THE FIRST FOSSIL RECORD OF A MANTIS LACEWING PUPA, AND A REVIEW OF PUPAE IN MANTISPIDAE AND THEIR EVOLUTIONARY SIGNIFICANCE

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Abstract. During ontogenetic development, insects can undergo quite drastic changes (metamorphosis) until the adult stage is reached. A substantial part of this development in one group of Insecta, Holometabola, takes place during the pupa stage. Despite the pupa being recognised as an important phase, rather few depictions of pupae exist in the literature. We report here the first find of a fossil pupa of the lacewing group Mantispidae. The specimen represents an exuvia and is enclosed in Ukrainian Rovno amber, Eocene in age (c. 35–40 million years). We review the entire record of extant pupae of Mantispidae depicted in the literature or in online image repositories. With the aid of elliptic Fourier analysis, we compare the outline of the femur of the foreleg (raptorial appendage in the adults) of pupae and adults of Mantispidae. The pupae are all very similar concerning the femur, while the adults show a larger morphological diversity, particularly the extinct forms. Furthermore, our results indicate that the forelegs do not become increasingly complex throughout ontogenetic stages, but instead undergo an indirect development. According to the low variation in morphology seen in the pupa stage in Mantispidae, it is plausible that it represents a phylotypic stage for the group, i.e. a phase characterised by a significantly lower variability than other stages.

Introduction

The ecological importance of the group Insecta in continental ecosystems remains undisputed (e.g. Suter & Cormier 2014; Jankielsohn 2018; Crespo-Pérez et al. 2020; Wermelinger 2021). The evolutionary success of the group in terms of species richness, abundance of individuals, and biomass is concentrated in its ingroup Holometabola, which includes bees, beetles, and butterflies, among many others (Grimaldi & Engel 2005). The success of the group Holometabola has been attributed, at least in part, to their developmental mode: the early post-embryonic stages, or larvae, are (usually) very different in morphology and ecology from their corresponding adults. This distinct niche separation between larvae and their adults reduces the exploitation competition between the two (Truman & Riddiford 2019).

A drastic morphological differentiation between larvae (for challenges of the term, see Haug 2020a) and adults, however, also imposes a series of developmental constraints, especially for moulting animals. This is not specific to the group Insecta, but to all crustaceans (Insecta is an ingroup of Crustacea sensu lato; Zhang et al. 2007; Haug & Haug 2015). The ontogenetic transition between strongly differing larvae and adults can become a major problem concerning ecological aspects, for example as the larvae need to find suitable environmental conditions for the adult to transform from their planktic lifestyle to a benthic adult lifestyle in marine malacostracan crustaceans (e.g. Haug & Haug 2013; Haug et al. 2013a), but can also simply be mechanically challenging during metamorphosis (Haug 2020b). Often there is not a direct change from the larval to the adult morphology, but additional intermediate stages occur (Haug & Haug 2016; Haug et al. 2019). This transition was ancestrally (plesiomorphically) often rather gradual (see Haug 2019 for terminological issues) as exemplified by some extant groups such as Anostraca (brine shrimps) or Notostraca (tadpole shrimps), also to a certain extant in Stomatopoda (mantis shrimps; Haug et al. 2016a), but being especially well documented in the fossil record (Walossek 1993; Haug et al. 2010, 2016b; Kiesmüller et al. 2019). The transition from larva to adult became independently more metamorphic in many lineages, also within Insecta (Haug et al. 2016b). In the extreme case, intermediate stages have been entirely lost (Haug 2020b), yet in many groups a single intermediate stage remains.

In holometabolans, this intermediate stage is called 'pupa' (Jindra 2019; Truman 2019). Different criteria support the view that the pupa is a specialised larval stage (see discussion in Haug 2020a). Yet, the evolutionary origin of the pupa has puzzled entomologists (e.g. Švácha 1992; Sehnal et al. 1996; Truman & Riddiford 1999, 2019; Jindra 2019 and references therein), as this stage is generally seen as unusual (but as pointed out, there are comparable stages in other lineages; see Haug 2020b) and is possibly central to the specific life history of holometabolans.

The pupal life stage, although thought to be so crucial in its function and of high evolutionary significance, seems to be the least depicted one in the literature (see discussion in Haug et al. 2017) for the extant fauna, but also for fossils. Quite counter-intuitive for an intermediate stage, the pupa is often assumed to be very similar in appearance to the adult (see discussion in Saltin et al. 2016).

Neuroptera, the group of lacewings, is no exception when it comes to research on pupae: adults are the most intensively studied forms, larvae rarely so, and the least studied post-embryonic life stage appears to be the pupa. Fossil neuropterans have been found in quite large numbers for adults (e.g. Engel & Grimaldi 2007; Menon & Makarkin 2008; Jepson 2015; Winterton et al. 2019), but also for larvae (e.g. Pérez-de la Fuente et al. 2020; Haug et al. 2021a), while fossil pupae are an absolute rarity (see discussion).

Within Neuroptera, Mantispidae, the group of mantis lacewings, has a comparably good record of pupa stages in the extant fauna (see further below). Mantis lacewing development has been generally considered to be hypermetamorphic (Tauber et al. 2003; Aspöck & Aspöck 2007; Ohl 2011): stage 1 larvae are highly mobile (campodeiform), stage 2 and 3 larvae are grub-like, and adults are elegant lacewings with powerful sub-chelate, 'spine'-bearing predatory front legs (Lucchese 1956; Parker & Stange 1965; Redborg & MacLeod 1985; Hoffman & Brushwein 1992). Hence, the morphological difference between the last larval stage and the adult is drastic, and it is mediated by the pupa stage.

We here review the knowledge on pupae of Mantispidae and report the first fossil pupal remains of this group. We also use quantitative as-

pects of pupae and compare these to a recent quantitative study of adults (Baranov et al. 2022a). Based on this comparison we can discuss some aspects on the pupa stage and its significance for understanding the evolutionary history of Mantispidae.

MATERIAL AND METHODS

Material

A single specimen was directly studied. It is deposited in the Palaeo-Evo-Devo Research Group Collection of Arthropods, Ludwig-Maximilians-Universität München, Germany under the repository number PED 1389. The specimen was legally purchased from Jonas Damzen (amberinclusions.eu). According to the available information, the specimen is preserved in Ukrainian Rovno amber (a southern, roughly contemporary analogue of Baltic amber) and is Eocene in age (ca. 35–40 million years old), with conservative dating to an age of 36 million years (Perkovsky et al. 2010; Baranov et al. 2016).

Investigation of all available extant pupae of mantis lacewings was based on images, either from the literature, from databases, or from image repositories (see Supplementary Table 1). All images were redrawn in vector graphic programs (Inkscape, Adobe Illustrator CS2, CS4) in order to provide a more uniform appearance of the specimens to enhance comparability. For comparison, also some aspects of larvae and adults were redrawn in a similar manner.

Documentation methods

The amber specimen PED 1389 was documented on a VHX-6000 digital microscope equipped with a ZST 20–2000 lens. Different settings were used during visualisation (black and white background, cross-polarised coaxial illumination, unpolarised low-angle ring illumination), and the photographs with the best contrast were used for presentation. Each image is a composite image (Haug et al. 2011): to overcome limitations of depth of field, a stack of images with gradually shifting focal depth was obtained and fused into a sharp image with the built-in software; to overcome limitations of field of view, several adjacent image details were recorded and stitched to a larger panorama with the built-in software (Haug et al. 2018). Each image was recorded with several exposure times (HDR; Haug et al. 2013b). Resulting images were further processed in Adobe Photoshop CS2.

Shape analysis

For a quantitative comparison between adult stages and pupae, we used the data set from Baranov et al. (2022a) and expanded it. We consider here all pupae known from groups that were traditionally considered as ingroups of Mantispidae (see below for details). The data set consists of drawings of the outlines of the femur (appendage element 3) of the foreleg in anterior or posterior view (for full list of specimens, see Supplementary Table 1 and Supplementary Text 1).

Outlines were analysed in SHAPE performing an elliptic Fourier analysis. Outlines were transformed into numerical chain codes, aligned and finally analysed with a principal component analysis (PCA) (Iwata & Ukai 2002; Braig et al. 2019).

Terminology

Terms for describing representatives of Insecta are highly specialised, differing even between the different lineages. This makes comparison in wider frames often very cumbersome, if not impossible. Beyond the limits of Insecta, in the frame of Euarthropoda, comparisons are even more problematic. As outlined, the pupa is a stage considered highly specific to Holometabola, but comparable stages have evolved convergently in other lineages of Euarthropoda. To further facilitate such comparisons, descriptive terms are accompanied by more neutral terms in square brackets.

Taxonomic integrity of Mantispidae and the use of associated common names

In their morphological phylogenetic analysis, Ardila-Camacho et al. (2021) recovered an otherwise generally accepted ingroup of Mantispidae, Symphrasinae, as sistergroup to the exclusively fossil group Paraberothinae, and Symphrasinae+Paraberothinae as sistergroup to Rhachiberothinae. For that reason, these authors excluded Symphrasinae from Mantispidae and interpreted it as an ingroup of Rhachiberothidae. Similar phylogenetic results recovering Symphrasinae as sistergroup to Rhachiberothidae were previously obtained by Winterton et al. (2018).

The phylogenetic interpretation of the group Rhachiberothidae (or Rhachiberothinae) has been unstable. Rhachiberotinae, also known as "thorny lacewings", was erected as a subfamily of Berothidae (Tjeder 1959, but questioned later by Tjeder 1968), then re-interpreted as an ingroup of Mantispidae (Willmann 1990) and then re-interpreted as a separate family (Rhachiberothidae), as sistergroup to Berothidae (Aspöck & Mansell 1994). This latter view was followed by several authors (Aspöck & Aspöck 1997, 2008; Aspöck et al. 2001; Beutel et al. 2010a, b; Petrulevicius et al. 2010; Zimmermann et al. 2011; Randolf et al. 2014).

On the other hand, Wang et al. (2017) suggested a sistergroup relationship of Rhachiberothidae to Mantispidae (in principle the same phylogeny as in Willmann 1990, but with different taxonomic views), also supported by numerous other studies (Liu et al. 2015; Engel et al. 2018). Other authors only interpreted Rhachiberothidae as closely related to Berothidae and Mantispidae (e.g. McKellar & Engel 2009; Aspöck et al. 2020). Some other authors still considered Rhachiberothinae as an ingroup of Berothidae (Schlüter & Stürmer 1984; Makarkin & Kupryjanowicz 2010; Makarkin 2015).

In addition, the group Paraberothinae is either interpreted as ingroup of Rhachiberothidae (e.g. Nel 2005; Nakamine & Yamamoto 2018; Pérez-de la Fuente & Peñalver 2019; Nakamine et al. 2020) or Berothidae (Makarkin & Kupryjanowicz 2010; Makarkin 2015). Alternatively, it was interpreted as closely related to Mantispidae including Rhachiberothinae (Willmann 1994).

Other detailed recent phylogenetic analyses remained undecided concerning the relationship of ingroups of Rhachiberothidae and of Mantispidae (e.g. Jandausch et al. 2018). Yet, many also recovered Symphrasinae as an ingroup of Mantispidae (Liu et al. 2015; Engel et al. 2018; Shi et al. 2020a).

The taxonomic instability of Mantispidae also renders any informal names associated to it, such as "mantis lacewings" or "mantispids", at an imprecise state. These terms may refer to: 1) only representatives of Drepacinae, Calomantispinae and Mantispinae (≈ "Mantispidae s. str.") following the stance of Ardila-Camacho et al. (2021); 2) representatives of Drepacinae, Calomantispinae, Mantispinae and Symphrasinae (Mantispidae in the common sense) following the interpretations of other authors such as Liu et al. (2015), Engel et al. (2018) and Shi et al. (2020a); or 3) representatives of Drepacinae, Calomantispinae, Mantispinae, Symphrasinae and Rhachiberothinae (≈"Mantispidae sensu lato") following the ideas of Willmann (1994).

The main question when using these names is therefore whether it is more appropriate to follow an exclusive (Ardila-Camacho et al. 2021) or an inclusive strategy (Willmann 1990, 1994). A comparable case dilemma also within Neuroptera is currently seen in the relationships of Ascalaphidae and Myrmeleontidae (Jones 2019 and Prost & Popov 2021 vs. Machado et al. 2019), although the present case is even more complex since the one might be an ingroup of the other or vice versa (Jones 2019; Prost & Popov 2021; Machado et al. 2019 vs. Badano et al. 2021). In general, the inclusive approach seems to be the more widely accepted one (e.g. Modesto & Anderson 2004). For our current study, there is no practical difference in the use of Mantispidae and associated common names such as "mantis lacewing" in cases 2 (Mantispidae in the common sense) and 3 (≈"Mantispidae sensu lato"). Therefore, herein we use these terms in that way, also considering the absence of known pupae from Rhachiberothidae and Paraberothidae.

RESULTS

Extant pupa specimens figured in the literature

All known occurrences of pupa stages of mantis lacewings figured in the literature 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 represents the most complete way of cross-referencing, avoiding interpreting the same specimens as two independent occurrences (see also Haug et al. 2020).

Marquez-López & Contreras-Ramos (2018) already provided a list of earlier studies on mantis lacewing pupae. Yet, not all of these figured the studied specimens (e.g. Smith 1934; Redborg & MacLeod 1985; Buys 2008, cited as Sandor 2008 in Marquez-López & Contreras-Ramos 2018). Also, these authors did not include some of the older literature as they focused on specimens from North and South America.

1) Brauer (1855) provided coloured drawings of a pupa of *Mantispa pagana* (specimen 1; Fig. 1; later *Mantispa styriaca*, e.g. Aspöck & Aspöck 2007). Images included the pupa in lateral view (fig. 7), in ventral view (fig. 8), the pronotum in dorsal view (fig. 9), the last tarsus element (fig. 10), and the cocoon within the ground (fig. 11). Size was provided as magnification factor, which is not informative with the electronic version available to the authors; a scale bar is included in the images, yet without a statement about its length. Some images were re-figured by Stitz (1931) and Aspöck & Aspöck (2007).

2) Stitz (1931) re-figured (fig. 334 p. 35.303) specimen 1, i.e. the specimen from Brauer (1855), in ventral and lateral view.

3) Lucchese (1956) provided several images of a pupa of *Mantispa perla* (current valid combination *Mantispilla perla*). Images included a drawing of an early phase pupa ("quiescent pupa") in lateral view (fig. LXXI p. 204) and a drawing of a late phase, free mobile pupa ("pharate adult"), also in lateral view (fig. LXXI [sic!] p. 205). It remains unclear if the early phase pupa and the late phase pupa are the same individual, but we consider this as possible, therefore we consider it as one (specimen 2; Fig. 1).

4) Parker & Stange (1965) provided several drawings of a pupa of *Plega yucatanae* (specimen 3; Fig. 1). Drawings included the head in anterior view (fig. 7 p. 609) and an overview in lateral view (fig. 13 p. 611). The specimen was most likely a mobile late phase pupa. No indication of size was provided.

5) Bissett & Moran (1967) provided a drawing of a pupa (specimen 4; Fig. 1) of "the chestnut mantispid" in lateral view (fig. 3b p. 87). According to the provided scale, the pupa was about 6.4 mm long.

6) Poivre (1976) re-figured specimen 2, i.e., the two drawings from Lucchese (1956).

7) Gilbert & Rayor (1983) provided two drawings of a pupa of *Mantispa fuscicornis* (specimen 5; Fig. 1) in dorsal view, one overview drawing (fig. 1B p. 579) and one detail drawing of two segments of the abdomen (fig. 1A p. 579). The provided scale indicates that the pupa is about 8.5 mm long.

8) Schremmer (1983) provided a micrograph of a pupa of *Mantispa styriaca* (specimen 6; Fig. 1) in lateral view (fig. 2 p. 23). No indication of size was provided.

9) Hoffman & Brushwein (1992, p. 193) provided several drawings of a pupa of *Mantispa pulchella* (specimen 7; Fig. 1; current valid combination *Leptomantispa pulchella*). Drawings included an overview in lateral view (fig. 20a), the head in frontal view (fig. 20b), a detail of the distal tip of thorax appendage 2 (fig. 20c), and the abdomen end in lateral view (fig. 20d). No clear indication of overall size was provided, yet the provided scale indicates that the head was 2.1 mm wide. Additional details from pupae of two other species were figured, i.e., *Mantispa interrupta* (fig. 14; current valid combination *Dicromantispa interrupta*) and *Mantispa viridis* (fig. 26a–c; current valid combination *Zeugomantispa minuta*).

10) Aspöck & Aspöck (2007) re-figured (fig. 110) the drawings from Brauer (1855) in lateral and ventral view.

11) Maia-Silva et al. (2013) provided several micrographs of the development of *Plega hagenella.* Images included a pupa in lateral view within an opened brood cell (fig. 1B p. 103) and a later pupa ("pharate adult"; fig. 1E p. 103) in dorso-lateral view (specimen 8; Fig. 1). It remains unclear whether both represent the same individual; in order not to consider the same individual twice, we only considered the image with more accessible details. According to the provided scale, the specimen was about 3.5 mm long. Additionally, simplified drawings of the two stages were shown (fig. 2 p. 104).

12) Monserrat (2014) provided a photograph of a pupa of *Mantispa styriaca* (specimen 9; Fig. 1) in lateral view (fig. 17 p. 7), as well as a photograph of a pupal exuvia in the same orientation (fig. 18 p. 7). It remains unclear whether this is the same individual; in order not to consider the same individual twice, we only considered the image with more accessible details. No indication of size was provided.

13) Dorey & Merritt (2017) provided several photographs of a late pupa ("pharate adult") of *Ditaxis biseriata* (specimen 10; Fig. 2). Images included a lateral view (fig. 1 left p. 5), a close-up on the anterior body in antero-lateral view (fig. 1 middle p. 5), and an antero-frontal view of the animal on a tree trunk (fig. 1 right p. 5). In addition, a series of images shows the eclosion of the adult from the pupa (fig. 2 p. 6; as movie file fig. 5 p. 8). No indication of size was provided.

14) Marquez-López & Contreras-Ramos (2018) provided several photographs of a pupa
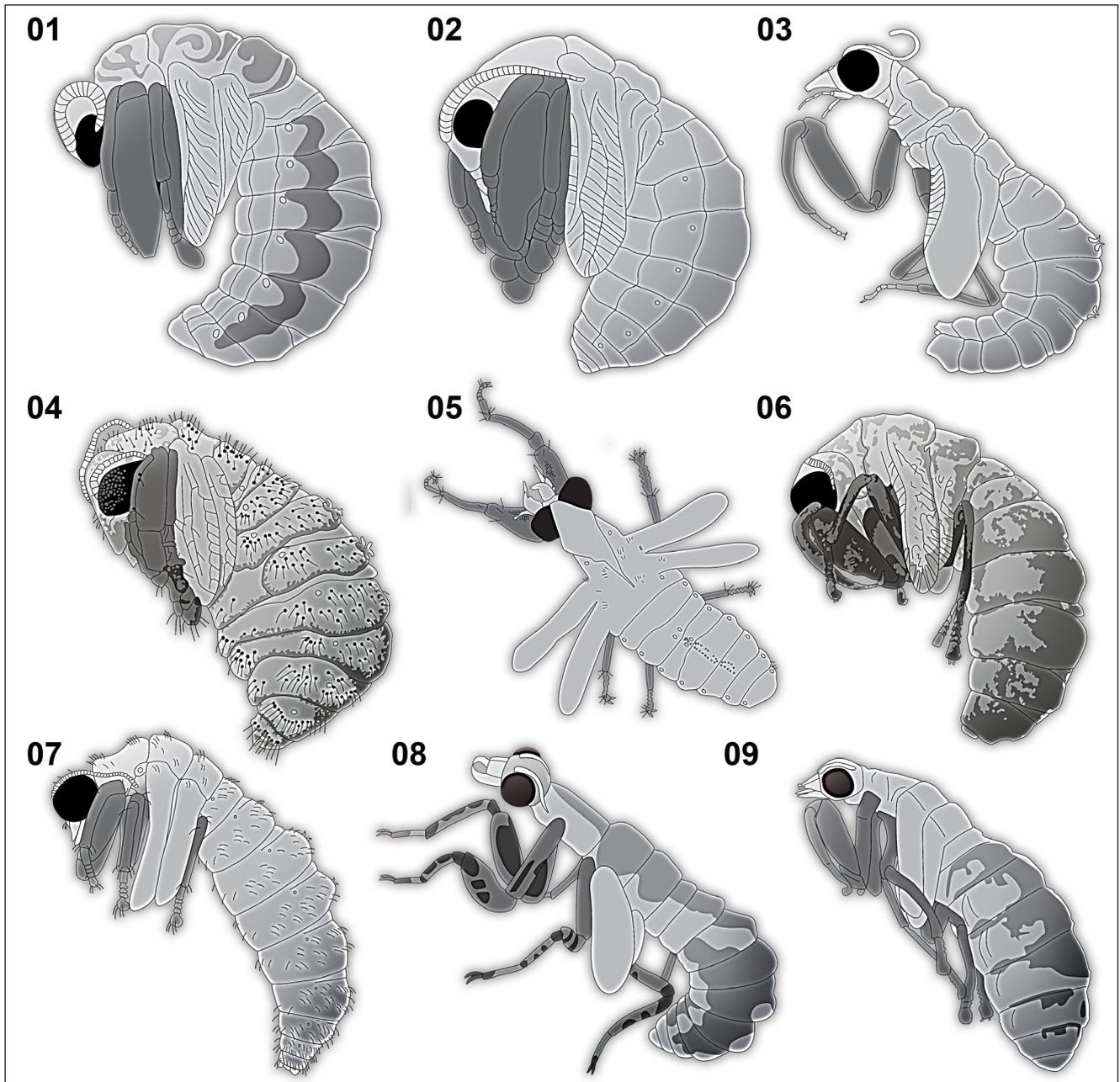
Fig. 1 - Known extant pupae of Mantispidae, redrawn from various sources, all in lateral view. 01) *Mantispa styriaca*, from Brauer (1855, fig. 7). 02) *Mantispilla perla*, from Lucchese (1956, fig. LXXI p. 204). 03) *Plega yucatanae*, from Parker & Stange (1965, fig. 13 p. 611). 04) Species undetermined, "the chestnut mantispid", from Bissett & Moran (1967, fig. 3b p. 87). 05) *Mantispa fuscicornis*, from Gilbert & Rayor (1983, fig. 1B p. 579). 06) *Mantispa styriaca*, from Schremmer (1983, fig. 2 p. 23). 07) *Leptomantispa pulchella*, from Hoffman & Brushwein (1992, fig. 20a p. 193). 08) *Plega hagenella*, from Maia-Silva et al. (2013, fig. 2 p. 104). 09) *Mantispa styriaca*, from Monserrat (2014, fig. 17 p. 7).

of *Climaciella brunnea* (specimen 11; Fig. 2). Images (all on fig. 1 p. 68) included a lateral view (fig. 1A), dorsal view (fig. 1B), and detail of the dorsal surface of the abdomen (fig. 1C, D). According to the provided scale, the specimen was 15 mm long. They also re-figured (fig. 2 p. 69) several drawings from Parker & Stange (1965) and Hoffman & Brushwein (1992).

15) Given the scarceness of data on pupae of Mantispidae, we used data available on websites as additional data source being aware of its limitations, particularly the lack of reliable determinations. In particular, the 'BugGuide' community (https://bugguide.net) is active and well sorted. This website is hosted by the Department of Entomology of the Iowa State University, and has
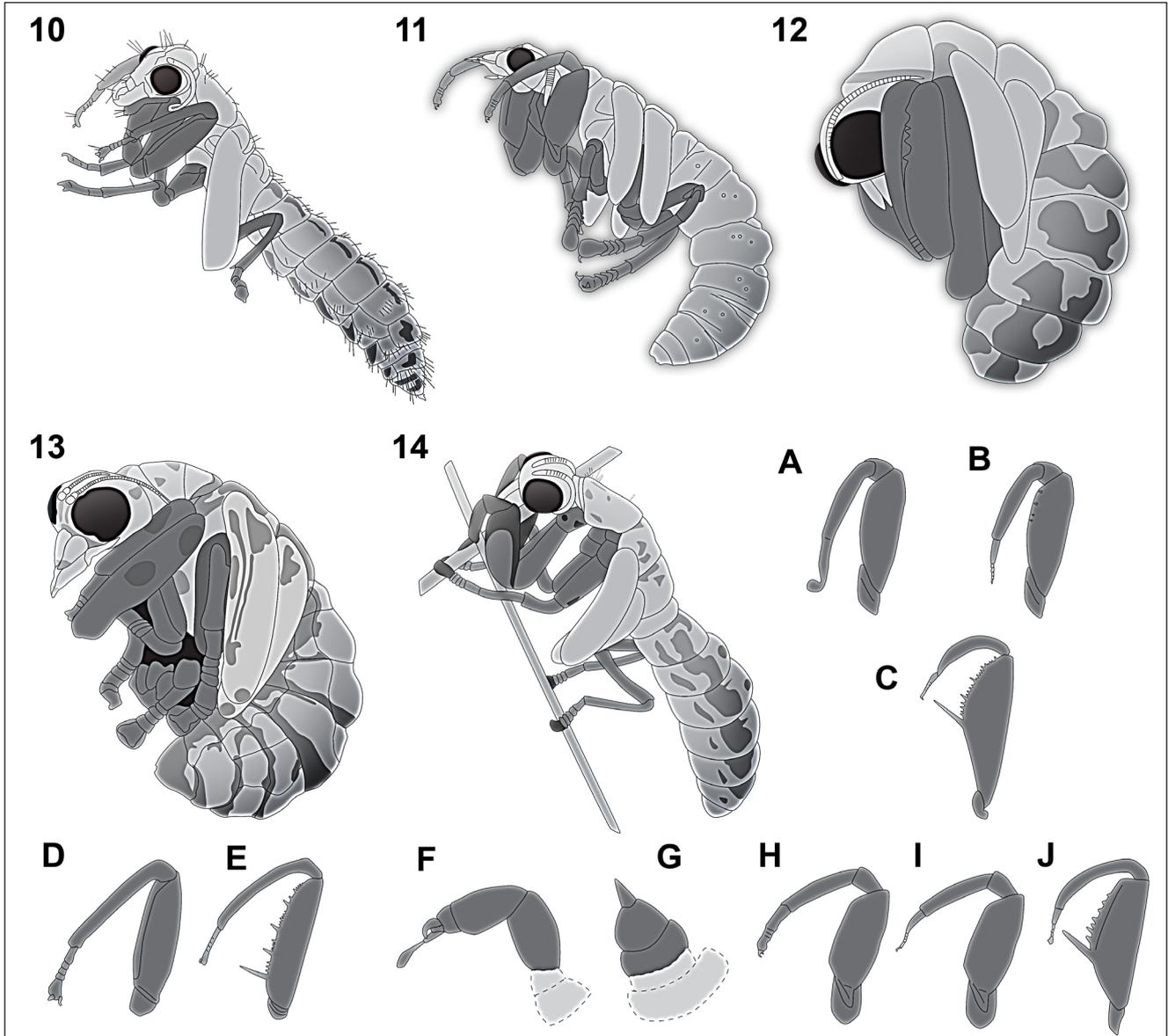
Fig. 2 - Known extant pupae of Mantispidae, redrawn from various sources, all in lateral view, continued, and details of front legs of various post-embryonic stages. 10) *Ditaxis biseriata*, from Dorey & Merritt (2017, fig. 2 p. 6). 11) *Climaciella brunnea* from Marquez-López & Contreras-Ramos (2018, fig. 1A p. 68). 12) From bugguide.net, image 1132526 (© 2015 Jennifer Thompson). 13) From bugguide. net, image 25293 (© 2005 Jeff Hollenbeck). 14) From 'The MacroClub project' (macroid.ru), image 26884. A–J) Further distal parts of front legs (mostly femur, tibia, tarsus). A–C) *Mantispa styriaca*. A) Pupa, from Monserrat (2014 fig. 17 p. 7). B) Pharate adult, from Monserrat (2014 fig. 17 p. 7). C) Adult, from Monserrat (2014 fig. 25 p. 22). D, E) *Ditaxis biseriata*. D) Pupa, from Dorey & Merritt (2017, fig. 2 bottom p. 6). E) Adult, from Dorey & Merritt (2017, fig. 2 top p. 6). F) Stage 1 larva of *Dicromantispa interrupta*, from Hoffman & Brushwein (1992 fig. 10b p. 186). G) Stage 3 larva of *Mantispa uhleri*, from Redborg & MacLeod (1985 fig. 6 p. 17). H–J) *Climaciella brunnea*. H) Pupa, from Marquez-López & Contreras-Ramos (2018, fig. 1A p. 68). I) Pharate adult, from Marquez-López & Contreras-Ramos (2018, fig. 1A p. 68). J) Adult, from bugguide.net, image 1540431 (© 2018 Marcie Oconnor) labelled 'Mantidfly – *Climaciella brunnea*'.

already been used as a source for similar studies (e.g. Haug & Haug 2019; Haug et al. 2021b).

Image 1132526 (© 2015 Jennifer Thompson) was labelled 'Mantidfly Larvae' (specimen 12; Fig. 2). The photograph shows the specimen in lateral view. Additional images of this specimen are available, but this one was most suitable for accessing details. No indication of size was provided.

Image 25293 (© 2005 Jeff Hollenbeck) was labelled 'Mantidfly – *Dicromantispa sayi*' (specimen 13; Fig. 2). The photograph shows the specimen in lateral view. No indication of size was provided.

A third image comes from the website 'The MacroClub project' (macroid.ru). Image 26884 (by Zabenok) was labelled '*Mantispa styriaca*' (specimen 14; Fig. 2).
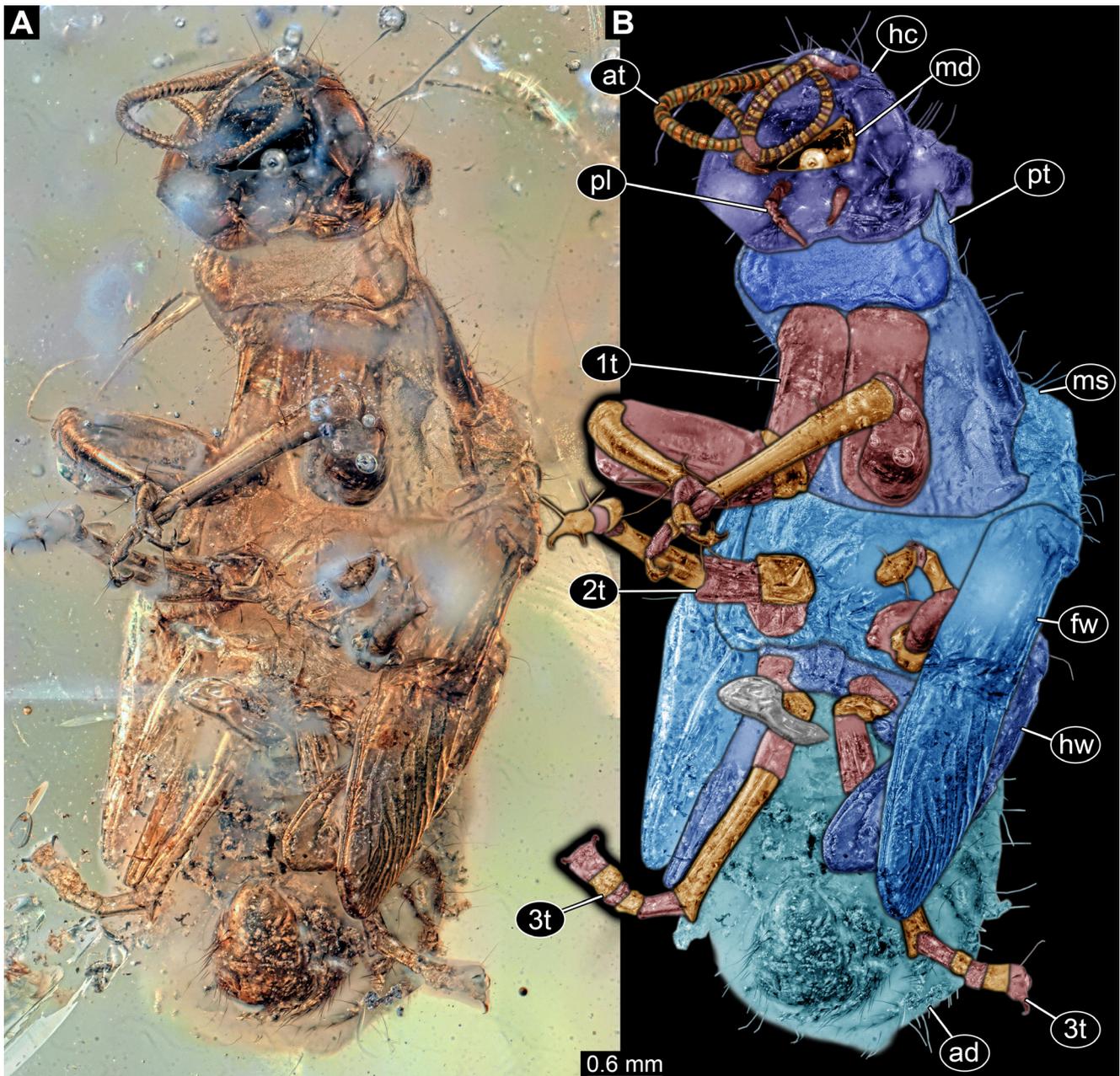
Fig. 3 - New specimen PED 1389, Eocene pupal exuvia, Rovno amber. A) Ventral view. B) Colour-marked version of A. Abbreviations: 1t–3t = trunk appendages 1–3; ad = abdomen; at = antenna; fw = forewing; hc = head capsule; hw = hind wing; md = mandible; ms = mesothorax; pl = palp; pt = prothorax.

New fossil specimen PED 1389

Remark. The fossil is an exuvia preserved within a piece of Eocene Rovno amber and therefore partly deformed, hence not all aspects are accessible in original morphology. Syninclusions: two immature mites and a badly preserved, undeterminable minute insect (Hymenoptera?).

General habitus. Immature lacewing, late stage pupa, with free appendages (exarate), including the mandibles (decticous; Fig. 3). Body organised into distinct capsulate head and trunk. Trunk further differentiable into an anterior region (thorax)

and posterior region (abdomen) [not corresponding to abdomen in other groups].

Head. Head assumed to be composed of six segments. First body segment, ocular segment (protocerebral segment), should be recognisable by prominent compound eyes and the clypeus-labrum complex, yet the cuticle in these regions is strongly distorted and both structures cannot be reliably distinguished as such.

Post-ocular segment 1 (deutocerebral segment) recognisable by its pair of appendages antennae [antennulae]. Antennae strongly curled, but
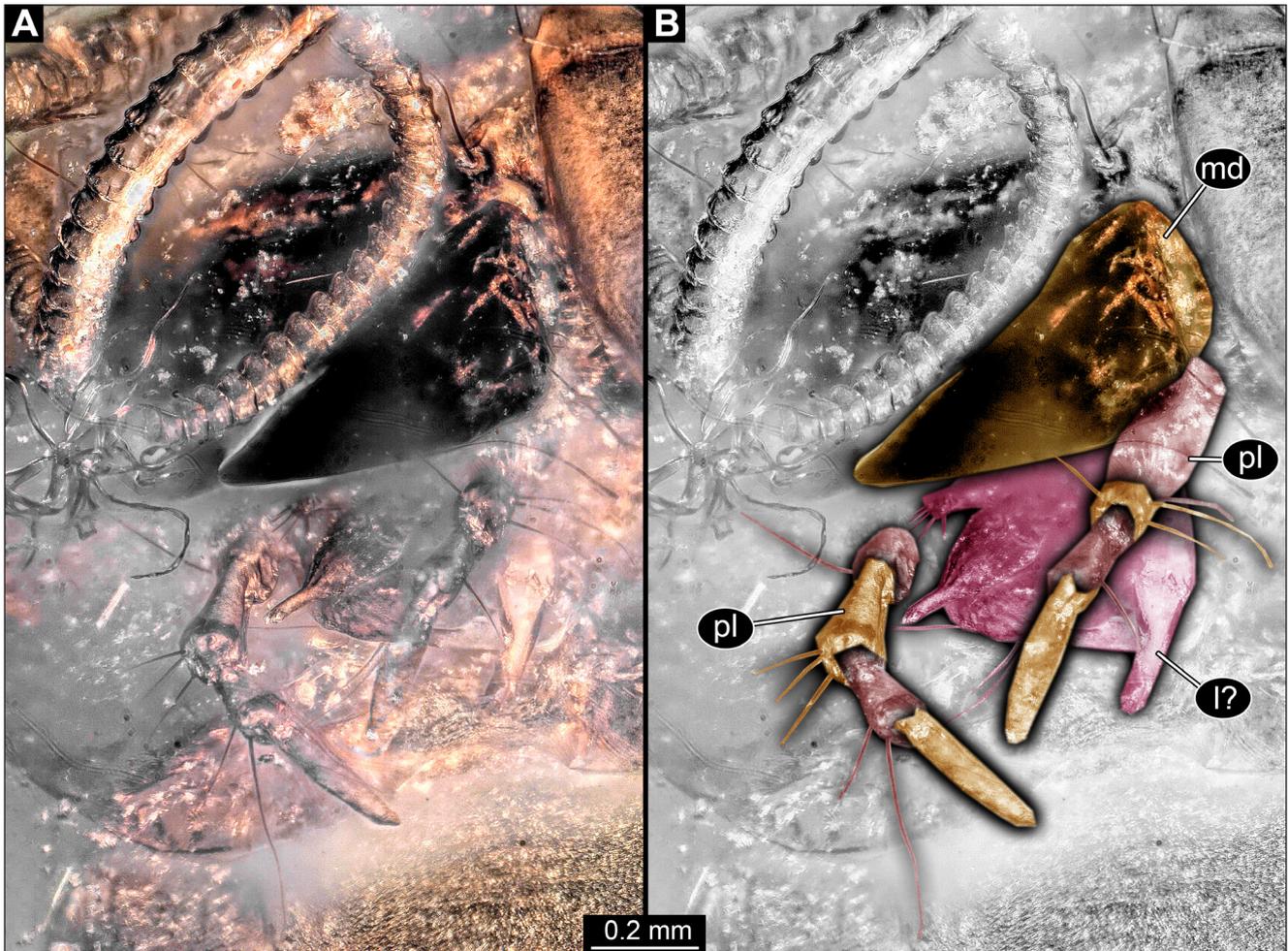
Fig. 4 - New specimen PED 1389, Eocene pupal exuvia, Rovno amber, continued. A) Detail of head region with mouthparts. B) Colour-marked version of A. Abbreviations: l? = possible labium; md = mandible; pl = palp (possibly of maxillae).

seem to have been longer than head capsule; subdivided into numerous elements (antennomeres), at least 45, transverse, gradually decreasing in width (diameter) distally; each antennomere slightly expanding in diameter distally, expansion greater towards the distal end. Post-ocular segment 2 (intercalary segment; tritocerebral segment) without externally visible structures.

Post-ocular segment 3 recognisable by its pair of appendages, mandibles (Fig. 4). Mandibles only accessible in overall anterior, functional lateral view; roughly triangular, longer than wide at the proximal joint region, about 2×.

Post-ocular segment 4 possibly recognisable by its pair of appendages, maxillae [maxillulae] (Fig. 4). Only supposed distal parts apparent, palps [endopod], with four elements (palpomeres). Length of proximal element partly unclear (proximal border uncertain). Element 2 longer than wide (diameter), at least 2×; distally widening; with at least four long

setae distally (exact arrangement unclear). Element 3 slightly shorter than preceding element; distally widening; with at least two long setae distally (exact arrangement unclear). Terminal element about as long as element 2, not widening distally, with a rounded tip, overall finger-like in appearance; no setae apparent.

Post-ocular segment 5 possibly recognisable by its pair of appendages, labium, medially conjoined to a single structure [maxillae] (Fig. 4). Appears partly deformed and largely concealed under the other mouthparts, laterally bearing a pair of protruding digitiform structures (palps?).

In dorsal view, posterior part of head capsule (occiput) with a pair of prominent setae on each side close to the midline (Fig. 5A).

Anterior trunk, thorax. With three segments, prothorax, mesothorax, and metathorax (Figs. 3, 5).

Prothorax in ventral view about as wide as head, longer than head, about 1.5×. With a distinct anteroventral region, apparently slightly sclerotised

membrane, slightly less than one third of overall length. Behind distinct anteroventral membrane, a pair of prominent appendages (forelegs) inserts. Dorsally, segment strongly deformed, medially split. With prominent longer setae along the lateral edge of a distinct sclerite (notum) [tergite], at least four such setae.

Appendages of prothorax with five major elements. Proximal element, coxa [basipod, not corresponding to coxa in other groups], very prominent; longer than wide (diameter), about 3×; about the same outline in ventral view as the ventral sclerite of the prothorax. Element 2, trochanter [endopod element 1], same diameter as preceding element, but much shorter. Element 3, femur [endopod element 2] moderately swollen, about the same length as coxa but higher, lacking integumentary specialisations. Element 4, tibia [endopod element 3], about as long as preceding element, but much more slender, less than 50%, slightly curved inwards; distally with at least two long setae. Element 5 [endopod element 4], tarsus, about 60% of the length of the tibia, further subdivided into smaller elements (tarsomeres), at least four recognisable. Proximal sub-element (basitarsus) slightly longer than wide; two subsequent sub-elements slightly shorter in length. Distalmost sub-element shorter, proximally narrower, then widening distally, bearing a pair of pretarsal claws, no arolium evident.

Mesothorax shorter in anterior-posterior axis than prothorax, about as long as the region of the prothorax behind the anterior membraneous region. Dorsally about the same length as ventrally. Close to the posterior rim, a pair of prominent appendages (midlegs) inserts. Dorsal sclerite, mesonotum, rectangular in dorsal view, medially split, one split half slightly wider than long. With several distinct setae (Fig. 5B): a row (from anterior to posterior) of four setae in the anterior half closer to the midline; a single seta further lateral at the same level as the most posterior setae of the group of four setae; a group of three setae further lateral at about the level of the anterior three setae of the group of four setae; further posterior a group of three setae (in median to lateral orientation); further lateral a group of eight setae more or less forming an anterior-posterior line at about the level of the group of four setae.

Pair of wing (forewing) pads inserted laterally to the mesonotum (Fig. 5B). Wing pads longer than mesothoracic segment ventrally about 2×. Pterostigma with numerous pterostigmal veinlets. Radial

posterior with long branches, 5 or 6 in number, not forming regular angular cells.

Appendages of mesothorax with five major elements. Proximal element, coxa [basipod, not corresponding to coxa in other groups], short, wider than long, not as wide as coxa of foreleg. Element 2, trochanter [endopod element 1], roughly the same size as preceding element. Element 3, femur [endopod element 2], longer, exact length difficult to estimate due to perspective, longer than preceding element. Element 4, tibia [endopod element 3], longer than preceding elements, also more slender. Element 5 [endopod element 4] further subdivided into smaller elements (tarsomeres), at least four recognisable. Distalmost tarsomere bearing a pair of pretarsal claws, no arolium evident. Further details not accessible due to perspective.

Metathorax in ventral view shorter, only about 30% of the mesothorax. Close to the posterior rim a pair of prominent appendages (hind legs) inserts. Dorsally similar in dimensions to mesothorax, also medially split. Metathorax with fewer setae, exact arrangement concealed by white froth (=Verlumung).

Pair of wing (hind wing) pads inserted laterally to the metanotum. Wing pads longer than metathoracic segment ventrally, about 2×.

Appendages of metathorax with five major elements. Proximal element, coxa [basipod, not corresponding to coxa in other groups], short, wider than long, not as wide as coxa of foreleg. Element 2, trochanter [endopod element 1], roughly the same size as preceding element. Element 3, femur [endopod element 2], longer than coxa and trochanter combined. Element 4, tibia [endopod element 3], longer than preceding elements combined, also slightly more slender. Element 5 [endopod element 4] further subdivided into smaller elements (tarsomeres), five recognisable. Tarsus as a whole slightly shorter than tibia, more slender. Sub-element 1 (basi-tarsus) slightly longer than wide. Sub-element 2 shorter than wide. Sub-elements 3 and 4 similar to 2. Distal sub-element slightly longer than preceding one, bearing a pair of pretarsal claws, no arolium evident.

Posterior trunk, abdomen. Recurved ventrad, with most details not accessible due to Verlumung. Exact number of externally recognisable segments unclear. Posterior segments narrower than anterior ones. All segments with numerous setae, exact arrangement not accessible.
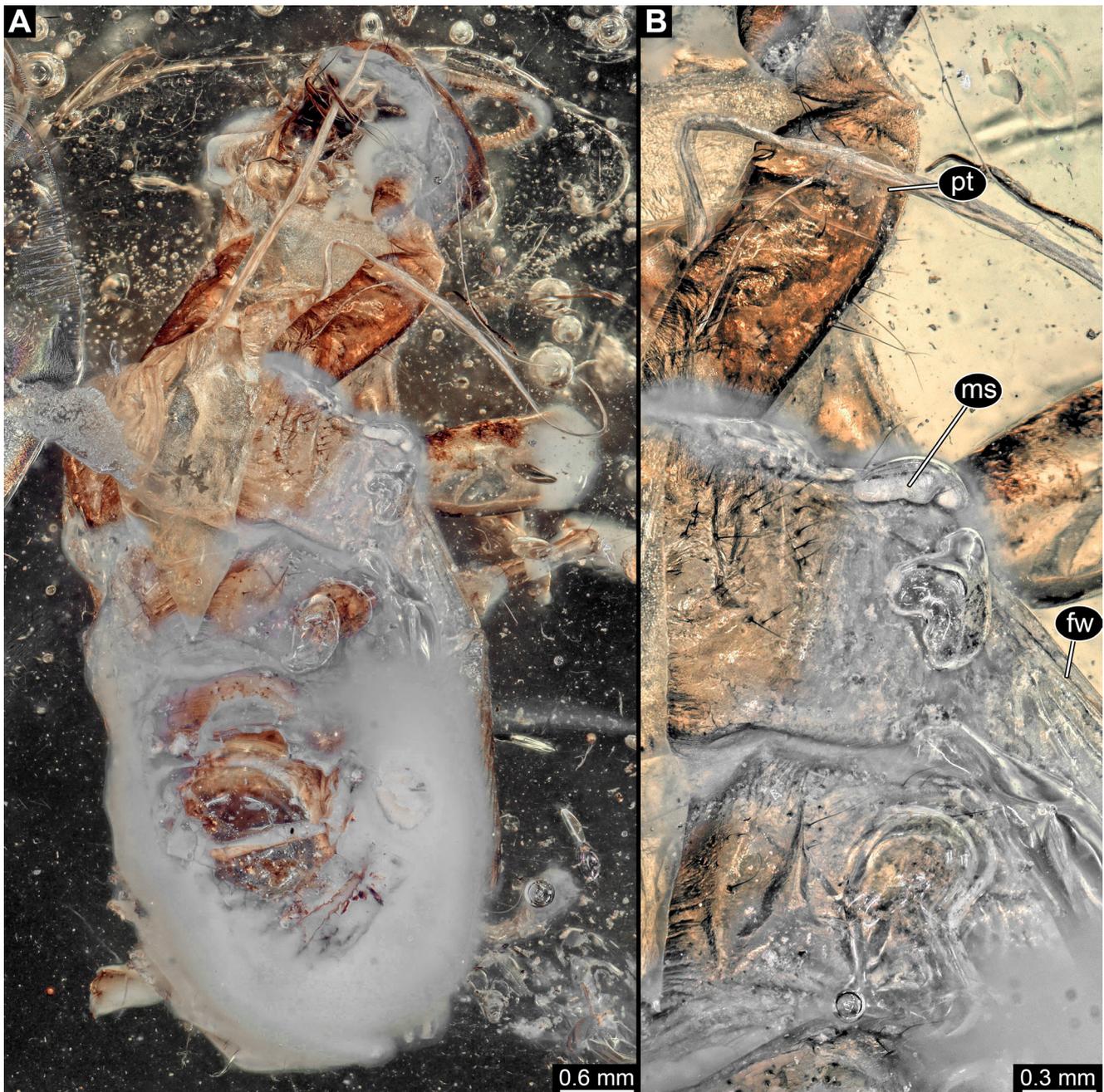
Fig. 5 - New specimen PED 1389, Eocene pupal exuvia, Rovno amber, continued. A) Dorsal view. B) Close-up on the setation of the nota. Abbreviations: fw = forewing; ms = mesothorax; pt = prothorax.

Shape analysis of femora of fossil and extant specimens

The shape analysis of the entire data set resulted in three effective principal components (PCs), together explaining 95.51% of the overall variation (Supplementary File 1).

PC1 explains 85.21% of the overall variation. It is dominated by the overall shape of the femur. High values indicate a simpler overall morphology, low values indicate an overall y-shaped outline (note:

the factor loadings extremes depict non-existing morphologies; Supplementary File 2).

PC2 explains 7.59% of the overall variation. It is dominated by the relative length of the femur. High values indicate a more elongate shape, low values a stouter shape (Supplementary File 2).

PC3 explains 2.72% of the overall variation. It is dominated by the proximal shape of the femur. A high value indicates a narrow proximal region, a low value a broader one (Supplementary File 2).

Shape analysis of femora of only extant specimens

The shape analysis of only the extant specimens resulted in four effective principal components (PCs), together explaining 93.73% of the overall variation (Supplementary File 1).

PC1 explains 74.23% of the overall variation. It is dominated by the relative length of the femur and presence of a prominent spine. A high value indicates a stout shape without a prominent spine, a low value indicates a more elongate shape with a prominent spine (Supplementary File 3).

PC2 explains 10.82% of the overall variation. It is dominated by the shape of the proximal region of the femur. A high value indicates a less drawn out proximal region, a low value a stronger drawn out proximal region (Supplementary File 3).

PC3 explains 5.86% of the overall variation. It is dominated by the shape of the proximal region of the femur. A high value indicates a broader proximal region, a low value a narrower proximal region (Supplementary File 3).

PC4 explains 2.82% of the overall variation. It is dominated by the shape of the proximal region of the femur. A high value indicates a broader proximal region, a low value a narrower proximal region (Supplementary File 3).

Discussion

Moult remains and the fossil record

The specimen reported here is clearly an exuvia due to the presence of an open wide ecdysial suture in typical position, i.e., dorsomedially from the head to the last thoracic segment, through which shed, tube-like tracheal cuticle is visible (Fig. 5). Exuviae can be challenging to interpret in moulting animals, as it can be impossible to differentiate between a moult remain and a half-rotten carcass. However, it is often quite straightforward to recognise exuvial remains of representatives of Insecta.

While an exuvia provides informative characteristics from the original morphology, it tends to be less reliable for quantifiable aspects due to the deformation of structures (a reason why the specimen was not included in the quantitative analysis). Assessing a pupal exuvia – particularly a fossil one – allows ensuring that the pupal development of that particular species was maximum at the moment of moulting, save from variation from environmental factors.

A philosophical aspect concerning exuviae is whether they should be considered body fossils or trace fossils (see discussion in Vallon et al. 2015). The usual argument for the latter is that a fossil exuvia does not represent the true individual, but a remain produced by it. Yet, this argument poses some challenges (see also Baranov et al. 2022b).

Most representatives of Euarthropoda spend their lives with two layers of cuticles; adults of the group Pterygota are in fact an exception. In many extant specimens, but also some fossil ones, it is possible to see both cuticles (evident in some figured extant pupae of mantis lacewings, e.g. Marquez-López & Contreras-Ramos 2018, fig. 1A p. 68). Both these layers are part of the individual. When the outer cuticle is moulted, it becomes separated from the original individual. Yet, does this make it a 'trace'? Different representatives of Euarthropoda can actively detach an appendage at predetermined 'breaking points' (i.e., autospasy). Does such a lost appendage also represent a 'trace'?

An exuvia clearly provides information of a specific semaphoront from an individual, i.e., the morphology at a specific time slice (see also Vallon et al. 2015). This is therefore not fundamentally different from an individual dying at a specific time slice. An exuvia would simply need to be treated as a slightly deformed individual.

In summary, the information provided by an exuvia is not fundamentally different from that provided by a carcass. Considering exuviae as trace fossils provides no practical advantages.

Identity of the new specimen

The new specimen PED 1389 can be readily identified as pupa due to the presence of wing pads in combination with its overall habitus clearly indicating an ingroup position within Neuroptera. Within this group, the prominent raptorial forelegs of the pupa are diagnostic for the monophyletic group Mantispidae + Rhachiberothidae within Mantispoidea. Further-reaching interpretations are more challenging than with adults, as many diagnostic features on the forelegs are not yet fully developed (see also further below for this aspect). Still the major ingroups (often considered subfamilies) of Mantispidae should be distinguishable at the pupa stage.
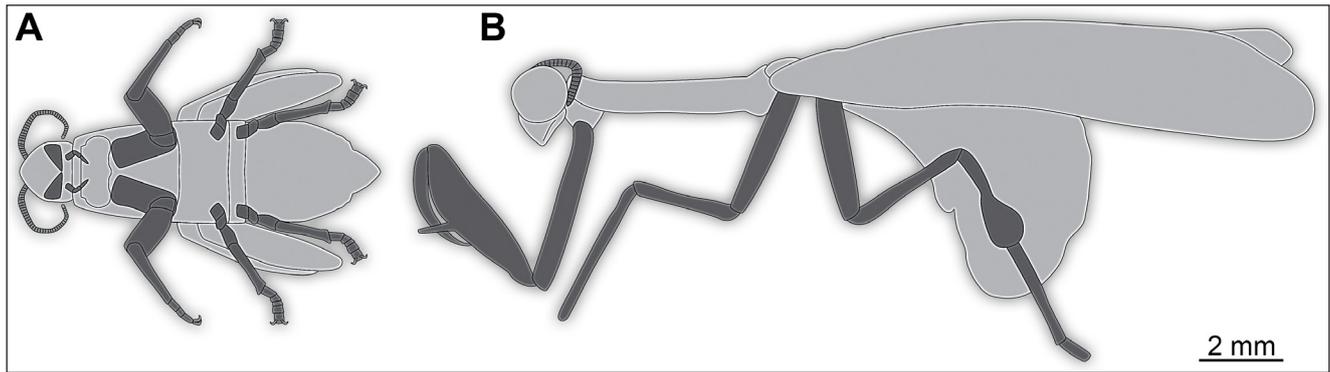
Fig. 6 - Size comparison of the new pupa (A) and the single known adult in Eocene amber (B, based on Baranov et al. 2022a).

According to the figured pupae of Mantispinae provided by Lucchese (1956) and Schremmer (1983), less evidently so in Marquez-López & Contreras-Ramos (2018), the wing venation pattern in the wing pads (at least in late pupal stages) is strongly consistent with that of the adult. Therefore, in pupae of Mantispinae the radial sector is formed by rather short branches forming rather angular cells in a consistent pattern due to the presence of a regular gradate series of crossveins.

A far anterior foreleg insertion on the prothorax, immediately posterior to the head, seems typical for all major ingroups of Mantispidae with the exception of Symphrasinae. Such an anterior insertion is evident in late pupae such as those of *Climaciella brunnea* (Mantispinae) and *Ditaxis biseriata* (Drepanicinae) (Dorey & Merritt 2017; Marquez-López & Contreras-Ramos 2018).

The pupa of *Plega yucatanae* (Symphrasinae) depicted by Parker & Stange (1965) was described as possessing a foretarsus with four elements. Also, in that specimen the foreleg insertion on the prothorax is not immediately behind the head, but further posterior. These two diagnostic characters also occur in adults of Symphrasinae (Ardila-Camacho et al. 2021). The venation pattern in the latter specimen is unclear as only costal veinlets were depicted (some basal ones twigging in contact with the costal margin). The further posterior foreleg insertion on the prothorax is also evident in the photographs of the pupa of *Plega hagenella* provided by Maia-Silva et al. (2013).

In sum, even though the four-segmented foretarsi cannot be ascertained from the present fossil, the further posterior foreleg insertion (not immediately posterior to the head, separated by an apparent membraneous region) and the venation of the wing pads (lacking angular cells) suggest that the specimen is a representative of Symphrasinae. Yet it cannot be fully excluded that it is a representative of Rhachiberothidae, as pupae for this group are still unknown.

The fossil record of Mantispidae

The fossil record of mantis lacewings is especially rich in the Mesozoic, including numerous fossils in sedimentary rocks and in different types of ambers (see recent summary in Baranov et al. 2022a). Fossils in sedimentary rocks are restricted to adult specimens. Mesozoic ambers have provided a wealth of different mantis lacewing adults (Lu et al. 2020; Shi et al. 2020a, b), but also some larvae, supposedly all stage 1 larvae (Haug et al. 2018, 2021c).

A more restricted number of mantis lacewings has been provided by Eocene ambers so far. Four possible larvae (Ohl 2011; Wunderlich 2012) and a single adult (Baranov et al. 2022a; Fig. 6) have been reported. Miocene ambers are, again, richer in adult mantis lacewings, with at least three specimens known (Engel & Grimaldi 2007); yet, no larvae have been hitherto reported.

The new fossil therefore expands the overall still scarce fossil record of mantis lacewings in the Eocene. It also represents the first record of a mantis lacewing in Rovno amber and the first fossil record of a pupal stage of Mantispidae.

Based on the scarcity of Mantispidae in Baltic amber and a likely ingroup position of the new fossil within Symphrasinae, it very likely represents a new species. However, we refrain from formally erecting a new species because providing a differential diagnosis would not be possible and would render the taxonomy for Eocene mantis lacewings challenging.
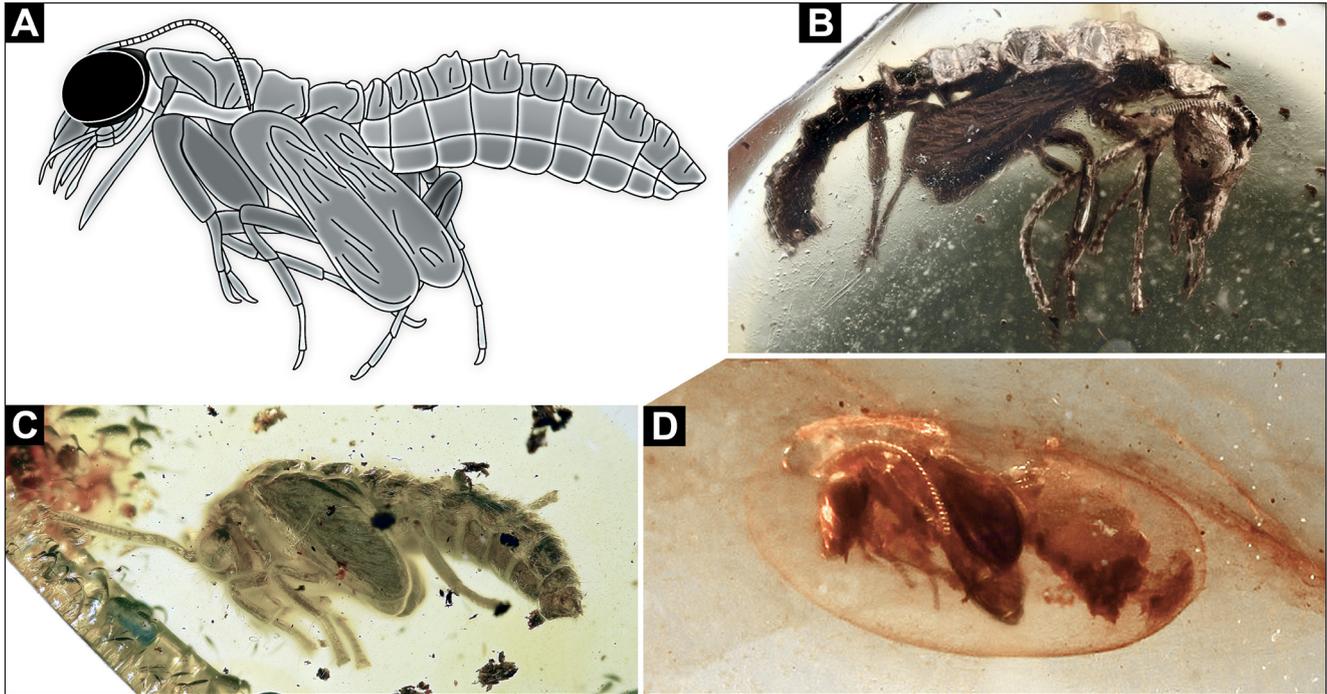
Fig. 7 - Other lacewing pupae in the fossil record. A) Specimen from Lower Cretaceous French amber, redrawn from Soriano et al. (2010, fig. 1 row three right p. 363). B) Specimen from Eocene Baltic amber, image provided by Jonas Damzen (amberinclusions.eu); now part of the Collection Gröhn (CCGG 7309; Makarkin 2022). C) Specimen from Eocene Baltic amber, image provided by Marius Veta (amber-treasure4u.com). D) Specimen from Cretaceous Kachin amber, Myanmar, image provided by Simon Chen (burmiteamberfossil.com).

The fossil record of lacewing pupae

Pupae of lacewings have been scarcely reported in the fossil record. A fossil in Lower Cretaceous French amber was identified as a snakefly pupa (Raphidioptera; Soriano et al. 2010); yet the rather short head and prothorax suggest that this specimen represents a pupa of a lacewing (a clear snakefly pupa was depicted in Zhang 2017).

Makarkin (2022) reported a pupa, more precisely a late stage pupa often referred to as a pharate adult, from Baltic amber. Makarkin (2022) interpreted the specimen as a representative of the group Hemerobiidae, possibly of the ingroup *Sympherobius*. Searching outside the scientific literature has provided two more specimens preserved in amber (Fig. 7).

All these pupae lack prominent specialisations known in pupae of specific ingroups of Neuroptera (such as elongate mouthparts and curled hind wings of thread-winged lacewing pupae: Pierre 1952 figs. 27, 28; Aspöck & Aspöck 1999 fig. 63 p. 23) and based on available information remain difficult to interpret. They seem unlikely to be pupae of mantis lacewings. Therefore, the new specimen is a rare find of a fossil pupa of Neuroptera – the first one for Mantispidae – and the first case of

a fossil pupal exuvia for Neuroptera, possibly even Neuropterida.

The femoral morphology of mantis lacewing pupae in comparison to the adults

All examples of lacewing pupae differ in significant morphological aspects from their corresponding adults, especially in the details of the raptorial legs (forelegs). These aspects seem to have gained little attention; although Brauer (1855) stated that the legs in the pupae are already fully developed as in the adult (pp. 482–483), that is apparently not the case.

In adults, the femur of the foreleg is armed with prominent 'spines' (actually not spines in the strict sense, but outgrowths of the femoral cuticle distally bearing modified setae, hence in principle drawn out sockets; see e.g. discussion in Pérez-de la Fuente & Peñalver 2019). The tibia forms the major part of the movable finger of the sub-chela, but the tarsus can variably contribute to the functional finger (Fig. 2C, E, J). The basi-tarsus (proximal element; proximal tarsomere) can, for example, be enlarged or be drawn out and spine-like. The further distal part of the tarsus is rather small in some mantis lacewings, partly concealed by the spine-like

protrusion (e.g. Alvim et al. 2019 fig. 2F p. 278). Alternatively, the entire distal tarsus can be a quite small structure sitting distally 'on top' of a cone-shaped basi-tarsus (e.g. Ohl 2004 fig. 3 p. 194). Pre-tarsal claws can be small (e.g. Reynoso-Velasco & Contreras-Ramos 2019 fig. 8C p. 144) or even be partially absent (e.g. Reynoso-Velasco & Contreras-Ramos 2019 fig. 9C p. 148).

In the pupae, these morphological aspects are quite different (Fig. 2A, D, H). The femur (still) lacks the 'spines' and the tarsus is average in size, not smaller or specialised. These differences are more apparent in some late stage pupae with a rather transparent cuticle with the (more or less developed) adult inside (pharate adult; Fig. 2B, I; e.g. Maia-Silva et al. 2013 fig. 1 p. 103, fig. 2 p. 104). This pronounced difference between adult and pupa is also evident in the quantitative analysis (Figs. 8, 9): extant pupae plot clearly outside the area occupied by extant adults based on femur morphology. However, pupae plot close to some fossil adults with barely developed femoral 'spines' (Fig. 8; especially specimen 0003, *Sinomesomantispa microdentata*). The Mesozoic adults occupy a large area of the morphospace, much larger than that of the extant adults. This is not surprising, as former studies have indicated that Mesozoic representatives of Mantispidae were in certain aspects more derived than modern ones (e.g. Lu et al. 2020; Shi et al. 2020a, b; Baranov et al. 2022a).

In sum, mantis lacewing pupae tend to have a less specialised morphology than the adults regarding the foreleg morphology. The pupa morphology of mantis lacewings in principle resembles the adult morphology of other lacewings, at least concerning the forelegs.

The morphology of mantis lacewing pupae in the light of the ontogenetic sequence
Stage 1 larvae of mantis lacewings have well-developed, functional locomotory legs. Femur and tibia are elongate. The tarsus is already present, but rather short and not subdivided into tarsomeres, distally carrying a pair of claws and a prominent trumpet-shaped empodium (attachment structure; Fig. 2F; e.g. Hoffman & Brushwein 1992).

In stage 2 and 3 larvae, legs are functionally no longer important due to the specific life habits of the larvae (see e.g. Riek 1970; Redborg & MacLeod 1985; Hoffman & Brushwein 1992). Femur

and tibia are stout and short. The tarsus is simple, spine-like without claws or other distal structures (Fig. 2G).

Together with the morphology of the pupae, this gives an ontogenetic sequence for the femur of (1) elongate (stage 1 larva), (2) stout (stages 2 and 3 larvae), (3) elongate (pupa), (4) elongate with 'spines' (adult). This is a classical example for an indirect development (see discussion in Haug 2019). The pupa here clearly serves as an intermediate stage to allow the transition from the stout unarmed morphology of the late larvae via the elongate but unarmed morphology of the pupa to the elongate and armed morphology of the adult. This sequence, together with the fact that the femur morphology of the pupa basically resembles that of adults of other lacewings, indicates that the raptorial legs, or more precisely the femur, of mantis lacewings likely evolved via heterochrony by adding a new morphology at the end of the ontogeny (hypermorphosis + predisplacement; see discussion in Haug et al. 2010).

For the tarsus, the ontogenetic sequence is: (1) developed, with distinct distal structures, e.g. pair of claws, but not subdivided (stage 1 larva), (2) reduced, simple, still not subdivided (stages 2 and 3 larvae), (3) well developed, again with a pair of claws, subdivided into tarsomeres (pupa), and (4) variably reduced in size, still with claws (although they can be reduced or only one present), still subdivided, with the basi-tarsus drawn out into spine-like structure in some forms (adult). For the tarsus, it also appears that the morphology is a result of a hypermorphosis + predisplacement. Still, it gives an impression of developed-underdeveloped-developed-underdeveloped, so forth and back, forth and back. The unusual condition here is the well-developed tarsus in the pupa. There is little functional use for it besides in the short period when the latest pupa/pharate adult (with the almost fully developed adult inside) is motile in order to find a suitable area for the adult eclosion. Most likely, the well-developed tarsus is a real evolutionary relict here. Developing it may simply not have enough costs to cause a negative selective pressure against it.

The pupa as a step in-between
It has often been assumed that the pupa is very similar to its corresponding adult (see discus-
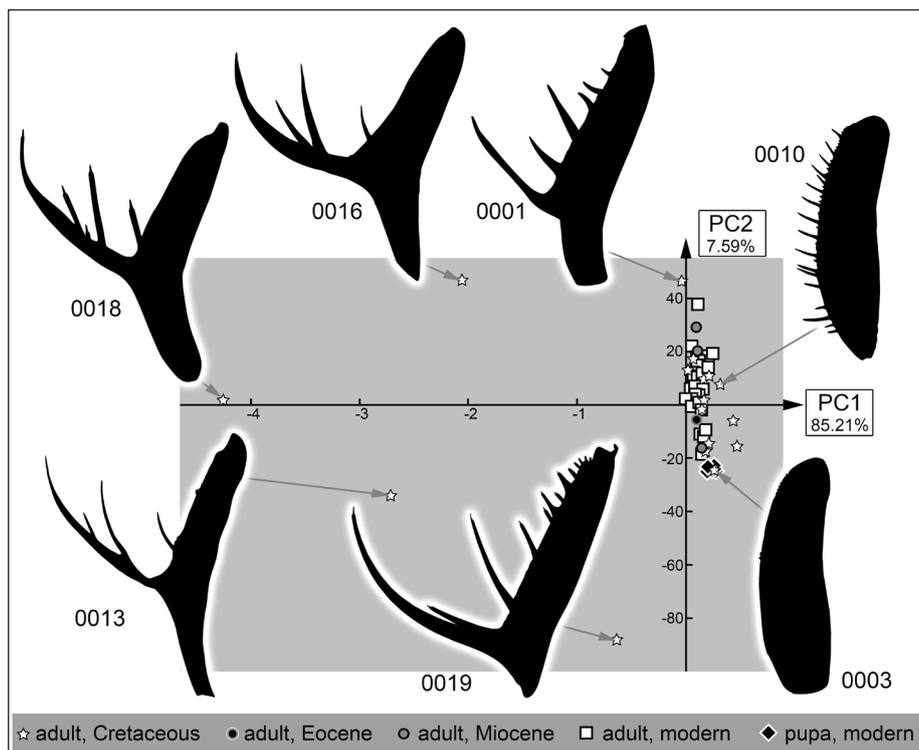
Fig. 8 - Morphospace of femur shape of the entire data set of Mantispidae. Note how large the occupied area of the Cretaceous specimens is and how densely the pupae plot. Numbers refer to Supplementary Table 1.

sion in Saltin et al. 2016). This may be certain for many ingroups of Neuroptera. The large transformation process from the highly specialised larval morphology, especially in the head region, appears to take place in the moult to the pupa, so basically the restructuring process occurs in the pre-pupa phase (Zhao et al. 2020). Hence, for many lacewings not much morphological change is apparent from pupa to adult.

Yet, whenever more extreme morphologies are to be expressed in the adult, the pupa provides the possibility to develop this very morphology in a step-wise manner. Whenever a strongly metamorphic moult occurs in a representative of Euarthropoda, there is an associated risk for the moulting animal. If the morphology of the inner cuticle is very different from the outer one, it can be difficult to fit it in at all (Saltin et al. 2016), and dragging it out without damaging it might be challenging. Therefore, strongly metamorphic moults could potentially kill larger parts of a population during this process (see discussion in Haug 2020b). Hence, a kind of 'two-moult transformation' offers a possibility of reducing this risk (Saltin et al. 2016).

It appears that for mantis lacewings the pupa allows the development of a complex armed raptorial appendage from a rather stout and overall reduced one appearing during late larval morphology. It would be interesting to know how the transition takes place in the likewise raptorial representatives of Rhachiberothidae (or Rhachiberothinae), yet so far no pupa seems to have been reported for this group.

Outlook: The pupa as a phylotypic stage?

Another aspect of the quantitative analysis is worthy of discussion. The occupied area of the pupae not only falls outside of the area of extant adults, but it is also remarkably reduced. It could be argued that the sample size is also smaller than that of the adults. Yet, this cannot explain the difference, as the area is not only smaller, but the individual points also plot very densely, indicating less morphological variation. A developmental stage showing less variability than other stages potentially could represent a phylotypic stage (see discussions in Cridge et al. 2019; Tautz 2019).

The pupa could be less affected by selective pressures than other post-embryonic stages since it is less active, it does not have to feed nor find a partner to reproduce. It is therefore quite possible that the pupa could represent a phylotypic stage, at least for Mantispidae. With the available data, despite being limited to a single structure, it remains im-

Fig. 9 - Morphospace of femur shape of only the extant specimens of Mantispidae. Note how densely the pupae plot. Numbers refer to Supplementary Table 1.
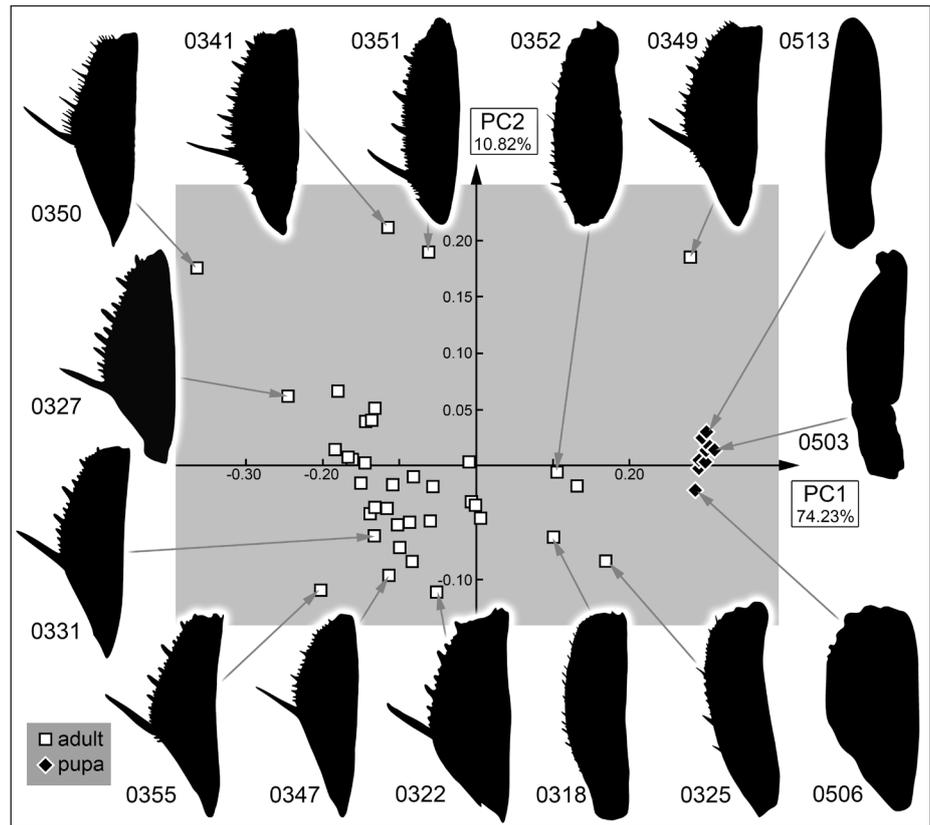
possible to make further quantitative explorations of this aspect. There are almost 20 stage 1 larvae available in the literature with aspects of the front legs accessible (Haug et al. 2021c). Yet, for stage 3 larvae not even a handful of comparable data is available. This leaves us with the observation that the pupa has less variability in the morphology of the raptorial legs than the adults, but whether pupal variability is lower than that of the larvae remains unclear. Expanding the data set will be necessary to further explore the pupa as a possible phylotypic stage.

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