overall variation. It is dominated by the differentiation of the 'spines'. A low value indicates fewer, well set off 'spines', while a high value indicates a greater proportion of not-so-well set off 'spines'.

4. Discussion

4.1. Remarks on the new species

Inclusion in amber is an exceptional form of preservation. Nonetheless, while some specimens appear almost life-like and provide access to the finest of details, certain phylogenetically informative structures can be obscured. Different kinds of x-ray microtomography have significantly improved this circumstance, revealing structures of interest, which are often concealed by different elements such as other body structures, air bubbles, debris, or even *Verlummung*. Still, this method also has its limitations, and it can only resolve structures that are sufficiently well preserved and/or have enough contrast relative to other materials, particularly the surrounding matrix. This is also the case in the new specimen.

The specimen clearly is a representative of the group Mantispiniae owing to, among other characters, the concave head vertex in frontal view (not domed); the forewing lacking trichosors, with 2A and 3A veins fused proximally with a thick common stem and a reduced jugal lobe; the mesonotal lobes angled anteriorly (rather than gently and broadly rounded); the procoxae lacking a transverse sulcus; the probasitarsus elongate, longer than remaining protarsomeres; the combined length of protibia and protarsus much shorter than that of the profemur; and the presence of simple, unbranched mesopretarsal claws (Lambkin 1986, Snyman et al. 2018). Assignment of the new species to the genus *Mantispa* is based on the head shape; the antennal flagellum being much shorter than the prothorax; all the flagellomeres being of similar shape, about as long as broad in profile; the presence of thick, erect setae on the occiput, prothorax, and mesothorax (diagnostic for *Mantispa* sensu Snyman et al. 2018); the prothorax generally cylindrical in shape and smooth, i.e., lacking corrugations or wrinkles; the forewing having Sc contacting C for a short distance prior to running along pterostigma; the elongate pterostigma; and the presence of a mesoscutal furrow, albeit weakly so (Snyman et al. 2018). Snyman et al. (2012, 2015) considered a pale band on the distal third of the antenna and a granulated prothorax as characters separating *Afromantispa* Snyman & Ohl, 2012 from *Mantispa*. The distal third of the antennae of the fossil appears to be lighter in colour as preserved and the texture of the prothorax seems to lack an obvious ornamentation, yet in fact both aspects remain unclear due to preservation, mostly because of the presence of *Verlummung*. Moreover, the integrity of *Afromantispa* has been put into question (Monserrat 2014). On the other hand, the inability to access the hind wing and the genitalia of the specimen would preclude a certain generic assignment of the present fossil for the sake of caution. In sum, the most conservative stance is to tentatively classify our specimen within *Mantispa*. We hope that future conspecific material can shed light on the present species, including a possible character gradation between *Mantispa* and *Afromantispa* as currently understood.

Mantispa? damzenogedanica sp. nov. represents the first record of an adult mantis lacewing in Baltic amber. The only two previous records of Mantispidae from Baltic amber were first-instar larvae (Ohl 2011, Wunderlich 2012). One was attached by its head to the pedicel of a spider, likely displaying what is termed 'boarding' behaviour (Ohl 2011, Jepson 2015). This circumstance explains why that fossil immature was interpreted as a representative of Mantispiniae, as spider-boarding is known to only take place among larvae of this group at present. Otherwise, the morphology of the first instar did not allow for a more detailed interpretation (Ohl 2011). It is also impossible to determine whether the adult reported here is conspecific with the previously described larvae (Ohl 2011, Jandausch et al. 2018).

The new species is among the oldest representatives of Mantispiniae currently known, certainly the oldest adult

of the group described in amber. The previously oldest representative of Mantispininae, *Vectispa relict* Cockerell, 1921, is from the Priabonian (upper Eocene) Bembridge marls, UK (Cockerell 1921, Jarzembowski 1980). The remaining fossils of the group described are either from the Oligocene, i.e., *Prosagittalata oligocenica* Nel, 1988 (Céreste, France, middle Oligocene) and *Climaciella? henrotayi* Nel, 1988 (Dauphin, France, middle Oligocene) (Nel 1988), or Miocene, i.e., *Dicromantispa electromexicana* Engel & Grimaldi, 2007 (Mexican amber, Burdigalian to Serravallian), *Dicromantispa moronei* Engel & Grimaldi, 2007 and *Feroseta prisca* Poinar, 2006 (Dominican amber, Burdigalian) (Poinar 2006, Engel and Grimaldi 2007). When compared to these other fossils of Mantispininae, *Mantispa? damzenogedanica* differs from (1) *V. relict* in the pterostigma distally ending at the mid-length of cell 3r (ending at the distal part of that cell in *V. relict*) and the presence of a fully closed cell 4r (Jarzembowski 1980); from (2) *P. oligocenica* in the longer pronotum ($3.3\times$ as long as wide in the Oligocene species), a higher number of posterior RP branches, and a different shape of the cell 4r (Nel 1988); from (3) *C.? henrotayi* (assuming it corresponds to a forewing) in the general wing shape, the shape of the radial cells, and the lower number of posterior RP branches (Nel 1988); from (4) *F. prisca* in the gradually tapering last flagellomere (abruptly changing in diameter in that species), pronotum lacking an anterior constriction (present immediately before the pronotal prozone in *F. prisca*), and a pterostigma well sclerotised (apparently not sclerotised on the Oligocene species) (Poinar 2006); and from both (5) *D. electromexicana* and *D. moronei* in its diagnostic stouter pronotal setation (these two species presumably lacking that sort of setation on the occiput as well), and considerably shorter pronotum than that of *D. electromexicana* ($3\times$ longer than the maximum width, vs $10\times$ longer than the maximum width in *D. electromexicana*) (Engel and Grimaldi 2007).

4.2. Scarcity of Mantispidae in Baltic amber

The fact that the present specimen is the first record of an adult mantis lacewing from Baltic amber is remarkable taking into account that the latter is among the most intensively studied ambers worldwide (Weitschat and Wichard 2002). There are over a dozen adults of Mantispidae known from Cretaceous ambers (Poinar and Buckley 2011, Pérez-de la Fuente and Peñalver 2019, Lu et al. 2020, Shi et al. 2020a, b), and three records from Miocene ambers (Poinar 2006, Engel and Grimaldi 2007). In many instances, Baltic amber has yielded significantly more specimens than are known from Miocene ambers (e.g., Haug et al. 2020a, 2021b). The lower number of specimens of Mantispidae in Baltic amber compared to that of Cretaceous ambers could be explained by the overall decline of Neuroptera during at least the last 100 million years (e.g., Aspöck and Aspöck 2007). Yet, this cannot account for differences to Miocene ambers. In the latter, the

three species known from Dominican amber do not seem to suggest much difference with the modern diversity of Mantispidae on present-day Hispaniola. Today, the fauna of Hispaniola includes at least five species of Mantispidae (Perez-Gelabert 2008, Hoffman et al. 2017). Modern Europe also has about five species of Mantispidae, but unlike Hispaniola where the current tropical environment is very similar to that of the Miocene, the regional climate of Europe has transitioned from a paratropical landmass and bordering archipelagos in the Eocene to a cooler temperate today. Thus, the potential for significant faunal alteration is greater. Nonetheless, given that mantis lacewings are generally more diverse and abundant in warmer habitats, one would presume that the Eocene fauna of Mantispidae in Baltic amber would be more prevalent than that of present-day Europe. In any case, there is an emerging understanding of the Baltic amber forest as a warm-temperate to temperate environment rather than a tropical forest (Kaasalainen et al. 2017, Sadowski et al. 2017, Rikkinen and Schmidt 2018). Thus, a more temperate climate in the area of Baltic amber deposition might partly explain the lower abundance of mantis lacewings in this deposit.

4.3. Changes on morphological diversity over time in Mantispidae

Already on a qualitative level, it is quite apparent that a significant loss in morphological diversity within Mantispidae has taken place since the Cretaceous (Lu et al. 2020). Our quantitative analysis of the raptorial appendages provides further support to that view. The Cretaceous specimens span a large area of the morphospace, while modern forms are restricted to a significantly smaller area. Hence, a significant part of the morphospace became lost over time in the group regarding one of their defining features, the raptorial foreleg, as well as their corresponding potential biologies. Furthermore, all the specimens from the Miocene plot within the area occupied by modern representatives of Mantispidae. This indicates that, already by the Miocene, the morphospace was restricted in a manner similar to that of modern diversity, although the rather low sample size makes this statement less conclusive. Regarding the Eocene specimens, the species described herein plots within the area of modern mantis lacewings, not far from extant species of *Mantispa*. Close, on the upper right of the new fossil plots a specimen of *Mantispa perla* (from Lucchese 1956); even closer, on the lower right to the new fossil, plots a specimen of *Mantispa styriaca* (from Poivre 1974); right under it a specimen of *Anchieta fumosella* (from Alvim et al. 2019); to the lower left a specimen of *Plega* (species unknown; from Reynoso-Velasco and Contreras-Ramos 2008); to the upper left *Symphrosis varia* (from Tjeder 1959). It is important to note that the low resolution of the time bins in our analysis prevents us from inferring if the decline in the diversity of mantispid raptorial appendages was steady or more irregular.

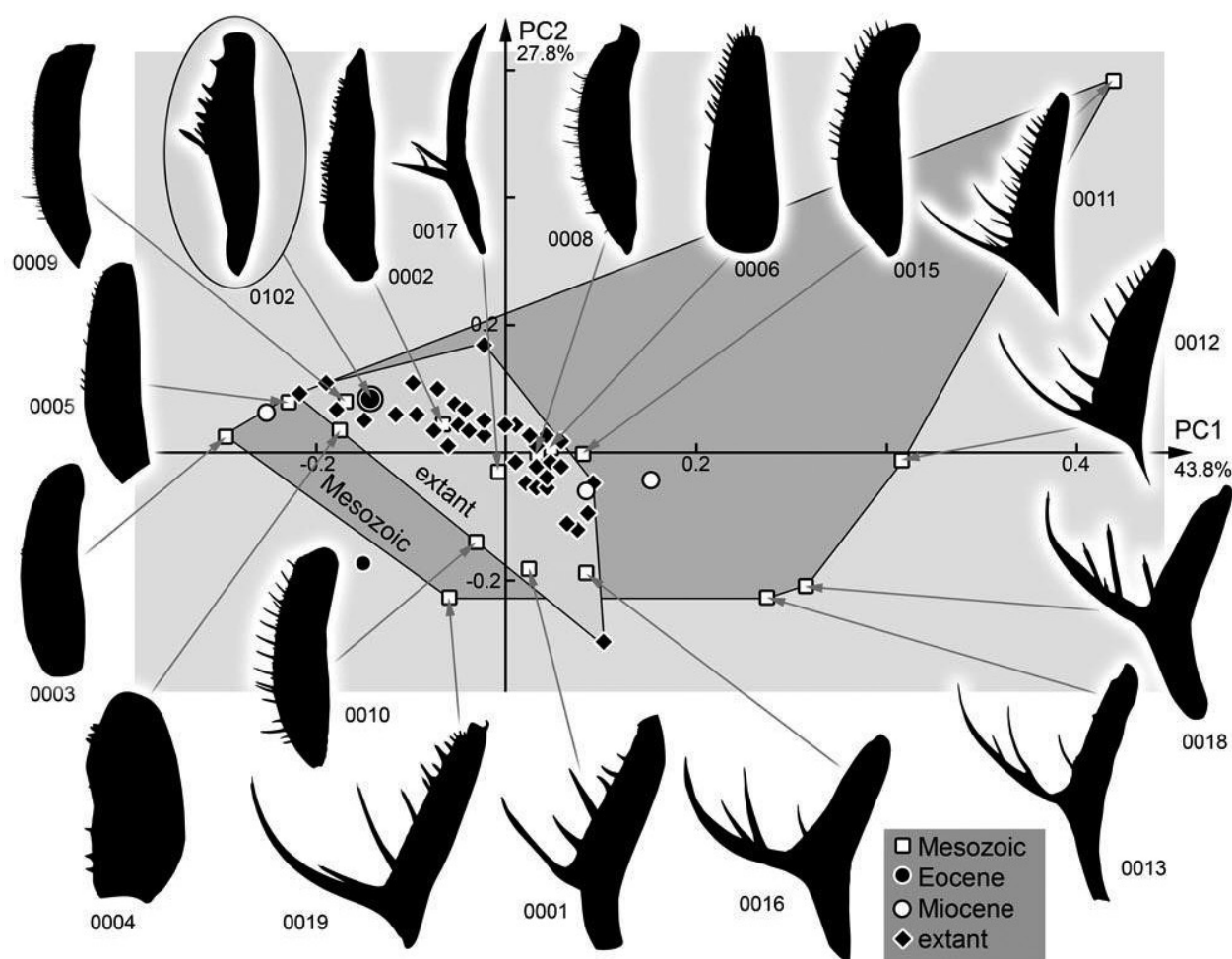


Figure 5. Morphospace occupied by the femora of raptorial legs of extant and fossil adult representatives of Mantispidae. The profemur of the new species has been circled. Total captured variation = 71.6%; 43.8% at PC1 and 27.8% at PC2. Numbers refer to Suppl. material 2: Table S1 (https://github.com/chironomus/Mantispidae-shape-analysis/blob/main/_CLEANED_FOR_EOCENE_Raptorial_Neuropterans.xls).

Although Winterton et al. (2018) and Ardila-Camacho et al. (2021) recovered Symphrasinae as sistergroup to Rhachiberothidae, with the latter work considering Symphrasinae as an ingroup of Rhachiberothidae, we prefer to follow here the classic view considering Symphrasinae as an ingroup of Mantispidae pending more supporting data. Note that even if Symphrasinae was not considered in the quantitative analysis this would not impact the overall results, as extinct species of Symphrasinae fall within or very close to extant representatives in the morphospace.

Although *Whalfera venatrix* was originally described as a representative of Mantispidae (Whalley 1983), subsequent works have generally regarded the species as a representative of Rhachiberothidae based on characters such as the protibia and protarsus being longer than the profemoral length, the presence of a first protarsal process, and the type of integumentary processes present in a dense group (Engel 2004, Wedmann and Makarkin 2007, Makarkin and Kupryjanowicz 2010, Pérez-de la Fuente and Peñalver 2019, Nakamine et al. 2020). However, universal consensus would appear to still be

lacking, mostly related to the inability to ascertain several diagnostic characters from the holotype (see Jepson 2015). The fact that *W. venatrix* plots out of the morphospace of even extinct forms of Mantispidae (see black circle in Fig. 5 and Suppl. material 1: Fig. S2) further supports regarding the species as a representative of Rhachiberothidae.

Mantispa? damzenogedanica sp. nov. represents the sole definitive Eocene adult of Mantispidae preserved in amber. As the species is well circumscribed within modern morphospace, it tends to support the notion that declines in diversity of Mantispidae occurred prior to the Eocene, differing in this respect from what has been inferred to occur in some other neuropteran lineages where comparable quantitative data are available, at least from larvae (e.g., Aspöck and Aspöck 2007, Wang et al. 2016, Liu et al. 2016, 2018, Badano et al. 2018, Haug et al. 2019a, 2020a, b, c, Zippel et al. 2021). Admittedly, though, given the small sample for Eocene individuals of Mantispidae ($n = 3$), such a conclusion might just as likely represent an extreme sampling artefact. Thus, considerable exploration for further Cenozoic adults of Mantispidae is needed to

enrich the available data from which patterns of diversity might be observed and conclusions on mantis lacewing evolution inferred.

5. Conclusions

The record presented herein illustrates a striking decline in the Mantispidae morphological diversity over the course of the Cretaceous and Cenozoic. This trend illustrates yet another case of the drastic decline of the morphological diversity in an ingroup of Neuroptera (Haug et al. 2021c).

Data availability

All data and results are presented in the main text, tables, figures and supplement. (https://github.com/chironomus/Mantispidae-shape-analysis/blob/main/_CLEANED_FOR_EOCENE_Raptorial_Neuropterans.xls).

Author contributions

Conceptualization: VB, RPF, ME, VB, JTH; Methodology: VB, RPF, ME, JTH; Formal analysis and investigation: RPF, ME, JTH, VB Writing – original draft preparation: JVB, ME, RPF, JTH; Writing – review and editing: all authors; Image preparation : JUH, JTH, CH, PGP, CK, MKH, CS, VB, ME, RPF; Analysis: JTH; Funding acquisition: JTH, VB, CH, JUH. Resources: JTH, VB, JUH.

Competing interests

The authors declare that they have no conflict of interest.

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Supplementary material 1

Graphical representation of the PC's correspondence to morpholog

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Data type: figures

Explanation note: Figure S1. Shape-drivers of the principal components in the PCA analysis. Figure S2. Numbered specimens used in the analysis. Legend to the numbers in the Suppl. material 2: Table S1 (https://github.com/chironomus/Mantispidae-shape-analysis/blob/main/_CLEANED_FOR_EOCENE_Raptorial_Neuropterans.xls).

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Link: <https://doi.org/10.3897/fr.25.80134.suppl1>

Supplementary material 2

Table S1. Cleaned for eocene Raptorial Neuropterans

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Data type: table

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