

Morphology of the primary larva of *Mantispa aphavexelte* Aspöck & Aspöck, 1994 (Neuroptera: Mantispidae) and phylogenetic implications to the order of Neuroptera

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Accepted 09.x.2018.

Published online at www.senckenberg.de/arthropod-systematics on 27.xi.2018.

Editors in charge: Martin Fikáček & Klaus-Dieter Klass

Abstract. The external and internal morphology of the primary larva of *Mantispa aphavexelte* was studied and documented with a broad spectrum of techniques. The cephalic anatomy, which is very similar to conditions found in other neuropteran immatures, is mainly affected by the formation of specialized mandibulo-maxillary sucking tubes and associated internal features. The postcephalic anatomy largely follows a generalized holometabolous pattern, with well-developed muscles in the thorax and the abdominal segments, an elongate, uncondensed ganglionic chain, and well-developed Malpighian tubules. The phylogenetic analysis of 70 larval characters suggests a weakly supported clade comprising Dilaridae, Berothidae, Rhachiberothidae and Mantispidae. Mantispoidea comprising Rhachiberothidae, Berothidae and paraphyletic Mantispidae is suggested by overlapping scales on antennae and maxillae, thoracic “trichobothria”, and hypermetamorphosis with scarabaeiform 2nd instar larvae. The relationships of the mantispoid terminals are not resolved, and *Mantispa* (Mantispinae) and *Plega* (Symphrasinae) are not retrieved as sister taxa. Spider parasitism and feeding in spider egg sacs is characteristic for Mantispinae, whereas immatures of Berothidae and non-mantispine mantispid larvae prey on the offspring of social or non-social aculeate Hymenoptera, on termites, or on immatures living in soil or under bark, for example scarab larvae. Specializations of the legs like a trumpet-shaped empodium and a fixed tarsal pseudoclaw, enable mantispine larvae to cope with functional challenges linked with their specialized form of parasitism, like entering a host or penetrating its egg sack. The largely immobilized and straight sucking stylets are suitable for piercing eggs of spiders, but not for grasping prey. The terminal eversible attachment structure probably provides anchorage of the abdominal apex and thus may facilitate the penetration of the egg sac or membranes of the body surface of a spider. It may also facilitate boarding a passing suitable host. Very small size of the 1st instars and hypermetamorphosis are likely linked with parasitism. Even though the primary larvae of *M. aphavexelte* belong to the smallest immatures in Neuroptera, the effects of miniaturization are very limited.

Key words. Neuroptera, *Mantispa*, larva, morphology, hypermetamorphosis, miniaturization, phylogeny.

1. Introduction

It was pointed out by ASPÖCK (1999) that the eminent naturalist Johan Christian Fabricius interpreted mantidflies as small praying mantises (Dictyoptera: Mantodea), whereas LINNAEUS (1758) and SCHNEIDER (1843) assigned the species known by that time to the genus *Raphidia* (Neuropterida: Raphidioptera). A reliable assessment of the systematic position was only possible when first instar larvae were discovered (BRAUER 1852a), and the

later stages during the course of the following 17 years (see ASPÖCK 1999). All immature stages and the development and biology of *Mantispa styriaca* Poda, 1761 were described by BRAUER (1852a) and ROGENHOFER (1862), pioneers in discovering the life-cycle of the genus (ASPÖCK 1999). A historical drawing of the 1st instar larva in BRAUER (1852a) and the convincing phylogenetic assignment based on the modification of the mouthparts

as sucking tubes (BRAUER 1852b) were milestones in the investigation of Neuroptera (ASPÖCK 1999).

Mantispidae or mantispid lacewings comprise about 410 extant species grouped in 44 genera (ASPÖCK & ASPÖCK 2005; OHL 2004, 2005). The small or medium sized adults (forewing length 5–35 mm) are characterized by an elongated prothorax, a triangular head with large compound eyes, and especially raptorial forelegs, features resulting in a habitus strongly reminiscent of the dictyopteran praying mantises (Mantodea).

The group is presently subdivided into four subfamilies, Symphrasinae (Nearctic, Neotropical), Drepanicinae Enderlein (Oriental, Australasian, Neotropical), Calomantispinae Navás (Australasian, Nearctic, Neotropical) and Mantispinae Leach (Oriental, Australasian, Palaearctic, Afrotropical, Neotropical, Nearctic) (LAMBKIN 1986 a,b; OHL 2004). The time of origin of the family is estimated as Late Triassic to early Jurassic (LIU et al. 2015). Presently less than 20 fossil named species of Mantispidae are known (ENGEL & GRIMALDI 2007; WEDMANN & MAKARKIN 2007; POINAR & BUCKLEY 2011; JEPSON et al. 2013; KHRAMOV 2013; SHI et al. 2014; JEPSON 2015). Despite of the very characteristic habitus and prey-catching habits of adults, the monophyletic origin of the family is presently contentious. It was supported in a study based on mitochondrial genes and morphology (LIU et al. 2015). In contrast, anchored phylogenomics suggested paraphyletic Mantispidae (WINTERTON et al. 2018), with Rhachiberothidae + Symphrasinae as sister-group of a clade comprising Berothidae + [(Drepanicinae + Calomantispinae) + Mantispinae].

The biology of Mantispidae was summarized in NEW (1986) and REDBORG (1998). One of its main characteristics is a transition field between larval predacious habits and parasitism. Females deposit tremendous numbers of stalked eggs. After hatching, the very small and agile primary larva remain in aggregations or drop to the ground (e.g. Drepanicinae; e.g. DOREY & MERRITT 2017). Finding a suitable food source is the vital factor. The tiny first instars either walk on the substrate or are dispersed by the wind. There are two major groups of prey or hosts, spiders in the case of Mantispinae (and possibly Drepanicinae; DOREY & MERRITT 2017) and social Hymenoptera in case of Symphrasinae. However, the prey or host spectrum of Mantispidae is distinctly broader, also including eggs or postembryonic stages of solitary wasps (BUYS 2008), roaches, termites, beetles, flies, and lepidopterans (MACLEOD & REDBORG 1982). Like in the related Berothidae (and likely Rhachiberothidae), the development of Mantispidae is characterized by a specific type of hypermetamorphosis (BRAUER 1869). Second and third larval instars are physogastric, grub-like, stump-legged (BRAUER 1852a, 1855a,b; ROGENHOFFER 1862). SCHREMMER (1983) observed that in egg cocoons of lycosid spiders (“*Tarentula*”) up to three *Mantispa* larvae developed to the pupal stage in addition to up to 240 immature spiders. This and the fact that larvae feed on spiders haemolymph before entering eggsacs suggested true parasitism and not predacious habits as

BRAUER (1852a,b) concluded when observing *Mantispa* in cocoons of Lycosidae. Larvae of Mantispinae feed exclusively on spider eggs as far as known at present. The first instar of *Mantispa styriaca* searches actively a spider egg sack (Lycosidae or Salticidae) and enters it (BRAUER 1869). The larva of *Mantispilla perla* Pallas, 1772, however, boards a passing spider, spends a period of time on it, and only in spring enters the completed egg sack (LUCCHESI 1956). Likewise, Nearctic Mantispinae are “spider-boarders” (REDBORG & MACLEOD 1982). In contrast to spider-associated Mantispinae, larvae of Symphrasinae and Calomantispinae are distinctly less specialized as pointed out above, rather preying upon slow moving or immobile immature stages of other insects. Recently it has been reported by DOREY & MERRITT (2017) that newly hatched larvae of Drepanicinae burrow in soil after dropping and possibly prey upon small spiders.

After several revisions the genus *Mantispa* has a palearctic distribution after some species from the new world were moved to other genera. (HOFFMAN 2002; SNYMAN et al. 2012, 2018). The type locality of *Mantispa aphavexelte* Aspöck & Aspöck, 1994, the species in the focus of this study, is on the Greek Island of Samothraki. The present distribution area comprises Southern Europe, Morocco, Anatolia, Caucasus, Armenia, Kazakhstan, Mongolia (ASPÖCK et al. 2001), and as recently demonstrated also Germany (NIEHUIS et al. 2014). Like the type species of the genus, *Mantispa styriaca* (type locality in Austria), *M. aphavexelte* belongs to *Mantispa* sensu stricto as originally defined.

The primary larva of *M. aphavexelte* is described here for the first time. Whereas larval head structures of Neuroptera, especially skeletal features, are quite well-known (e.g. WUNDT 1959; MACLEOD 1964; BEUTEL et al. 2010), the anatomy of the postcephalic body was almost completely unknown, as it is also the case in other groups of Holometabola (e.g. BEUTEL et al. 2009, 2011). Consequently, the aim of this study was to document external and internal features of the entire larva, using a broad spectrum of techniques, especially scanning electron microscopy, microphotography, histology and computer-based 3D reconstruction. The morphological findings are interpreted with respect to possible effects of miniaturization and correlations with parasitic data. The new data are also entered in a data matrix mainly based on BEUTEL et al. (2010). The data set was analyzed cladistically after adding some characters and the genus *Plega* Navás, 1927 of the subfamily Symphrasinae.

2. Material & methods

2.1. Material

The specimens used for this work were obtained from an egg-laying female. This specimen was collected by H. Pohl at the 28.VIII.2012 in Italy, Umbria south of Monte

del Lago, Castello di Zocco, ruins, olive grove, ruderal, 260 m (43°8'9.47"N 12°9'57.73"E). Primary larvae were hatching from the eggs in Jena under laboratory conditions. The material was fixed overnight in Dubosq-Brasil and stored in 70 % ethanol. The larvae were determined by the identification of the mother animal after ASPÖCK & ASPÖCK (1994) by H. Pohl.

Additional larval material. Psychopsidae: *Psychopsis* Newman, 1842 sp., Queensland, Footprint Scrub, 19°41.3'S 146°26.4'E, 10.II.2007, C.J. Burwell & G.B. Monteith coll., det. Sh. Winterton. — Nymphidae: *Nymphes myrmeleonoides* Leach, 1814 Brisbane S.E., 27.IV.1987, J. Grimshaw coll., det. Sh. Winterton. — Nemopteridae: *Nemopteridae* sp., S. Namibia, Tok Tok-kie trails, XI. 2000, V. Grebennikov coll.

2.2. Methods

SEM-micrographs were taken with a Philips ESEM XL30 (Philips, Amsterdam, Netherlands). The larva was dehydrated and dried with CO₂ at the critical point with an Emitech K850 Critical Point Dryer (Sample preparation division, Quorum Technologies Ltd., Ashford, England) and sputter coated with gold with an Emitech K 500 (Sample preparation division, Quorum Technologies Ltd., Ashford, England). Specimens were glued to a micro-needle and fixed on a rotatable specimen holder (POHL 2010).

SEM pictures were used for morphological description of external structures of the primary larva of *Mantispia aphavexelte*. Images were processed with Adobe Photoshop CS2 (brightness, tone, picture arrangement). They were also used as template for vector graphics carried out with Adobe Illustrator CS2.

Two specimens were embedded in Araldite CY 212 (Agar Scientific, Stansted/Essex, England) and sectioned crosswise and lengthwise with a Microtome HM 360 (Microm, Walldorf, Germany) equipped with a diamond knife and stained with toluidine blue and pyronin G. The slides were digitalized with a Zeiss Axioscope (Carl Zeiss AG, Oberkochen, Germany) with a 40×-objective (1.5× post-enlargement) and a camera (PixeLink Capture Oem) equipped with PixeLink Capture OEM software (PixeLink, Ottawa Canada). To document some selected sections in higher resolution image were taken with an Olympus dot. Slide microscope (BX51, software version 3.4, Olympus, Tokyo, Japan).

The crosswise images were arranged and elastically aligned with ImageJ Fiji (SCHINDLER et al. 2012) and the Plugin Track_EM2 (CARDONA et al. 2012). The arrangement was corrected manually in Amira 6.0.1. and 6.1. (Visage Imaging GmbH, Berlin, Germany). The same software was also used for sectioning as basis data for 3D reconstruction. The data were transferred as image stacks to Imaris (Bitplane AG, Zürich, Switzerland) to generate 3D surfaces and converted into Wavefront-files (.obj) using Amira 6.1.

The size of the materials was reduced with Transform 2 Version 8.3.24 (Heiko Stark, Jena, Germany, URL: <http://starkrats.de>). Surfaces were then reduced and smoothed in AUTODESK MAYA 2017 (Alias Wavefront, Toronto/Ontario, Canada) to minimize artifacts in the reconstructions. The same software program was also used to produce illustrations with the rendering mode.

For phylogenetic analysis the data (72 characters of larvae and adults mostly from BEUTEL et al. 2010) were entered with Winclada (NIXON & CARPENTER 1993) and parsimony analyses were carried out with NONA (ratchet, 1000 replicates).

3. Morphological results

3.1. General appearance

(Figs. 1, 2)

The larvae are slender and of the campodeiform type. Head, thorax and abdomen are distinctly separated. The first instars are ca. 1 mm long and the maximum diameter is ca. 0.15 mm at the broadest part of the abdomen. The prognathous head is well sclerotized, especially the piercing-sucking paired mouthparts. Well-developed antennae, labial palps are present and three stemmata on each side. The three thoracic segments are of similar size. Three pairs of well-developed legs are present, all of them bearing an elongate trumpet-shaped adhesive empodium at the tip of the tarsus. The abdomen is composed of ten segments. Abdominal segment I is nearly the same size as the thorax segments. The following segments gradually decrease in size towards the abdominal apex. Segment X is elongated and bears an attachment structure. The dorsal regions of the thoracic and abdominal segments bear sclerotized tergites, whereas the ventral parts appear mostly semimembranous. Setae of different length are present on all body regions, with a higher concentration on the head capsule and mouthparts.

3.2. Head capsule

(Figs. 2, 3, 4, 10)

The prognathous head is strongly sclerotized dorsally and laterally and less so on the ventral side (Fig. 2A,B,C). The head capsule appears approximately quadratic in dorsal view; in lateral view it appears wedge-shaped, with the dorsal and ventral surfaces converging towards the anterior clypeolabral edge (Fig. 3C). The cuticular surface on the lateral parts of the head capsule forms a pattern of flat, elongated scale-like structures; the cuticular surface of the dorsal side is characterized by numerous fine ridges and enclosed furrows, resulting in a leaf-like pattern; two grooves are present on the frontal region, corresponding with the internal attachment sites of dorsal tentorial arms. The frontal and coronal

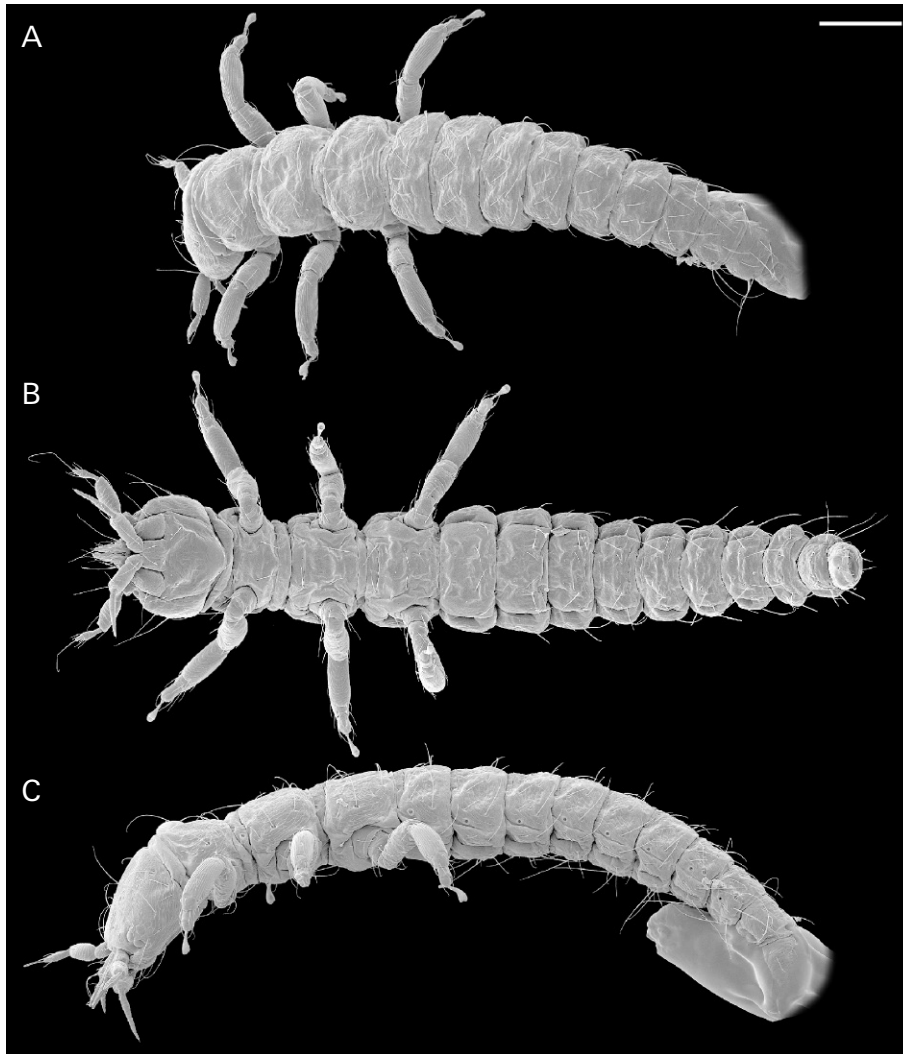


Fig. 1. SEM micrographs of 1st instar larva of *Mantispa aphavexelte*; **A:** dorsal view; **B:** ventral view; **C:** lateral view. — **Scale bar:** 100 μ m.



Fig. 2. Photographs of 1st instar larva of *Mantispa aphavexelte*; **A:** dorsal view; **B:** ventral view; **C:** lateral view. — **Scale bar:** 100 μ m.

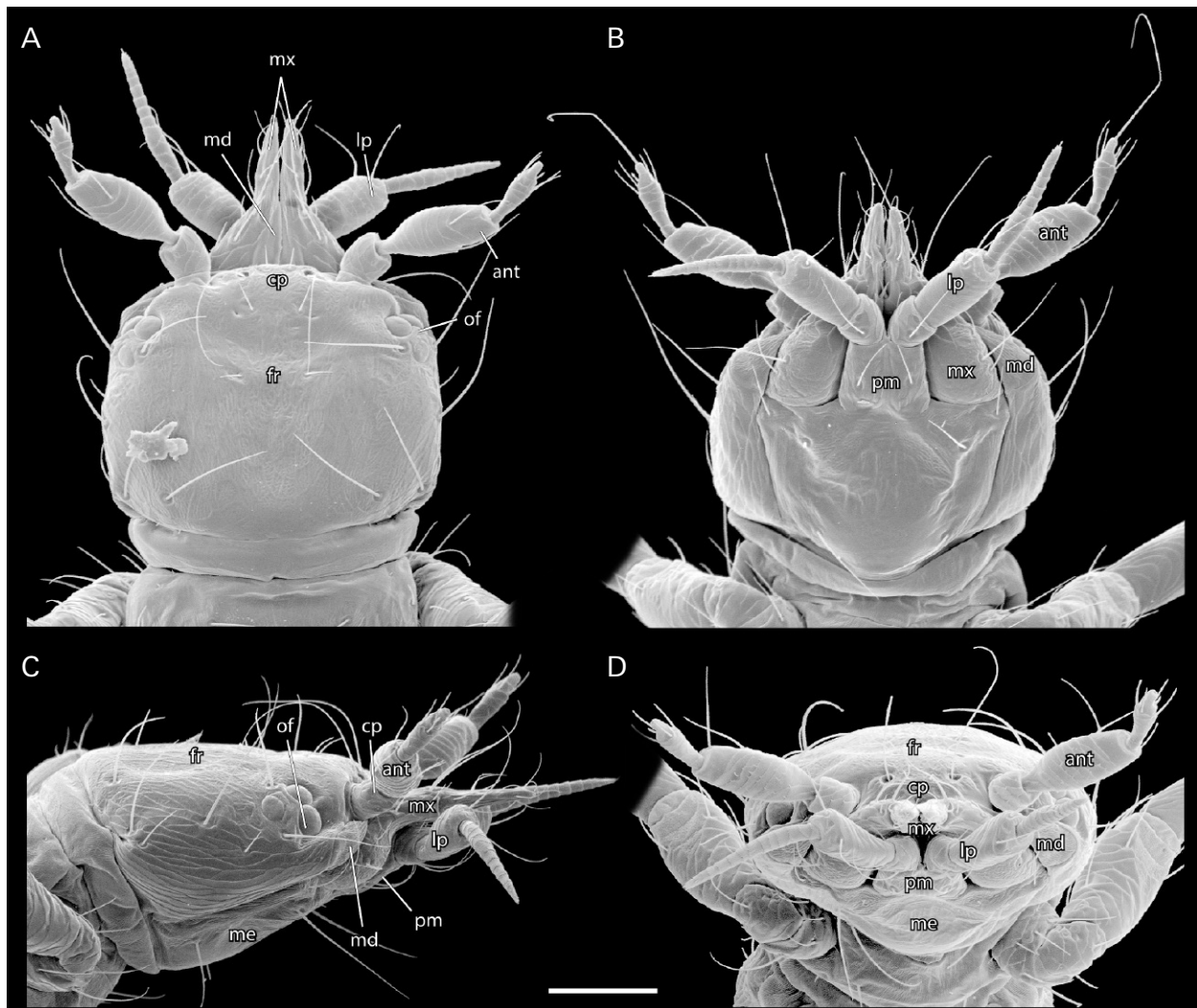


Fig. 3. SEM micrographs of head of 1st instar of *Mantispa aphavexelte*; **A:** dorsal view; **B:** ventral view; **C:** lateral view; **D:** frontal view. — **Abbreviations:** ant – antenna, atg – anterior tentorial groove, cp – clypeus, fr – frons, lp – labial palps, md – mandible, me – mentum, mx – maxilla, of – ocular field, pm – prementum. — **Scale bar:** 50 μ m.

ecdysial sutures are absent. Three well-developed stemmata are present on both sides, arranged in a triangular formation. The antennae are inserted anterior to the ocular field, very close to the anterior edge of the head capsule (Fig. 3A,D, ant); an exposed articular membrane is missing. The clypeolabral region is located between the antennal insertion areas. The ventral side of the head is largely occupied by proximal elements of the labium, especially the mentum, a condition referred to as “maxillary head” (e.g. ASPÖCK & ASPÖCK 2007); a gula is not developed and a hypostomal or postgenal bridge is also absent; the mentum is laterally enclosed by narrow ventrolateral parts of the head capsule, with a surface structure resembling that of the dorsal side. The head capsule and maxillary elements are distinctly separated by a ridge reaching into the cephalic lumen. The posterior part of the head is connected to a short collar-like cervical region; this semimembranous bulge completely encloses the occipital region but overlaps only very slightly with the posteriormost part of the head (Fig. 3A,B).

3.3. Internal skeletal structures (Figs. 7, 10–12, tt, tb)

The tentorium is well-developed. The anterior arms originate at distinct anterior tentorial grooves; the short dorsal arms arise in the middle region of the tentorium; the posterior arms originate posteroventrally close to the cervical region; thin lateral elements of a tentorial bridge arise from the posterior arms close to their area of origin; a very thin fusion area of these thin structures lies below the pharynx.

3.4. Stemmata (Figs. 4, 9)

The ocular fields are located posterior to the antennae and mandibles. The closely adjacent anterior two stemmata (Fig. 4, sm2, sm3) (diameter ca. 11 μ m) are placed above each; the posterior one (Fig. 4, sm1) (diameter ca. 9 μ m) is separated from their hind margin by slightly less than its diameter. The cuticular lenses are very distinctly delimited from the surrounding cuticle and distinctly convex.

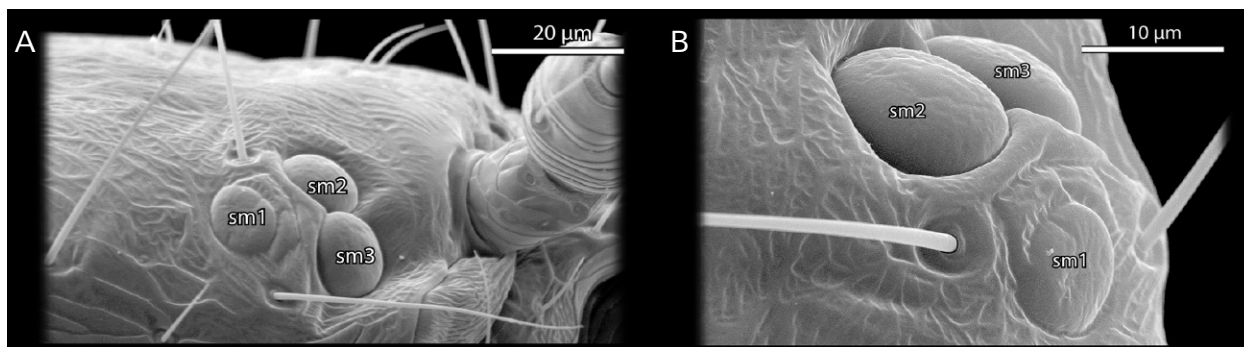


Fig. 4. SEM micrographs of ocular field of 1st instar of *Mantispa aphavexelte*; **A:** overview; **B:** dorsal view. — **Abbreviations:** sm1–3 – stemmata 1–3.

3.5. Labrum

(Fig. 3)

Not recognizable as a separate structure. Main labral sclerite completely fused with the clypeus and associated structures like tormae also absent. Labral muscles are also completely missing.

3.6. Antenna

(Figs. 5, 10)

The three-segmented antenna is inserted anterolaterally, laterad the lateral clypeal edge and very close to the anterior margin of the head capsule (Figs. 5, 3A,D). The first segment is inserted in a sclerotized narrow socket, but without an externally exposed articulatory membrane (Fig. 5, scp). The total length is around 0.1 mm. All antennomeres show a surface pattern of large, transverse scale-like areas separated by fine ridges, with minute cuticular thorns on the ridges on the antennomere 2. Antennomere 1 is ca. 15 µm broad and 20 µm long; few circular sensilla are embedded in the cuticle of the distal part, but setae are missing on this segment; the sharp oblique distal edge bears 1–2 minute sensilla. The club-shaped antennomere 2 inserts on a circular articulatory membrane (Fig. 5, mb); it is about 3 × longer than antennomere 1 and of equal width in its middle region, but very distinctly narrowed proximally and also slightly narrowing towards the apex; an apical articulatory membrane bearing the ultimate segment is enclosed by a well-defined circular edge; a sensorial appendage is missing; two long setae inserted on the distal half are pointing towards the antennal apex. The ultimate antennomere 3 is slightly more than half as long as the second segment and much less voluminous; it is also widened in its middle region, whereas the distal part is distinctly narrowed and peg-like; four distally directed setae of ca. 15 µm length are inserted on the distal third of this antennomere; one sensillum basiconicum is present in the same region; a conspicuous long seta arises from the tip of the last segment (MACLEOD 1964: specialized terminal seta of flagellum [abbreviation used by MACLEOD: FITS]).

Musculature: three extrinsic muscles are present (Fig. 10A, M1, M2, M3), two of them composed of two

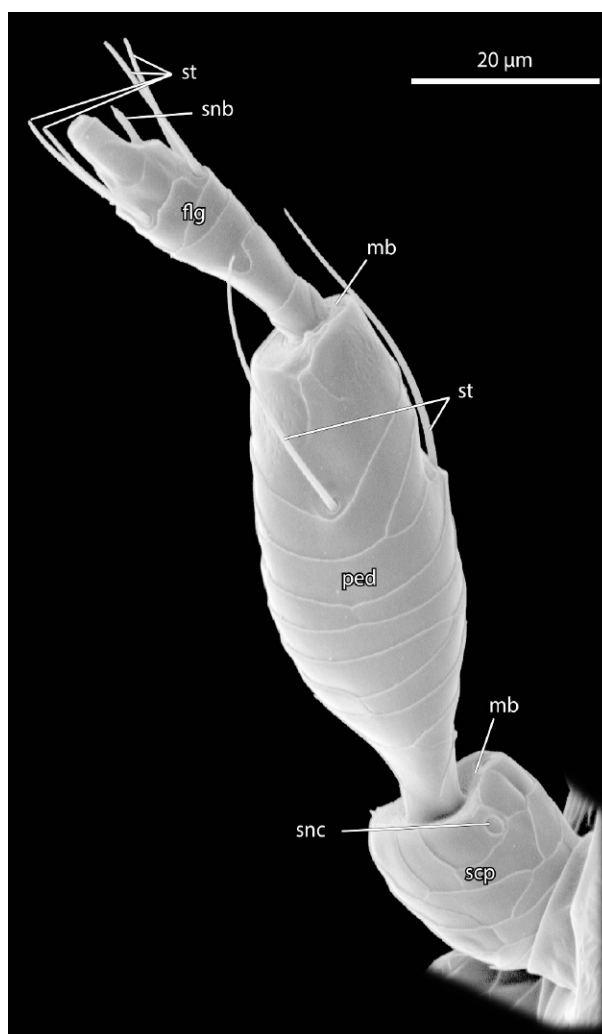


Fig. 5. SEM micrograph of antenna of 1st instar of *Mantispa aphavexelte*. — **Abbreviations:** flg – antennomere 3, mb – membrane, ped – antennomere 2, scp – antennomere 1, snb – sensillum basiconicum, snc – sensillum campaniformium, st – seta.

bundles. M. tentorioscapalis anterior/posterior/lateralis, O: two bipartite muscles on anterior frontal region, muscle with single bundle on dorsal tentorial arm; I: dorsally on anterior, posterior and lateral base of antennomere 1, respectively.

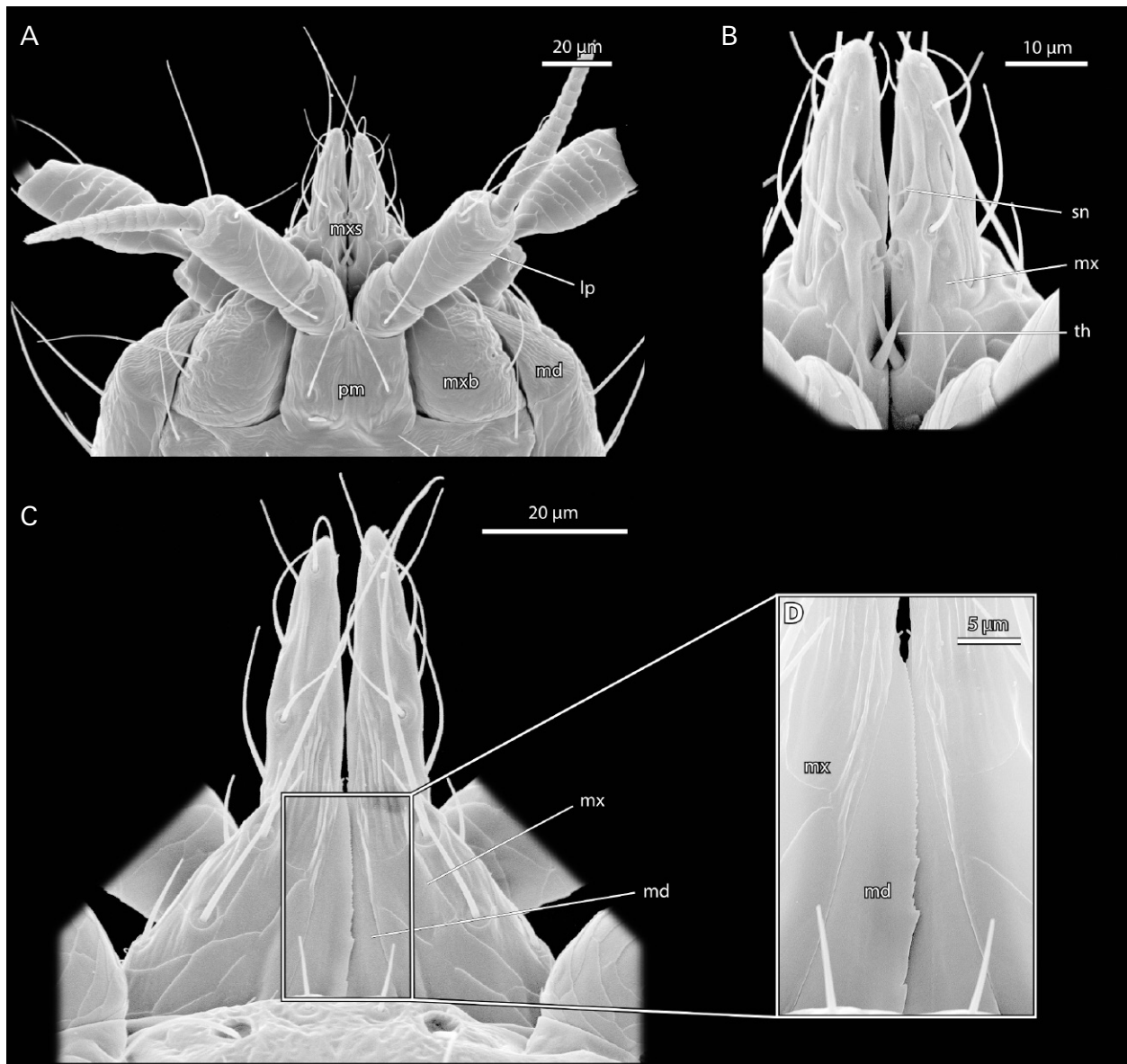


Fig. 6. SEM micrographs of mandibulo-maxillary complex of 1st instar of *Mantispa aphavexelte*; **A:** ventral view; **B:** maxillary stylet, ventral view; **C:** dorsal view; **D:** distal mandible, dorsal view. — **Abbreviations:** lp – labial palps, md – mandible, mxb – maxillary base, mxs – maxillary stylet, pm – prementum, sn – sensillum, th – thorn.

3.7. Mandibulo-maxillary complex (Figs. 6, 7, 9)

The mandibles and maxillae form a closely connected functional unit. Each of the partly immobilized symmetrical mandibles can only move together with the corresponding maxilla. The ventral mandibular base is distinctly separated from the head capsule, but the ventral primary joint is obsolete; a dorsal secondary mandibular joint is present but distinctly reduced and probably non-functional. The broad and relatively high mandibular bases are inserted posteroventrad the antennal insertions and mesad the maxillary bases (Fig. 6A, mxb). The main parts of the mandibles are flattened, blade-like sinuate structures, largely concealed by the clypeolabral region, but with protruding distal parts with straight, very slightly serrated mesal edges closely adjacent to each other in

midline (Fig. 6A,B). Dorsally the distal parts are overlapped by the distal maxillary elements and both paired mouthparts are closely connected by a lateral groove and spring mechanism. A sucking channel is present between the dorsal maxillary surface and the ventral surface of the mandible.

The maxillae are inserted ventrally and moderately retracted, with the posterior edge aligned with the posterior mandibular margin laterally and the posterior margin of the prementum mesally. A cardo is not present as a distinct separate element. The maxillary body is probably mostly formed by the stipes (BEUTEL et al. 2010; but see ASPÖCK & ASPÖCK 2007 for an alternative interpretation). The distal maxillary part is undivided, without galea or lacinia as recognizable separate structures. Maxillary palps are also absent. The distal part is closely connected with the distal mandible (see above, Fig. 6C, md, mx)

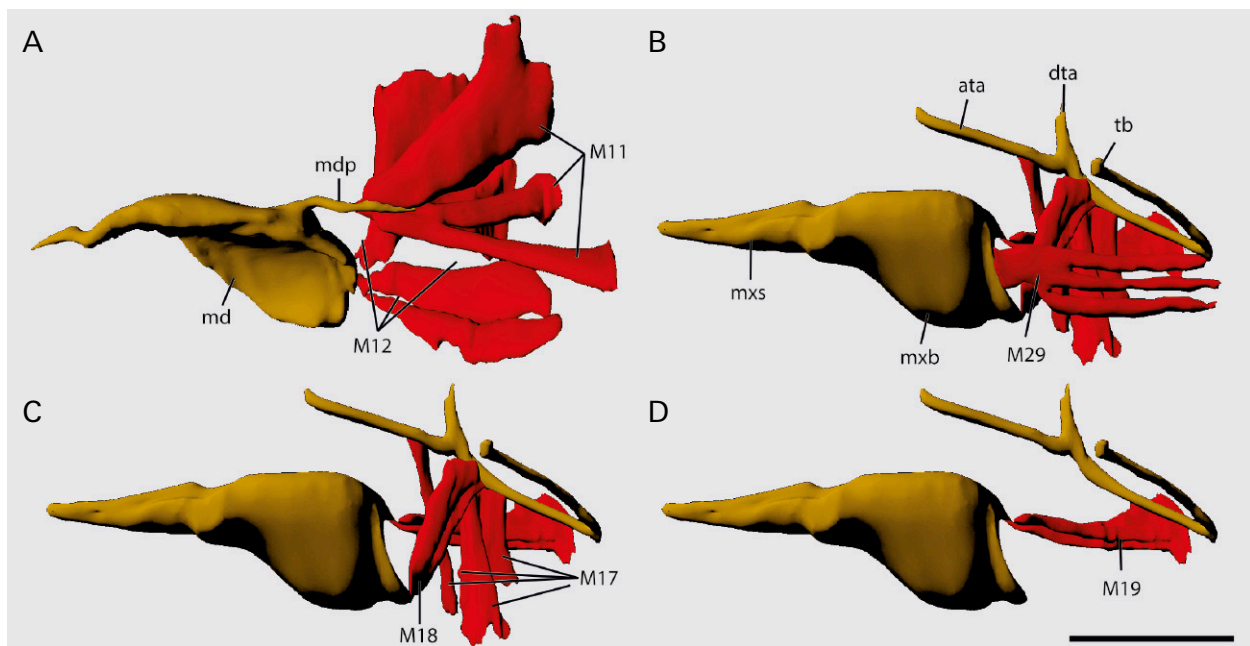


Fig. 7. 3D reconstruction of mandibulo-maxillary complex of 1st instar of *Mantispa aphavexelte*; **A:** mandible, median view; **B–D:** maxillary base, median view. — **Abbreviations:** ata – anterior tentorial arm, dta – dorsal tentorial arm, M11/12 – *M. craniomandibularis internus/externus*, M17 – *M. tentoriocardinalis*, M18 – *M. tentoriostipitalis*, M19 – *M. craniolacinalis*, M29 – *M. tentoriopremental*, md – mandible, mdp – mandibular process, mxb – maxillary base, mxs – maxillary stylet, tb – tentorial bridge. — **Scale bar:** 50 μ m.

and partly forms a sheath around it. The cuticle on the proximal maxillary region is slightly sculptured with a pattern of fine ridges; the sculpture gets more distinct on the proximal stylet. Few setae are present on the distal part of the maxilla. Ventrally a small opening is visible between the mesal edges of the left and right maxilla; this region displays minute structures, presumably sensilla, and additionally two larger thorns which intercross in midline. A bar-like structure on the dorsal proximal region of the maxilla fits with an elongate mandibular depression, thus linking both structures (Fig. 9A, mmc). A posteriorly pointing maxillary process is also present.

Mandibular musculature (Figs. 7A, 9B, 10A): M11 (*M. craniomandibularis internus*), very large muscle, divided into 4 subcomponents, O: large areas of head capsule, dorsally, laterally and ventrally; I: medially on small process of mandibular base with a tendon (Fig. 7A, mdp). M12 (*M. craniomandibularis externus*), almost as large as M11, with two subcomponents, O: one unit dorsolaterally on head capsule, second ventrolateral; I: laterally on mandibular base with a tendon. M13 (*M. tentoriomandibularis*) absent.

Maxillary musculature (Figs. 7C,D, 9B,C, 10A,B): imms (intrinsic muscle of maxillary stylet), connecting dorsal and ventral side of proximal part of maxillary stylet, associated with glands. M15 (*M. craniocardinalis*), absent. M17 (*M. tentoriocardinalis*), strongly developed muscle composed of several bundles with different insertion sites, O: ventral side of tentorium, together with M18, one bundle slightly shifted anterad; I: most bundles at retracted proximal parts of maxilla, successively from median area to lateral region, one bundle inserting slightly anterior to the rest. M18 (*M. tentoriostipitalis*),

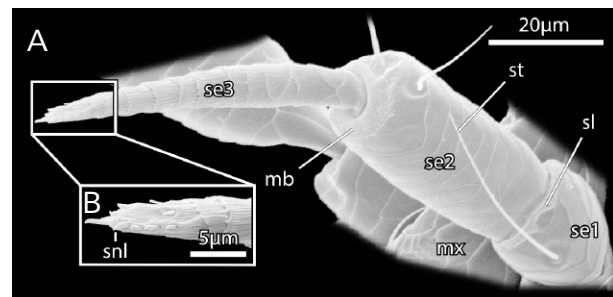


Fig. 8. SEM micrograph of labial palp of 1st instar of *Mantispa aphavexelte*; **A:** overview; **B:** tip of 3rd segment. — **Abbreviations:** mb – membrane, se1–3 – segment 1–3, sl – sclerite, snl – sensillum, st – setae.

strongly developed muscle, O: ventrally on tentorial arm, near dorsal arms; I: proximal parts of maxillary base, anterior to bundles of M17. M19 (*M. craniolacinalis*), thin muscle composed of two bundles, O: ventrolaterally on head capsule, I: proximally on dorsal edge of maxilla, one bundle slightly laterad the other.

3.8. Labium (Figs. 3B,C,D, 8–10)

The labium forms a large part of the ventral closure of the head. Three parts are distinguishable, mentum, prementum and well-developed palps (Fig. 3B,C,D, me, lp, pm). The shield-like mentum, which occupies about two thirds of the ventral side of the head, is nearly as broad as long; a strongly developed bulge is present posteriorly and the hind margin is adjacent with the ventral part of the cervix; few setae are present on the mentum; the

cuticle has a leathery surface structure comprising more distinct and finer micro-sculptural elements; the surface pattern is gradually fading on the posterior region.

The prementum, which is about as long as wide, is connected with the mentum by a membrane. Two symmetrical halves with rounded hind margins are separated by a thin suture. A pair of setae is inserted in the middle region of the prementum. The cuticle of the proximal regions of the segments shows a scale-like surface structure, whereas the distal regions display a pattern of fine ridges.

The three-segmented palps are well-developed. The short and cup-shaped first palpomere inserts on the anterior margin of the prementum (Fig. 8A, se1), with the mesal edges adjacent in midline; its cuticular surface shows the typical pattern with fine ridges, similar to the surface structure of antennomere 1; a distinct pore is present on the distal edge of palpomere 1, likely a sensillum; a small elongated sclerite (Fig 8A, sl) recognizable close to this minute structure likely articulates with palpomere 2; a long seta is inserted ventrally on this structure. Palpomere 2 is slightly narrower than palpomere 1 but about twice as long; its cuticle displays the typical pattern with fine ridges; two long setae are inserted on its distal part (Fig 8A, se2). The apical palpomere 3 articulates on a wide apical articulatory membrane; it is very thin compared to the proximal segments and ca. 0.06 mm long; its proximal part shows a scale-like cuticular surface structure which obliterates distally; the distal two thirds of this palpomere appear segmented, with small cylindrical subunits seemingly stacked into each other; each of these small elements shows a pattern of longitudinal ridges, and additionally minute thorns on the edges; the apical segment is equipped with ten small conical sensilla, nine of them forming a circle on the apex and the tenth placed in the center of them; no setae are present on palpomere 3 (Fig. 8A, se3).

Musculature (Figs. 7B, 9B,C): M29 (*M. tentoriopraementalis inferior*), large and composed of three bundles, O: base of posterior tentorial arms; I: laterally on hind margin of prementum. M30 (*M. tentoriopraementalis superior*), a single bundle, well-developed, O: tentorium near M17, below origin of dorsal tentorial arms; I: lateral wall of prementum with a thin tendon.

3.9. Epipharynx (Fig. 9A, eph)

The anterior section of the epipharynx below the anterior clypeolabral region and above the middle part of the mandibles is sclerotized, with concavities closely fitting with the dorsal mandibular surface and medially separated by a shallow longitudinal ridge. The cuticle entirely lacks microtrichia or other recognizable surface modifications. A strongly flattened and laterally closed preoral chamber forms at the level of the lateral mandibular base. The median ridge obliterates in this intermediate epipharyngeal section and is followed by a median longitudinal rim; the cuticle in this area is semimembranous. The

median rim widens posteriorly and is completely filled out by the pistil-like dorsal part of the hypopharynx. This interconnected median section almost completely separates two posteriorly narrowing and strongly flattened preoral spaces, which connect with the posterior opening of the mandibulo-maxillary channel. Posteriorly a strongly flattened closed prepharyngeal tube with conspicuous upward directed lateral edges is formed by the posteriormost epipharynx and the posteriormost section of the dorsal hypopharyngeal surface; the width of the tube decreases towards the oval anatomical mouth and the upward directed edges obliterate posteriorly.

Musculature (Figs. 9A, 10A, 12): M43 (*M. clypeopalatalis*), large muscle consisting of four linear bundles of similar length and diameter, O: clypeolabral region, bundles originate successively from anterior to posterior; I: anterior part of epipharynx. M44 (*M. clypeobuccalis*), a short straight muscle, O: clypeolabral area posterior to M43; I: posteriormost M43 on epipharyngeal roof near anatomical mouth opening.

3.10. Hypopharynx (Fig. 9A, hph)

The hypopharynx is fused to the dorsal parts of the prelabium but separated from it by distinct lateral folds. It extends dorsad between the rounded mesal maxillary edges as a narrow structure, almost reaching the intermediate epipharyngeal section in its midline. Posteriorly the upper hypopharyngeal part forms a pistil-like structure closely fitting with the median rim of the epipharynx (Fig. 9A, eph, hph). Posteriorly the hypopharynx widens distinctly. The dorsal part of the posteriormost section forms the prepharyngeal tube with the posteriormost epipharynx, whereas the lateral walls gradually merge with the mesal maxillary bases.

Musculature (Figs. 9B, 10A, 12): M41 (*M. frontohypopharyngalis*), muscle composed of two small bundles with different origin. O: one portion anterior to frontal ganglion laterad third bundle of M44, second subunit posterolaterad the frontal ganglion; I: dorsolateral folds at anatomical mouth opening.

3.11. Digestive tract and associated structures (Figs. 11, 12)

The prepharyngeal tube with its well-developed preoral pumping apparatus is followed by a short and slightly widened pharynx with longitudinal folds for muscle attachment; it is posteriorly continuous with a much less wide tube-shaped esophagus (Fig. 11B, oes), which expands posteriorly before it connects with the midgut in the mesothoracic region without a distinct border; an ingluvies and proventriculus are not developed. The midgut is very wide and fills out almost two thirds of the lumen of the thorax and abdominal segments I–III. It ends in abdominal segment III (Fig. 11B, mg). At the beginning of abdominal segment IV Malpighian tubules

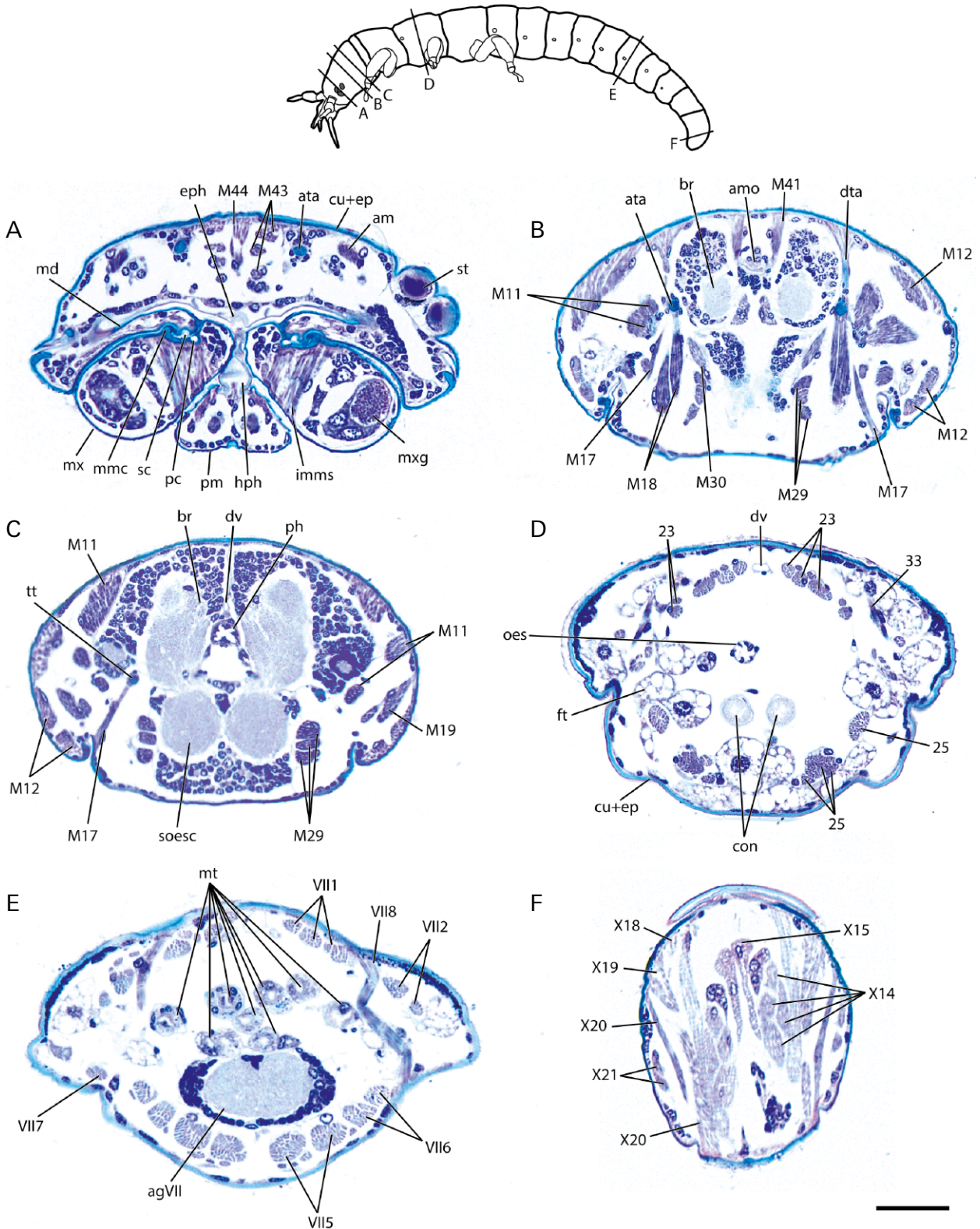


Fig. 9. Cross sections of 1st instar of *Mantispa aphavexelte*, position of sections indicated in habitus drawing; **A:** anterior head capsule; **B:** posterior head capsule; **C:** far posterior head capsule; **D:** anterior mesothorax; **E:** abdominal segment VII; **F:** abdominal segment X. — **Abbreviations:** 23, 25, 33 – muscles of the mesothorax, ag – abdominal ganglion VII, am – antennal muscles, amo – anatomical mouth opening, ata – anterior tentorial arm, br – brain, con – connectives, cu – cuticula, dv – dorsal vessel, ep – epidermis, eph – epipharynx, ft – fat tissue, hph – hypopharynx, imms – intrinsic muscle of maxillary stylet, M11 – M. craniomandibularis internus, M12 – craniomandibularis externus, M17 – M. tentoriocardinalis, M18 – M. tentoriostipitalis, M19 – M. craniolacinalis, M29 – M. tentoriopraementalis inferior, M30 – tentoriopraementalis superior, M41 – M. frontohyopharyngalis, M43 – M. clypeopalatalis, M44 – M. clypeobuccalis, M45 – M. frontobuccalis anterior, md – mandible, mmc – mandibulo-maxillary connection, mt – Malpighian tubes, mx – maxilla, mxg – maxillary glands, oes – oesophagus, pc – poison channel, ph – pharynx, pm – prementum, sc – sucking channel, soesc – suboesopharyngeal complex, st – stemmata, tt – tentorium, VII1–8 – muscles of the 7th abdominal segment, X15–21 – muscles of the 10th abdominal segment. — **Scale bar:** 20 μ m.

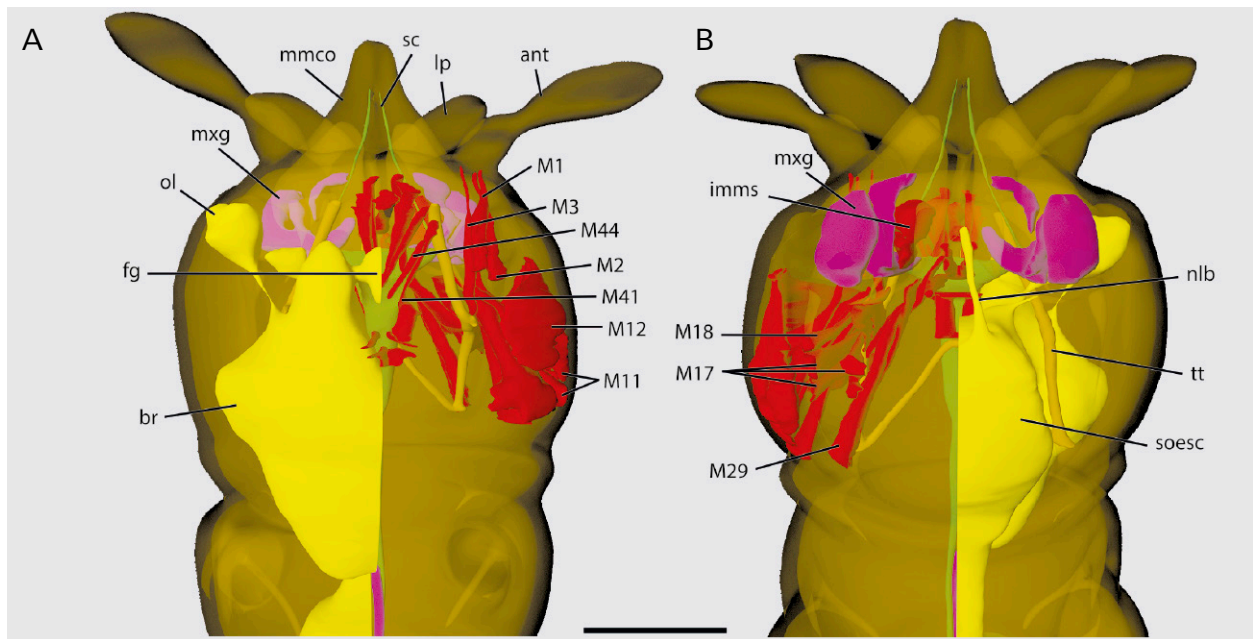


Fig. 10. 3D reconstruction of 1st instar head of *Mantispa aphavexelte*; **A:** dorsal view; **B:** ventral view. — **Abbreviations:** ant – antenna, br – brain, fg – frontal ganglion, imms – intrinsic muscle of the maxillary stylet, lp – labial palps, M1/2/3 – M. tentorioscapales anterior/posterior/lateralis, M11/12 – M. craniomandibulares internus/externus, M17 – M. tentoriocardinalis, M18 – M. tentoriostipitalis, M29 – M. tentoriopraementalis, M41 – M. frontohypopharyngalis, M44 – M. clypeobuccalis, mmco – mandibulomaxillary complex, mxg – maxillary gland, nlb – nervus labialis, ol – optical lobe, sc – sucking channel, soesc – suboesopharyngeal complex, tt – tentorium. — **Scale bar:** 50 μ m.

arise at the midgut-hind gut border (Fig. 11B, mt). A distinctly extended pyloric region is not developed. Two of the tubules run anterad close to the midgut and end in abdominal segment II. The other five form loops in the posterior abdomen, where they connect with the hindgut (Fig. 11B, hg), forming a pyriform organ (e.g. GAUMONT 1965) or cryptonephric complex. A short hindgut is connected to an expanded rectum (Fig. 11B, rec). The latter reaches from the sixth to the ninth abdominal segment and enters a short tube which opens at the anal opening.

Glands: A massive glandular complex is present in the proximal part of the maxillary stylet (Figs. 9A, 10A,B, mxg), apparently comprising a lateral and two mesal subcomponents, one of the latter separated from the remaining parts by the vertical intrinsic muscles. It is likely that these glandular elements are equivalent with the lateral and mesal maxillary glands (WUNDT 1959; ROUSSET 1966; BEUTEL et al. 2010). The cephalic gland, which appears rather indistinct on the microtome sections, is located posterolaterad the maxillary base, between bundles of the mandibular flexor and extensor.

Musculature (Fig. 12): M45 (M. frontobuccalis anterior), slender muscle, O: frontal area posterior to anterior bundle of M41, laterad frontal ganglion; I: dorsally on pharynx at anatomical mouth, between insertion sites of M41. M46 (M. frontobuccalis posterior), two thin bundles, O: two slightly separated areas on frons, posterad second bundle of M41; I: posterad M45 on dorsal folds. M48a (M. tentoriobuccalis anterior), short but thick, O: thin median part of tentorial bridge; I: ventral side of posterior prepharyngeal tube. M48b (M. tentoriobuc-

calis anterior), long and slender, O: posterior prementum; I: ventral side of prepharyngeal tube anterad M48a. M48c (M. tentoriobuccalis), one thin bundle, O: lateral wall of prementum; I: ventral side of prepharyngeal tube anterad M48b, slightly shifted laterad.

3.12. Cephalic central and stomatogastric nervous system (Figs. 10, 11)

The compact brain is very large in relation to the head size and occupies a large proportion of the cephalic lumen (Figs. 10A, 11A, br). A small part of the protocerebrum is shifted into the anterior prothorax. The antennal nerves and optic lobes are present and well-developed (Figs. 10A, 11A, ol). The circumoesophageal connectives are short and the brain and suboesophageal ganglion together form a nearly spherical compact unit. A separated tritocerebral commissure is missing. The proximal parts of the nerves of the mouth-parts are recognizable on the microtome sections. The frontal ganglion is located above the anatomical mouth, anterad the frontal region of the brain (Fig. 10A, fg).

3.13. Cervix (Fig. 3A,B,C)

The cervix is a narrow semimembranous collar between the head and prothorax. It is as broad as the head but only ca. 0.2 mm long. It is slightly conical and narrows slightly posteriorly. The cuticle surface is smooth, without sensilla or setae. The cervix is straight on the dorsal side behind the head but is curved ventrally to fit with

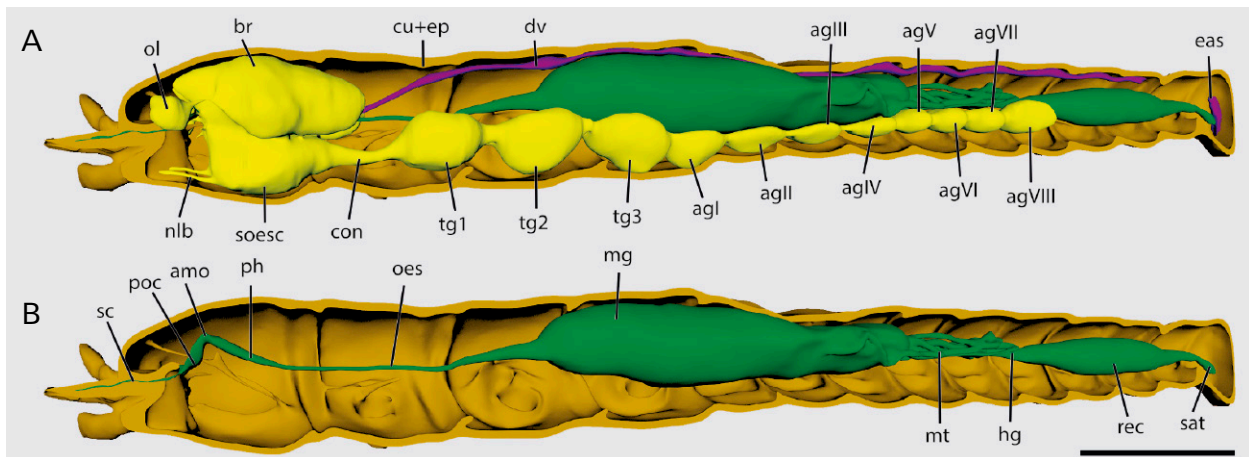


Fig. 11. 3D reconstruction of 1st instar of *Mantispa aphavexelte*, lateral view, sagittally sectioned; **A:** nervous system, digestive tract and dorsal vessel; **B:** digestive tract. — **Abbreviations:** amo – anatomical mouth opening, br – brain, con – connective, cu – cuticle, dv – dorsal vessel, eas – eversible attachment structure, ep – epidermis, ggl I–3 – thoracic ganglia, ggl I–VIII, hg – hind gut, mg – mid gut, mt – Malpighian tubes, nlb – nervus labialis, oes – oesophagus, ol – optic lobe, ph – pharynx, poc – preoral chamber, rec – rectum – sat – short anal tube, sc – sucking channel, soesc – suboesophageal complex. — **Scale bar:** 100 μ m.

the posterior edge of the mentum. Internally the cervix bears a short apodeme pointing slightly posteromesad (Fig. 14A, ca).

3.14. Prothorax (Figs. 2, 13, 14)

The prothorax is about as large as the following segments. The collar-like cervix connects the prothorax with the posterior head capsules (Fig. 13A, cer). Cervical sclerites are missing (Fig. 2). A posteroventral collar-like element is similar in length and degree of sclerotization to the anterior cervix. A moderately sclerotized, brownish pronotal region is medially interrupted by a broad, weakly pigmented and unsclerotized ecdysial stripe (Figs. 2A, 13A, pno). Its lateral edge is a rounded bulge. An almost circular median region has a very smooth cuticular surface and is almost completely lacking setae. The lateral pronotal areas display a scale like surface structure like some cephalic regions and bear a vestiture of setae of different length. A seta inserted in a deep, cup-like depression, similar to the articulation of a trichobothrium, is present on the lateral pronotal area (Fig. 13B, t6), and also on the corresponding regions of the meso- and metanotum. The anterior part of the lateral pronotal margin is connected with a folded semimembranous anterolateral region, which is ventrolaterally continuous with the completely weakly pigmented sternal part of the segment. The pleural region is a relatively small element between the posterolateral tergal margin and the dorsal and anterior coxal edge. A very short pleural suture subdivides it into an anterior episternal part and a posterior epimeral element. A crescent shape bulge along the anterior coxal margin is possibly a trochantin. The well-developed legs are inserted between the pleural and sternal regions. The main anterior part of the sternal region is very weakly pigmented but has a shiny surface and is apparently lightly sclerotized. It bears only few setae. The ventral pos-

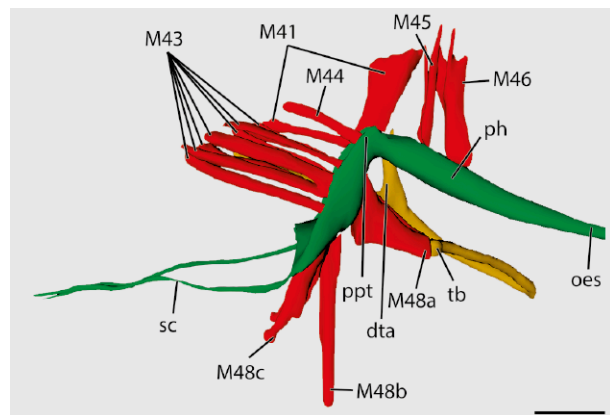


Fig. 12. 3D reconstruction of anterior digestive tract and associated muscles of 1st instar of *Mantispa aphavexelte*, lateral view. — **Abbreviations:** dta – dorsal tentorial arm, M41 – *M. frontohypopharyngalis*, M43 – *M. clypeopalatalis*, M44 – *M. clypeobuccalis*, M45 – *M. frontobuccalis anterior*, M46 – *M. frontobuccalis posterior*, M48 – *M. tentoriobuccalis anterior*, oes – oesophagus, ph – pharynx, ppt – prepharyngeal tube, sc – sucking channel, tb – tentorial bridge. — **Scale bar:** 20 μ m.

terior element of the segment is a bulge-like postcoxal bridge. It is similar to the cervix in shape, length and degree of sclerotization. It likely represents a spinasternum, but invagination sites of the prospina or profurca are not recognizable. Internally, a long spine-like process is present, projecting posteriorly above the coxa (Fig. 14A, slp). Another small spine is present posterolaterad the coxal insertion. Several muscles originate on these processes.

Musculature (Fig. 14A,B,C,D): The homologization of the thoracic and abdominal muscles is impeded by missing skeletal landmarks like furcal arms or well-defined sclerites. Therefore, they are successively numbered and possible equivalents in the systems of LARSÉN (1966) and FRIEDRICH & BEUTEL (2006) are given in brackets.

Dorsal musculature: 1 (M1, *M. pronoti primus*), short and fan-shaped, composed of three bundles, with a slight-

ly oblique orientation, O: median pronotal area; I: two bundles on postoccipital ridge, passing the collar-like cervix, one shorter bundle reaches posterior edge of cervix. 2 (M2, *M. pronoti secundus*), long and slender, with three subcomponents, O: dorsal area of postoccipital ridge; I: one shorter bundle attached to posterodorsal hind margin of pronotum, two bundles on anterior mesonotal region. 13 (M4, *M. pronoti quartus*), strong straight muscle with a broad origin, O: anterolateral mesonotal edge; I: anterior region of pronotum laterad 1 and 14.

Ventral musculature: 3 (M5, *M. prosterni primus*), long and strongly developed, with oblique, almost transverse orientation, O: ventrolaterally on hind margin of prothorax; I: ventromedially on postoccipital ridge. 4 (M6, *M. prosterni secundus*), similar to 3, both intercrossing in ventromedian region of prothorax, O: hind margin of prothorax mesad 3; I: laterad 3 on postoccipital ridge.

Dorsoventral musculature: 5 (M7, *M. dorsoventralis primus*), long and slender, slightly widening towards insertion, O: mesal pronotal region; I: laterally on postoccipital ridge, laterad 4. 6 (M8, *M. dorsoventralis secundus?*), slender muscle, O: anterolateral corner of mesonotum; I: tip of long spine-like process near procoxa. 7 (M11, *M. dorsoventralis quintus*), similar to 6, small and short, O: anterolateral mesonotal edge slightly posterad 6; I: ventrolaterally posterior to coxal insertion. 8 (alternative: 7b), thin muscle anterad 6 and 7, O: like 7 on anterolateral mesonotal edge, anterad 7; I: laterally on hind margin of prothorax (postcoxal bridge). 9, short bipartite muscle. O: dorsolaterally on postoccipital ridge; I: both subcomponents laterally on cervical ridge at transition to prothorax.

Lateral musculature: 10, short and slender straight muscle, O: anterolaterally on pronotum; I: on cervical spine close to its tip. 11, same shape and size as 10, O: lateral region of prothorax, posterior to 10; I: tip of cervical spine. 12, same shape and size as 10 and 11, O: anteroventral part of prothorax slightly anterior to coxa; I: ventrally on tip of cervical spine.

Extrinsic leg musculature: 14a (M14, *M. noto-trochantinalis*), long and strongly developed, O: middle region of pronotum; I: anterior procoxal base. 14b (M14, *M. noto-trochantinalis*), bifurcated, O: anterolateral pronotum, close to 14a; I: anterolaterally on basal region of spine-like procoxal process. 15 (M17, *M. epimero-coxalis*), bipartite, but with both bundles closely adjacent and with same origin and insertion, O: middle region of pronotum, close to 14; I: on small spine-like process near epimeron. 16 (M15, *M. noto-coxalis*), thin and straight, thinner than 15, O: lateral pronotal region, near origin of 5; I: lateral procoxal base, slightly anterad 15. 17 (M16, *M. episterno-coxalis*), slender and straight, O: anterolateral pronotal region, anterior to 18 and 13; I: lateral coxal base posterad trochantin and spine-like process. 18, same shape as 17, O: anterolateral pronotal region, posterior to 17; I: tip of spine-like coxal process. 19, short and thick, O: base of spine-like coxal process; I: tip of spine-like coxal process. 20, short and thin, O: mesal edge of coxa;

I: tip of spine-like process. 21, small, O: lateral edge of coxal base; I: tip of spine-like process. 22, short and compact, O: lateral edge of coxal base, near 21; I: tip of spine-like process.

3.15. Mesothorax

(Figs. 13, 14)

The mesothorax is divided into a small, collar-like anterodorsal portion and a large posterior subunit (Fig. 13A, B, mspsc, msno). The almost completely unpigmented and weakly sclerotized anterodorsal element is arguably a prescutum, also referred to as spiracular sclerite (TAUBER 1987); it narrows towards its ventrolateral edge, where it is connected with the pleura; dorsolaterally it bears a distinct annular spiracle (Fig. 13A,B, sp), and few anteriorly directed very short sensilla are inserted on this area. The larger dorsal notal region is medially divided by a median unpigmented and unsclerotized ecdysial stripe (Fig. 2), distinctly broader than its prothoracic counterpart; the lateral notal region is rounded and its anterior part connects with a folded semimembranous anterolateral area, similar to this region of the prothorax; like on the pronotum an almost circular median mesonotal region has a very smooth surface and is lacking setae, whereas the lateral areas bear a vestiture of setae of different length; it also displays a scale-like cuticular surface structure. The pleural parts of the mesothorax are similar to the prothoracic equivalents, with an episternum, an epimeron and a crescent-shaped element likely representing a trochantin (Fig. 13A,B, est, eme, trn). A ventral transverse suture separates the unpigmented and weakly sclerotized sternal region from a small sclerite possibly representing a presternum. The postcoxal bridge is half the size of its prothoracic equivalent and extends less far towards the pleural parts. Two sclerotized disk-like structures in the lumen of the mesothorax serve as attachment areas of several muscles; the larger anterior one is located anterolaterad the coxal insertion, the posterior one is closely adjacent to the lateral coxal edge.

Musculature (Fig. 14A,E,F,G): *Dorsal musculature*: 23 (M28, *M. mesonoti primus*), large, with 3 subcomponents, O: one bundle on anterior mesoprescutal margin, two at hind margin; I: anterior margin of metaprescutum. 24 (M29, *M. mesonoti secundus*), short and fan-shaped, O: median part of metanotum; I: anterolateral margin of metaprescutum.

Ventral musculature: 25 (M30, *M. mesosterni primus*), large, composed of two strongly developed subcomponents and one thin bundle. O: anterior margin of mesosternal region, two bundles medially, one shifted laterad; I: lateral component on hind margin of mesothorax, two bundles mesally on sternal region. 26 (M31, *M. mesosterni secundus*), long and slender, O: hind margin of mesothorax, near lateral bundle of 3; I: mesally on sternal region of prothorax.

Dorsoventral musculature: 31 (M32, *M. dorsoventralis*), long and thin, O: posterior region of sternal area; I: anterior mesoprescutal margin.

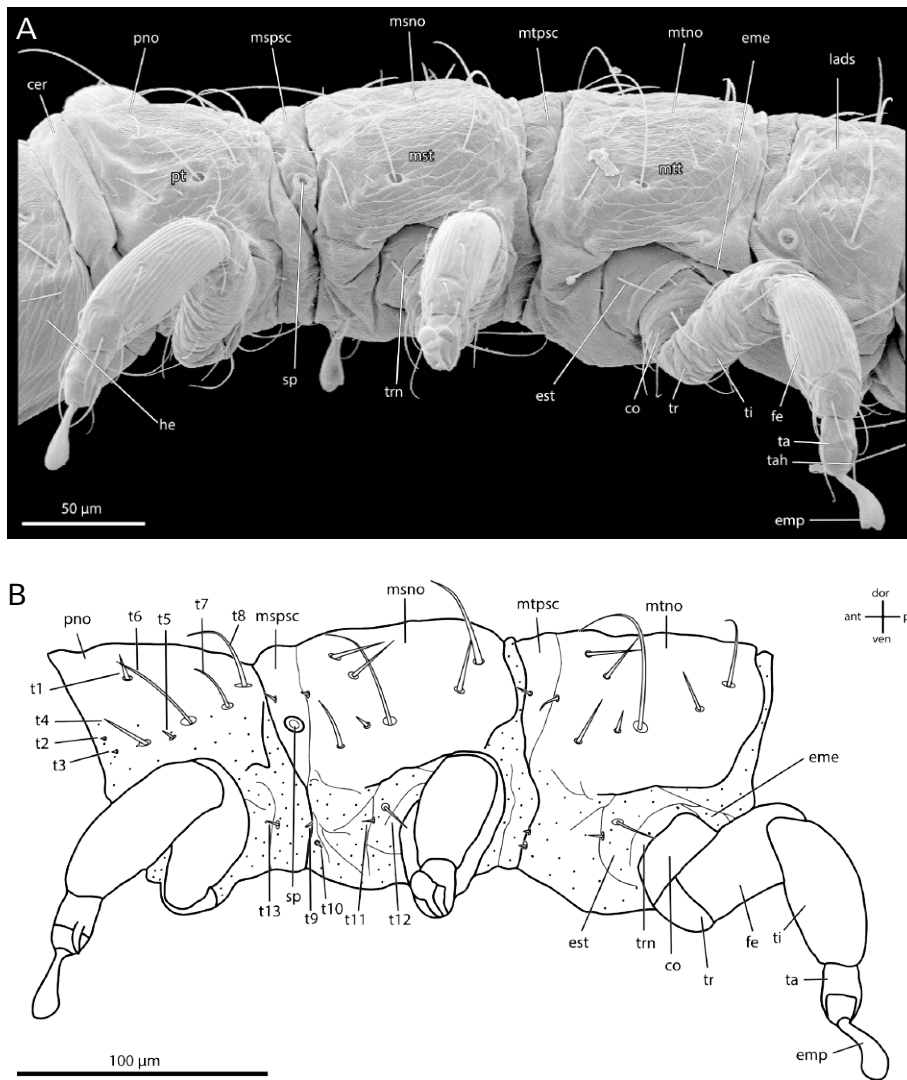


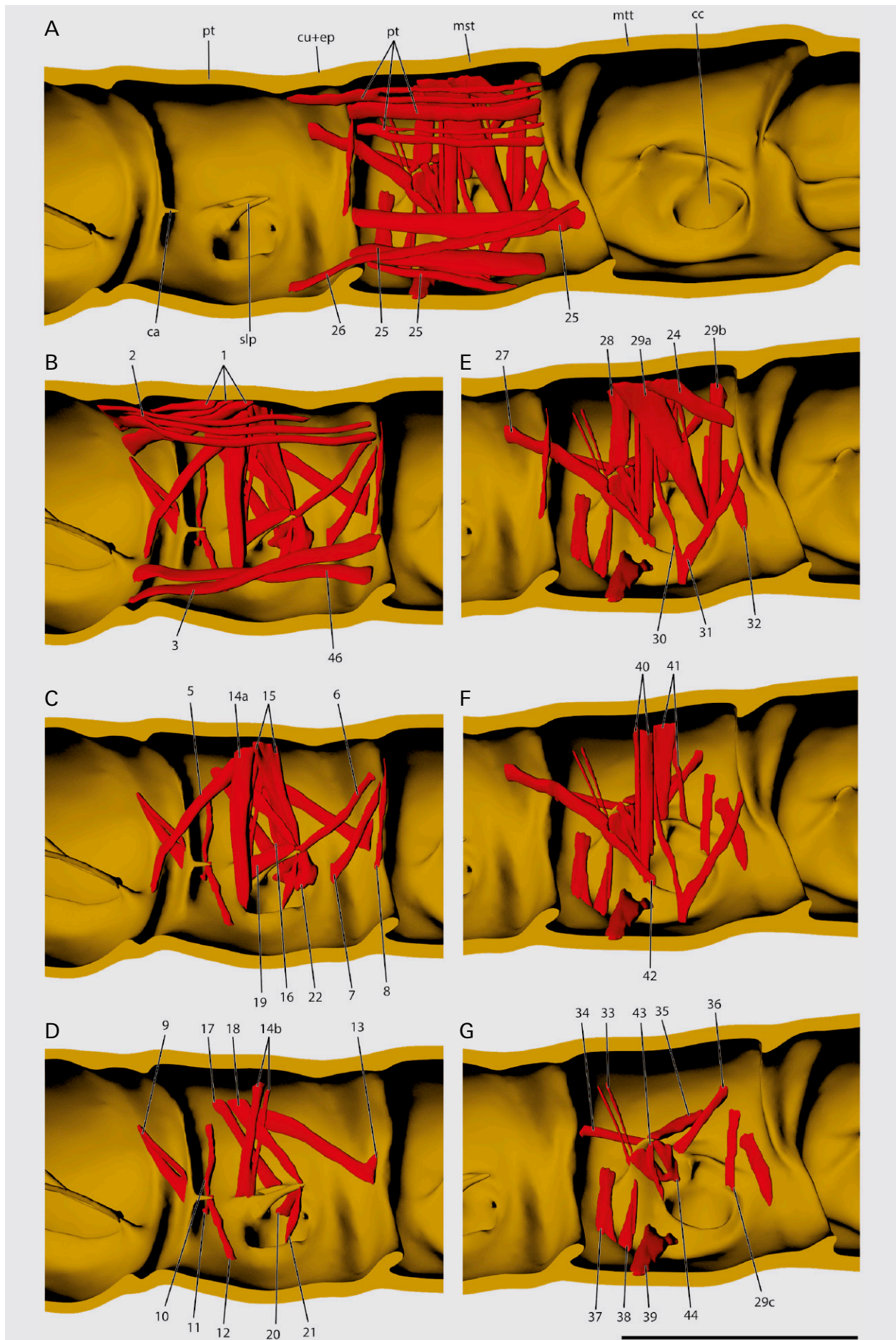
Fig.13. Thorax of 1st instar of *Mantispa aphavexelte*, lateral view; **A:** SEM micrographs; **B:** Drawing. — **Abbreviations:** lads – first abdominal segments, cer – cervix, co – coxa, eme – epimeron, emp – empodium, est – episternum, fe – femur, he – head, msno – mesonotum, mspsc – mesoprescutum, mtno – metanotum, mtpsc – metaprescutum, pno – pronotum, sp – spiracle, t1–13 – thoracic setae 1–13, ta – tarsus, ti – tibia, tr – trochanter, trn – trochantin.

Lateral musculature: 27 (M33, *M. noto-pleuralis*), straight, with oblique orientation, O: laterally on anterior margin of mesoprescutum; I: anterior part of cryptopleural region. 28, short and straight, O: medial part of mesonotal area; I: dorsally on cryptopleura, posterior to 27. 30 (M37, *M. furca-pleuralis*), same shape as 31, O: posterior region of sternal area, together with 31; I: paramedially on mesonotum. 32 short and flat, O: posterior mesopleural region, anterior to insertion of 31; I: sternal area posterior to coxa. 33, two very thin bundles. O: anterior mesonotum, slightly laterad of midline; I: anteriorly on dorsal side of cryptopleura. 34, straight and thin, O: posterolateral mesoprescutal margin; I: dorsally on cryptopleura, posterior to 33. 35, same shape as 34, O: lateral mesonotal edge, slightly posterior to midlength; I: together with 34 on cryptopleura. 36 (M20, *M. pleuralaris*), short and straight, O: mesonotum, slightly dorsad 35; I: posterior to 35 on cryptopleura. 37, short and com-

pact, O: lateral edge of anterior mesonotum, anterior to cryptopleura; I: anterolateral sternal region, 38, O: ventral base of anterior cryptopleura; I: slightly posterior to 37. 39, short and compact, O: mesally on anterior coxal base; I: medially on sternal region, posterior to 38 and 39.

Extrinsic leg musculature: 40 (M39, *M. noto-trochantinalis*), strongly developed and long, with two sub-components with same origin and insertion, O: middle region of mesonotum; I: anterior procoxal base. 41, long, with a strongly developed and a thin subunit, O: mesonotum posterior to 40; I: dorsally on middle region of cryptopleura. 42, short and thin, O: ventrally on cryptopleura; I: anterolaterally on coxal base. 43 (M41, *episterno-coxalis*), several short bundles, O: anterior coxal base, laterad 42; I: ventrally on cryptopleural area, posterior to 42. 29a (M43, *M. coxa-subalaris*), large and fan-shaped, O: median region of mesonotum, between

→ **Fig. 14.** 3D reconstruction, thorax of 1st instar of *Mantispa aphavexelte*; **A–G:** medial view, with muscles of prothorax (B, C, D) and mesothorax (A, E, F, G). — **Abbreviations:** 1–22 – muscles of prothorax, 23–44 – muscles of mesothorax, ca – cervical apodeme, cc – coxal cavity, cu – cuticule, ep – epidermis, mst – mesothorax, mtt – metathorax, pt – prothorax, slp – spine like process. — **Scale bar:** 100 µm.



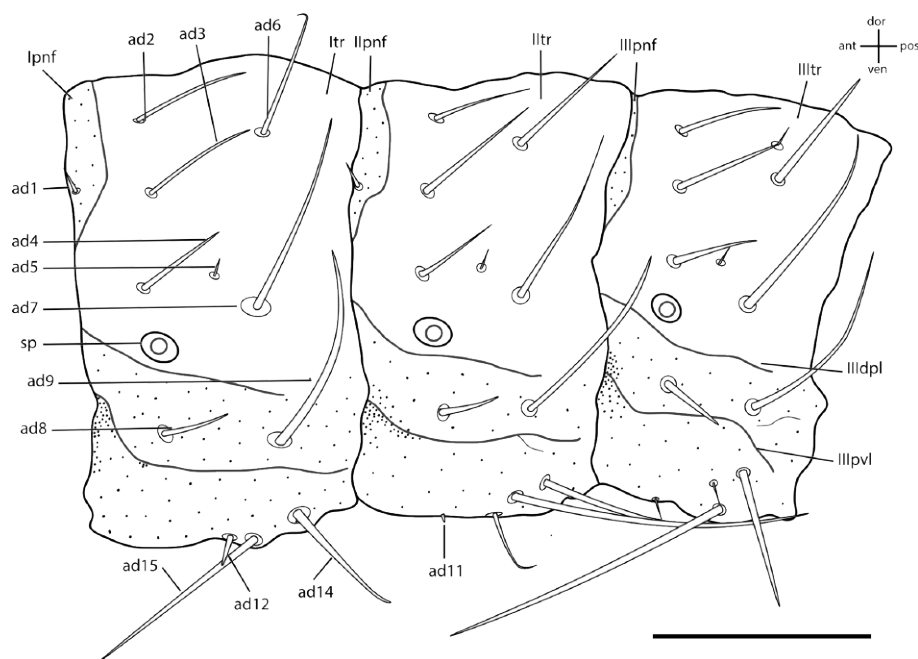


Fig. 15. Drawing of abdominal segments I–III of 1st instar of *Mantispa aphavexelte*. — **Abbreviations:** ad1–15 – abdominal setae 1–15, dpl – dorsopleural line, pl – pleural region, pnf – prenatal fold, pvl – pleuroventral line, sp – spiracle, st – sternal region, tr – tergal region. — **Scale bar:** 50 μ m.

24 and 28. 29b (M43, *M. coxa-subalaris*), long and strongly developed, O: posterior mesonotum; I posterior coxal base. 29c (M43, *M. coxa-subalaris*), shorter than 29b, O: lateral edge of posterior mesonotum; I: posterior coxal base together with 29b and 29c. 44, fan-shaped and bifurcated, very compact, O: anterolaterally at coxal base; I: ventrally on cryptopleural area.

3.16. Metathorax (Fig. 13, 14)

Similar in its configuration to the mesothorax, very slightly larger than the other two thoracic segments. The distinctly sclerotized tergal region is less elevated in lateral view than its mesothoracic counterpart. A spiracle is missing on the slightly smaller prescutum. A postcoxal bridge is absent.

Musculature: Very similar to that of the mesothorax. Some muscles show minor differences in size, but this is probably within the range of variation between individuals. The general configuration and arrangement in both segments is the same.

3.17. Legs (Fig. 13A,B)

For a detailed description of the leg and its intrinsic musculature, see JANDAUSCH et al. (2018).

3.18. Abdominal segments I–VIII
(Figs. 15, 16)

The abdomen with ten recognizable segments is about $2 \times$ as long as the thorax. The single segments are distinctly separated and slightly decreasing in size posteriorly. The general shape and configuration of segments

I–VIII are very similar. Each segment is divided into three areas. The distinctly pigmented and sclerotized terga are separated from the pleural region by the dorsopleural line (Fig. 15A, dpl); anterolaterally they bear very distinct annular spiracles (Fig. 15A, sp); anteriorly a semimembranous region is present, resembling the thoracic prescutal areas and referred to as prenotal fold by (TAUBER 1987) (Fig. 15A, pnf); this bulge-like structure decreases in size from segment I to VIII: the tergal region is medially divided by a broad unpigmented and unsclerotized zone of weakness; the sclerotized tergal areas display a scale-like cuticular structure as present on parts of the head and thorax. The pleural elements ventrad the dorsopleural line lack well-defined sclerites and the degree of sclerotization and pigmentation of the pleural region increases posteriorly; the pleural area is separated from the sternal region by the pleuroventral line or tergosternal fold (Fig. 15A, pvl). The venter is completely unpigmented but lightly sclerotized and shiny; distinctly defined sclerites are missing. Short sutures are present on the posterior areas of segments I–IV, possibly separating an anterior larger basisternum from a small bulge-like sternellum; they are absent on segments V–VIII. A vestiture of setae of different length is distributed on the tergal, pleural and sternal regions. The cuticular surface of the pleura and sternal areas is smooth. Inner cuticular apodemes or projections are missing, but the dorsopleural and pleuroventral lines form inner bulges in the single segments, decreasing in size from anterior to posterior and completely missing in segments IX and X.

Musculature (Fig. 16A,B,C): Abdominal muscles are successively numbered and abdominal segments are marked with roman numerals. Possible equivalents in the system of v. KÉLER (1963) are given in brackets. Alary muscles are present but only faintly recognizable in cross sections (not displayed in reconstructions).

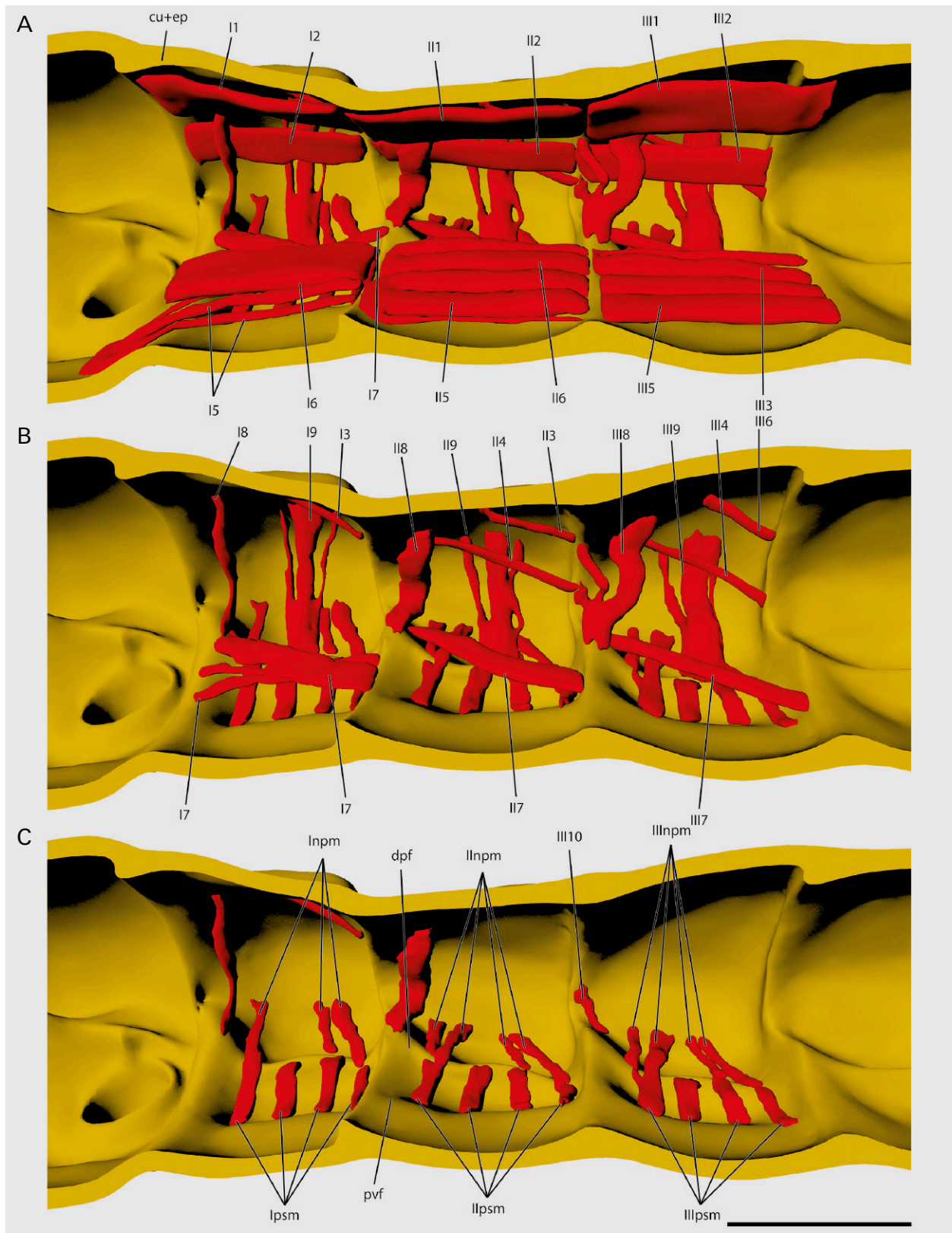


Fig. 16. 3D reconstruction, abdominal segments I–III of 1st instar of *Mantispa aphavexelte*; A–C: medial view, with muscles of abdominal segments I–III. — **Abbreviations:** 1–10 – abdominal muscles, cu – cuticle, dpf – dorsopleural fold, ep – epidermis, npm – notopleural muscles, psm – pleurosternal muscles, pvf – pleuroventral fold. — **Scale bar:** 50 μ m.

Dorsal musculature: 1 (170, *M. antecostaantecostalis* uronotum medialis), strongly developed and broad, O: anterior margin of segment; I: anterior margin of follow-

ing segment. 2 (171, *M. antecostaantecostalis* uronotum lateralis), same shape and size as 1, O: anterior margin of segment, laterad 1, I: anterior margin of following seg-

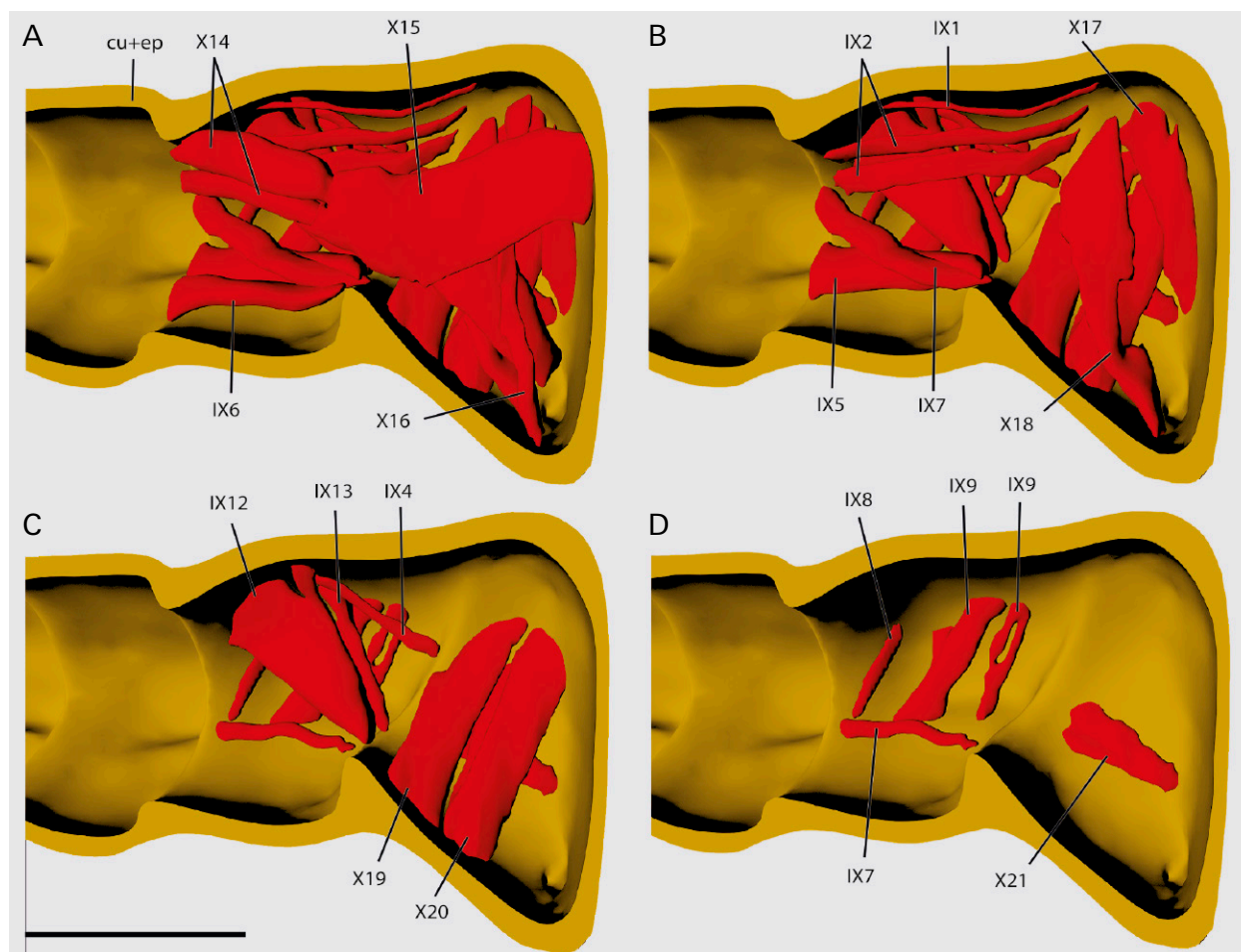


Fig. 17. 3D reconstruction, abdominal segments IX and X of 1st instar of *Mantispa aphavexelte*; **A–D**: medial view, with muscles of abdominal segments IX and X. — **Abbreviations:** 1–21 – abdominal muscles, cu – cuticle, ep – epidermis. — **Scale bar:** 50 μ m.

ment. 3 (172, *M. uronotoantecostalis obliquomedialis*), straight and slender, with oblique orientation, missing in segment VIII, O: middle region of tergal areas; I: dorsolaterally on anterior margin of following segment. 4 (173, *M. uronotoantecostalis lateralis*), single straight bundle similar to 3, missing in segments I and VIII, O: on tergal area anterolaterad origin of 3; I: anterior margin of following segment, laterad 3 on pleural regions. Alary muscles present as series of very thin muscles (precise number cannot be assessed with available cross section); O: tergal region near segmental border, I: ventral side of dorsal vessel.

Ventral musculature: 5 (175, *M. antecostaantecostalis urosterni medialis*), large and flat muscle with two sub-components, O: in segment I on posteroventral region of mesothorax, in all other segments on anteroventral segmental margin; I: anterior margin of following segment. 6 (177, *M. antecostaantecostalis urosterni lateralis*), strongly developed muscles present in all segments. O: anterior segmental margin laterad 5; I: anterior margin of following segment. 7 (178, *M. urosternoantecostalis externus*), in abdominal segment I divided into several sub-components, in following segments one slightly oblique bundle, O: laterally on anterior margin of following segment; I: in segment I two mesally directed slightly

oblique bundles insert on anterior segmental margin and on posterior sternal region of metathorax, one bundle laterally on anterior segmental margin, like single bundle in all other segments.

Dorsoventral musculature: 8 (179, *M. urotergosternalis internus primus*), strongly developed, in some segments with two bundles, in segment I smaller and missing in VIII, O: anteriorly on dorsopleural fold; I: anterior parts of tergal region posterior to prenotal fold. 9 (180, *urotergosternalis internus secundus*), also strongly developed with several bundles, O: middle part of dorsopleural fold; I: middle region of tergum, slightly laterad to midline. 10, small and short muscle, missing in segment I, II and VIII, O: anterior dorsopleural fold; I: anterolaterally on anterior margin of same segment.

Lateral musculature: completely missing in segment VIII. Notopleural muscles, npm (185, *M. tergopleuralis anterior*; 186, *tergopleuralis posterior*), several small but distinct muscles, O: successively on dorsopleural fold; I: successively on lateral tergal region. Pleurosternal muscles, psm (182, *M. urotergosternalis externus primus*; 183, *M. urotergosternalis externus secundus*), like npm composed of several small bundles, O: successively on dorsopleural fold; I: successively on pleuroventral fold (Fig. 16, dpf, pvf).

3.19. Abdominal segments IX and X (Fig. 17)

Abdominal segments IX and X are distinctly modified, especially the latter. Segment IX is separated into a distinctly pigmented and sclerotized dorsal area and a slightly pigmented and unsclerotized ventral region. It is smaller than segment VIII but of similar shape. A dorso-pleural line is missing. A longitudinal ridge separating dorsal and ventral areas is possibly a tergosternal fold. The cuticle displays a scaly surface pattern and bears a vestiture of setae comparable to those of the anterior abdominal segments. The conical segment X is distinctly sclerotized and pigmented. It is $2 \times$ as long as segment IX and lacks any ridges or recognizable lines. At its tip it bears a retractile membranous adhesive structure, with a pouch-like appearance when everted. This segment also bears setae of different length. Segment IX and X lack internal sclerotized structures.

Musculature of segment IX (Fig. 17): muscles 1, 2, 4, 5, 6, 7, 8 and 9 are also present in segment IX, with some variation in size. As in segment VIII several muscles are missing. A homologization with numbers of v. KÉLER (1963) is impeded by the missing genital apparatus.

Dorsoventral musculature: 12, large fan-shaped muscle, very distinct in segment IX. O: anteriorly on tergal region near anterior margin of segment VIII; I: ventrally at hind margin of segment IX. 13, small and straight muscle, slightly posteriad 12. O: tergal region posterior to 12. I: together with 12 at hind margin of segment IX.

Lateral musculature: lateral muscles like psm and npm are absent.

Musculature of segment X (Fig. 17): distinctly different from muscles of other abdominal segments. 14, bifurcated muscle, O: anterodorsally on posterior margin of segment IX, one bundle near midline, second slightly laterad; I: dorsally at eversible attachment structure of segment X. 15, strongly developed muscle, largest of entire abdomen, interacts with 14 by surrounding it in its middle region, O: dorsal wall of segment X; I: ensheathing parts of 14 near short tube-like part of digestive tract ending in anal opening. 16 (216, M. tergorectalis dorsalis), thin, straight muscle passing through entire segment, O: anterodorsal tergal region, near anterior segmental border. 17, fan-shaped large muscle in posterior part of segment X, O: anterolateral tergal region; I: laterad eversible attachment structure. 18, elongated fan-shaped muscle, strongly developed. O: laterally on anterior margin of segment X; I: posteroventrally on eversible attachment structure with short tendon. 19 (probably 179, M. urotergosternalis internus primus), flattened muscle with a broad origin. O: anterior sternal region near midline; I: medially on middle tergal region. 20 (probably 180, M. urotergosternalis internus secundus), same shape and size like 19. O: slightly posterad 19; I: slightly posterad 19. 21, small compact muscle, close associated with pleural wall. O: pleural region posterior to anterior margin of segment X; I: posterolateral tergal region.

3.20. Central nervous system of postcephalic body (Fig. 11)

The three thoracic ganglia are relatively large in relation to the size of the segments and linked by well-developed connectives (Fig. 11A, tg1-3). The eight abdominal ganglia are distinctly smaller; those lying below the mid gut are flattened; the last abdominal ganglionic complex is larger than each of ganglia I–VII and appears wedge-shaped (Fig. 11A, agI–VIII). The position of the ganglia does not correspond with the segment they belong to due to a shift towards the thorax.

3.21. Circulatory system (Fig. 11)

A well-developed dorsal vessel extends almost through the entire postcephalic body.

3.22. Fat body (Fig. 9D,E,F, ft)

The postcephalic body is filled with very loose fat body tissue.

3.23. Chaetotaxy (Figs. 13, 15, 18)

The line drawings in each chapter give an overview of the setation. Setae are assigned the following abbreviations: dorsal side of head – d, ventral side of head – v, labial palps – l, antenna – a, maxilla – m, thorax – t and abdomen – ad. The setae are numbered successively as shown in the figure plate.

Head capsule (Fig. 18): forty-two pairs of regular setae and one pair of specialized setae with a large socket (“trichobothria”) are inserted on the head. All setae are acute at the tip end none of them is split. Two very short adjacent setae are inserted at the posterior margin of the head capsule close to each other (d1 & d2). Anterior to them two longer and anteriorly directed setae are inserted on the dorsolateral head capsule pointing anterad (d3 & d14). Setae d4, d5 and d6 on the anterior part of the head are inserted successively from anterior to posterior, slightly laterad the mid line. The elongate and posteriorly directed “trichobothrium” d7 is inserted laterad d6. A long seta is present mesad the posterior stemmata (d8). Setae d9 and d10 are inserted laterally on the posterior half of the head capsule; both are long and pointing anteriorly. The lateral seta d11 is much shorter and located further anteriorly. A second seta of the ocular field (d12) is inserted below the posterior stemmata and as long as d8. The long and anteriorly directed seta d13 is located at the posterior margin of the head capsule, slightly laterad d3. The ventral side of the head bears less setae than the dorsal surface. The moderately long v1 is inserted at the ventral hind margin of the head capsule. Two short setae are located on the anterior part of the mentum (v2 &

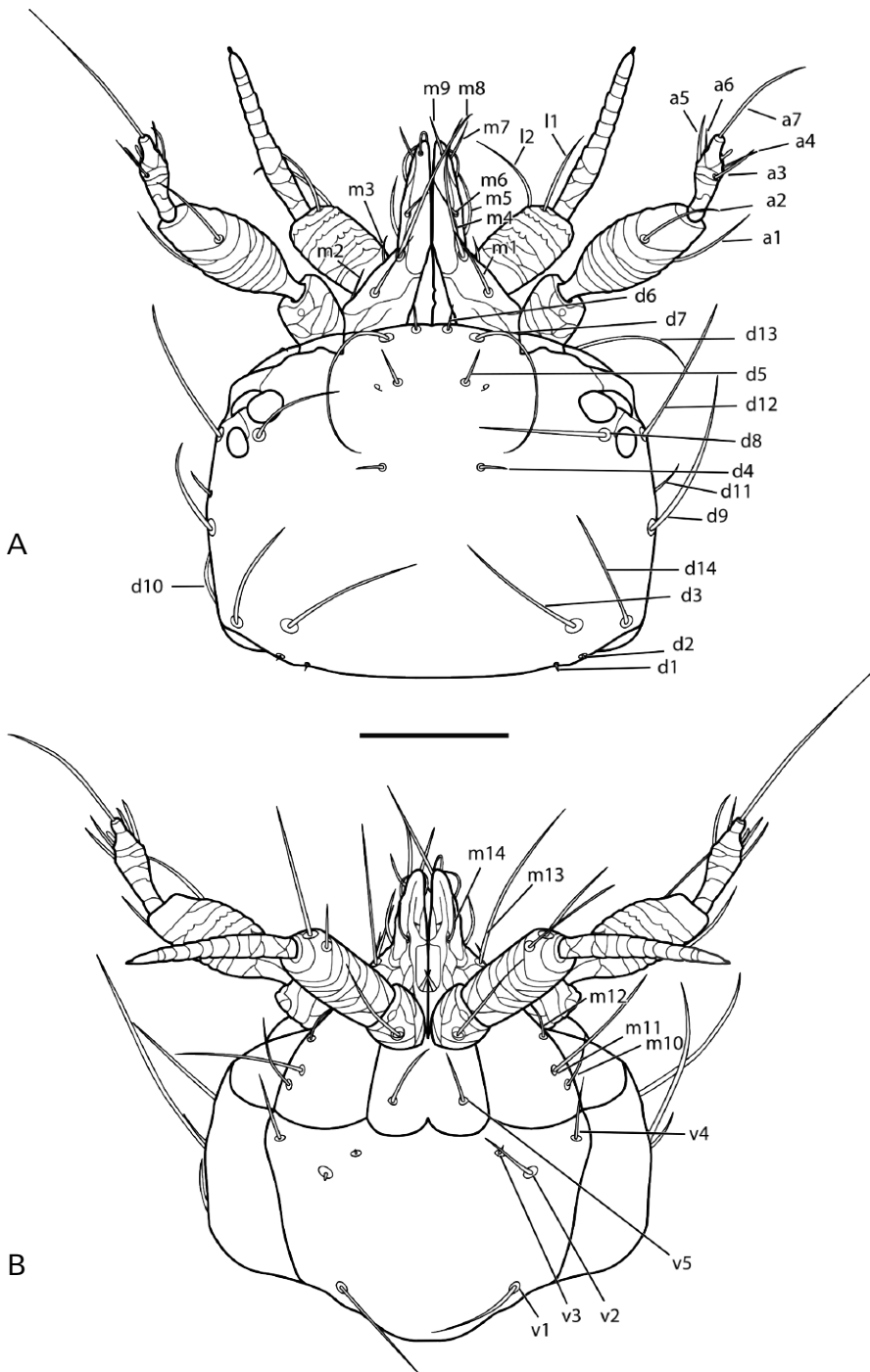


Fig. 18. Chaetotaxy of head capsule; **A:** dorsal view; **B:** ventral view. — **Abbreviations:** a1–a7 – antennal setae, d1–d14 – dorsal setae, l1–l3 – labial palp setae, m1–m14 – maxillary setae, v1–v5 – ventral setae. — **Scale bar:** 50 μ m.

v3), both short and v3 shorter than v2. Seta v4 is inserted laterad v3, close to the ventrolateral margin of the head capsule. A moderately long seta is inserted on the central region of the prementum.

Antenna: the antenna bears seven setae of different length. Antennomere 1 is completely glabrous. Two setae are inserted on the distal half of antennomere 2, both pointing apicad and of moderate length. Four short setae are inserted on the distal half of antennomere 3. A long and specialized seta (FITS) is located on the tip of the antenna.

Maxilla: thirteen pairs of seta are inserted on the maxilla. Only three of them are located on the proximal stipi-

tal region; they are arranged successively from anterior to posterior near the margin of the proximal mandibular part (m10,11 & m12). Additional setae of different length are inserted on the maxillary stylets (m1–9, m13 & m14), all of them oriented towards the tip of the stylets.

Labial palps: one seta is inserted on the ventral side of the first palpomere (l1), two on the distal half of palpomere II (l2 & l3); all three are long and pointing apicad.

Thorax (Fig. 13B): meso- and metathorax show very similar patterns; the slight differences will be pointed out below. One short seta is inserted on the central pronotal region laterad the midline (t1). A pair of setae is located at the anterolateral edge of the sclerotized notal region

(t2 & t3); both are very short and pointing anterad; their meso- and mesothorax equivalents are shifted mesad; one of them retains its position on the notum (t3) whereas t2 is located on the prescutum near the anterior margin of the respective segment. A series of setae of different length is inserted on the lateral notal regions (t4–t8), t4 slightly posterior to t3; the other four setae are arranged successively from anterior to posterior, accompanied by slight shifts towards the midline; all of them are long except for t5 which is greatly shortened, and all are directed anteriorly; seta t6 is inserted in a very deep cuticular pit and thus resembles a trichobothrium. Two very short setae are located at the anterolateral margin of each thoracic segment (t9 & t10). Another pair is inserted anterior to the episternum (t11 & t12); while t11 is short and pointing anterad, t12 is slightly longer and directed posteriorly. The short seta t13 is inserted slightly anterad t9 and pointing anteriorly. Three setae are present on the ventral side of the thoracic segments; one located close to the midline (t14) is missing on the prothorax; a long seta is inserted posterior to t14 on the posterior half of the respective segment; a short seta (t16) is inserted antero-laterad t14; it is located near the anterior margin of each segment and pointing anteriorly.

Abdomen (Fig. 15A): a very short and anteriorly directed seta is laterally inserted on the prenatal fold (ad1); a row of three setae is inserted on the tergal region posterior to the fold (ad2–ad4), successively arranged from the median region towards the lateral areas; all three are long and pointing posteriorly. A small seta is inserted posteriorly and slightly mesad to ad4 and also pointing posteriorly (ad5). Setae ad6 and ad7 are inserted on the posterior half of the tergal region, the former mesally and the latter laterally. Two setae are present between the dorsopleural and pleuroventral line. One seta of moderate length is inserted anteriorly on the pleural region (ad8) and one long seta (ad9) on the posterior half on the same level as ad7. The sternal regions bear only few setae as in the case of the thoracic segments. Like the dorsal ad1, the small seta ad8 is inserted near the anterior segmental border. One very short seta is located on the anterior half close to the midline (ad9). The long posteriorly oriented ad10 is inserted posterolaterad ad9, and the long antero-laterally directed ad11 close to ad10. Two additional setae are inserted on the posterior parts of the pleuroventral line (ad12 & ad13); they are placed close to each other, ad13 slightly posterior to ad12; on segment III both setae are moderately long, whereas ad 12 is very short on the other abdominal segments; seta ad12 is missing on segment.

3.24. List of phylogenetically relevant characters
(mainly from BEUTEL et al. 2010)

Characters of larval head

1. Cervix: (0) absent; (1) present. A cervix as a separate collar-like element between the head and prothorax is present in all groups of Neuroptera, in contrast

to a direct connection by a cervical membrane in other groups of Holometabla (e.g. MACLEOD 1964; MANSELL 1983; BEUTEL et al. 2010). Cervix short but distinctly developed in primary larvae of *Mantispa* (Fig. 4) and Berothidae (MÖLLER et al. 2006). Longer in *Plega* (Symphrasinae) (MACLEOD 1964: figs. 45, 46) and *Ditaxis biseriata* Westwood, 1852 (Drepanicinae) (DOREY & MERRITT 2017: fig. 4).

- 2. Head shape of later instars: (0) dorsoventrally compressed; (1) dorsoventral depth approximately equals anterior-posterior length.** Head of first instar of *Mantispa* moderately flattened (Fig. 4) like in most neuropteran primary larvae. Strongly flattened in Nevrothidae and some other groups (e.g. Dilariidae, Berothidae, *Plega*; MACLEOD 1964; BEUTEL et al. 2010). The dorsoventral depth exceeds the anterior-posterior length of the head in Ithonidae (incl. Polystoechotidae) and Sisyridae (MACLEOD 1964: fig. 31), and to a slightly lesser degree in mature larvae of Mantispidae and Coniopterygidae (MACLEOD 1964) (coded as 1).
- 3. Orientation of mouthparts: (0) subprognathous; (1) prognathous, head horizontal, dorsal and ventral wall of head capsule nearly horizontal.** Distinctly prognathous in first instars of Mantispidae (Fig. 3) and other groups of Neuroptera (e.g. WUNDT 1959; ROUSSET 1966; ASPÖCK & ASPÖCK 1971; BEUTEL & GE 2008; GREBENNIKOV 2004; BEUTEL et al. 2010). Subprognathous in *Sialis* (RÖBER 1942).
- 4. Shape of frontoclypeal region: (0) without abrupt change in the slope; (1) with abrupt change in the slope.** An abrupt change in the slope of the frontoclypeal region is an unusual feature of Ithonidae (MACLEOD 1964; GREBENNIKOV 2004).
- 5. Gula: (0) present, large; (1) absent or vestigial; (2) small, triangular; (3) very narrow, appearing like a longitudinal double suture.** Absent in first instars of Mantispidae (Fig. 3) and other hemerobiform larvae, with the exception of Polystoechotidae (MACLEOD 1964; BEUTEL et al. 2010). Present as well-developed more or less parallel-sided plate in Raphidioptera (ASPÖCK et al. 1991; BEUTEL & GE 2008), Corydalidae, and Nevrothidae (ZWICK 1967; BEUTEL et al. 2010). Also present but relatively small in *Polystoechotes punctatus* Fabricius, 1793 (MACLEOD 1964) and represented by small sclerotizations in *Ithone fusca* Newman, 1838 (MACLEOD 1964). Present as small and triangular sclerite in Myrmeleontiformia (BEUTEL et al. 2010).
- 6. Narrowed neck region: (0) distinctly developed; (1) indistinct or absent.** Absent in Mantispidae (Fig. 3) and other hemerobiform groups, and vestigial in most groups of Myrmeleontiformia. Very distinct in Nevrothidae and also present in Psychopsidae and Nemopteridae (usually hidden in Nemopterinae; BADANO et al. 2017) (MACLEOD 1964; BEUTEL et al. 2010). Also distinct in Corydalidae (BEUTEL & FRIEDRICH 2008) and Raphidioptera (ASPÖCK et al. 1991; BEUTEL & GE 2008).

- 7.* Paired postoccipital pads: (0) absent; (1) present.** A postoccipital ridge is present in Mantispidae and other neuropteran groups. It is transformed into paired sclerotized pads in larvae of Coniopterygidae (ROUSSET 1966).
- 8. Temples of later instar larvae: (0) distinct; (1) obsolete or absent.** The head capsule is evenly rounded posterolaterally in first instars of *Mantispa* (Fig. 3), Berothidae and Rhachiberotidae (MINTER 1990; MÖLLER et al. 2006: figs. 7–9) (coded as 0). Temples are completely absent in *Plega* (MACLEOD 1964: figs. 45, 46) and they are also missing in Ithonidae, Osmylidae, Chrysopidae, Hemerobiidae, Sisyridae, Coniopterygidae, and Dilaridae (*Nallachius*; MACLEOD 1964; MINTER 1992; BEUTEL et al. 2010). Distinct temples are present in Raphidioptera, Corydalidae, and Nevrothidae. They are strongly pronounced in larvae of the myrmeleontiform lineage (MACLEOD 1964).
- 9. Hypostomal bridge: (0) absent; (1) present.** Absent in first instars of Mantispidae and other hemerobiform larvae, and also missing in Nevrothidae. Generally present in Myrmeleontiformia (MACLEOD 1964).
- 10. Lateral remnant of frontoclypeal sulcus: (0) present; (1) absent.** Completely missing in Mantispidae, Berothidae and Dilaridae (MACLEOD 1964). Present in Nevrothidae and most other groups of Neuroptera. Very distinct and long in myrmeleontiform larvae (MACLEOD 1964; BEUTEL et al. 2010).
- 11. Finger-like mid-dorsal cervical apodeme: (0) absent or short; (1) strongly developed.** Finger-like mid-dorsal cervical apodeme absent in first instars of *Mantispa* and also absent or short in most other groups of Neuroptera. Strongly developed in Ascalaphidae, Myrmeleontidae and Nemopteridae (SUNDERMEIER 1940; MACLEOD 1964).
- 12. Dolichasterine setae: (0) absent; (1) present.** Present in myrmeleontiform larvae (HENRY 1978; MONSERRAT 1996).
- 13. Shape of tentorium: (0) H-shaped; (1) X-shaped, with distinctly constricted central part.** Tentorium more or less H-shaped, with posteriorly diverging posterior arms in first instars of *Mantispa* and most other neuropteran groups (e.g. MACLEOD 1964; BEUTEL et al. 2010). X-shaped with distinctly constricted central part and very broad tentorial bridge in Ithonidae (MACLEOD 1964). A reduction of the tentorium was ascribed to larvae of Mantispidae by MACLEOD (1964). This may apply to Symphrasinae (e.g. *Plega*) or other subgroups, but not to the larva of *Mantispa* described here.
- 14. Posterior tentorial grooves: (0) central region of head capsule; (1) close to hind margin of head capsule; (2) anterior third of head capsule, close to anterior margin.** Close to hind margin of head capsule in Mantispinae and other hemerobiform groups (WUNDT 1959; MACLEOD 1964; ROUSSET 1966). In central region of head capsule in Raphidioptera, Megaloptera, and Nevrothidae (BEUTEL et al. 2010). In anterior third in Myrmeleontiformia (MACLEOD 1964). Tentorial grooves not recognizable in Symphrasinae (MACLEOD 1964).
- 15. Tentorial bridge: (0) well developed, (1) very thin or absent.** Very thin in first instars of *Mantispa* and Dilaridae. Absent in Berothidae and *Plega* (MACLEOD 1964).
- 16. Position of anterior tentorial pits: (0) within anterior third of head capsule; (1) posterad of anterior third of head capsule.** Anterior tentorial arms not shifted posteriorly in Mantispidae (Figs. 3, 10) and most other neuropteran larvae, and only slightly in *Ithone fusca* (MACLEOD 1964; coded as 0). Strongly shifted posteriorly in Coniopterygidae (MACLEOD 1964; ROUSSET 1966).
- 17. Number of convex corneae (lenses): (0) seven; (1) six; (2) five; (3) four; (4) three; (5) two; (6) one; (7) absent.** Three distinct and convex cornea lenses are present in first instars of *Mantispa* (Fig. 3, 4) and in Hemerobiidae. Two are present in *Plega* and Berothidae (MACLEOD 1964), and only a single large eyespot with a completely flat and undivided lens and large internal pigment spot in Nevrothidae (ZWICK 1967; coded as 7). A single cornea is present in *Nallachius americanus* McLachlan, 1881 but a cornea is absent in *Nallachius krooni* Minter, 1986 (coded as 6&7 for Dilaridae; MACLEOD 1964; MINTER 1992). Seven stemmata are present in Nymphidae (partim, coded as 0&1; HENRY 1978), Nemopteridae (with few exceptions in Nemopterinae; BADANO et al. 2017), Myrmeleontidae and Ascalaphidae (MACLEOD 1964; MANSELL 1983; MONSERRAT 1996) and Raphidiidae (partim). Six occur in Polystoechotidae (very small), Osmylidae, Chrysopidae (ROUSSET 1966), Sisyridae, and Nymphidae (partim; MACLEOD 1964; HENRY 1978), and also in Megaloptera (RÖBER 1942; BEUTEL & FRIEDRICH 2008) and Raphidiidae [partim]. Five corneae are present in Coniopterygidae and Psychopsidae (MACLEOD 1964).
- 18. Shape of ocular region: (0) not forming a distinctly raised, well defined elevation; (1) forming a moderately raised, well defined elevation; (2) forming a strongly convex elevation.** Distinctly raised ocular region absent in primary larvae of *Mantispa* like in most other groups Neuroptera. Stemmata located on moderately distinct elevation in most Nemopteridae (coded as 1) (not in *Derhynchia* [eyes reduced]; MANSELL 1983) and Nymphidae. Placed on strongly pronounced ocular tubercle in most Myrmeleontidae (coded as 2), Ascalaphidae and *Coniopteryx* (MACLEOD 1964; HENRY 1978; MONSERRAT 1996).
- 19. Articulation of labrum: (0) labrum movably articulated with anterior clypeal margin with membrane; (1) membranous articulation missing, labrum and clypeus firmly connected.** Fused with clypeus in primary larvae of *Mantispa* (Fig. 3) like in all other groups of Neuroptera (e.g. WUNDT 1959; MACLEOD 1964; ROUSSET 1966; GREBENNIKOV 2004; BEUTEL et al. 2010).

20. ***Pseudolabral prominence (0) absence; (1) present.** A structure resembling an articulated labrum is present in Coniopterygidae: It has evolved secondarily as shown by MACLEOD (1964).
21. **Antennomere 1 and 2: (0) not fused; (1) fused.** Antennomeres 2–3 fused in Coniopterygidae (MACLEOD 1964).
22. **Fixed curvature of antenna: (0) absent; (1) present.** Fixed curvature present in Ithonidae (MACLEOD 1964; GREBENNIKOV 2004).
23. **Shape of flagellum: (0) diameter of flagellomeres subequal to diameter of basal antennomere; (1) very slender, flagellum very small; (2) reduced, club-shaped antennomere 2 terminal.** Flagellomeres and entire flagellum greatly reduced in size in Nymphidae, Myrmeleontidae, and Ascalaphidae (MACLEOD 1964). Antennomere 2 club-shaped and terminal in Nemopterinae (MONSERRAT 1996).
24. **Specialized terminal seta of flagellum (MACLEOD 1964: FITS): (0) absent; (1) present.** Specialized long terminal flagellar seta present in Mantispidae, Hemerobiidae, Chrysopidae, Osmylidae, Sisyridae, Dilaridae, Berothidae, Mantispidae and Coniopterygidae (MACLEOD 1964: FITS; MÖLLER et al. 2006: fig. 17, “flagellum”). Absent in Nevrothidae, Ithonidae, and the myrmeleontiform groups (MACLEOD 1964; BEUTEL et al. 2010). The paired, slender spines on the apical antennomere of Nevrothidae (ZWICK 1967: fig. 5d) are cylindrical, stiff, distinctly shorter than the apical antennomere, and bear minute hairs on their apex (BEUTEL et al. 2010: coded as 0).
25. **Sensorium of antepenultimate antennomere: (0) absent; (1) present.** Only present in megalopteran larvae (BEUTEL & FRIEDRICH 2008).
26. **Overlapping scales on antennae and maxillae: (0) absent; (1) present.** Present in first instars of Mantispidae (Fig. 5, 6) and also in Berothidae and Rhachiberothidae (ASPÖCK & MANSELL 1994; MINTER 1990). Apparently absent in Dilaridae (MINTER 1992) and also missing in the other groups (e.g. WUNDT 1959; MACLEOD 1964; ROUSSET 1966).
27. **Tricondylic articulation of mandible: (0) absent; (1) present.** Only present in Coniopterygidae (ROUSSET 1966).
28. **Mandibulo-maxillary stylets: (0) absent; (1) present.** Present in primary larvae of *Mantispa* and all other groups of Neuroptera (WUNDT 1959; MACLEOD 1964; ROUSSET 1966; GAUMONT 1976; ASPÖCK & ASPÖCK 2007; BEUTEL et al. 2010).
29. **Length of mandibulo-maxillary stylets: (0) elongate and slender, longer than head capsule; (1) compact, not longer than head capsule.** Short and compact in Mantispidae, Ithonidae (nearly as long as head capsule), Coniopterygidae (partim, long in *Helicoconis*?) and Nemopterinae (MACLEOD 1964; MONSERRAT 1996; ASPÖCK & ASPÖCK 2007; BEUTEL et al. 2010). Elongate and slender in Nevrothidae and most other groups of Neuroptera including Symphrasinae and Drepanacinae (MACLEOD 1964; ASPÖCK & ASPÖCK 2007; DOREY & MERRITT 2017).
30. **Shape of mandibulo-maxillary stylet: (0) curved inwards; (1) straight and nearly subparallel; (2) straight distal inner margin, external margin concave; (3) curved outwards.** Curved inwards in most families and also in *Plega* (Symphrasinae) and outgroup taxa (MACLEOD 1964; ASPÖCK & ASPÖCK 2007), but with straight inner distal margin and concave outer margin in Coniopterygidae, Mantispidae and Drepanacinae (MACLEOD 1964; ASPÖCK & ASPÖCK 2007; BEUTEL et al. 2010; DOREY & MERRITT 2017: fig. 4). Straight and subparallel in Dilaridae, Berothidae, and Rhachiberothidae and curved outwards in Osmylidae and Sisyridae (MACLEOD 1964; ASPÖCK & ASPÖCK 2007).
31. **Distal region of mandibular stylet: (0) thin; (1) stout.** Distal part of mandibular stylet stout in Ithonidae (MACLEOD 1964; GREBENNIKOV 2004). Only present as thin lamella in first instars of *Mantispa* and other groups of Neuroptera (BEUTEL et al. 2010).
32. **Slender mesally directed teeth of mandibular element of stylet: (0) absent; (1) present.** Absent in Mantispidae and other hemerobiform groups. Also missing in Nevrothidae (BEUTEL et al. 2010). Present in some Nemopteridae (not in Nemopterinae and most Crocinae; BADANAO et al. 2017; MANSELL 1983; MONSERRAT 1996; ASPÖCK & ASPÖCK 2007), Nymphidae, Myrmeleontidae and Ascalaphidae (MACLEOD 1964; ASPÖCK & ASPÖCK 2007).
33. **Length of mesally directed slender mandibular teeth: (0) shorter than width of stylet; (1) most teeth longer than width of stylet.** Short in Crocinae (MACLEOD 1964). Most or all teeth are long in Nymphidae, Myrmeleontidae and Ascalaphidae (MACLEOD 1964; ASPÖCK & ASPÖCK 2007).
34. **Number of mesally directed slender mandibular teeth: (0) one; (1) two or more.** One long tooth in Nymphidae (MACLEOD 1964) and two or more in Myrmeleontidae, Ascalaphidae and Nemopteridae (partim) (MACLEOD 1964; MANSELL 1983; ASPÖCK & ASPÖCK 2007).
35. **Position of maxillary base: (0) protracted, maxillary groove absent; (1) slightly retracted, maxillary groove short, one third as long as ventral head capsule or shorter; (2) considerably retracted, maxillary groove half as long as ventral head capsule or longer.** Maxillae strongly retraced in first instar of *Mantispa* and other hemerobiform groups (BEUTEL et al. 2010). Maxillary groove greatly reduced in larvae of Myrmeleontiformia and maxillae protracted (MACLEOD 1964; BEUTEL et al. 2010).
36. **Width of proximal elements of maxilla: (0) about as broad as base of maxillary stylet; (1) very narrow.** Very narrow in Mantispidae, Sisyridae and Coniopterygidae (MACLEOD 1964; ASPÖCK & ASPÖCK 2007).
37. **Longitudinal sulcus of basal maxillary element: (0) absent; (1) present.** Present in Hemerobiidae

and Chrysopidae (MACLEOD 1964: cds; ROUSSET 1966: scldc).

38. **Longitudinal apodemal ridge of intermediate maxillary element: (0) absent; (1) present.** Apodemal ridge of intermediate maxillary element present in Hemerobiidae, Chrysopidae and Osmylidae (WUNDT 1959; MACLEOD 1964; ROUSSET 1966; BEUTEL et al. 2010).
39. **Poison channel of maxillary stylet: (0) absent; (1) present.** Separate mesal poison channel present on mesal side of maxillary stylet of *Mantispa*, Nevrothidae (BEUTEL et al. 2010) and other neuropteran larvae (WUNDT 1959; ROUSSET 1966; GAUMONT 1976). Absent in Sisyridae (GAUMONT 1976).
40. **Galea: (0) present as distinct element; (1) absent or completely fused with lacinia.** Completely absent in Mantispidae and other groups of Neuroptera (e.g. CRAMPTON 1921; WUNDT 1959; MACLEOD 1964; ROUSSET 1966).
41. **Maxillary palp: (0) present; (1) absent.** Missing in Mantispidae and other groups of Neuroptera (MACLEOD 1964; ROUSSET 1966; GREBENNIKOV 2004; ASPÖCK & ASPÖCK 2007).
42. **M. craniocardinalis: (0) present; (1) absent.** Absent in first instar of *Mantispa* and other groups of Neuroptera (WUNDT 1959; ROUSSET 1966; BEUTEL et al. 2010).
43. **Teeth on lateral surface of the maxillary blade: (0) absent; (1) present.** Only present in Coniopterygidae (MACLEOD 1964).
44. **Intrinsic muscle of the stylet: (0) absent; (1) present.** Present in first instars of *Mantispa* and also in Nevrothidae (BEUTEL et al. 2010) and other groups of Neuroptera (WUNDT 1959; ROUSSET 1966).
45. **Subdivision of postmentum: (0) subdivided into mentum and submentum; (1) undivided.** Undivided in *Mantispa* and other groups of Neuroptera except for Nevrothidae (WUNDT 1959; MACLEOD 1964; ROUSSET 1966; BEUTEL et al. 2010). Also subdivided in Raphidioptera (mentum distinctly reduced and membranous; BEUTEL & GE 2008) and Megaloptera (CRAMPTON 1921; BEUTEL & FRIEDRICH 2008).
46. **Shape of postmentum: (0) not distinctly longer than wide; (1) at least 2 × longer than wide.** Usually about as wide as long, but at least twice as long as wide in *Plega*, Dilaridae, Berothidae and Rhachiberothidae (MACLEOD 1964; ASPÖCK & ASPÖCK 2007). Coded as inapplicable for groups with divided postmentum.
47. **Median separation of paired premental (prelabial) elements: (0) adjacent; (1) widely separated.** Medially adjacent, only divided by a cleft and corresponding internal ridge in Mantispidae (Fig. 3), Nevrothidae, and other hemerobiform groups (WUNDT 1959; MACLEOD 1964; BEUTEL et al. 2010). Premental elements widely separated in myrmeleontiform larvae.
48. **Large internal process of prementum: (0) absent; (1) present.** Median sclerotized strut-like prelabial structure (ROUSSET 1966: “baguette”) present in Coniopterygidae. A much smaller structure is present in Berothidae (MACLEOD 1964: fig. 40, PrlbAP), coded as 0.
49. **Number of labial palpomeres: (0) three or more; (1) two.** Only two in Coniopterygidae and Crocinae (MACLEOD 1964; ROUSSET 1966; MONSERRAT 1996, 2006).
50. ***Widely separated premental halves: (0) similar in shape and size to palpomeres; (1) strongly developed and ventrally flattened** (BADANO et al. 2017 [erroneously interpreted as palpigers]). The premental halves are similarly shaped like the palpomeres in larvae of Psychopsidae (MACLEOD 1964: fig. 69). It is strongly developed and dorsoventrally flattened in all other Myrmeleontiformia (BADANO et al. 2017: fig. 10F,G). Coded as inapplicable for non-myrmeleontiform groups.
51. **Size of labial palpomeres: (0) normally sized; (1) proximal palpomere unusually large; (2) all palpomeres appear inflated.** Palpomeres appear strongly inflated in Coniopterygidae (MACLEOD 1964; ROUSSET 1966). Proximal palpomere large in *Plega* (MACLEOD 1964: fig. 69).
52. **Sensory pit of distal labial palpomere: (0) absent; (1) present.** Present on apical labial palpomere of Ascalaphidae, Myrmeleontidae and Nemopteridae (MACLEOD 1964; MONSERRAT 1996; BADANO et al. 2017).
53. **Elongate sensory area on distal labial palpomere: (0) absent; (1) present.** Present on apical labial palpomere in Coniopterygidae (MACLEOD 1964).
54. **Mandibulo-maxillary cephalic gland: (0) absent; (1) present.** Present in Nevrothidae, Osmylidae, Chrysopidae, Hemerobiidae, Sisyridae, Coniopterygidae (partim), Myrmeleontidae (WUNDT 1959; ROUSSET 1966; GAUMONT 1976), and Crocinae. Also present in first instars of *Mantispa* but composed of delicate tissue with a single duct. The gland is absent in *Coniopteryx*, but present in other genera of the family (ROUSSET 1966).
55. **Mesal gland of maxillary stylet: (0) absent; (1) present.** The median internal gland or poison gland of the maxillary stylet is present in *Mantispa* and also in larvae of other families of Neuroptera (WUNDT 1959; ROUSSET 1966; GAUMONT 1976), with the noteworthy exception of *Sisyra* (GAUMONT 1976).
56. **Lateral gland of maxillary stylet: (0) absent; (1) present.** The large lateral gland of the maxillary stylet is represented by a hollow compartment delimited by an extremely thin endothelium in larvae of Nevrothidae (BEUTEL et al. 2010). A similar condition is found in other groups of Neuroptera (e.g. hemerobiid and crocine larvae; WUNDT 1959; ROUSSET 1966; GAUMONT 1976).

Additional larval characters

57. ***Shape of postcephalic body: (0) subparallel- or parallel-sided, abdomen elongate; (1) meso- and**

- metathorax and abdomen strongly rounded laterally, abdomen compact. The postcephalic body is parallel-sided in most families of Neuroptera including Mantispidae and also the myrmeleontiform family Psychopsidae. The body region posterior to the prothorax is strongly rounded laterally and forms a compact unit in Myrmeleontiformia excluding Psychopsidae (BADANO et al. 2017: figs. 1, 8). The body is also distinctly rounded in larvae of Coniopterygidae (TAUBER 1987).
58. **Proportion of head and postcephalic body in 2nd or 3rd instars: (0) head normally sized in relation to postcephalic segments; (1) small in size relation to postcephalic segments.** Head greatly reduced in size in relation to postcephalic body in later instars of Mantispidae, Dilaridae and Berothidae (ASPÖCK & ASPÖCK 2007; PARKER & STANGE 1965). Condition in *Mucroberotha* (Rhachiberothidae) unknown (MINTER 1990).
59. ***Long setae inserted in deep sockets on thoracic tergites (“trichobothria”): (0) absent; (1) present.** Present in Mantispidae, Berothidae and Rhachiberothidae (MINTER 1990; MÖLLER et al. 2006; PARKER & STANGE 1965).
60. **Regular series of scoli on abdomen: (0) absent; (1) present.** Present in Nymphidae, Myrmeleontidae and Ascalaphidae (HENRY 1978).
61. **Fusion of tibia and tarsus in the hind leg: (0) absent; (1) present.** Tibia and tarsus of hind legs fused in Myrmeleontidae and Ascalaphidae (HENRY 1978).
62. ***Deep transverse furrow on proximal ventral tibia: (0) absent; (1) present.** Present in first instar of *Mantispa*. Absent in Berothidae and Rhachiberothidae (MINTER 1990; MÖLLER et al. 2006) and other groups of Neuroptera.
63. ***Pseudoclaw on proximal tarsus: (0) absent; (1) present.** Present on all legs of first instars of *Mantispa*. Absent in Berothidae and Rhachiberothidae (MINTER 1990) and other groups including Symphrasinae (PARKER & STANGE 1965: “post-tarsal claws”).
64. **Trumpet-shaped, elongate empodium of first instar larvae: (0) absent; (1) present.** Present in Mantispidae, Chrysopidae, Hemerobiidae, Berothidae, Rhachiberothidae, Dilaridae and Psychopsidae (TILLYARD 1918; PARKER & STANGE 1965: “clavate empodium”; MINTER 1990, 1992; MÖLLER et al. 2006), but absent in the other groups (ZWICK 1967; HENRY 1978; MONSERRAT 1996; GREBENNIKOV 2004; BEUTEL et al. 2010).
65. **Scarabaeiform 2nd instar larva: (0) absent; (1) present.** Present in Mantispidae and Berothidae, and possibly also in Rhachiberothidae (coded as ?) (PARKER & STANGE 1965; ASPÖCK et al. 2001; MÖLLER et al. 2006). This condition is likely correlated with specialized predacious (e.g. in nests of termite) or parasitic habits (ASPÖCK et al. 2007).
66. **Urogomphi: (0) present on segment IX; (1) absent.** Urogomphi occur in most lineages of Coleoptera but are absent in Neuropterida.
67. ***Adhesive structure of segment X: (0) absent; (1) present.** An adhesive organ formed by segment X is present in larvae of Mantispinae (Fig. 3), Berothidae and Chrysopidae. (TAUBER 1987). The presence in larvae of *Plega* is not confirmed (PARKER & STANGE 1965) (coded as ?).
68. ***Exposure of segment X: (0) visible externally; (1) retracted.** Retracted in larvae of Nemopteridae, Myrmeleontidae and Ascalaphidae (pers. obs. R. Beutel; TAUBER 1987).
69. **Cryptonephry: (0) absent; (1) five or six Malpighian tubules attached; (2) one Malpighian tubule attached (ASPÖCK et al. 2001, modified).** The cryptonephric condition with two free tubules is found in *Mantispa*, and also in Myrmeleontidae, Hemerobiidae, Osmylidae and Chrysopidae (GAUMONT 1976). Apparently one tubule is lost in *Osmylus* (GAUMONT 1976). All tubules are free in *Nevrorthus* and *Sialis* (ASPÖCK et al. 2001), and all except one in *Sisyridae*. The condition for several families is unknown (ASPÖCK et al. 2001).
70. **Habitat: (0) aquatic; (1) terrestrial.** Larvae of Megaloptera, Nevorthidae and Sisyridae are aquatic.

Characters of adults (coleopteran outgroup taxa)

71. **Elytra: (0) absent; (1) present.** Present in Coleoptera.
72. **Exposed body parts sclerotized, without exposed membranes: (0) absent; (1) present.** Present in Coleoptera.

4. Discussion

The first instar larvae of *Mantispa* (Mantispinae) were shaped by different but interrelated phenomena, the phylogenetic background, functional requirements linked with the specific parasitic lifestyle, hypermetamorphosis, and effects of miniaturization. These aspects will be discussed in the following.

4.1. Phylogeny

The morphological features analyzed here represent the largest larval data set for Neuroptera analyzed so far. It is largely based on BEUTEL et al. (2010), but several characters were added, data missing for *Mantispa* were inserted, and *Plega* (Symphrasinae) was added to the taxon sampling. The parsimony analysis of the 72 larval characters (Fig. 19) places *Mantispa* and *Plega* in the ‘dilarid clade’ (ASPÖCK & ASPÖCK 2008; BEUTEL et al. 2010) (branch support [= BS] 2) comprising Dilaridae, Berothidae, Rhachiberothidae and Mantispidae. Potential synapomorphies are the complete absence of lateral remnants of the frontoclypeal sulcus (10.1), straight and nearly subparallel mandibulo-maxillary stylets (30.1), a small head of secondary larvae (in relation to the post-

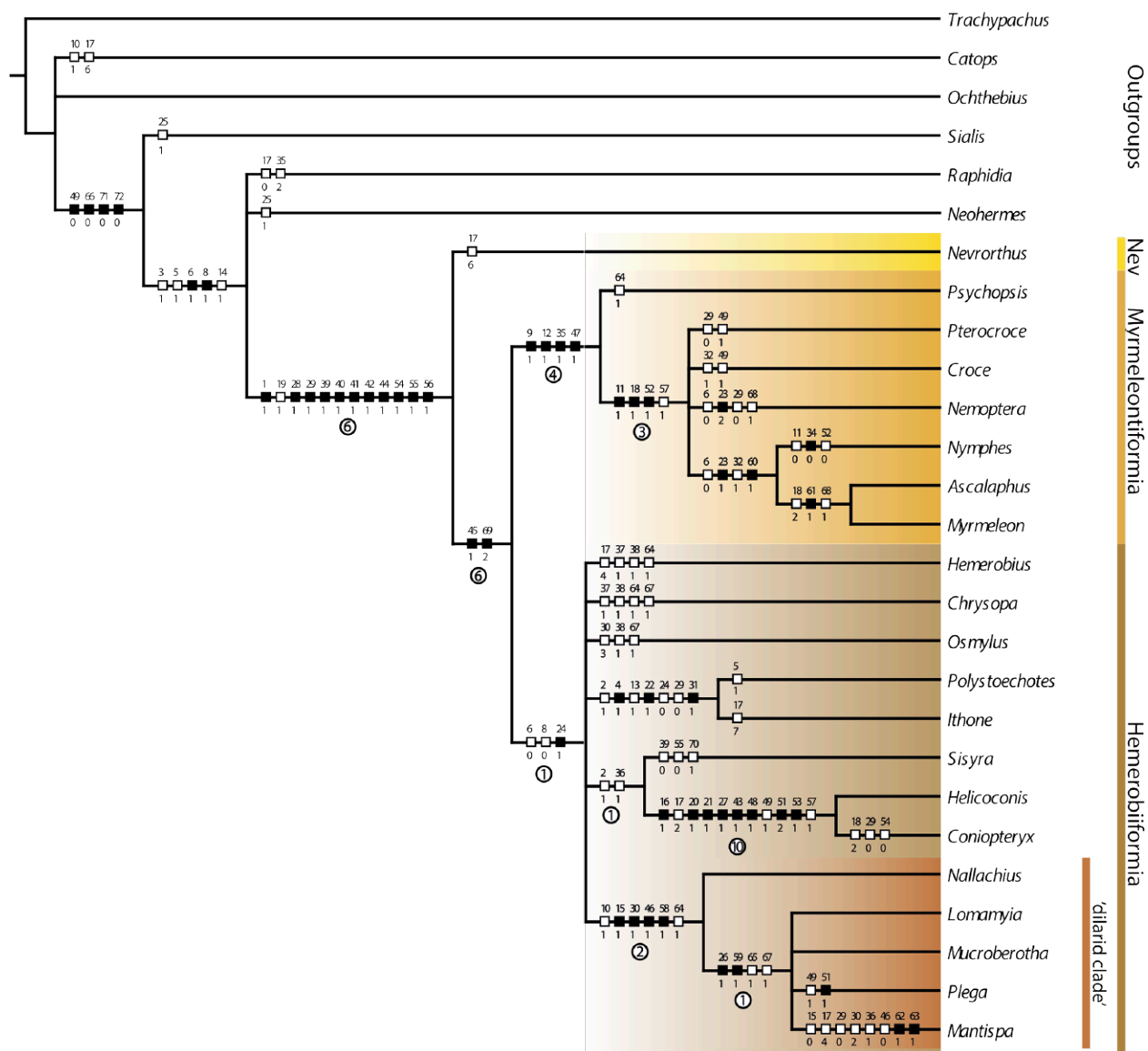


Fig. 19. Cladogram – Strict consensus of 249 minimal length trees with 135 steps, consistency index 0.63, retention index 0.81. Apomorphies mapped on tree – non-homoplasious changes full quadrangles. Bremer support in circles. — **Abbreviations:** Nev – Nevrorthidae. — Datamatrix in Electronic Supplement File 1.

cephalic body) (58.1), and a trumpet-shaped pretarsal empodium (64.1). None of these characters is really convincing. Loss of the frontoclypeal sulcus is a frequent feature in holometabolous larvae (BEUTEL et al. 2009, 2011), the stylets vary considerably in shape among the four families, and a trumpet-shaped empodium does also occur in other hemerobiform families and also in Psychopsidae. Parallel evolution of this highly unusual pretarsal adhesive device is very unlikely. We assume that it evolved early in the evolution of the order, possibly as a derived groundplan feature of Neuroptera excl. Nevrorthidae, Coniopterygidae, Sisyridae and Osmylidae, with secondary loss in Myrmeleontiformia excluding Psychopsidae. This interpretation is also supported by the presence of a well-developed empodium in Mesozoic stem-Myrmeleontiformia (BADANO et al. 2018). A similar scenario may apply to the terminal abdominal attachments structure. Its presence is confirmed for Mantispinae

(e.g. KUROKO 1961: pl. X), Berothidae and Chrysopidae, but reliable data are missing for most groups (e.g. Dilaridae, Symphrasinae). Mantispodea in the sense of WINTERTON et al. (2018), comprising Rhachiberothidae, Berothidae and paraphyletic Mantispidae, appear reasonably well supported despite of the low support value (BS 1). Shared larval apomorphies of Berothidae, Rhachiberothidae and Mantispidae are overlapping scales on antennae and maxillae (26.1), long setae inserted in large sockets on the thoracic tergites (“trichobothria”) (59.1), and hypermetamorphosis with scarabaeiform 2nd instar larvae (65.1). The relationships of the mantispoid terminals are not resolved, and *Mantispa* (Mantispinae) and *Plega* (Symphrasinae) are not retrieved as sister taxa. Within this lineage, larvae of *Mantispa* (Mantispinae) differ distinctly from those of *Plega* (see MACLEOD 1964) and also from those of Drepanicinae (DOREY & MERRITT 2017: figs. 3, 4), Berothidae and Rhachiberothidae. The

shortened mesal edges of the compact mandibular stylets, the large and broadened mentum, and the fixed tarsal pseudoclaw are possible autapomorphies of Mantispiniae (see also KUROKO 1961). *Ditaxis* (Mantispiniae) differs from *Mantispa* by the laterally rounded and posteriorly widening head (KUROKO 1961: pl. X). *Plega* differs from both by the elongate head and mentum, the distinctly longer cervix, the presence of only two stemmata, inwardly curved sucking stylets with small apical teeth on the maxillary component, and the presence of only two labial palpomeres, with the proximal one strongly inflated (MACLEOD 1964: figs. 42, 44).

Not surprisingly the results concerning the other groups are similar to the phylogeny of BEUTEL et al. (2010), which was based on a slightly smaller and less complete data set. Nevrothidae were recovered as sister to all remaining groups, monophyletic Hemerobiformia as sister to a clade Myrmeleontiformia, and Psychopsidae as sister to the remaining myrmeleontiform families. The branching pattern will not be discussed in detail in this study focused on larval Mantispidae. It is clear however, that hemerobiform relationships remain a problem, whereas the myrmeleontiform lineage appears largely clarified (e.g. RANDOLF et al. 2013, 2014, 2017; WANG et al. 2016). In a recent study based on anchored hybrid enrichment (AHE) data, WINTERTON et al. (2018) retrieved Coniopterygidae as sister to all other neuropteran families, Nevrothidae in a clade Osmyoidea together with Sisyridae and Osmylidae, and like in the present contribution paraphyletic Mantispidae in a clade with Rhachiberothidae and Berothidae (Mantispoidea). In contrast to the present study, Dilaridae were placed as sister to Neuroptera excl. Coniopterygidae and Osmyoidea (with Sisyridae, Nevrothidae, Osmylidae), and Ithonidae as sister to Psychopsidae, which means paraphyletic Myrmeleontiformia. This pattern, which requires 20 additional steps with the data set presented here (Mesquite; MADDISON & MADDISON 2015), implies that the gula and subdivided postmentum have evolved secondarily in Nevrothidae (see WINTERTON et al. 2018: fig. 5). However, there is no supporting proof for this argumentation. These features were interpreted as part of the neuropteran groundplan in BEUTEL et al. (2010) with the corresponding apomorphic conditions as potential synapomorphies of Neuroptera excl. Nevrothidae. In WANG et al. (2016) Dilaridae are placed as sistergroup to the rest, excluding Coniopterygidae, Sisyridae, Nevrothidae, Osmylidae.

4.2. Parasitism and specialized predacious habits

First instars of species of the subfamily Mantispiniae are well known for their spider parasitism and feeding in spider egg sacs (SCHREMMER 1983; REDBORG 1998). Two distinctive types are described: species searching for egg sacs on the substrate like *Campio vittatus* (Guerin-Ménéville, 1831) (McKEOWN & MINCHAM 1948) and *Mantispa styriaca* (BRAUER 1869) or spider boarders like *Dicromantispa interrupta* (Say, 1825) (GUARISCO 1998). Due to missing

observations it remains unclear if *M. aphavexlete* follows a single strategy or a combination of both like *Dicromantispa sayi* (Banks, 1897) (REDBORG & MACLEOD 1984). It is likely that the highly specialized life style of immature Mantispiniae has evolved from a transition field between parasitism and specialized carnivorous habits, with prey with a distinctly reduced mobility. Larvae of the related Berothidae and non-mantispid mantispid larvae prey on the offspring of social or non-social aculeatan Hymenoptera or Isoptera (termites), or on immature insects living in soil or under bark (e.g. TAUBER 1987).

Both strategies of mantispine larvae imply different challenges. Firstly, the larvae must find an egg sac or a suitable spider to board, for example species of Lycosidae, Thomisidae, Clubionidae or Salticidae (BRAUER 1869; KASTON 1938; REDBORG 1998; OHL 2011). This makes high mobility essential, which is guaranteed by differentiated thoracic legs and well-developed extrinsic and intrinsic leg muscles of the tiny larvae. The legs display several unusual structural modifications. The trumpet-shaped empodium is a partly membranous structure likely facilitating efficient movements and adhesion on different substrates with its flexibility and fine ridges on its surface. This includes spider egg sacs and in the case of spider-boarding species also the body surface of hosts. The wide distribution of the trumpet-shaped empodium in non-parasitic neuropteran families (see above) implies that this is not a special adaption to the parasitic lifestyle of Mantispiniae. It is apparently useful in this context but has certainly evolved early in the evolution of Neuroptera. A very unusual feature of the legs of mantispine larvae is the well-sclerotized, fixed tarsal pseudoclaw, which likely also improves locomotion on different surfaces, thus complementing the structurally very different empodium. It is likely that this solid hook-shaped structure also facilitates the rupturing of the egg sac of the host spiders.

Compared to larvae of other families (e.g. Nevrothidae, Myrmeleontiformia), the sucking jaws of first instars of Mantispiniae are largely immobilized and not curved mesad as it is usually the case, but straight and anteriorly directed (Fig. 3A,B). Unlike in some other neuropteran groups, the combined paired mouthparts are not used for grasping prey. However, the modified mandibulo-maxillary stylets are well suited for penetrating immobile surfaces, i.e. piercing eggs of spiders (BRAUER 1869; KASTON 1938; REDBORG 1998; OHL 2011), and in the case of spider boarding species also for penetrating articulatory membranes or other weakly sclerotized areas of the host. Despite of the partial immobilization, the mandibular adductor (M11) and abductor (M12) are well-developed (Fig. 11A), whereas the tentorio-mandibular muscle (M13), which it is present in Nevrothidae, Osmylidae, Chrysopidae, and Myrmeleontidae (WUNDT 1959; ROUSSET 1966; BEUTEL et al. 2010), is missing like in Coniopterygidae (ROUSSET 1966; see also BEUTEL et al. 2010). In contrast to the usual condition in insects, the abductor (M12) of *Mantispa* is distinctly enlarged, according to v. KÉLER (1963) a condition typical for insects with piercing-sucking feeding habits with an active

stroke. The abductor is also slightly enlarged in Osmylidae, where the mandibles are slightly bent outwards and elongated. The musculature of the maxilla is similar to the configuration in other neuropteran larvae examined so far. The well-developed tentorio-cardinal and tentorio-stipital muscles (M17, M18) are likely linked with penetration and possibly the injection of gland secretions as described by WUNDT (1959) for the larva of *Osmylus*. A similar function was postulated for non-related insects with piercing-sucking feeding habits, Hemiptera and Thysanoptera (v. KÉLER 1963). The well-developed cranio-lacinal muscle (M19) functions as retractor of the maxillary stylet.

The cephalic gland of *Mantispa* is poorly developed compared to the condition found in other neuropteran groups, like for instance Nevrothidae, where it is large and tube-shaped (BEUTEL et al. 2010). The vestigial condition in *Mantispa* is possibly related with the specific feeding habits and parasitic lifestyle. In contrast to active prey, eggs do not need to be immobilized by poison. Spider boarding species would not inject venom in their host, as they depend on the production of egg sacs for completing their postembryonic development.

A noteworthy feature of the abdomen is the terminal eversible attachment structure. As its function WUNDT (1959) suggested the fixation of the larval abdominal apex on the ground. In the case of Mantispinae the anchorage of the abdominal apex likely facilitates the penetration of the egg sac or articulatory membranes of a host spider. It may also provide anchorage on the cuticle of a spider in the case of spider boarding species. Another possible function would be fixing the body on the substrate, while the free legs can attach to a passing spider host. However, observations confirming this are missing so far.

4.3. Size of 1st instars and hypermetamorphosis

Far-reaching size reduction is a typical feature of parasitic holometabolous larvae (e.g. OSSWALD et al. 2010; POHL & BEUTEL 2008; GE et al. 2012; BEUTEL et al. 2016; KNAUTHE et al. 2016). In the case of spider boarding species, this makes it possible to avoid detection and attack when entering the host. A second factor is the size of the spider egg sac, which obviously limits the size of the larva. Aside from this, the small size of first instars is linked with the production of very large numbers of offspring in parasitic insects.

Hypermetamorphosis (or heteromorphosis) (SNODGRASS 1954) is another feature typical for holometabolous parasitic insects (e.g. POHL & BEUTEL 2008), but not restricted to such groups (e.g. NORMARK & POLLOCK 2002: *Micromalthus debilis* LeConte, 1878 (Coleoptera: Micromalthidae)). It is defined as a premature metamorphosis between different larval stages, which strongly affects the morphology of the instars. It often occurs in Hymenoptera, in few groups Coleoptera (e.g. PAOLI 1938; SNODGRASS 1954), and also in Lepidoptera (BODY et al. 2015). Strikingly different larval stages are also

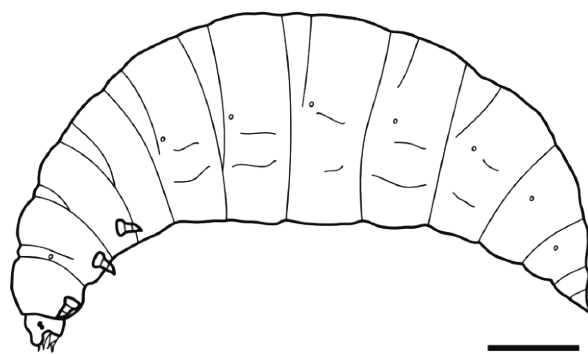


Fig. 20. Later instar of *Dicromantispa sayi*. Redrawn after REDBORG (1982) and STEHR (1987). — Scale bar: 1 mm.

a feature of the highly specialized endoparasitic Strepsiptera (e.g. POHL & BEUTEL 2008, 2013). Two different types are classified (PINTO 2009), type I referring to insects with the site of egg deposition distant from the feeding place of the larva, and type II with eggs placed at the feeding site of the first instars. *M. aphavexelte* clearly belongs to type I, as their eggs are positioned on ground substrate, on grass or on twigs, while the first instars feed on spider eggs or in the case of spider boarders also on hemolymph of the host.

Not surprisingly, first instars of *M. aphavexelte* show characteristics of type I hypermetamorphosis. As they hatch not at their feeding site, the larvae are highly mobile, and were therefore called planidium (“little wanderer”) by SNODGRASS (1954). Like in Strepsiptera or the coleopteran Meloidae and Rhipiphoridae, the first instar is very slender and of the agile campoideiform type. Three differentiated pairs of six-segmented legs are present, equipped with a well-developed set of extrinsic and intrinsic muscles (JANDAUSCH et al. 2018).

As later larval stages of *M. aphavexelte* are unknown, observations made on *Dicromantispa sayi* (Fig. 20; REDBORG & MACLEOD 1984) and *M. styriaca* (BRAUER 1869; HANDSCHIN 1959) will be discussed here. The largely immobilized 2nd stage hatching after the first moult (“metamorphosis”) is referred to as scarabaeidiform type. The size increases dramatically after the first molt. In *D. sayi* the mature third larval stage is about 10 × larger than the first instar (REDBORG & MACLEOD 1984). Once an egg sac is infested, efficient locomotion is not required any more. The trunk appears bloated and desclerotized, and the legs small and simplified. The head is very small compared to the rest of the body. A specific feature of the third instar is the transformation of abdominal segment X into a spinneret (REDBORG & MACLEOD 1984).

4.4. Effects of miniaturization

First instars of *M. aphavexelte* belong to the smallest known larval stages in Neuroptera. The total length is ca. 1 mm and the size during this stage increases only slightly while feeding.

The head shows only minimal effects of miniaturization, compared for instance to minute parasitic 1st instars

of Strepsiptera, which measure ca. 0.2 mm on average (POHL 2000; KNAUTH et al. 2016). The head capsule and appendages are not simplified compared to larger neuropteran larvae (e.g. WUNDT 1959; MACLEOD 1964; ROUSSET 1966; BEUTEL et al. 2010). In contrast to MACLEOD (1964) the endoskeleton of primary larvae of *Mantispa* is well-developed, except for the vestigial tentorial bridge, and also the cephalic set of muscles, with the exception of *M. tentorio-mandibularis*, which is also missing in the small larvae of Coniopterygidae (ROUSSET 1966). A typical feature occurring in very small insect larvae is a shift of the brain and suboesophageal ganglion into the thorax. In *M. aphavexelte* these parts of the central nervous system remain largely within the head capsule, with only the posterior ¼ of the protocerebrum reaching the prothorax. In contrast, the brain of larvae of *Tenomerga mucida* Chevrolat, 1844 (Coleoptera: Cupedidae) is completely dislodged to the thoracic segments (YAVORSKAYA et al. 2015), and this is also the case in larvae of *Mikado* sp. (Coleoptera: Ptiliidae), where the brain reaches the second abdominal segment (POLILOV & BEUTEL 2009). An extreme condition is reached in the minute first instars of Strepsiptera, where the entire central nervous system forms a compact unit in the middle body region (BEUTEL et al. 2005).

Except for indistinct or missing pleural and sternal sclerotized elements, the postcephalic exoskeleton is not differing distinctly from larger neuropteran larvae. However, endoskeletal elements are completely missing. Furcal arms are absent and likely replaced spine-like apodemes in the coxal region of each thoracic segment. Additionally, a similar spine-like structure is present in the cervical region. A complete reduction of the thoracic endoskeleton was also observed in *Mengenilla chobauti* Hofeneder, 1910 (Strepsiptera: Mengenillidae), whereas the muscular system is well-developed in these minute first instars of Strepsiptera (POHL 2000; OSSWALD et al. 2010). Like in strepsipteran primary larvae and recently examined small or very small 1st instar beetle larvae (GE et al. 2012; YAVORSKAYA et al. 2016), the postcephalic muscle system of *Mantispa* is complex and apparently not affected by miniaturization, with complex muscle sets of the neck region and legs, and well-developed dorsal and ventral longitudinal muscle, muscles of the pleural region, and also muscles of the terminal abdominal segments.

In contrast to the extremely condensed central nervous system of 1st instars of Strepsiptera, the ventral ganglionic chain is not recognizably affected by small size in *M. aphavexelte*. All thoracic ganglia and abdominal ganglia I–VIII are separated by connectives, as it is also the case in 1st instars of *Tenomerga mucida* (YAVORSKAYA et al. 2015).

5. Conclusions

The phylogenetic relationships of non-myrmecoleontiform Neuroptera are presently still contentious, with different data sets yielding different results (e.g. BEUTEL et al. 2010; RANDOLF et al. 2014, 2017; WANG et al. 2017; WIN-

TERTON et al. 2018). However, Mantispoidea comprising Mantispidae, Berothidae and Rhachiberothidae appear solid. The monophyletic status of Mantispidae remains ambiguous. The larvae of the specialized Mantispinae differ very distinctly from those of other subfamilies. Different structural features of 1st instars of *M. aphavexelte* are likely well suited for behaviour in the context of spider parasitism but have apparently evolved long before this life style was established as a preadaptation. Very small 1st instars and hypermetamorphosis are probably linked with a trend towards parasitism in Mantispoidea, with the majority of the group feeding on largely immobilized offspring of other insects, mainly aculeate hymenopterans or termites. In contrast to minute primary endoparasitic larvae of Strepsiptera, effects of miniaturization on 1st instars of *Mantispa* are very limited.

6. Acknowledgements

We are very grateful to Ronald Bellstedt (Museum der Natur Gotha) for the donation of valuable larvae. We are very grateful to Martin Fikáček (National Museum & Charles University, Prague), Leonidas Davranoglou (University of Oxford) and an anonymous reviewer for very helpful comments, which greatly helped to improve this study.

7. References

- ASPÖCK H. 1999. Beschreibungen und Abbildungen von Mantispiden in der frühen entomologischen Literatur und Österreichs Beitrag zur Erforschung der Fanghafte (Neuroptera: Neuroptera: Mantispidae). – *Stapfia* **60**: 209–244.
- ASPÖCK H., HÖLZEL H., ASPÖCK U. 2001. Kommentierter Katalog der Neuroptera (Insecta: Raphidioptera, Megaloptera, Neuroptera) der Westpaläarktis. – *Denisia* **2**: 606 pp. + 6 Abb.
- ASPÖCK H., ASPÖCK U. 1971. Raphidioptera (Kamelhalsfliegen). Handbuch der Zoologie, Vol. 4: Insecta. Inst. 25. – Berlin: Walter de Gruyter 1–50.
- ASPÖCK U., ASPÖCK H. 2005. 30. Ordnung Neuroptera (Planipennia), Netzflügler. In: DATHE H.H. (Hrsg.): **5**. Teil: Insecta. In: Lehrbuch der Speziellen Zoologie. Begründet von A. Kaestner. Zweite Auflage. Korrigierter Nachdruck. H.-E. GRÜNER (Hrsg.): Band I: Wirbellose Tiere. – Spektrum Akademischer Verlag Heidelberg, Berlin: pp. 564–884 and 890–892.
- ASPÖCK U., ASPÖCK H. 2007. Verbliebene Vielfalt vergangener Blüte. Zur Evolution, Phylogenie und Biodiversität der Neuroptera (Insecta: Endopterygota). – *Denisia* **2**: 451–516.
- ASPÖCK U., ASPÖCK H. 2008. Phylogenetic relevance of the genital sclerites of Neuroptera (Insecta: Holometabola). – *Systematic Entomology* **33**: 97–127.
- ASPÖCK U., MANSELL M.W. 1994. A revision of the family Rhachiberothidae Tjeder, 1959, stat.n. (Neuroptera). – *Systematic Entomology* **19**: 181–206.
- ASPÖCK U., PLANT J.D., NEMESCHKAL H.L. 2001. Cladistic analysis of Neuroptera and their systematic position within Neuroptera (Insecta: Holometabola: Neuroptera). – *Systematic Entomology* **26**: 73–86.
- ASPÖCK H., ASPÖCK U., RAUSCH H. 1991. Die Raphidiopteren der Erde, Vol.2. – Krefeld: Goecke & Evers. 730 pp.
- BADANO D., ASPÖCK U., ASPÖCK H., CERRETTI P. 2017. Phylogeny of Myrmecoleontiformia based on larval morphology (Neuroptera: Neuroptera). – *Systematic Entomology* **42**(1): 94–117.

- BADANO D., MILLER R., STANGE L.A. 2018. Rediscovery and revision of the antlion genus *Ripalda* Navás within a phylogeny of Nemoleontini (Neuroptera, Myrmeleontidae). – *Invertebrate Systematics* **32**(4): 931–947.
- BEUTEL R.G., FRIEDRICH F. 2008. Comparative study of larval head structures of Megaloptera (Hexapoda). – *European Journal of Entomology* **105**: 917–938.
- BEUTEL R.G., FRIEDRICH F., ASPÖCK U. 2010. The larval head of Neurothridae and the phylogeny of Neuroptera (Insecta). – *Zoological Journal of the Linnean Society* **158**: 533–562.
- BEUTEL R.G., FRIEDRICH F., HÖRNSCHEMEYER T., POHL H., HÜNEFELD F., BECKMANN F., MEIER R., MISOF B., WHITING M.F., VILHELMSEN L. 2011. Morphological and molecular evidence converging upon a robust phylogeny of the megadiverse Holometabola. – *Cladistics* **26**: 1–15.
- BEUTEL R.G., KRISTENSEN N.-P., POHL H. 2009. Resolving insect phylogeny: The significance of cephalic structures of the Nannomecoptera in understanding endopterygote relationships. – *Arthropod Structure and Development* **38**(5): 427–460.
- BEUTEL R.G., GE S.-Q. 2008. The larval head of *Raphidia* (Raphidioptera, Insecta) and its phylogenetic significance. – *Zoology* **111**: 89–113.
- BEUTEL R.G., ZHANG W.W., POHL H., WAPPLER T., BAI M. 2016. A miniaturized beetle larva in Cretaceous Burmese amber: reinterpretation of a fossil “strepsipteran triungulin”. – *Insect Systematics & Evolution* **47**(1): 83–91.
- BEUTEL R.G., POHL H., HÜNEFELD F. 2005. Strepsipteran brains and effects of miniaturization (Insecta). – *Arthropod Structure & Development* **34**(3): 301–313.
- BODY M., BURLAT, V., GIRON D. 2015. Hypermetamorphosis in a leaf-miner allows insects to cope with a confined nutritional space. – *Arthropod-Plant Interactions* **9**(1): 75–84.
- BRAUER F. 1852a. Verwandlungsgeschichte der *Mantispa pagana*. – *Archiv für Naturgeschichte* **18**: 1–2 + 1 table.
- BRAUER F. 1852b. Versuch einer Gruppierung der Gattungen in der Zunft Planipennia mit besonderer Rücksicht auf die früheren Stände. – *Stettiner Entomologische Zeitung* **13**: 71–77.
- BRAUER F. 1855a. Beiträge zur Kenntnis der Verwandlung der Neuropteren. – *Verhandlungen des Zoologischen-Botanischen Vereins in Wien* **5**: 479–484.
- BRAUER F. 1855b. Beiträge zur Kenntnis des inneren Baues und der Verwandlung der Neuropteren. – *Verhandlungen des Zoologisch-Botanischen Vereins in Wien* **5**: 701–726.
- BRAUER F. 1869. Beschreibung der Verwandlungsgeschichte des *Mantispa styriaca* Poda und Betrachtung über die sogenannte Hypermetamorphose Fabre's. – *Verhandlungen der Kaiserlichen-Königlichen Zoologischen-Botanischen Gesellschaft in Wien* **19**: 831–840.
- BREMER K. 1994. Branch support and tree stability. – *Cladistics* **10**: 295–304.
- BUYS S.C. 2008. Observations on the biology of *Anchieta fumosella* (Westwood 1867) (Neuroptera Mantispidae) from Brazil. – *Tropical Zoology* **21**(1): 91–95.
- CARDONA A., SAALFELD S., SCHINDELIN J., ARGANDA-CARRERAS I., PREIBISCH S., LONGAIR M., TOMANCAK P., HARTENSTEIN V., DOUGLAS R.J. 2012. TrakEM2 software for neural circuit reconstruction. – *PLoS ONE* **7**: e38011.
- CRAMPTON G.C. 1921. The sclerites of the head and the mouthparts of certain immature and adult insects. – *Annals of the Entomological Society of America* **14**(2): 65–103 + pls.
- DOREY J., MERRITT D. 2017. First observations on the life cycle and mass eclosion events in a mantis fly (family Mantispidae) in the subfamily Drepanicinae. – *Biodiversity Data Journal* **5**: e21206. doi:10.3897/BDJ.5.e21206
- ENGEL M.S., GRIMALDI D.A. 2007. The neuropterid fauna of Dominican and Mexican amber (Neuropterida: Megaloptera, Neuroptera). – *American Museum Novitates* **3587**: 1–58.
- FRIEDRICH F., BEUTEL R.G. 2006. The pterothoracic skeletomuscular system of Scirtoidea (Coleoptera: Polyphaga) and its implications for the high-level phylogeny of beetles. – *Journal of Zoological Systematics and Evolutionary Research* **44**(4): 290–315.
- GAUMONT J. 1965. L'appareil digestif de la larve d'un Planipenne associé aux éponges d'eau douce: *Sisyra fuscata*. – *Annales de la Société Entomologique de France (N.S.)* **1**: 335–357.
- GAUMONT J. 1976. L'appareil digestif des larves de Planipennes. – *Annales des Sciences Naturelles, Zoologie et Biologie Animale* **18**: 145–250.
- GE S.-Q., WIPFLER B., POHL H., HUA Y., ŚLIPIŃSKI A., YANG X.-K., BEUTEL R.G. 2012. The first complete 3D reconstruction of a Spanish Fly primary larva (*Lytta vesicatoria*, Meloidae, Coleoptera). – *PLOS ONE* **7**(12): e52511.
- GREBENNIKOV V.V. 2004. Grub-like larvae of Neuroptera (Insecta): A morphological review of the families Ithonidae and Polytoechotidae and a description of *Oliarces clara*. – *European Journal of Entomology* **101**: 409–417.
- GUARISCO H. 1998. First observation of egg sac predation of the mantisfly, *Mantispa interrupta* (Neuroptera, Mantispidae) upon the wolf spider, *Gladicosa gulosa* (Araneae, Lycosidae). – *Transactions of the Kansas Academy of Science* **101**(1/2): 60–62.
- HANDSCHIN E. 1959. *Mantispa styriaca* (Poda 1761). – *Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich* **104**: 105–114.
- HENRY C.S. 1978. An unusual ascalaphid larva (Neuroptera: Ascalaphidae) from Southern Africa, with comments on larval evolution within the Myrmeleontoidea. – *Psyche* **85**: 265–274.
- HOFFMAN K.M. 2002. Family Mantispidae. In: PENNY N.D. (ed.), *A Guide to the Lacewings (Neuroptera) of Costa Rica*. – *Proceedings of the California Academy of Sciences* **53**(4): 251–275.
- JANDAUSCH K., BÜSSE S., POHL H., GORB S., BEUTEL R.G. 2018. The legs of “spider associated” parasitic primary larvae of *Mantispa aphavexelte* (Mantispidae, Neuroptera) – attachment devices and phylogenetic implications. – *Arthropod Structure and Development* **47**(5): 449–456.
- JEPSON J.E., HEADS S.W., MAKARKIN V.N., REN D. 2013. New fossil mantidflies (Insecta: Neuroptera: Mantispidae) from the Mesozoic of north-eastern China. – *Palaeontology* **56**. doi:10.1111/pala.12005
- JEPSON J.E. 2015. A review of the current state of knowledge of fossil Mantispidae (Insecta: Neuroptera). – *Zootaxa* **3964**(4): 419–432.
- KASTON B.J. 1938. Mantispidae parasitic on spider egg sacs. – *Journal of the New York Entomological Society* **46**: 147–153.
- KÉLER S.V. 1963. *Entomologisches Wörterbuch*. – Berlin: Akademie Verlag. 3. Auflage. 753 pp.
- KHRAMOV A.V. 2013. New mantidflies (Neuroptera: Mantispidae) from the Upper Jurassic of Kazakhstan. – *Insect Systematics & Evolution* **44**: 221–230.
- KNAUTHE P., BEUTEL R.G., HÖRNSCHEMEYER T., POHL H. 2016. Serial block–face scanning electron microscopy sheds new light on the head anatomy of an extremely miniaturized insect larva (Insecta, Strepsiptera). – *Arthropod Systematics and Phylogeny* **74**(2): 107–126.
- KUROKO H. 1961. On the eggs and first-instar larvae of two species of Mantispidae. – *Esakia* **3**: 25–32.
- LAMBKIN K.J. 1986a. A revision of the Australian Mantispidae (Insecta: Neuroptera) with a contribution to the classification of the family. I. General and Drepanicinae. – *Australian Journal of Zoology (Suppl. Ser.)* **116**: 142 pp.
- LAMBKIN K.J. 1986b. A revision of the Australian Mantispidae (Insecta: Neuroptera) with a contribution to the classification of the family. II. Calomanatipinae and Mantispininae. – *Australian Journal of Zoology* **117**: 1–113. doi:10.1071/AJZS117
- LARSÉN O. 1966. On the morphology and function of the locomotor organs of the Gyrinidae and other Coleoptera. – *Opuscula Entomologica (Supplementum)* **30**: 1–241.
- LINNAEUS C. 1758. *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. – Editio decima, reformata. Tom. I.–L. Salvii, Holmiae. 823 pp.
- LIU X., WINTERSTON S.L., WU C., PIPER R., OHL M. 2015. A new genus of mantidflies discovered in the Oriental region, with a higher-level phylogeny of Mantispidae (Neuroptera) using DNA

- sequences and morphology. – *Systematic Entomology* **40**: 183–206.
- LUCCHESI E. 1956. Recherche sulla *Mantispa perla* Pallas (Neuroptera Planipennia – Fam. Mantispidae). – *Annali della Facoltà di Scienze Agrarie dell'Università degli Studi di Perugia* **12**: 83–213.
- MACLEOD E.G. 1964. A comparative morphological study of the head capsule and cervix of larval Neuroptera (Insecta). – Unpublished PhD Thesis, Harvard University, Cambridge, Massachusetts.
- MACLEOD E.G., REBORG K.E. 1982. Larval platymantispine mantispids (Neuroptera: Planipennia): possibly a subfamily of generalist predators. – *Neuroptera International* **2**(1): 37–41.
- MACLEOD E.G., REBORG K.E. 1984. The developmental ecology of *Mantispa uhleri* Banks (Neuroptera: Mantispidae). – *Illinois Biological Monographs* **53**: 1–130.
- MADDISON W.P., MADDISON D.R. 2015. Mesquite: a modular system for evolutionary analysis. Version 3.04.
- MANSSELL M.W. 1983. New Crocinae (Neuroptera: Nemopteridae) from South America, with descriptions of larvae. – *Journal of the Entomological Society of South Africa* **46**: 115–130.
- MCKEOWN K.C., MINCHAM V.H. 1948. The biology of an Australian mantispid (*Mantispa vittata* Guérin). – *Australian Zoology* **11**: 207–224.
- MINTER L.R. 1990. A comparison of the eggs and first instar-larvae of *Mucroberotha vesicaria* Tjeder with those of other species in the families Berothidae and Mantispidae (Insecta: Neuroptera). – Pp. 261–269 in: MANSSELL M.W., ASPÖCK H. (eds), *Advances in Neuropterology: Proceedings of the Third International Symposium on Neuropterology*, Bergen Dal, Kruger National Park, R.S.A., 1998. – Department of Agricultural Development, Pretoria.
- MINTER L.R. 1992. The egg and larval stages of *Nallachius krooni* Minter (Insecta: Neuroptera: Dilaridae). Pp. 101–113 in: CANARD M., ASPÖCK H., MANSSELL M.W. (eds), *Current Research in Neuropterology*. – SACCO, Toulouse.
- MONSERRAT V.J. 1996. Larval stages of European Nemopterinae, with systematic considerations on the family Nemopteridae (Insecta, Neuroptera). – *Deutsche Entomologische Zeitschrift* **43**: 99–121.
- MONSERRAT V.J. 2006. Nuevos datos sobre la taxonomía y la faunística de los coniopterígid de Senegal (Insecta, Neuroptera, Coniopterygidae). – *Graellsia* **62**(1): 13–24.
- MÖLLER A., MINTER L.R., OLIVIER P.A.S. 2006. Larval morphology of *Podallea vasseana* Navás and *Podallea manselli* Aspöck & Aspöck from South Africa (Neuroptera: Berothidae). – *African Entomology* **14**(1): 1–12.
- NEW T.R. 1986. A review of the biology of Neuroptera Planipennia. – *Neuroptera International*, Supplemental Series **1**: 1–57.
- NIEHUIS M., BLANKE A., PETERS R. 2014. Der Verwechselte Fanghaft (*Mantispa aphavexelte* ASPÖCK et ASPÖCK, 1994) in Rheinland-Pfalz nachgewiesen (Neuroptera: Mantispidae). – *Fauna Flora Rheinland-Pfalz* **12**(4): 1393–1402.
- NIXON K.C., CARPENTER J.M. 1993. On outgroups. – *Cladistics* **9**: 413–426.
- NORMARK B.B., POLLOCK D.A. 2002. The life cycle of *Micromalthus debilis* (Coleoptera: Archostemata: Micromalthidae): historical review and evolutionary perspective. – *Journal of Zoological Systematics and Evolutionary Research* **40**(2): 105–112.
- OHL M. 2004. Annotated catalog of the Mantispidae of the world (Neuroptera). – *Contributions on Entomology, International*, **5**, **3**: 131–262.
- OHL M. 2005. Towards a global inventory of Mantispidae – the state of the art in mantispid taxonomy. – *Annali del Museo Civico di Storia Naturale di Ferrara* **8**: 79–86.
- OHL M. 2011. Aboard a spider – a complex developmental strategy fossilized in amber. – *Naturwissenschaften* **98**(5): 453.
- OSSWALD J., POHL H., BEUTEL R.G. 2010. Extremely miniaturised and highly complex: The thoracic morphology of the first instar larva of *Mengenilla chobauti* (Insecta, Strepsiptera). – *Arthropod Structure and Development* **39**(4): 287–304.
- PAOLI G. 1938. Note sulla biologia e sulla filogenesi dei Meloidi (Coleoptera). – *Fratelli Pagano*.
- PARKER F.D., STANGE L.A. 1965. Systematic and biological notes on the tribe Platymantispini (Neuroptera: Mantispidae) and the description of a new species of *Plega* from Mexico. – *The Canadian Entomologist* **97**(6): 604–612.
- PINTO J.D. 2009. Hypermetamorphosis. – Pp. 484–486 in: *Encyclopedia of Insects Vol. 2*. – Elsevier.
- POHL H. 2000. Die Primärlarven der Fächerflügler – evolutive Trends (Insecta, Strepsiptera). – *Kaupia* **10**: 1–144.
- POHL H. 2010. A scanning electron microscopy specimen holder for viewing different angles of a single specimen. – *Microscopy Research & Technique* **73**(12): 1073–1076.
- POHL H., BEUTEL R.G. 2008. The evolution of Strepsiptera (Hexapoda). – *Zoology (Jena)* **111**(4): 318–338.
- POHL H., BEUTEL R.G. 2013. The Strepsiptera-Odyssey: the history of the systematic placement of an enigmatic parasitic insect order. – *Entomologia* **1**(1): 4.
- POINAR G.O., BUCKLEY R. 2011. *Doratomantispa burmanica* n. gen., n. sp. (Neuroptera: Mantispidae), a new genus of mantidflies in Burmese amber. – *Historical Biology* **23**: 169–176.
- POLILOV A.A., BEUTEL R.G. 2009. Miniaturisation effects in larvae and adults of *Mikado* sp. (Coleoptera: Ptiliidae), one of the smallest free-living insects. – *Arthropod Structure and Development* **38**(3): 247–270.
- RANDOLF S., ZIMMERMANN D., ASPÖCK U. 2013. Head anatomy of adult *Sisyra terminalis* (Insecta: Neuroptera: Sisyridae) – functional adaptations and phylogenetic implications. – *Arthropod Structure & Development* **42**(6): 565–582.
- RANDOLF S., ZIMMERMANN D., ASPÖCK U. 2014. Head anatomy of adult *Nevrorthus apateli* and basal splitting events in Neuroptera (Neuroptera: Nevrothidae). – *Arthropod Systematics & Phylogeny* **72**(2): 111–136.
- RANDOLF S., ZIMMERMANN D., ASPÖCK U. 2017. Head anatomy of adult *Coniopteryx pygmaea* Enderlein, 1906: Effects of miniaturization and the systematic position of Coniopterygidae (Insecta: Neuroptera). – *Arthropod Structure & Development* **46**(2): 304–322.
- REDBORG K.E. 1998. Biology of the Mantispidae. – *Annual Review of Entomology* **43**: 175–194.
- RÖBER H. 1942. Morphologie des Kopfes und des Vorderdarmes der Larve und Imago von *Sialis flavilata*. – *Zoologische Jahrbücher, Abteilung für Anatomie* **67**: 61–118.
- ROGENHOFER A. 1862. Beitrag zur Kenntnis der Entwicklungsgeschichte von *Mantispa styriaca* Poda (*pagana* Fab.). – *Verhandlungen der k. k. Zoologisch-Botanischen Gesellschaft in Wien* **12**: 583–586.
- ROUSSET A. 1966. Morphologie céphalique des larves de Planipennes (Insectes Névroptéroïdes). – *Mémoires du Muséum National d'Histoire Naturelle A* **42**: 1–199.
- SCHINDELIN J., ARGANDA-CARRERAS I., FRISE E., KAYNIG V., LONGAIR M., PIETZSCH T., PREIBISCH S., RUEDEN C., SAALFELD S., SCHMID B., TINEVEZ J.-Y., WHITE D.J., HARTENSTEIN V., ELICEIRI K., TOMANCAK P., CARDONA A. 2012. Fiji: an open source platform for biological-image analysis. – *Nature Methods* **9**: 676–682.
- SCHNEIDER W.G. 1843. Monographia generis Rhaphidia Linnaei. Continens et novas de huius generis singulis speciebus institutas observationes, et integram omnium, quae hucusque inventae sunt, specierum descriptionem. – Grass, Barth & Co., Vratislaviae. 96 pp. + 7 tables.
- SCHREMMER F. 1983. Beitrag zur Entwicklungsgeschichte und zum Kokonbau von *Mantispa styriaca*. – *Zeitschrift der Arbeitsgemeinschaft Österreichischer Entomologen* **35**. Jg. (1/2).
- SHI C.-F., OHL M., WUNDERLICH J., REN D. 2014. A remarkable new genus of Mantispidae (Insecta, Neuroptera) from Cretaceous amber of Myanmar and its implications on raptorial foreleg evolution on Mantispidae. – *Cretaceous Research* **52**: 425–426.
- SNODGRASS R.E. 1954. Insect metamorphosis. – *Smithsonian Miscellaneous Collections* **122**(9): 1–124.

- SNYMAN L.P., OHL M., MANSELL M.W., SCHOLTZ C.H. 2012. A revision and key to the genera of Afrotropical Mantispidae (Neuroptera, Neuroptera), with the description of a new genus. – *ZooKeys* **184**: 67–93.
- SNYMAN L.P., SOLE C.L., OHL M. 2018. A revision of and keys to the genera of the Mantispinae of the Oriental and Palearctic regions (Neuroptera: Mantispidae). – *Zootaxa* **4450**(5): 501–549.
- SUNDERMEIER W. 1940. Der Hautpanzer des Kopfes und des Thorax von *Myrmeleon europaeus* und seine Metamorphose. – *Zoologische Jahrbücher, Abteilung Anatomie und Ontogenie der Tiere* **66**: 291–348.
- TAUBER C.A. 1987. Order Raphidioptera. Order Neuroptera. – Pp. 123–143 in: STEHR F.W. (ed.), *Immature Insects*, Vol. I. Dubuque, Iowa: Kendall/Hunt Publishing Company.
- TILLYARD R.J. 1918. Studies in Australian Neuroptera. No. 7. The life-history of *Psychopsis elegans* (Guérin). – *Proceedings of the Linnean Society of New South Wales* **43**: 787–818.
- WANG Y., LIU X.-Y., GARZÓN-ORDUÑA I.J., WINTERTON S.L., YAN Y., ASPÖCK U., ASPÖCK H., YANG D. 2016. Mitochondrial phylogenomics illuminates the evolutionary history of Neuropterida. – *Cladistics* **33**: 617–636. doi: 10.1111/cla.12186
- WEDMANN S., MAKARKIN V.N. 2007. A new genus of Mantispidae (Insecta: Neuroptera) from the Eocene of Germany, with a review of the fossil record and palaeobiogeography of the family. – *Zoological Journal of the Linnean Society* **149**: 701–716.
- WINTERTON S.L., LEMMON A.R., GILLUNG J.P., GARZON I.J., BADANO D., BAKKES D.K., BREITKREUZ L.C.V., ENGEL M.S., MORIARTY LEMMON E., LIU X., MACHADO R.J.P., SKEVINGTON J.H., OSWALD J.D. 2018. Evolution of lacewings and allied orders using anchored phylogenomics (Neuroptera, Megaloptera, Raphidioptera). – *Systematic Entomology*. doi:10.1111/syen.12278
- WUNDT H. 1961. Der Kopf der Larve von *Osmylus chrysops* L. (Neuroptera, Planipennia). – *Zoologische Jahrbücher, Abteilung Anatomie und Ontogenie der Tiere* **79**: 557–662.
- YAVORSKAYA M.I., KOJIMA K., MACHIDA R., BEUTEL R.G. 2015. Morphology of the first instar larva of *Tenomerga mucida* (Chevrolat, 1829) (Coleoptera: Archostemata: Cupedidae). – *Arthropod Systematics & Phylogeny* **73**(2): 239–258.
- YAVORSKAYA M.I., POLILOV A.A. 2016. Morphology of the head of *Sericoderus lateralis* (Coleoptera, Corylophidae) with comments on the effects of miniaturization. – *Entomological Review* **96**(4): 395–406.
- ZWICK P. 1967. Beschreibung der aquatischen Larve von *Neurorthis fallax* (Rambur) und Errichtung der neuen Planipennierfamilie Neurorthidae fam. nov. – *Gewässer und Abwässer* **44/45**: 65–86.

Authors' Contributions

K.J. took the SEM pictures and was in charge of 3D reconstructions, drawings and design of the figures. R.G.B. supported the work in all stages and carried out the phylogenetic analysis. R.G.B. and K.J. have written the manuscript. U.A. was strongly involved in writing the introduction and provided a lot of background information. H.P. provided help with figures and methods and has provided some helpful insights on the manuscript. S.L.W. provided background information.

Electronic Supplement File

at <http://www.senckenberg.de/arthropod-systematics>

File 1: jandausch&al-mantispalarva-asp2018-electronic-supplement-1.winc — Data matrix mainly from BEUTEL et al. (2010) with some additional characters from this study.