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A remarkable fossil berothoid larva (Neuroptera) from the late Eocene Rovno amber (Ukraine)

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ABSTRACT

The larva of Berothidae or Rhachiberothidae (Neuroptera) is described from the late Eocene Rovno amber; it is the first record of either family from this amber. The larva is in particular characteristic with a four-segmented antenna, at least five stemmata, and lateral sutures on the head capsule connecting the coronal suture and lateral margins of the head. Based on these characters, the larva probably may belong to one of basal taxa of Berothidae, possibly to a suprageneric taxon which includes an undescribed small species from Baltic amber which is closely related to the mid-Cretaceous *Haploberotha*, or to Rhachiberothidae. This larva was most likely free living, possibly occurring under/on tree bark. In addition, the genus *Protomenocria* Emeljanov and Shcherbakov 2009 (Hemiptera: Achilidae) is recorded from Rovno amber for the first time.

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Berothidae; Rhachiberothidae; Mantispidae; Rovno amber; late Eocene; *Protomenocria*

Introduction

Knowledge of the preimaginal stages is very important for understanding the taxonomic composition and phylogeny of taxa. In recent years, the larvae of many fossil Neuroptera have been described (e.g. Liu et al. 2016, 2018, 2022; Pérez-de le Fuente et al. 2016; Pérez-de la Fuente et al. 2018; Badano et al. 2018; Herrera-Flórez et al. 2020; Du et al. 2023). Unfortunately, there are few adequate descriptions of fossil larvae in Mantispoidea. We can mention only descriptions of the larvae from the late Albian Spanish amber (Pérez-de la Fuente et al. 2020) and the late Eocene Baltic amber (Wedmann et al. 2013). However, many fossil larvae of Mantispoidea are reported, but their descriptions are incomplete and presented mainly by illustrations, especially from the mid-Cretaceous Kachin amber (e.g. Whalley 1980; Engel and Grimaldi 2008; Wunderlich 2012; Haug et al. 2018, 2021; Haug and Haug 2022).

Fossil larvae of Berothidae are known from the Barremian Lebanese amber (Whalley 1980); the late Albian Spanish amber (Pérez-de la Fuente et al. 2020); the mid-Cretaceous Kachin amber (Engel and Grimaldi 2008; Haug et al. 2021); the Campanian Canadian amber (Engel and Grimaldi 2008; Wedmann et al. 2013); and the late Eocene Baltic amber (Wedmann et al. 2013). No fossil larvae of Rhachiberothidae are known.

Here, we describe in detail a larva of Berothidae or Rhachiberothidae from the late Eocene Rovno amber.

Material and methods

The fossil larva described herein is preserved in a piece of Rovno amber from the Pugach quarry (Klesov deposit), Sarny District, Rovno Region, Ukraine. The amber piece was rather large before primary treatment with numerous syninclusions (31 grams after primary treatment); later, it was cut to several pieces. The piece with the larva is 14.5 × 9 × 5 mm.

Amber from the Pugach quarry was mined by the 'Ukramber' factory (Rovno). This quarry was the single legal amber mine in Ukraine for many years (Perkovsky et al. 2010). Before 2014, the Klesov deposit was the main and almost the only source of information about the biota of the Rovno amber forest (Perkovsky et al. 2010; Makarkin et al. 2019, 2022; Mitov et al. 2021; Legalov et al. 2023; Loktionov et al. 2023). Then a rapid growth in illegal amber mining produced abundant material, primarily from the Varash District of the Rovno Region (Perkovsky and Makarkin 2019, 2020; Yamamoto et al. 2022) and the Zhitomir Region (Radchenko et al. 2021 and references therein). The late Eocene Rovno amber is coeval with Baltic amber (Perkovsky et al. 2010; Telnov et al. 2023).

The Rovno fauna contains a number of thermophile forms, which are absent in coeval Baltic amber (Anisyutkin and Perkovsky 2023; Lyubarsky et al. 2023; Nabozhenko and Perkovsky 2023; Jenkins Shaw et al. 2023, and references therein). At the same time, the volume of the Rovno material is incomparably smaller than Baltic one. The vast majority of morphotypes, including those of exceptional interest and importance (e.g. Olmi et al. 2022), are represented by single specimens. Fortunately, the Rovno amber collection is unbiased, which facilitates the study of community composition through the study of syninclusions (Perkovsky et al. 2012; Perkovsky and Rasnitsyn 2013).

Photographs were taken by A.P. Rasnitsyn using a Leica M165 stereomicroscope and an attached Leica DFC 425 digital camera (Figure 1A), and by V.M. Loktionov using a SteREO Discovery V12 stereomicroscope (Figures 1B–E, 2). The line drawing was prepared by VM using Adobe Photoshop SC3.

General terminology follows Snodgrass (1935), MacLeod (1964) and Beutel et al. (2010); head chaetotaxy terminology follows Hoffman and Brushwein (1992).

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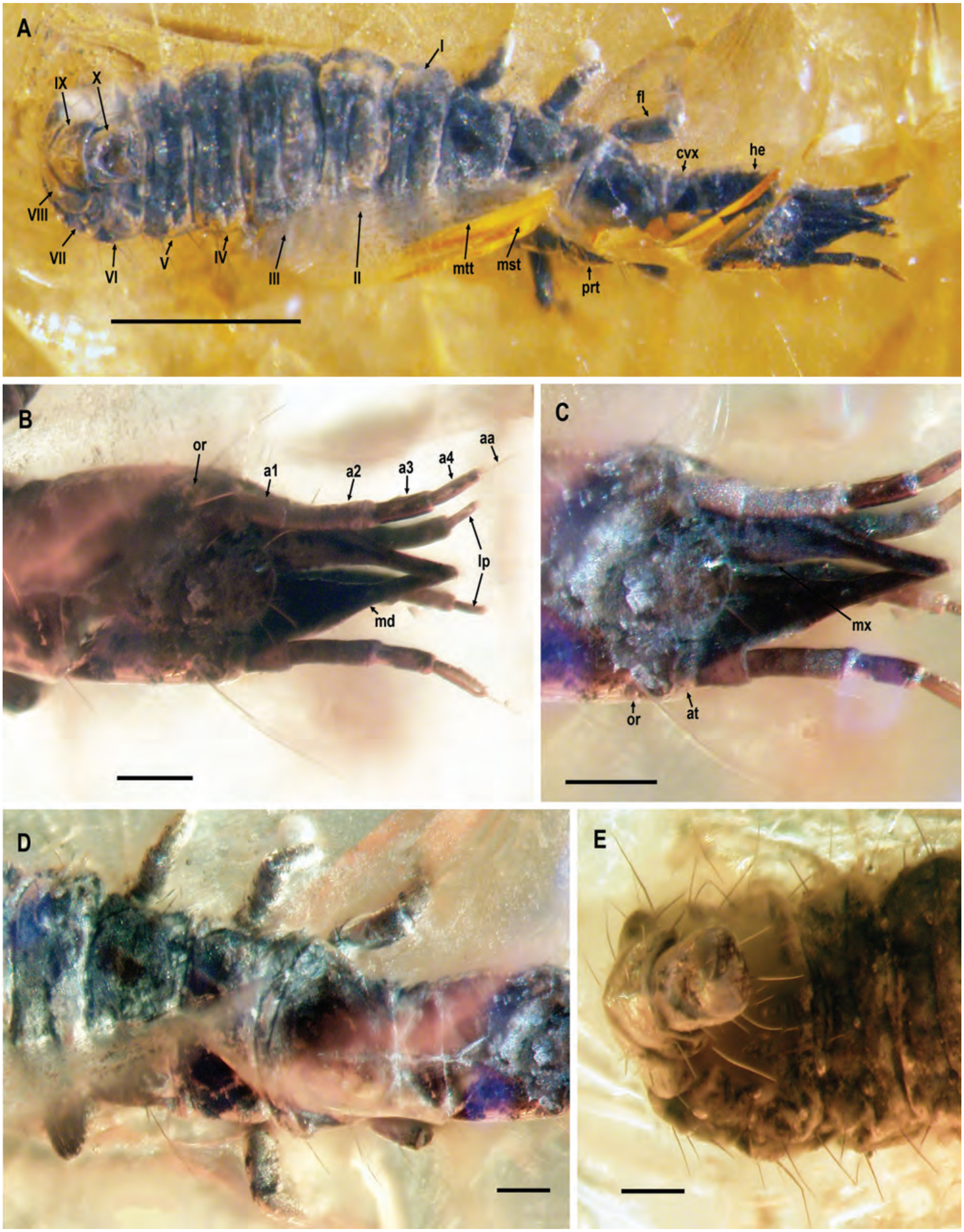

Figure 1. Berothoid larva, fam., gen. et sp. indet., specimen SIZK K-7926 (dorsal view). A, whole larva as preserved; B, head; C, part of head under alternative lighting; D, thorax; E, caudal part of abdomen. aa, apical arista of antennae; a1 to a4, 1st to 4st antennomeres; as, apical setae; at, antennal tubercle; cvx, cervix; fl, foreleg; he, head; lp, labial palps; md, mandible; mx, maxilla; mst, mesothorax; mtt, metathorax; or, ocular region; prt, prothorax. I to X, 1st to 10th abdominal segments. Scale bars = 0.5 mm (A); 0.1 mm (B – E).

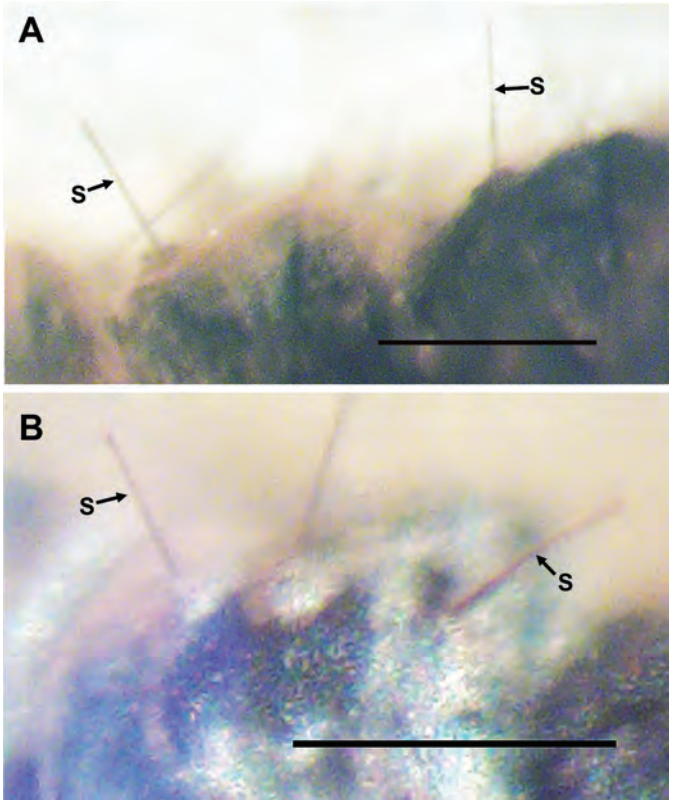

Figure 2. Berothoid larva, fam., gen. et sp. indet., specimen SIZK K-7926. Clubbed setae (s) on 4st (on the right) and 5st segments (A), and 1st segment of abdomen (B). Scale bars = 0.1 mm.

Order Neuroptera Linnaeus, 1758
Superfamily Mantispoidea *sensu* Engel et al. 2018

Berothoid larva, fam., gen. et sp. indet.(Figures 1–3)

Material

Specimen SIZK K-7926, a complete larva in amber, viewed only dorsally with the caudal part of the abdomen curved upwards. Klesov, Rovno amber; late Eocene.

Syninclusions: Acari (SIZK K-7915); Collembola: Arthropleona (SIZK K-7918); Hemiptera: Achilidae: *Protomenocria* sp. (SIZK K-7919); Anthocoridae: *Electrocoris* sp. prop. *brunneus* Usinger (Yu. Popov det.) (SIZK K-7924); Coleoptera: Scirtidae (SIZK K-7917); Staphylinidae: Paederinae? (SIZK K-7929); Hymenoptera: Ichneumonidae (SIZK K-7916); Scelionidae (SIZK K-7925b); Formicidae: two workers of *Formica* sp. (SIZK K-7925) and worker of *Prenolepis henschei* Mayr, 1868 (SIZK K-7927); Bethylidae: *Lytopsenella kerneggeri* Ohl, 1995 (SIZK K-7923) (Ramos et al. 2014); Diptera: Sciaridae: one specimen (SIZK K-7922), female (SIZK K-7920), male (SIZK K-7921); Tipuloidea: two specimens (SIZK K-7927a and SIZK K-7929a); Nematocera incertae sedis: one specimen (SIZK K-7924a); Insecta incertae sedis: two specimens (SIZK K-7930); stellate hairs.

Description

Body 2.26 mm long as preserved, from tip of mandibles to visible end of abdomen (estimated complete length when extended ca. 2.7 mm).

Head

Capsule elongate, 0.38 mm long (from anterior margin of labrum to visible end of head), 0.23 mm wide (length/width ratio ca. 1.65). Anterior margin of labrum rounded. Ocular areas located dorsolaterally; stemmata rather distinctly discernible; at least five preserved at left side (viewed dorsally, other possible if located more ventrally). Ecdysial cleavage lines distinct in posterior part of head capsule, consisting of frontal, coronal, and lateral sutures. Two arms of frontal suture converge at relatively acute angle, their anterior parts poorly discernible. Coronal suture rather short (third of head capsule), appearing duplicate for short distance. Lateral sutures straight, connecting coronal suture at its anterior quarter with lateral margins of head; both lateral sutures form straight line. Chaetotaxy: four clypeal ordinary setae long; S4, S9 very long; S1 (or S2), S7, S11, S12 relatively short; three maxillary setae visible in dorsal view.

Mandibles dilated basally, narrowed towards apex, blunt apically. Maxillary blades only fragmentarily discernible in dorsal view; strongly dilated basally, their basal part (at least along inner margin) sparsely and finely serrate. Mandibles and maxillae closely associated together to form mandibulomaxillary stilets, 0.3 mm long.

Antennal sockets located at relatively low projections (= antennal tubercles of MacLeod 1964). Antennae four-segmented, 0.33 mm long. Basal antennomere broadest, cylindrical, 0.06 mm long. Second antennomere longest (0.12 mm long), narrower than basal segment, distally annulated with one to two visible pseudosegments; bearing long fine seta. Third antennomere elongate, annulation not visible, slightly narrowed than second segment, 0.07 mm long. Four antennomere narrow-most, slightly fusiform, 0.07 mm long, bearing apically at least two minute setae and rather long apical seta (= FITS of MacLeod 1964), 0.05 mm long.

Labial palps longer than mandibles, probably 4-segmented (basal segment not visible dorsally). Second segment elongate, broad, annulation not discernible. Third segment 0.08 mm long, slightly thinner than second. Fourth segment clearly separated from third, markedly thinner than third, 0.04 mm long.

Cervix

In dorsal view, visible as two lateral triangle structures (left one well discernible). One relatively short lateral seta on each side.

Thorax

Prothorax 0.24 mm long, maximum 0.29 mm wide, most broad posteriorly, narrowed anteriad, consisting of one subsegment. Longitudinal middle ecdysial cleavage line distinct in anterior half, continuing coronal suture of head. Dorsal sclerites (= nota of Ardila-Camacho et al. 2021b) distinctly discernible at left half, almost undiscernible at right half; rather large, oval, almost approaching one another posteriorly. Chaetotaxy: two long fine ordinary setae on each side (one dorso-lateral; other near or on dorsal sclerites); clubbed seta not detected.

Mesothorax transverse, maximum 0.2 mm long, 2.8 mm wide (at mid-line), consisting of two subsegments. Anterior subsegment short. Posterior subsegment relatively long with two oval dorsal sclerites. Chaetotaxy: one rather short lateral ordinary seta on anterior subsegment; one dorsolateral long ordinary seta on posterior subsegment; clubbed seta (relatively short, slightly clubbed) one each side, near anterior dorsolateral edge of posterior subsegment.

Metathorax transverse, 0.18 mm long, 0.29 mm wide (at mid-line), consisting of two subsegments. Anterior subsegment very short without discernible setae. Posterior subsegment relatively long with two oval dorsal sclerites. Chaetotaxy: one dorsolateral long, one lateral ordinary setae on each side; two clubbed setae on

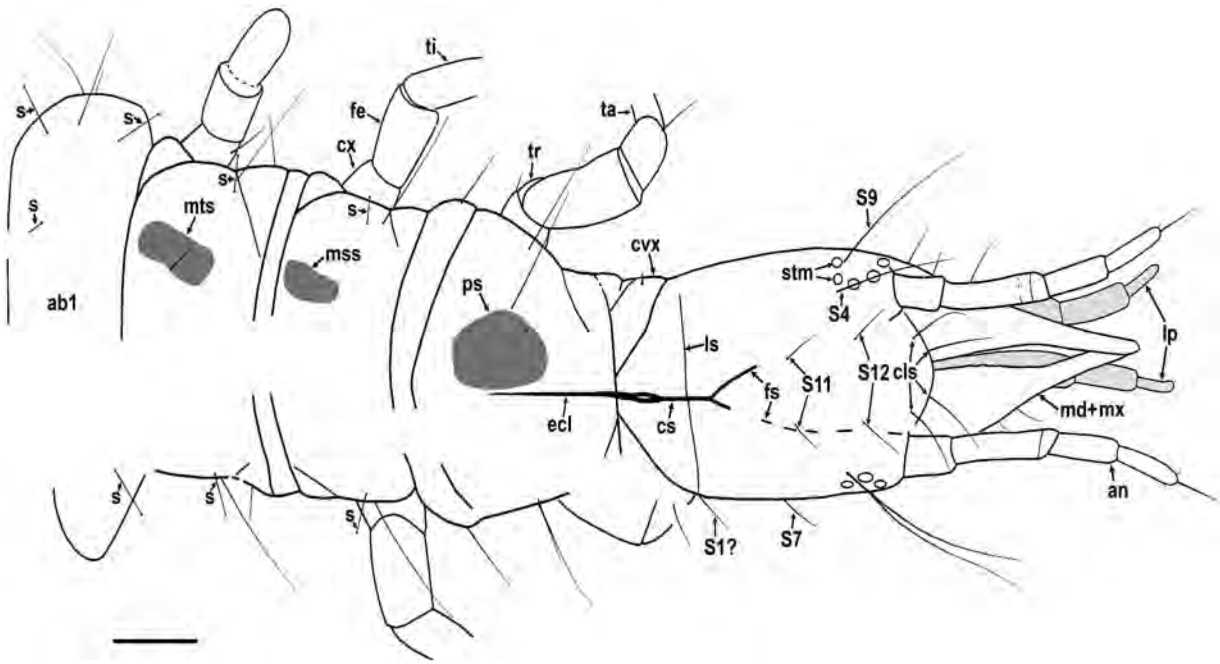

Figure 3. Berothoid larva, fam., gen. et sp. indet., specimen SIZK K-7926. Drawing of head, thorax and 1st segment of abdomen (dorsal view). ab1, 1st segment of abdomen; an, antenna; cls, clypeal setae; cs, coronal suture; cvx, cervix; cx, coxa; ecl, thoracic ecdysial cleavage line; fe, femur; fs, frontal suture; lp, labial palps; ls, lateral suture; md, mandible; mss, mesonotal sclerite; mts, metanotal sclerite; mx, maxilla; ps, pronotal sclerite; s, clubbed seta; S1, S4, S7, S9, S11, S12, head capsule setae; stm, stemmata; ta, tarsus; ti, tibia; tr, trochanter. Scale bar = 0.1 mm.

each side (relatively short, slightly clubbed): one near dorsolateral edge (similar to location of this seta on mesonotum); one near sclerite (detected on left half, not on right half due to poor preservation).

Legs rather short, robust: coxa short in dorsal view; trochanter small; femur stout; tibia narrowed then femur; tarsus not visible. Setae scarce.

Abdomen

Length 1.05 mm as preserved (estimated complete length when extended ca. 1.45 mm), maximum width ca. 0.4 mm (at second and thirds segments), divided into ten segments. Segments 1 to 5 transverse, with lateral lobes and transversal median depression. Structure of segments 6 to 8 not clear. Segment 9 markedly narrower than anterior segments. Segment 10 viewed ventrally, narrow, slightly broadens towards apex, almost straight posteriorly; with several very long setae. Caudal sucker not detected.

Chaetotaxy. First to seven segments: one long dorsolateral and two lateral ordinary setae; clubbed setae: two at anterior and posterior dorsolateral edges on each side; one posterior near midline on left and right halves (altogether six setae on a segment). Eighth to tenth segments: several long and short ordinary setae on a segment; clubbed setae not detected.

Remarks

The body length of the larvae in moderately-large berothines (*Lomamyia* Banks, 1904, *Isoscelipteron* Costa, 1863, *Podallea* Navás, 1936, and *Spermophorella* Tillyard 1916: forewings 6.5–11.5 mm long) is 1.2–2.6 mm (1st instar), 2.5–3.9 mm (2nd instar), and 3.0–6.4 mm (3st instar) (Tillyard 1916; Brushwein 1987; Möller et al. 2006; Komatsu 2014). The first-instar larva of the rhachiberothid *Mucroberotha vesicaria* Tjeder 1968 is 1.06 mm long (Minter 1990); its forewing length is 6–7 mm (Tjeder 1968). Those of *Berothimerobius reticulatus* Monserrat and Deretsky 1999 (Nyrminae) is 1.25 mm long, and the forewing is 3.2–4.3 mm long (Monserrat 2006). Clubbed setae are present only in third-instar larvae of the *Podallea* (see below).

Therefore, the described larva is most probably a third instar based on its size (ca. 2.7 mm) and the presence of clubbed setae. It is likely that this larva belongs to a relatively small imago.

Comparative analysis of most important characters of the larva

Antennae

It is often difficult to determine actual number of antennal segments (antennomeres) in Berothidae (and other mantispoid) larvae because of their secondary annulation. The distinctly 4-segmented antenna is present in *Mucroberotha* Tjeder 1959 (Rhachiberothidae; Minter 1990, fig. 6). The antennae of an undetermined berothid larva from Australia (Riek 1970, fig. 29.5) is also 4-segmented, but their second anntenomere is distally annulated like in the Rovno larva. The first-instar larva of Nyrmidae (*Nyrma* Navás, 1933; *Berothimerobius* Monserrat and Deretsky 1999) possibly possess 4-segmented antennae but the boundary between the second and third antennomeres is unclear because of their strong annulation; alternatively, their antennae are three-segmented and the second antennomere has a medial constriction (see Monserrat 2006, fig. 11; Dobosz and Górski 2008, figs. in Poster). Such antennae are found in an Early Cretaceous berothid larva from Spain (Pérez-de la Fuente et al. 2020, fig. 2).

The three-segmented antennae with long apical arista are present in all larva of Berothinae including fossils (Tillyard 1916; Gurney 1947; MacLeod 1964; Toschi 1964; Tauber and Tauber 1968; Möller 2003; Möller et al. 2006; Wedmann et al. 2013).

The antennae in some Baltic amber larvae are six- to seven-segmented (Wedmann et al. 2013, figs. 7C, 9C).

The antenna is three-segmented in all Mantispidae, with a club-shaped second antennomere (less distinct in Drepanicinae) (Dorey and Merritt 2017; Jandausch et al. 2018b; Ardila-Camacho et al. 2021a). The antenna of first-instar larvae in Dilaridae is very similar in structure to that of Mantispidae (Monserrat 1988, fig. 20; Minter 1992, fig. 2; Badano et al. 2022, fig. 3C; Li et al. 2023, fig. 4A); it is also three-segmented and has a club-shaped second antennomere, which becomes proximally annulated in later instars (e.g. Ghilarov 1962, fig. 2a; Minter 1992, figs. 2, 4, 6; Monserrat 2014, figs. 6a, b).

Lateral sutures

The dorsal ecdysial cleavage lines on the head of the berothid larvae consist usually of the coronal, lateral and frontal sutures (Wedmann et al. 2013). The lateral sutures connect the frontal sutures and lateral margins of the head in Berothinae (including fossils) and possibly Nyrminae (Möller 2003; Möller et al. 2006; Dobosz and Górski 2008; Wedmann et al. 2013). Sometimes, the lateral sutures are located posterior to the frontal sutures, connecting the coronal suture and lateral margins of the head as in this Rovno larva. This condition is found in extant Rhachiberothidae (Minter 1990, figs. 5, 6), an undetermined larva of Berothidae from Australia (Riek 1970, fig. 29.5), one larva of Berothidae or Rhachiberothidae from Kachin amber (Haug et al. 2021, fig. 5). This Kachin amber larva was incorrectly assigned by the authors to 'Mantispidae?', but the structure of antennae and dorsal ecdysial cleavage lines indicates berothid/rhachiberothid affinity.

The long frontal sutures together with the absence of lateral sutures are found in some larvae from Baltic amber (Wedmann et al. 2013, figs. 7, 9, 10, 11) and one larva (specimen 5839 PED 0828) from Kachin amber (Haug et al. 2021, fig. 15).

In Mantispidae, the dorsal head ecdysial cleavage lines are weakly developed: these are represented by incomplete coronal and frontal sutures in Symphrasinae (Ardila-Camacho et al. 2021a), and these sutures are lost in Mantispinae (Jandausch et al. 2018b).

The head ecdysial cleavage lines are lacking in Dilaridae (MacLeod and Spiegler 1961; Ghilarov 1962; MacLeod 1964; Monserrat 1988, 2005, 2014; Minter 1992; Badano et al. 2022).

Subdivision of thorax

Each segment of the thorax is divided into two subsegments in many neuropteran larvae: the short anterior and the much longer posterior. The thoracic spiracle is located on the short anterior subsegment of the mesothorax in Berothidae (Tauber and Tauber 1968), Chrysopidae (see e.g. Tauber 2003), Osmylidae (see e.g. Matsuno and Yoshitomi 2016), Mantispidae (Jandausch et al. 2018b; Ardila-Camacho et al. 2021a) while this subsegment is incorrectly considered as belonging to the prothorax in Hemerobiidae (see e.g. Withycombe 1925; Miller and Cave 1987). Moreover, it was interpreted as an intersegmental membrane by Möller (2003, fig. 32). This subsegment is long and clearly separated from the prothorax by membrane in Nevrorthidae (see Malicky 1984, fig. 5B).

In general, the thorax of Mantispidae is similar to that of Berothidae (Jandausch et al. 2018b; Ardila-Camacho et al. 2021a).

Thoracic sclerites

The pronotal sclerites of this larva are rather large and separated; sclerites on the meso- and metanotum are smaller. This condition is typical for Berothidae. In extant Berothidae, the size of the pronotal sclerites varies from relatively small in *Lomamyia* (Gurney 1947, fig. 5) to relatively large in *Podallea* (Möller 2003, figs. 16, 63). The notal sclerites are not mentioned in the only described first-instar larva of Rhachiberothidae (Minter 1990); that article, however, also does not mention these sclerites in either Berothidae or Mantispidae. The form and size of the notal sclerites of *Podallea* are similar to those of the late Albian Spanish amber berothid-like larva (Pérez-de la Fuente et al. 2020, fig. 5B) and the Baltic amber berothine-like larvae (Wedmann et al. 2013, figs. 1, 3). The pronotal sclerites of other berothid larvae from Baltic amber are closely approaching mantispid-like (Wedmann et al. 2013, figs. 7B, 9A, 11). In this, these are similar to those of one of the larvae from the mid-Cretaceous Kachin amber (Haug et al. 2021, fig. 6).

In Nevrorthidae, the pronotal sclerite is single covering the entire notum, with a median ecdysial cleavage line; sclerites on the meso- and metanotum are paired and relatively large (see Malicky 1984, figs 5A, B). In Mantispidae, the notal sclerites are similar to those of Nevrorthidae: the single pronotal sclerite covers almost the entire notum; sclerites on the meso- and metanotum are slightly larger than in Nevrorthidae (Ardila-Camacho et al. 2021a).

In Osmylidae, the pronotal sclerite is also large, covering almost the entire notum, but narrowly divided into two halves by the median ecdysial cleavage line; sclerites on the meso-and metanotum are paired and relatively large, together with four to six smaller additional (secondary) sclerites in posterior subsegments (see Matsuno and Yoshitomi 2016, figs 18, 20, 22; Martins et al. 2018, figs 6a, b).

In Hemerobiidae, there are small to minutest paired sclerites on the meso- and metanotum, and larger ones on the pronotum (Killington 1936; Monserrat 2003). The structure of notal sclerites in Chrysopidae is generally similar to that Hemerobiidae (Killington 1936; Tauber 2014). In Dilaridae, the notal sclerites are probably lost; at least their integuments are weakly sclerotised (Ghilarov 1962; Badano et al. 2022).

Therefore, the notal sclerites in this larva are most similar to those of some Berothidae.

Clubbed (clavate, spatulate) setae

These setae are found only in the larvae of three families of Neuroptera, i.e. Berothidae, Hemerobiidae and Chrysopidae. They are detected on the dorsal side of 1st to 7th abdominal segments of the described larva (Figure 2). Third larval instars of *Lomamyia* and *Podallea* bear rather numerous clubbed setae on dorsal part of the head, thorax and abdomen (Tauber and Tauber 1968; Möller 2003; Möller et al. 2006). At least in the *Podallea* larvae, first and second instars do not possess such setae (see Möller 2003, figs. 16, 32, 52). The most dorsal setae on the abdomen are clubbed in the third larval instars of the hemerobiid *Micromus tasmaniae* (Walker 1860) (New and Boros 1983); and at least one dorsal clubbed seta is found on 8th abdominal segment of the mature larva of *M. timidus* Hagen 1853 (VM, pers. obs.). Some dorsal setae are clubbed on the head, thorax and abdomen of Nothochrysinae (Chrysopidae) (Tauber 2014).

Taxonomical affinity of the larva

The characters of the described larva show that it certainly belongs to a taxon with straight-jawed larvae (Mantispoidea, Dilaridae or Osmylidae).

The superfamily Mantispoidea is thought to include up to five families: the Triassic Mesoberothidae (presumably; this group is poorly known), the Cretaceous Dipteromantispidae, Berothidae (Early Jurassic to Recent), Mantispidae (Early Jurassic to Recent), and Rhachiberothidae (Early Cretaceous to Recent) (Engel et al.

2018). The Mantispoidea are often considered together with Dilaridae as a dilarid clade based on similarity of their larvae (e.g. Aspöck et al. 2001; Engel and Grimaldi 2008).

Therefore, this larva may theoretically belong to one of the following families, which are known from the late Eocene amber of Europe: Berothidae, Rhachiberothidae, Mantispidae, Dilaridae or Osmylidae. Of these, it certainly does not belong to the three latter families.

All known larvae of Osmylidae (including fossil) have numerous additional sclerites on the thorax and abdomen, the antennae are strongly annulated, and the lateral sutures on the head are absent (e.g. Killington 1936; CoBabe et al. 2002; Matsuno and Yoshitomi 2016; Martins et al. 2018).

The larvae of Dilaridae also strongly differ from the Rovno larva by the complete absence of head sutures and thoracic sclerites, and by club-shaped one of antennomeres (Monserrat 2014; Badano et al. 2022).

The larvae of extant Mantispidae differ from the Rovno larva by possessing a 3-segmented antenna, the club-shaped 2nd antennomere, the absence of completely-developed coronal and frontal sutures, and the possession of much larger pronotal sclerites (Kuroko 1961; MacLeod 1964; Hoffman and Brushwein 1992; Dorey and Merritt 2017; Jandausch et al. 2018a, b; Ardila-Camacho et al. 2021a; De Lira-Ramos et al. 2022).

Therefore, this larva belongs to Berothidae or Rhachiberothidae.

The systematic position of Rhachiberothidae is very controversial. The taxon is considered as a subfamily of Berothidae (e.g. Tjeder 1959; Makarkin and Kupryjanowicz 2010), as a subfamily of Mantispidae (Willmann 1990, 1994), and as a distinct family (Aspöck and Mansell 1994), comprising usually Paraberothinae and Rhachiberothinae (e.g. Nakamine and Yamamoto 2018; Aspöck et al. 2020; Nakamine et al. 2020).

Ardila-Camacho et al. (2021b) assigned to Rhachiberothidae (in addition to these two subfamilies) the mantispid subfamily Symphrasinae based on morphological characteristics of imagoes. However, the characters of the first-instar larva of *Plega* Navás, 1928 (Symphrasinae) described by Ardila-Camacho et al. (2021a) indicate that its morphology is typical for Mantispidae, and differs from that of larval Rhachiberothidae. The larvae of Paraberothinae are unknown. If we consider Rhachiberothidae as a family, the inclusion of only Rhachiberothinae may be confirmed by the larvae.

The position in Mantispoidea of two fossil taxa with raptorial forelegs is also debatable: Mesithoninae (Middle Jurassic to Early Cretaceous) and Paraberothinae (Early to mid-Cretaceous) (see Makarkin and Kupryjanowicz 2010; Makarkin et al. 2012; Makarkin 2015).

Six subfamilies with cursorial (non-raptorial) forelegs are recognised in Berothidae: the early Eocene to extant Berothinae, and the extant Cyrenoberothinae, Protobiellinae, Nyrminae, Trichomatinae, and Nosybinae (= Berothimerobiinae) (Aspöck and Randolf 2014). However, three fossil genera (two Cretaceous and one early Eocene) were recently assigned to Cyrenoberothinae by Machado et al. (2022).

Among extant Berothidae, the larvae are known only in Berothinae and Nyrminae (Tillyard 1916; Toschi 1964; Tauber and Tauber 1968; Möller 2003; Möller et al. 2006; Monserrat 2006; Dobosz and Górski 2008), in addition to a larva from Australia which has not been determined to a subfamily (Riek 1970, fig. 29.5).

Three species of Berothidae/Rhachiberothidae belonging to three different suprageneric taxa based on imagoes are known from contemporaneous Baltic amber, i.e. *Elektroberotha groehni* Makarkin and Ohl 2015 (Berothinae); *Whalfera wiszniewskii* Makarkin and Kupryjanowicz 2010 (Rhachiberothidae); and a small undescribed species with the venation similar to that of *Haploberotha* Engel and Grimaldi 2008, a mid-Cretaceous Kachin amber genus (uncertain subfamily) (VM, pers. data).

The larvae of Berothidae/Rhachiberothidae known from Baltic and Rovno amber also belong to three different suprageneric taxa. Five larvae described from Baltic amber belong to two different types: two are certainly berothine-like (Wedmann et al. 2013, figs. 1–5); they may theoretically belong to the berothine *Elektroberotha groehni*. Some characters of three other larvae are unknown today in Berothidae (Wedmann et al. 2013, figs. 6–11); in particular, six- to seven-segmented antennae, and the pronotal sclerites being in close contact are dissimilar to other larvae of Berothidae, and similar to those of Mantispidae, Osmylidae and Nevrorthidae (see also below).

The Rovno larva belongs to a third type. It may certainly not be assigned to Berothinae as it bears (1) four-segmented antenna [three-segmented in Berothinae], (2) at least five stemmata [up to two in Berothinae], and (3) lateral sutures on the head capsule connecting the coronal suture and lateral margins of head [connecting frontal sutures and lateral margins of head in Berothinae]. Also, the larva does not belong to Nyrminae, in which ecdysial cleavage lines are probably similar to those of Berothinae (Dobosz and Górski 2008, figs. at Poster).

The Rovno larva shares these three characters with basal Berothidae and Rhachiberothidae, e.g. the rhachiberothid *Mucroberotha* (see Minter 1990, figs. 5–7), and an undetermined larva of Berothidae from Australia (Riek 1970, fig. 29.5). Except Berothinae, two berothid subfamilies occur in Australia, i.e. Protobiellinae and Trichomatinae (Aspöck and Randolf 2014). Therefore, the Australian larva belongs to one of these two subfamilies. Of these, the Trichomatinae are not a basal taxon (see Aspöck and Randolf 2014, fig. 57), and they are similar to Berothinae. But the venation of Protobiellinae is similar to that of some mid-Cretaceous Berothidae from Kachin amber and an undescribed species from Baltic amber. The Rovno larva may belong to this group. The Protobiellinae now include two genera restricted to Australia and New Zealand (Tillyard 1923; Aspöck and Aspöck 1985, 1988). The venation of Protobiellinae is also similar to that of Cyrenoberothinae, another basal berothid subfamily, but these are now absent in Australia (see Machado et al. 2022).

Therefore, the Rovno larva may equally belong to Rhachiberothidae or basal Berothidae: Protobiellinae, Cyrenoberothinae or an uncertain subfamily closely related to these.

Unfortunately, only first-instar larva of one extant species of Rhachiberothidae is known (Minter 1990). The structure of antennae may be changed in later instars, as was found in Dilaridae: the number of pseudo-segments increase due to secondary annulation (see above). Therefore, the mature larvae from the Baltic amber with six- to seven-segmented antennae (Wedmann et al. 2013, figs. 6–11) may theoretically belong to Rhachiberothidae, e.g. *Whalfera*. In this case, the Rovno larva belongs more confidently to some basal taxon of Berothidae, possibly to an undescribed Baltic amber genus with the venation similar to that of the mid-Cretaceous Kachin amber *Haploberotha*, or closely related taxon.

Possible habitat and biology of the larva

The large size of the amber piece, the abundance and composition of syninclusions indicate the location of the «amber trap» in the lower part of the trunk (Perkovsky 2010). In particular, this is evidenced by the presence of Collembola, three specimens of Sciaridae and Scirtidae in this piece. The abundance of workers of Formicinae indicates the likely presence of aphids or scale insects on the trunk (Perkovsky 2011; Radchenko and Perkovsky 2021 and references therein). Of other syninclused insects in the amber piece, the hemipteran genus *Protomenocria* Emeljanov and Shcherbakov, 2009 (Achilidae) is recorded from Rovno amber for the first time.

The Rovno larva possibly lived under/on bark, similar to the larvae of the Australian berothids which live under the bark of eucalypts (Riek 1970). We can assume that these are the larvae, one of which was illustrated by Riek (1970, fig. 29.5) which is similar to the Rovno larva. This is the only evidence of the habitats of extant non-berothine larvae in the wild. The presence of five stemmata in the Rovno larva confirms the idea that it is free living. If a larva lives in hidden habitats (in soil, for example Dilaridae, or in termite colonies, for example Berothinae), the number of stemmata is reduced: to two (Berothinae) or none (Dilaridae).

Some conclusions about larval food can be drawn from attempts to feed first-instar larvae of the Chilean *Berothimerobius reticulatus* hatched from eggs (Monserrat 2006). The author divided ten larvae into five groups of two and provided as food (1) flower nectar; (2) nymphs and imagoes of aphids; (3) larvae of Syrphidae; (4) larvae of ants; (5) immobilized nymphs, soldiers and workers of termite *Neotermes fulvescens* (Silvestri, 1901) (Kalotermitidae).

Five days later none of the ten specimens had prospered, except for one specimen to which ant larvae had been provided, this specimen remained alive for nine days, and the two who had been provided with nymphs, soldiers and workers of termites, remained alive for 15 and 19 days, with a marked and evident growth. From this the author suggested that the development of this species is likely associated with termite colonies.

All other available data on life habits of berothid larvae refer to Berothinae. They are associated with termite colonies (see a review in Wedmann et al. 2013). Also, one larva of *Lomamyia* was found in an ant nest, 'in the fungus garden (nest) of *Atta occidentalis* [almost surely *Trachymyrmex septentrionalis* (McCook 1881)] in wooded knoll' (Gurney 1947, p. 154).

The life habits of larval Rhachiberothidae are unknown.

Conclusions

The described larva from the late Eocene Rovno amber is of great importance in understanding the phylogenetic relationships between Berothidae and Rhachiberothidae. It is similar to both the basal Berothidae and Rhachiberothidae in having four-segmented antenna, at least five stemmata, and lateral sutures on the head capsule connecting the coronal suture and lateral margins of the head. This similarity means that Rhachiberothidae is more closely related to Berothidae than to Mantispidae, and the view of some authors that Rhachiberothidae is a subfamily of Berothidae appears justified. However, this issue may be further clarified when more fossil larvae will be described in detail, i.e. the numerous Mantispoidea from the mid-Cretaceous Kachin amber.

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