Straight-jawed lacewing larvae (Neuroptera) from Lower Cretaceous Spanish amber, with an account on the known amber diversity of neuropterid immatures

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Abstract

Three larval neuropterans (Insecta: Neuropterida) with straight mandibulomaxillary stylets are described from Lower Cretaceous (late Albian, ~105 Ma) Spanish amber: a third-instar beaded lacewing (Berothidae) from the Peñacerrada I locality (Burgos, Spain), and two specimens from the San Just locality (Teruel, Spain), i.e., a tentative first-instar beaded lacewing and a remarkable specimen considered a berothid-like mantispoid or dilaroid (instar unknown) displaying a combination of potentially plesiomorphic characters and some unique features. These morphotypes are among the oldest straight-jawed neuropteran larvae described. According to the morphology of the specimens and the taphonomy of the amber pieces where they are embedded, the described forms are regarded as active predators of small soft-bodied arthropods, probably living among bark or other vegetation of the resin-producing forest although they could have frequented the soil. An account of the diversity of larval Neuropterida described and/or figured from amber localities worldwide is provided, including reassessments of some specimens. The gathering diversity of fossil immature neuropterans, like that of their adult counterparts, already leans towards reflecting a greater diversity and disparity of the group in deep time –particularly during the Cretaceous– than in modern days, and it is worthy of increased research efforts due to the evolutionary and palaeobiological potential that it holds.

Keywords: insects, amber, Neuroptera, Albian, Spain, larvae

1. Introduction

Neuropteran larvae typically are active or sit-and-wait predators that use their mandibulomaxillary stylets, which form piercing and sucking tubes when conjoined, to absorb the fluids and liquefied tissues of their prey (Withycombe, 1925; Engel et al., 2018). These stylets (often referred to as “jaws”) are curved inwards to a lesser or greater extent (and, therefore, opposable) in the families Hemerobidae, Chrysopidae, Ithonidae, Nymphidae, Nemopteridae, Ascalaphidae, Myrmeleontidae, and Psychopsidae, all of which appear to form a monophyletic clade recently termed Neoneuroptera (Engel et al., 2018). In the remaining neuropteran larvae, however, the mandibulomaxillary stylets are straight, therefore non-opposable, with their bases usually inserted closer to each other into the cephalic capsule. Rather than being adapted to grasp mobile prey, they are more suitable to feed on immobile animals and/or those inhabiting confined or sheltered spaces, such as under the bark or in the soil (Withycombe, 1925). The straight-jawed condition occurs in the larvae of a grade of lineages leading to the Neoneuroptera and comprised by the extant families Coniopterygidae, Sisyridae, Osmylidae, Dilaridae, Berothidae, Rhachiberothidae, and Mantispidae, the three last families (together with the Mesozoic Mesoberothidae) included in the superfamily Mantispoidea (Engel et al., 2018; Winterton et al., 2018). Withycombe (1925) also included Ithonidae within this category, but the blunt mandibles and maxillae of these larvae actually slightly incurve (Grebennikov, 2004) and the lineage is recovered nested amongst the opposable-jawed neuropterans in the latest phylogenetic frameworks (Winterton et al., 2018). Therefore, it appears as if possessing straight mandibulomaxillary stylets was the original condition in Neuroptera and it appeared only once during their evolution. It should be noted that the Nevrorthidae, currently classified together with the Sisyridae and the Osmylidae within Osmyloidea, show straight stylets but their tips are recurved as a likely autapomorphic state (Engel et al., 2018).

Larval biology in straight-jawed Neuroptera is in most cases largely unknown and based on a few observations (all species' recounts and geographical distribution shown below extracted from Oswald and Machado, 2018). Coniopterygidae (dustywings) are a relatively large cosmopolitan group with about 570 species described. Larvae are active terrestrial predators commonly found on trees and shrubs (Meinander, 1972). Sisyridae (spongillaflies or sponge lacewings) are composed of about 70 species distributed worldwide. Larvae are fully aquatic (they possess tracheal gills) and are obligate predators/parasites of freshwater invertebrates, such as sponges and bryozoans, using their thread-like stylets (Parfin and Gurney, 1956). Osmylidae (lance lacewings) are composed of about 210 species distributed worldwide except North and Central America. All known larvae feed on soft-bodied insects, including aquatic insect larvae, and although fully aquatic forms are lacking, some osmylid larvae are known to be semiaquatic (tolerating immersion facultatively) (New, 1986; Martins et al., 2018). Most of them, however, live in riparian habitats or moist terrestrial environments such as in decaying logs, on mosses, under wet stones or under loose bark (ibid.). Dilaridae (pleasing lacewings), with almost 80 extant species, are an almost cosmopolitan group (absent from Australia). Larvae have been found living in the soil or under bark or decaying wood, and prey on small arthropods (New, 1986; Monserrat, 2005). Berothidae (beaded lacewings) comprise about 110 species distributed worldwide. First and third instars are active predators, whereas second instars are C-shaped and inactive (Möller et al., 2006). Known larvae (*Lomamyia* spp.) are termitophiles, living in termite galleries and secreting chemical substances that prevent being attacked by the termites and/or can immobilise the hosts prior to feeding on them (Johnson and Hagen, 1981; Wedmann et al., 2013). Rhachiberothidae (thorny lacewings, herein considered a separate family from Berothidae) have 13 described extant species living in sub-Saharan Africa. To date only the larva of one species has been described and its biology is unknown (Minter, 1990). Lastly, Mantispidae (mantidflies or mantis lacewings) have almost 400 species distributed worldwide. First instar larvae (planidia) are campodeiform and ectoparasites, usually of spider eggs or the spiders themselves, to a lesser degree, insects such as hymenopterans and lepidopterans, whereas the two remaining instars are scarabaeiform, with largely reduced cephalic appendages, and increasingly sedentary (MacLeod, 1964; New, 1986; Redborg, 1998).

A few neuropterids have been previously described from Spanish amber. These are some adult snakeflies (Raphidioptera), including the hitherto only known baissopterid described from amber (Pérez-de la Fuente et al., 2012a), a debris-carrying chrysopoid larva, *Hallucinochrysa diogenesi* (Pérez-de la Fuente et al., 2012b, 2016), an adult dustywing (Coniopterygidae) (Pérez-de la Fuente et al., 2019a) and an adult mantidfly (Pérez-de la Fuente & Peñalver, in press). Further adult neuropterid material available from Spanish amber (Peñacerrada I, San Just, and El Soplao localities) will be published elsewhere.

2. Material and Methods

Specimens described herein are housed at the Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain (specimens with MCNA number) and the Fundación Conjunto Paleontológico de Teruel-Dinópolis, Teruel, Spain (specimens with SJ number). Other institutional abbreviations (used in Table A.1): AMNH –American Museum of Natural History, New York, USA; CES – El Soplao amber Collection, El Soplao Cave, Celis, Cantabria, Spain; CNC – Canadian National Collection, Ottawa, Canada; EMTG – Three Gorges Entomological Museum, Chongqing, China; GPIMH – Geologisch-Paläontologisches Institute and Museum, University of Hamburg, Germany; GZG – Geowissenschaftliches Zentrum, Georg-August-Universität, Göttingen, Germany; IGR.ARC – Geological Department and Museum of the University of Rennes 1, France; LPAM BA – Lingpoge Amber Museum in Shanghai, China; LU, FSII – Natural History Museum of the Lebanese University, Faculty of Sciences II (Azar Collection), Fanar, Lebanon; MCZ – Museum of Comparative Zoology, Cambridge, MA, USA; MHU – Museum of Humboldt University, Berlin, Germany; MNHN – Laboratoire de Paléontologie, Muséum national d'Histoire naturelle, Paris, France; NHML – Natural History Museum, London, UK; NIGP – Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China; PIN – Palaeontological Institute, Russian Academy of Sciences, Moscow, Russian Federation; SF – Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Frankfurt am Main, Germany; SMNS – Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany.

The specimens were isolated within small amber pieces by removing most of the surrounding amber, and then prepared in Epoxy resin (Nascimbene and Silverstein, 2000). A Discovery.V12 Zeiss stereomicroscope, and two compound microscopes (an Olympus BX51 and a Zeiss AXIO) were used to study the specimens. Specimens were drawn using a camera lucida attached to the stereomicroscope and to the Olympus BX51 compound microscope, and photographed using an Axiocam 105 colour digital camera attached to both the stereomicroscope and the Zeiss AXIO. Series of images were taken with the software ZenPro v.2.3 and then digitally stacked using the software Helicon Focus v.6.8.0.

Descriptions generally follow the nomenclature used by MacLeod (1964) and Beutel et al. (2010). Cephalic capsule chaetotaxy follows the nomenclature of Hoffman and Brushwein (1992) used for mantispid larvae, which was an attempt to homologise the nomenclature used in Chrysopidae since Rousset (1966). All measurements provided are in millimetres if not otherwise stated.

3. Geological Setting

The specimens studied herein belong to two Lower Cretaceous localities from Spain: the Peñacerrada I outcrop, in Basque-Cantabrian Basin and, the San Just outcrop, in the Maestrazgo Basin (Fig. 1). Both basins are related to the opening of the North Atlantic, during a period of intense rifting (Oxfordian–Aptian) (Salas et al., 2001; Martín-Chivelet et al., 2002; Mas et al., 2004).

The Peñacerrada I amber outcrop is located close to Moraza village (Burgos Province). The amber bearing-deposit is dated as late Albian and was included in the Escucha Fm. (Peñalver and Delclòs, 2010), which was more recently proposed as a part of the lower unit of the informal stratigraphic unit Utrillas Group (Barrón et al., 2015). The amber is associated to coal levels, more abundant in the upper part of the stratigraphic series. Amber is namely found at the top of filling sequences of interdistributary bays, but it is also present in filling deposits of abandoned fluvial channels or crevasse splay with abundant plant remains developed in delta plain areas (Martínez-Torres et al., 2003). Although spores of cryptogams are common and diverse in some levels, including several schizaceous fern spore species, the dominant group of pollen is from conifers, namely from Araucariaceae, whereas that from angiosperms is sparse and not diverse (Barrón et al., 2015).

The San Just amber outcrop is located in the Utrillas municipality (Teruel Province). The amber-bearing deposit is dated as middle–late Albian (Villanueva-Amadoz et al., 2010; Barrón et al., 2015), within the recently named –yet not formally defined– Utrillas Group (sensu Rodríguez-López et al., 2009). Until recently, the fossil site was included in the upper member of the Escucha Fm., defined by Cervera et al. (1976) and Pardo and Villena (1979). For Rodríguez-López et al. (2009), the San Just deposit is included in a sedimentary succession taking part of the development of an erg, corresponding to wet areas close to the sea (fore-erg) where swamps and mangroves related to the arid coast of the sedimentary system developed. Amber levels correspond to marls and fine sands rich in organic matter and with a high content of charcoal, which suggests that fires were recurrent at the time (Peñalver et al., 2007) and that some of the levels correspond to deposits of post-fire washed floors. From the floristic point of view, ferns of the *Cladophlebis* type, conifers such as *Arctiopitys*, *Brachyphyllum*, *Glenrosa*, and *Frenelopsis*, the ginkgoales *Eretmophyllum* (=*Nehvizdya*) and *Pseudotorellia*, and different groups of seeds have appeared (Gomez et al., 2012; Delclòs et al., 2016; Barral et al., 2019). Amber-rich levels show a high angiosperm pollen content and consistent with a humid environment (Villanueva-Amadoz, 2010).

4. Results

Systematic palaeontology

Order Neuroptera Linnaeus, 1758

Superfamily Mantispoidea Leach, 1815

Family Berothidae Handlirsch, 1906

Berothid larva

Figs 2–3

Material. MCNA 9294, from Peñacerrada I amber, an almost complete specimen (all the left legs are incomplete) with generally good preservation and visibility, although some areas of the cephalic capsule appear cleared or might have been lost. The fossil's body and cephalic region appear to present a minor taphonomic deformation in dorsoventral direction, but legs do not appear affected. The specimen is prepared in a 11 × 6 × 1 mm prism of Epoxy resin.

Description (immature). Third (second?) instar. Body slender, campodeiform, dorsoventrally flattened (flattening regarded as real in life, not fully explained by taphonomic deformation), small size, total length 1.72 (excluding mandibulomaxillary stylets).

Cephalic capsule longer than wide, 0.26 long (excluding mandibulomaxillary stylets), 0.17 wide, gently tapering posteriorly (L/W ratio = 1.52), with integument (including mouthparts and antennae) light to dark brown, apparently smooth to finely imbricate. Dorsal cuticle of cephalic capsule partially missing (perhaps peeled away) or strongly cleared on areas outside the frontal suture. Frontal suture arrow-shaped, with sides first converging and then diverging at about distal third of cephalic capsule's length to gently converge again and meet at coronal suture beyond proximal third of cephalic capsule. Lateral sutures not evident, if present. Clypeolabral region not particularly pronounced. Ventrally, prementum and postmentum strongly depressed towards dorsal side or lost (perhaps peeled away). Ocular regions not placed on a distinct tubercle, contiguous to base of antennae, laterally placed, with six small stemmata. Two elongate setae (S4 and S9) on ocular regions. Additional setae (S7? and S2/S1?) visible. Antennae with three elongate articles progressively thinning distally, second and third articles with rather wide annulations, creating effect of undulating margins. First article 0.05, dark brown but basally. Second article with a medial constriction, 0.14 long, darkened in its distal two thirds. Terminal antennal article 0.07 long, fully darkened, distally bearing an elongate seta, 0.10 long, and a few very short setae. Mandibulomaxillary stylets straight, slender, as long as cephalic capsule, 0.26 long. Maxillae with broad bases, 0.05 width. Mandibles or maxillae without visible serrations on their distal inner margin, with a few sensillae present along their length. Labial palpi 0.18, with four slender, cylindrical palpomeres. Terminal palpomere with a distal digitation preserved in right labial palp (absent in left palp).

Thorax and abdomen with integument light brown with darkened areas as shown in Fig. 2 (some could correspond to dorsal sclerites, but not well enough defined as preserved as to ascertain that); with fine, sparse setae dorsally, laterally with pair of fine, elongate setae medially. Legs relatively small, slender, dark brown, all equal in size: protrochanter 0.03 long, profemur 0.09 long, protibia 0.08 long, protarsus (with fused tarsomeres) 0.04 long. Pretarsal claws simple, 0.02 long; trumpet-shaped empodia well-developed, 0.04 long; paired setae-like pulvilli present, almost reaching distal end of empodium.

Abdominal segments I–VIII wider than long, IX–X longer than wide, cylindrical and bent ventrally. Caudal sucker present.

Remarks. The affiliation of this specimen within Berothidae is straightforward due to (1) its cephalic capsule longer than wide, (2) straight mandibulomaxillary stylets as long as the cephalic capsule, (3) maxillae expanded basally, (4) three-articled antennae with articles thinning distally, (5) terminal antennal article bearing a long and strong terminal seta, (6) tetramerous labial palps, and (7) trumpet-shaped empodia (see Table 1).

In spite of its small size, we consider MCNA 9294 a third-instar larva based on the much greater relative proportions of the head and legs when compared to first instars (e.g., Möller et al., 2006). However, the possibility of the new specimen being a second instar with a different ecology than extant relatives, the second instars of which are inactive and show morphological reductions (Möller et al., 2006), should not be ruled out. Even though the dorsal margins of the cephalic capsule's cuticle (those externally to the frontal suture) could be partially missing, and ventrally the capsule appears to be compressed, the specimen does not appear to be an exuvia due to the integrity of the remainder of the body, aside from that being incongruent with its inferred developmental stage.

The most differing character of the fossil when compared to known extant berothid larvae is the structure of the frontal ecdysial suture, which is arrow-shaped (Figs 2, 3). In modern berothid larvae, the frontal suture, when present, has sides that run gently converging or parallel to each other for a fairly long stretch, and then converge in a V- or U-shape fashion typically around the proximal quarter of the cephalic capsule's length (Gurney, 1947; MacLeod, 1964; Tauber and Tauber, 1968; Minter, 1990; Möller et al., 2006). A pair of lateral sutures are also typically present in modern berothid larvae where the sides of the frontal suture start to converge more steeply, although in the present fossil the corresponding areas from the dorsal cuticle appear peeled off or strongly cleared and therefore it is unclear whether the specimen presented them. On the other hand, an arrow-shaped frontal suture bearing some resemblance to that of MCNA 9294 is known from some osmylid larvae (Matsuno and Yoshitomi, 2016).

The new morphotype differs from the Burmese amber larva described by Engel and Grimaldi (2008) in its palpal and antennal morphology, and from the Lebanese amber specimen described by Whalley (1980) in its narrower cephalic capsule. Further differences between the latter and MCNA 9294 are not possible to evaluate due to the limited description and figures provided by the last author. In any case, the specimen described by Whalley (1980) appears to be missing (Azar, 2018 pers. comm.). The new specimen is remarkably smaller than these two previously described larvae, i.e., 1.7 mm (excluding mandibulomaxillary stylets) vs. 3.9 and 6–8 mm long, respectively.

Berothid? larva

Fig. 4

Material. SJ-10-25, from San Just amber. An almost complete specimen, the thorax of which is partially obscured by the abdomen and a leg of a rhagionid fly (SJ-10-27) preserved as a syninclusion. A *Microphorites* sp. fly (Dolichopodidae) is also preserved as syninclusion (SJ-10-26). The distalmost parts of the mandibulomaxillary stylets, antennae, and labial palpi are not preserved. The specimen is preserved in an amber piece with abundant surrounding debris, and prepared in a 2.4 × 1.5 × 0.4 mm prism of Epoxy resin.

Description (immature). First instar? Body slender, campodeiform, medium-sized, total length about 3.36 (excluding mandibulomaxillary stylets). Integument dark brown.

Cephalic capsule trapezoid, slightly wider anteriorly than long (L/W ratio = 0.92), 0.48 long (excluding mandibulomaxillary stylets), gently tapering posteriorly, 0.52 wide anteriorly, 0.41 wide posteriorly. Frontal sutures elongate, subparallel to each other (slightly converging) distally; basal part of the frontal sutures and further sutures not visible, if present. Ocular regions slightly elevated, maculated, located next to base of antennae, with at least four clearly discernible stemmata (Fig. 4D), probably with five of six in total. Cephalic capsule setation not discernible. Antennae inserted on an elevated mound, progressively thinning distally, with two preserved articles; basal article cylindrical, elongate, 0.11 long, 0.04 wide; second article apparently annulated. Total antennal article number and length unknown. Mandibulomaxillary stylets straight, slender, total length unknown. Maxillae expanded basally, not meeting in the middle. Labial palpi with two visible articles, slender; first article elongate, second article probably with annulations. Total palpomere number and length unknown.

Thorax with cervical sclerites not visible, if present. Legs slender, relatively large; metathoracic leg with tibiae 0.49 long, tarsus 0.26 long; pretarsal claws simple and equal, with a well-developed trumpet-shaped empodium between them, 0.16 long. Abdomen with sparse setae visible dorsally, up to about 0.20 long; laterally with a few elongate setae, longest 0.30 long. Abdominal segments I–VIII wider than long, IX–X longer than wide, cylindrical and bent ventrally. Abdominal segments VIII and IX with at least two pairs of particularly elongate, laterally placed, setae, 0.45 long (Fig. 4C).

Remarks. The high relative proportion of head and legs when compared to the body suggests that SJ-10-25 is a first-instar larva (e.g., see Minter, 1990; Möller et al., 2006), although the relatively large size of the specimen conflicts with that notion.

An affiliation of the present specimen within Berothidae based on the shape of its cephalic capsule, maxillae expanded basally and well separated (not meeting in the midline), at least four stemmata on each ocular region, equal claws, and trumpet-shaped empodia is the most consistent. However, because the full morphology of the antennae, labial palpi, and cephalic capsule sutures are unclear, and the total length of the mandibulomaxillary stylets is unknown, it cannot be ruled out that the present specimen could have dilaroid affinities and, therefore, be more closely related to the specimen SJNB2012-04 (see below). A relationship within other groups of mantispoids, such as Mantispidae, for the present specimen can be ruled out due to mandibulomaxillary stylets typically forming a triangle meeting at the midline when in rest in first-instar mantispids (although this feature appears to be absent in symphrasines such as *Plega*, see MacLeod, 1964), the number of stemmata is reduced to three or less, second antennal article and palpomere are rather swollen, and they lack a pair of well-developed claws (i.e., they show just one claw that can be reduced and possess a more or less developed unguitractor process) (Minter, 1990; Hoffman and Brushwein, 1992). Note that although first extant first-instar mantispine larvae have a subquadrangular cephalic capsule, first-instar symphrasine and drepanicine larvae have elongate cephalic capsules (MacLeod, 1964; Dorey and Merritt, 2017).

Superfamily incertae sedis
Mantispoid or dilaroid larva
Figs 5–6

Material. SJNB2012-04, from San Just amber, a well-preserved larval specimen partially missing the abdomen beyond its third segment and surrounded by relatively abundant debris. The amber sample is prepared in a 21 × 13 × 2 mm prism of Epoxy resin.

Description (immature). Instar uncertain. Body slender, campodeiform, total length unknown (preserved length 1.58, excluding mandibulomaxillary stylets).

Cephalic capsule oval, longer than wide, 0.62 long (excluding mandibulomaxillary stylets), maximum wide 0.42 between ocular regions (L/W ratio = 1.35), gently tapering posteriorly, light in colour. Frontal suture apparently absent but two subparallel grooves projecting beyond inner margin of antennal insertion and reaching slightly beyond half of cephalic capsule’s length (Fig. 5A). Coronal or lateral sutures not present. Clypeolabral region not particularly pronounced (not forming a rostrum), distally convex, with at least four short setae, 0.04 long. Remaining visible dorsal setation of cephalic capsule with a pair of elongate setae at the cephalic capsule’s midlength below inner margin of ocular region (S7), 0.16 long, and five pairs of shorter setae, about 0.04 long, arranged as follows (Fig. 6): S2 most proximal setae, followed by S5 in a slightly more distoexternal position; S1/S3? present more distomedially; S11 on inner margin of parallel cephalic grooves, aligned with S7; and S8?

placed next to ocular region's ventroproximal margin. Stipes + cardo large, bulging, widest at middle. Prementum not visible. Postmentum reduced, narrow. Ocular region contiguous to antennal insertion, slightly tuberculate, trianguloid in shape, distinctly darkened, with six stemmata, five arranged in a "C" fashion and a central one, flanked by two short setae (S4 and S9). Most proximal-inner stemma of five arranged in a "C" with a bar-shaped appearance (Fig. 5D). Antennae 0.69 long, with 11 articles. Antennal socket on an elevated projection, trapezoidal in shape, 0.05 long, 0.07 wide basally, 0.05 wide distally. Basal antennal article cylindrical, elongate, 0.12 long, 0.05 wide, with distal margin crenulate (visible only in right antenna). Antennal articles 2–7 cylindrical, slightly longer than wide, 0.04 long, 0.03 wide, with basal 2/3 of each article distinctly darkened. Antennal article 8 cylindrical, about twice as long as wide, 0.06 long, 0.03 wide, fully darkened. Antennal article 9 like articles 2–7 in shape but fully darkened. Antennal article 10 elongate, 0.13 long, slightly expanding until distal 2/3 then tapering, maximum width 0.04, proximally darkened, lacking visible sensorium, bearing two setae on external side, basalmost one at 1/4 of article's length and distalmost one at 1/2 of article's length. Antennal article 11 (terminal) expanding (not tapering) distally, cowbell-shaped, 0.08 long, 0.02 wide basally, 0.03 wide distally, light in colour, with four short and one longer (0.13 long) setae distally (Fig. 5D). Antennal articles 10 and 11 with a faint scaly texture. Mandibulomaxillary stylets straight, slender, slightly curving upwards, about 1.4× longer than cephalic capsule, 0.87 long. Mandibles thin, 0.50 wide basally. Maxillae with basal third moderately broadened, 0.12 wide. Mandibles or maxillae without visible serrations on their distal inner margin, with a few distal sensillae present. Labial palpi about 0.58 long, with nine palpomeres. First palpomere elongate, about 0.9 long. Palpomeres 2–7 slightly transverse to slightly cylindrical, partially darkened (apparently distally but palpomere 7, which appears fully darkened). Palpomere 8 cylindrical, 0.07 long, 0.03 wide, darkened on its basal half. Terminal palpomere particularly elongate, 0.26 long, with very fine annulations; slightly club-shaped, i.e., 0.02 wide basally and very gently expanding distally, reaching a maximum width of 0.03 at about 3/5 of its length then thinning into a distal cylindrical digitation, lacking setae distally.

Prothorax with a pair of large dorsal sclerites, 0.22 long, 0.18 wide, not meeting at midline, darkened. Pairs of smaller dorsal sclerites on proximal side of meso- and metathorax, 0.09 long, 0.10 wide. Further sclerites not discernible. All thoracic segments dorsally with transverse rows of short, rather strong setae; these rows on posteromedial margin of all thoracic dorsal sclerites comb-like, with more densely packed, peg-like short setae (Fig. 5C). Legs relatively large, robust, with dark maculations (Fig. 5), meso- and metafemora with basal half darkened. Pretarsal claws from all legs paired, equal, recurved, 0.07 long. Trumpet-shaped empodia well developed, 0.12 long. Paired seta-like pulvilli present, faint, about as long as pretarsal claws. Tarsi with fused tarsomeres. Pro- and metathoracic leg subequal in length, mesothoracic leg slightly shorter. Prothoracic leg 1.32 long (without pretarsal claws nor empodia); coxa 0.20 long; trochanter 0.16 long; femur 0.43 long, tibia 0.35 long, tarsi 0.18 long. Mesothoracic leg about 1.18 long; coxa + trochanter 0.25 long; femur 0.39 long; tibia 0.32 long; tarsus 0.22 long. Metathoracic leg about 1.36 long; coxa + trochanter + femur 0.68 long; tibia 0.46 long; tarsus 0.22 long.

Abdomen with the three first segments preserved, uniformly darkened, with setae longer than thoracic setae, setae not forming rows.

Remarks. As the larval specimen presents a combination of potentially plesiomorphic characters found in modern Dilaridae and Berothidae, as well Osmylidae to a lesser extent (see Table 1), the taxonomic placement of the new morphotype within the current extant and extinct larval diversity of these groups is challenging. References used for the data discussed below regarding extant larval diversity are only shown at Table 1 to avoid repetition (only references on fossil larvae are provided in the following text).

Ocular regions with six stemmata are present in all known extant osmylid and some berothid larvae, as well as all known Cretaceous and Eocene amber fossils classified in the latter (Whalley, 1980; Engel and Grimaldi, 2008; Wichard et al., 2009; Wedmann et al., 2013). On the contrary, described modern dilarid larvae have no or only a single stemma developed on each ocular region.

Both dilarid and berothid larvae have basally expanded maxillae and elongate cephalic capsules, although in berothid larvae the head tends to be more angulated, less oval-shaped as in dilarids. On the other hand, in known osmylid larvae the maxillae do not expand basally as significantly, and the head is subcircular or wider than long.

Frontal and coronal ecdysial sutures more or less Y-shaped are present in osmylids and berothids, but they are lacking in known sisyrids. Additionally, lateral sutures can exist in berothids.

The antennae of the new morphotype are most similar to those of Dilaridae, although those of Osmylidae show a similar pattern. Whereas extant berothid larvae have three or four-segmented antennae with segments typically thinning distally and a particularly enlarged terminal seta, extant dilarid and osmylid larvae (at least the third instars) have an antennae not narrowing distally, lacking a particularly enlarged terminal seta and showing three distinct regions, i.e., a basal article that is elongate, a multi-articulated median region (as occurs in other neuropteran larvae), and a distal region composed by two much more elongate articles, the penultimate one the largest, expanded beyond its midlength. The median region of the antennae has four to five articles/annulations in described extant dilarid larvae, and between 17 and 38 in known extant osmylid larvae. In the new fossil morphotype, the median region of the antennae has eight articles. Also, the penultimate antennal article, although distally expanded, lacks a distinct sensorium in the fossil, as occurs in *Dilar* larvae (Dilaridae). This sensorium is always present in the known osmylid larval diversity. It is important to note that larvae with a greater number of antennal articles (and sometimes of palpomeres) when compared to extant relatives, although lacking an expanded penultimate segment, have been described from straight-jawed larvae assigned to Berothidae in Burmese and Baltic ambers (Engel and Grimaldi, 2008; Wedmann et al., 2013).

Similarly, the new morphotype's labial palps are most similar to those of some dilarids, particularly those classified within the genus *Nallachius* Navás, 1909, which show octamerous labial palps with a median region composed of five equally-sized palpomeres, and therefore highly resembling antennae. Labial palps of extant osmylid larvae have five palpomeres in total, which are thinner and more elongate than in *Nallachius* and the new morphotype. Interestingly, although a club-shaped last palpomere with a distal digitation is absent from the known modern diversity of osmylid, dilarid, and berothid larvae, this morphology is commonly found in hemerobiid (Beutel, 2010) and chrysopid larvae, including Cretaceous forms (Pérez-de la Fuente et al., 2012, 2019b). Some osmylid larvae have a distal digitation on their cylindrical terminal labial palpomeres.

Whereas known osmylid and berothid larvae have dorsal thoracic sclerites, known dilarid larvae lack these. Moreover, described osmylid larvae have empodia that are triangular and pointed across all instars, whereas the empodia of berothid larvae and most described dilarid larvae is trumpet-shaped across all instars (empodia in the latter can also be filiform).

Three (four) potentially apomorphic characters from the new larval morphotype have not been described from the known larval diversity of dilarids, berothids or osmylids, extinct or extant: (1) The last antennal article expanding distally, not tapered (cowbell-shaped) (Fig. 5D); (2) the presence of an apparently bar-shaped stemma, visible in both eyes and therefore not regarded as an artefact (Fig. 5D), and (3) the presence of comb-like rows of peg-like short setae on the posteromedial margin of all thoracic dorsal sclerites (Fig. 5C). Additionally, the degree of elongation of the mandibulomaxillary stylets in relation to the cephalic capsule (~1.4×) is higher when compared to extant dilarid and berothid larvae, as well as previously described fossil berothid-like larvae (about as long as cephalic capsule) but lower than in extant osmylid larvae (2× longer than cephalic capsule). Only further discoveries will reveal if these characters deserve considering the current form as belonging to a separate group of straight-jawed neuropterans. For now, however, two hypotheses appear to be evenly likely for the taxonomic affiliation of the present specimen: a berothid-like mantispoid with a higher number of antennal articles and palpomeres than modern taxa, a condition that is known from some forms described from Baltic amber and which was hypothesised as plesiomorphic (Wedmann et al., 2013), or, conversely, a dilaroid with well-developed stemmata and thoracic sclerites, as well as with equal claws. A relationship with Osmylidae appears less likely with the present data.

5. Discussion

5.1. Palaeoecological remarks

In berothid larvae, the sharpness of the mandibulomaxillary stylets has been suggested to be indicative of the type of prey that they are adapted to feed on, with those forms showing more acutely pointed stylets (such as those present in MCNA 9294 and SJNB2012-04) piercing soft-bodied prey, namely arthropods, and those with blunter stylet tips better equipped to feed on prey with a stronger cuticle (Wedmann et al., 2013). Moreover, a reduction of the number of stemmata in the group (from the plesiomorphic condition of six) has been assumed to be related to the hypogeous and termitophilous habits of the larvae

(Wedmann et al., 2013), and so the lack of reduction could reflect the plesiotipic condition of an epigeous ecology.

From the taphonomic standpoint, the specimen SJNB2012-04 is surrounded by relatively abundant debris that clouds the amber piece in which it is included, which might indicate that the resin entrapped it closer to the ground. Although the specimen SJ-10-25 also shows abundant surrounding debris, it is included together with two dipterans, a rhagionid and a dolichopodid, which suggests that the two flies or the three insects altogether came from at a certain elevation above the forest floor.

Lastly, at least MCNA 9294 and SJNB2012-04 have bodies that are rather flattened dorsoventrally (Figs 3A, 5A–B), although in the first specimen taphonomic deformation is likely partially contributing to the depressed appearance. This morphology is commonly found today in straight-jawed lacewing larval forms that are well suited to crawl under bark, or among soil particles, looking for prey.

5.2. Described or figured palaeobiodiversity of neuropterid immatures

An account of the described or figured amber neuropterid larvae provides some interesting insights. When compared to other types of inclusions, namely those of adult insects, neuropterid larvae are relatively rare in amber. A total of at least 93 described or figured neuropterid immature morphotypes preserved in amber have been recounted (Table A.1). About a quarter of them are held by private collectors.

It has been experimentally proven that the ecology of an organism, larval in this case, biases their preservation and relative abundance depending on the nature of the fossiliferous material and deposit in question (Martínez-Delclòs et al., 2004; Solórzano-Kraemer et al., 2018). Rock deposits lacustrine or palustrine in origin namely preserve aquatic larvae, megalopterans in the case of neuropterids (Illies, 1967; Ponomarenko, 1976, 2012; Nel, 1991;

Wang and Zhang, 2010; Liu et al., 2012), which is also explained by their relative larger size in late instars. A few non-aquatic Neuroptera larvae are also known from rock deposits (e.g., Dayvault et al., 1995; Bechly, 1998; Martins-Neto et al., 2007). For amber deposits, it is well known that the more active and closer to the resin-producing sources an organism is, the higher its probability to become entombed in resin and therefore preserved in amber. Thus, arboreal forms that live on the tree trunk are expected to be more frequently trapped in resin and therefore more present in the amber record (Solórzano-Kraemer et al., 2018), whereas for instance larvae that live on or in the soil (epi- or hypogeous) or that are aquatic (even more so if they are fully aquatic) are expected to be less abundant. Another important factor that conditions potentially being exposed to fresh resin is how active and fast-moving larval forms are, particularly when seeking for prey. In that regard, raphidiopteran larvae, active predators on vegetation, are quite abundant in the amber record, with 12 morphotypes described/figured since the Early Cretaceous (Barremian) in Lebanese amber (Table A.1). Likewise, within Neuroptera, described/figured mantispoid, chrysopoid, myrmeleontoid (particularly ascalaphids and nymphids), and to a lesser extent psychopsoid larvae, are relatively well-represented in the amber record (Table A.1). Of special note is the palaeodiversity of chrysopoid larvae unearthed thus far, which includes various morphotypes with extreme morphological specializations for debris-carrying such as the hyperdevelopment of dorsal setose tubercles (Pérez-de la Fuente et al. 2012, 2018, 2019b; Wang et al., 2016), or hyperspecialised, non-debris-carrying forms with ecologies unknown in modern representatives, such as long-legged larvae posited as predators or kleptoparasites of web-spinning spiders (Liu et al., 2016) and forms mimetic with liverworts (Liu et al., 2018). By contrast, and quite surprisingly due to the alleged ecology of extant representatives (relatively similar to the groups noted above), coniopterygid and hemerobiid larvae are each represented by only a single specimen described/figured from Eocene Baltic amber, respectively (Table

A.1), although a larval coniopterygid preserved Charentese amber (France), Albian-early Cenomanian in age, was mentioned by Perrichot (2004).

Likely due to their soil-dwelling lifestyles, myrmeleontid (ant lion) larvae are only known from a few morphotypes in Miocene Dominican amber (Poinar and Poinar, 1999; Engel and Grimaldi, 2007) (Table A.1), although the larva figured by Poinar and Poinar (1999) might actually be better aligned with ascalaphids due to the high relative length of the mandibulomaxillary stylets, the alleged presence of short scoli, and the attachment of debris. On the other hand, no ithonid or definitive nemopterid (although see Haug et al., 2019) larvae have been described from amber yet, but their absence could be also explained by their expected geophilous – often hypogeous – habitat (Oswald and Machado, 2018).

Lastly, some morphotypes of neuropterid larvae considered as fully aquatic have been reported from amber: a few megalopterans and nevrorthids, and a sisyrid (Table A.1). Although very scarce, aquatic organisms (namely of freshwater habitats, but also living in marine or marine-influenced waters) can also become entombed in resin and potentially preserved as amber inclusions (Martínez-Delclòs et al., 2004; Schmidt and Dilcher, 2007; Sánchez-García et al., 2015). Potentially semiaquatic neuropterids, such as osmylids, are rather infrequent as well, with only one first instar from Baltic amber unequivocally belonging to this group.

5.3. Reassessment of some described neuropteran larvae

Some formerly described larvae appear to be more closely related to Berothidae than to other groups originally considered, often tentatively. The first instar larva clinging to a long-stalked egg described as "Chrysopid Egg and Larva" by Engel and Grimaldi (2008) (CAS-1096) from Canadian amber (Campanian in age) was regarded as belonging to Berothidae by Wedmann et al. (2013) based on head morphology, straight mandibulomaxillary stylets, and trimerous antennae bearing a long and strong terminal seta, and herein we agree with this assessment. Additionally, it is important to note that, like most chrysopids, known berothid eggs are also ovoid, show microornamented egg chorions (papillae), and have long silky stalks (Gepp, 1990; Pérez-de la Fuente et al., 2019b). Likewise, the mandibulomaxillary stylets of another larval specimen, AMNH Bu-126 from Burmese amber (early Cenomanian in age), described by Engel and Grimaldi (2008) as a "First-Instar Larva [Psychopsidae?]" are straight, with quite broad maxillae basally, and therefore their affiliation appears to be closer to Berothidae rather than to Psychopsidae. Lastly, the immature described as a "Coniopterygid? Larva" by Engel (2016) from Burmese amber (AMNH JZC Bu-275), appears to be related to a mantispoid group, probably assignable to Berothidae, due to its campodeiform habitus, subquadrate cephalic capsule with clypeolabral region not pronounced (not forming a rostrum, cf. Rousset, 1966), antennae with (likely three) articles thinning distally and bearing a terminal elongate seta, and labial palp structure (two thin palpomeres described but at least one more is perhaps present proximally). However, the mandibulomaxillary stylets are not particularly well developed, the maxillae do not appear to be expanded basally in the way characteristic of other berothids and appear to be meeting at the midline, so the affiliation of this specimen with mantispids (particularly with drepanicines, see Dorey and Merritt, 2017) should not be ruled out.

On the other hand, the larva reported by Engel and Grimaldi (2008) from Burmese amber as well classified within Osmylidae (AMNH Bu-267) shows characters that differ with known modern representatives of the group, such as head longer than wide (subcircular to wider than long in modern representatives), a different palpal and antennal structure (with lower and greater number of palpomeres and articles when compared to extant osmylids, respectively), and trumpet-shaped empodia (not triangular and pointed like in extant osmylids) (Table 1). For these reasons, it is interesting to note that AMNH Bu-267 could correspond to a stem-osmylid.

6. Conclusions

The three fossil larvae described herein, together with a single specimen from lower Barremian Lebanese amber briefly described by Whalley (1980) and which is currently lost, are among the oldest described straight-jawed neuropteran larvae known. From the systematic point of view, they are mantispoid neuropterans, although one of the described specimens could have dilaroid affinities. In that regard, once further similar fossil material is described and the much necessary descriptions of further extant neuropteran larvae are carried out, proper character polarization and phylogenetic analyses should be able to reveal a more satisfactory affiliation for said specimen and for other problematic straight-jawed neuropteran larvae (see Wedmann et al., 2013).

The morphology of the mandibulomaxillary stylets, the lack of stemmata reduction, the dorsoventrally flattened bodies of two of the specimens, and the taphonomy of the amber pieces are consistent with an ecology for the fossil forms analogous to that of extant representatives, and therefore we interpret them as active predators feeding on soft-bodied prey living on vegetation (including subcortical spaces and/or decaying wood) and often visiting the soil. In any case, it is likely that each larval morphotype showed habit and habitat particularities.

The fossil diversity of neuropteran larvae, like that of their adult counterparts (Engel et al., 2018), already appears to be more disparate from the morphological (and likely from the ecological) point of view than that of the present time. Although neuropterid larvae are scarce in amber when compared to records of adults (neuropterid or otherwise), their record is actually quite abundant when compared to that of the larvae from other holometabolous groups of insects. This can be explained by most groups of neuropterid larvae typically being terrestrial predators that are commonly rather active and that usually live on the vegetation. A study bias promoted by the campodeiform body plan of neuropterid larvae, spectacular insects showing plenty of external characters when compared to other insect larvae, can be another factor explaining their apparent relative abundance in the amber fossil record. In any case, said high relative abundance and campodeiform body plan make neuropterids an ideal group to study the deep past and evolution of larval morphology, ecology and behaviour in holometabolous insects. In that respect, the amount of palaeobiological information that can be extracted from immature insects is substantial, and in the case of neuropterid larvae, their palaeobiological potential has only recently begun to unfold (Peñalver and Pérez-de la Fuente, 2014; Tauber et al., 2014; Badano et al., 2018). Awareness of this importance needs to be raised in order to stop considering larval insects (and immature organisms, in general) second-class fossils with little information to provide. To achieve such goal, however, thorough descriptions of the fossil immatures are necessary, as well as targeted efforts in palaeontological collections, both public and those held by private collectors.

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Supplementary Material

The following file is published as supplementary material and can be found here.

Table A.1. Neuropterid larvae described or figured from amber.

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FIGURE CAPTIONS

Fig. 1. Paleogeographic map of the Iberian Peninsula during the late Aptian–early Albian, showing the location of the Peñacerrada I and San Just amber localities (black dots). Modified from Mas et al. (2004).

Fig. 2. Berothid larva, specimen MCNA 9294. **A**, microphotograph of ventral habitus. **B**, camera lucida drawing of ventral habitus. **C**, detail of the head in ventral view. **D**, camera lucida drawing of head in ventral view. Scale bars: A, B – 0.5 mm (both to the same scale); C, D – 0.2 mm (both to the same scale).

Fig. 3. Berothid larva, specimen MCNA 9294. **A**, lateral habitus. **B**, ventral view of the cephalic capsule as seen with incidental light, showing colour patterns and frontal suture (its proximal part seen by transparency through the interpreted depressed postmentum). **C**, dorsal view of the cephalic capsule as seen with incidental light, showing arrow-shaped frontal suture. Arrowhead #1 marks the point at which the sides of the frontal suture converge the most before diverging, and arrowhead #2 marks the point at which the sides of the frontal suture meet at the coronal suture. **D**, lateral view of cephalic capsule as seen with incidental light. Arrowheads provide the same information than in subfigure C. **E**, pretarsal claws (arrowheads mark their distal end), trumpet-shaped empodium, and two setae-like pulvilli (arrows) from the right mesothoracic leg in dorsal view. Scale bars: A – 0.5 mm; B, D – 0.2 mm (B and C to the same scale); E – 0.05 mm.

Fig. 4. Berothid? larva, specimen SJ-10-25, partially masked by the abdomen and a leg of a rhagionid fly. **A**, microphotograph of the habitus in dorsal view. **B**, camera lucida drawing. **C**, detail of the abdomen using transmitted light only. **D**, detail of the cephalic capsule. Arrow shows the ocular tubercle. Scale bars: A – 1 mm (A and B to the same scale); C, 0.5 mm; D, 0.2 mm.

Fig. 5. Mantispoid or dilaroid larva, specimen SJNB2012-04. **A**, right dorsolateral habitus. Black rectangle corresponds to top inset seen from the other side of the amber piece, showing the pretarsal claw and trumpet-shaped empodium from the left metathoracic leg. White rectangle corresponds to subfigure C. **B**, left dorsolateral habitus. The thoracic sclerites have been tagged: pr – prothoracic sclerites; ms – mesothoracic sclerites; mt – metathoracic sclerites. **C**, prothoracic sclerites. Arrow points to the comb-like row of peg-like setae on the posteriomedial margin of the prothoracic sclerites. **D**, right antenna and ocular tubercle.

Arrow points to the bar-shaped stemma. **E**, ventrolateral view of the cephalic capsule, showing the two bulging stipes + cardines and the narrow postmentum (arrowhead). **F**, right? labial palp. Arrowheads mark the limits of palpomeres 2–7. Scale bars: A, B – 0.5 mm; C, F – 0.1 mm; D, E – 0.2 mm; inset in A – 0.05 mm.

Fig. 6. Camera lucida drawings of mantispoid or dilaroid larva, specimen SJNB2012-04. **A**, cephalic capsule in dorsal oblique view, including the visible cephalic capsule setae and interpreted chaetotaxy. **B**, Best exposed labial palp (probably the right one) in lateral view. Scale bars: A, 0.2 mm; B, 0.1 mm.

TABLE

Table 1. Comparative chart of characters known from extant larvae of Osmylidae, Dilaridae, and Berothidae. In bold, characters shared with (or, for the number of antennal articles and palpomeres, closely resembling to) those of the new fossil morphotype SJNB2012-04.

	OSMYLIDAE	DILARIDAE	BEROTHIDAE
Cephalic capsule shape	Subcircular to wider than long	**Elongate, oval**	Elongate, subquadrate or trapezoid (slightly wider anteriorly)
Ecdysial sutures	Present, two arms of frontal suture converging anteriorly, arrowhead- or V-shaped	Absent	Present, two arms of frontal suture running parallel for most of their length and meeting rather proximally. Lateral sutures may exist.
Nº of stemmata in ocular region	**6**	0 or 1	**0–2, 5 or 6**
Mandibulomaxillary stylets: elongation	2x longer than cephalic capsule	As long as cephalic capsule	As long as cephalic capsule
Maxillary basal expansion	Absent	**Present (moderate)**	**Present**
Antennal structure	**Articles not tapering distally, terminal strong seta absent**	**Articles not tapering distally, terminal strong seta absent**	Articles tapering distally, terminal strong seta present
Antennal midregion	17–38 articles/annulations	**4–5 articles (third instar)**, single and globose (known in first instars)	Usually one middle article (can have a medial constriction), very elongate, scaly
Penultimate antennal article sensorium	Present	Present (*Nallachius*) or **absent (*Dilar*)**	**Absent**
Terminal antennal article	Elongate, cylindrical	Moderately elongate to papilliform	Very elongate, cylindrical
Palpal structure	5 palpomeres, all elongate	5 or **8 palpomeres** (3 palpomeres known in first instars)	4 palpomeres
Terminal palpomere	Papilliform to cylindrical, sometimes **with a distal digitation**	Papilliform	Elongate to very elongate, cylindrical
Thoracic sclerites	**Present**	Absent	**Present**
Empodium	Triangular and pointed	Filiform to **trumpet-shaped**	**Trumpet-shaped**
Pretarsal claws	**Equal**	Unequal	**Equal**
Taxa with species which larval stages are known	*Isostenosmylus* sp., *Kempynus* sp., *Osmylus* spp., *Stenosmylus* sp.	*Dilar* spp., *Nallachius* sp.	*Berothimerobius* sp., *Lomamyia* spp., *Podallea* spp., *Spermophorella* sp.
References	MacLeod, 1964; New, 1974; Gepp, 2003; Martins et al., 2016, 2018; Matsuno and Yoshitomi, 2016	Tillyard, 1916; Gurney, 1947; Ghilarov, 1962; MacLeod, 1964; Monserrat, 1988, 2005	Tillyard, 1916; Gurney, 1947; MacLeod, 1964; Tauber and Tauber, 1968; Minter, 1990; Möller et al., 2006; Monserrat, 2006