Beaded lacewings (Neuroptera: Berothidae) in amber from the Lower Cretaceous of Spain

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ABSTRACT

Five new beaded lacewings (Neuroptera: Berothidae) are described from ca. 105 Ma Spanish amber. A new genus and species, *Cantabroberotha soplaensis* gen. et sp. nov., are erected based on a complete amber specimen from the El Soplao outcrop (Cantabria, northern Spain). Four indeterminate berothids based on incomplete specimens are described from Peñacerrada I amber (Burgos, northern Spain). One of these provides a rare instance of an amber fossil being partially preserved as an impression rather than as a complete inclusion. This was the result of the lacewing not fully penetrating into a resin flow, its wings getting caught on the resin surface and leaving an imprint. The preservation of this delicate impression fossil allows us to infer that a low grade transport likely occurred, at least partly, during the biostratinomic phase of the genesis of the Peñacerrada I amber deposit, similar to what was inferred for the El Soplao amber deposit. Moreover, one of the incomplete berothid inclusions has an indeterminate, likely immature mesostigmatan mite attached to the proximal part of its hind wing, most parsimoniously resulting from a symbiotic interaction, probably phoresy.

Keywords: insects, amber, Neuroptera, Spain, amber impression, phoresy

HIGHLIGHTS

- New beaded lacewing morphotypes, including a new genus and species, are described from Spanish amber
- A fragmentary specimen is a partial inclusion, with wings preserved as a delicate amber impression
- The latter implies that low transport took place during the genesis of the Peñacerrada I outcrop
- A mite is associated to another specimen, possibly representing a case or phoresy

1. Introduction

Berothidae, also known as beaded lacewings, are a small family of neuropteran insects, with about 120 species distributed worldwide yet particularly diverse in Africa and Australia (Aspöck and Randolf, 2014; Oswald and Machado, 2018; Engel et al., 2018). Berothid biology remains poorly known. First and third instar larvae are active predators which use their straight mandibulomaxillay stylets to pierce and liquefy the tissues of their prey, whereas second instars are inactive (Möller et al., 2006). The larvae for which biology is known 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; Möller et al., 2006; Wedmann et al., 2013; Komatsu, 2014). Adults are polyphagous, feeding on pollen, small arthropods and fungal hyphae (Monserrat, 2006), and, although they are assumed to be nocturnal, some observations point to some species possibly being diurnal (Aspöck and Randolf, 2014). In the most recent phylogenetic analyses, the group is recovered together with the Rhachiberothidae, the thorny lacewings, and the Mantispidae, or mantidflies, the three groups together grouped in the superfamily Mantispoidea, although the precise relationships between the three lineages remain contentious (Wang et al., 2017; Winterton et al., 2018). About 35 fossil adult berothid species, from the Middle Jurassic to the Late Eocene, are currently recognised; an updated list of the described fossil Berothidae was provided by Yang et al. (2019) (complemented by Shi et al., 2019 and Yang et al., 2020). The fossil larval diversity of the group, and that of other neuropterids, was summarised by Pérez-de la Fuente et al. (2020).

2. Material and methods

Specimens described herein are housed at the Institutional Collection from the El Soplao Cave, Celis, Cantabria, N Spain (specimen with CES number), and at the Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain (specimens with MCNA number).

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

General body terminology is after Tjeder (1959) and that of the genitalia is after Aspöck and Aspöck (2008). Nomenclature on wing venation follows the revision by Breitkreuz et al. (2017) using wing tracheation. As these authors showed, MA does not fuse to the last branch of RP (or “Rs”, “radial sector”) and, therefore, the so-called “basal piece/stem of MA” or “b vein”, which sometimes can be sinuous (sigmoid) in Neuroptera, should be treated as a crossvein, herein named rp-m. Most of the literature on Neuropterida was accessed using the online resource Lacewing Digital Library (Oswald, 2020). Descriptive notes on the mite use general terminology after Lindquist et al. (2009). All provided measurements are in millimetres if not otherwise stated.

Abbreviations: A, anal vein; Ant, antenna; Ch, chelicera (mite); Cl, clypeus; CuA, cubital anterior vein; CuP, cubital posterior vein; Cx, coxa; FC, Forewing costal vein; Fe, femur; Ga, galea; GcxIX, gonocoxite IX (RGcxIX, right gonocoxite IX; LGcxIX, left one); GcxX, complex of gonocoxites, gonapophyses and gonostyli X (formerly known as paramere-mediuncus complex); GcxXI, gonocoxite XI (formerly known as gonarcus); H, humeral vein; HC, hind wing costal vein; Hy, hypocauda; LI, LII, LIII, left fore-, mid- and hind leg, respectively; L1–L4, legs (mite); La, labrum; Lb, labium; Lc, lacinia; LPl, labial palp; M, medial vein; MA, medial anterior vein; Mn, mandible; MP, medial posterior vein; MPl, maxillary palp; Pa, palp (mite); Pe, pedicel; RI, RII, RIII, right fore-, mid- and hind leg, respectively; RA, radial anterior vein; RP, radial posterior vein; SVIII, sternite VIII; SIX, sternite IX; Sc, subcostal vein; Sp, scape; St, stipe (maxillary); Su, subgenitale; TVIII, tergite VIII; TIX+e, tergite IX + ectoproct; Ti, tibia; Ta, tarsus.

3. Geological setting

The specimens studied herein belong to two Spanish localities dated as Albian from the Basque-Cantabrian Basin (BCB), the El Soplao and the Peñacerrada I amber localities (Fig. 1) (Alonso et al., 2000; Najarro et al., 2009, 2010; Barrón et al., 2015). The BCB is related to the opening of the North Atlantic during the Oxfordian–Aptian rifting period (Fig. 1) (Salas et al., 2001; Martín-Chivelet et al., 2002; Mas et al., 2004).

The El Soplao amber outcrop is found near the village of Rábago, within the El Soplao Territory (Autonomous Community of Cantabria, northern Spain), on the western margin of the BCB (Fig. 1). The deposit is included in the Las Peñosas Fm, a unit of continental to transitional marine siliciclastic deposits (Najarro et al., 2009). Although the depositional environment shows a certain marine influence, amber is found in a unit of heterolithic sandstone-siltstone and carbonaceous mudstone related to broadly coastal delta-estuarine environments (Najarro et al., 2009, 2010). Dinoflagellate cysts, cryptogam spores, gymnosperm and angiosperm pollen (the latter very scarce), gymnosperm macroremains, fusainised wood, and marine or brackish water invertebrates such as gastropods, bivalves, and bryozoans have been found associated with the amber (Najarro et al., 2009, 2010).

The Peñacerrada I amber outcrop is located nearby Moraza village (Burgos Province, northeastern Spain) on the eastern margin of the BCB (Alonso et al., 2000) (Fig. 1). The amber bearing-deposit is included in the Escucha Fm. (Peñalver and Delclòs, 2010), which takes part of the lower unit of the informal stratigraphic Utrillas Group (Barrón et al., 2015). Amber is associated to coal levels, more abundant up in the stratigraphic series. Although amber is namely present at the top of filling sequences of interdistributary bays, it is also found in filling deposits of abandoned fluvial channels or crevasse splay with abundant plant remains developed in delta plain areas (Martínez-Torres et al., 2003). Cryptogam spores are common and diverse in some levels, including those of schizaceous ferns, but the dominant palynomorph is represented by conifer pollen grains, namely from Araucariaceae; angiosperm pollen is scarce and not diverse (Barrón et al., 2015).

4. Results

Systematic palaeontology

Order Neuroptera Linnaeus, 1758

Superfamily Mantispoidea Leach, 1815

Family Berothidae Handlirsch, 1906

Cantabroberotha gen. nov.

--- Zoobank ID to be inserted upon acceptance ---

Type species. *Cantabroberotha soplaensis* sp. nov.

Diagnosis. Head with vertex prominently raised in a single dome; scape about 3× as long as high; pedicel relatively elongate, about ¾× scape length; antennae with 27 flagellomeres; all flagellomeres elongate, about 2× longer than wide. Pro- and mesothorax each with at least two pairs of tubercles with long setae. Wings with all costal veinlets simple except apicalmost. Forewing with rounded apex and membrane without maculations; humeral vein recurrent, simple; one sc-r crossvein present slightly before origin of RP; two ra-rp crossveins present, separated by two RP branches; RP with seven posterior branches; gradate series of crossveins absent. Hind wing RP with five posterior branches, rp-m crossvein elongate and sigmoidal.

Etymology. The new genus-group name is a combination of Cantabria, the Spanish Autonomous Community where the El Soplao outcrop is located, and *Berotha*, type genus of the family. The name is feminine.

Remarks. *Cantabroberotha* gen. nov. mostly resembles *Magniberotha* Yuan, Ren, and Wang, 2016 from Burmese amber. Both are similar in size (larger than other amber berothids), forewing RP with six or seven posterior branches and two ra-rp crossveins, hind wing RP with five posterior branches, and one oblique ra-rp crossvein in a rather distal position. The very similar genitalic configuration of *C. soplaensis* gen. et sp. nov. and *M. recurrens* Yuan, Ren, and Wang, 2016 (both females) also reinforces a close relationship between these two taxa. However, the new species has elongate flagellomeres (vs. subspherical), forewing with recurrent humeral vein simple (not branched), forewing RP branching off after sc-r crossvein, and costal veinlets simple in fore- and hind wings (except the most distal one). Additionally, the paratype of *M. recurrens* does not appear to have such an elongate scape and pedicel (base of the antennae not preserved in the holotype) (Yuan et al., 2016).

The new species has a rp-m crossvein in the hind wing that is elongate and sinuous, a shape highly unusual for berothids. In fact, this vein morphology has not been previously described from any fossil berothid, and was otherwise documented only in some extant taxa, namely species within the genus *Lekrugeria* Navás, 1929 (Aspöck and Aspöck, 1985). Typically, when present in Berothidae, the rp-m crossvein is rather short and slightly oblique or straight. An elongate and curved/sinuous rp-m crossvein in the hind wing (sometimes clearly sigmoid and/or more distally placed, after the branching of RP and M) occurs in different families within Neuroptera, and it would appear to represent a plesiomorphy within the whole lineage (Aspöck and Nemeschkal, 1998). Within Mantispoidea, it occurs in extant symphrasine and some drepanicine Mantispidae (Lambkin, 1986; Willmann, 1990) as well as in all extant (Aspöck and Mansell, 1994; Aspöck and Aspöck, 1997) and some fossil Rhachiberothidae (Whalley, 1983; Nel et al., 2005). The character also occurs in other neuropteran families such as Sisyridae, Osmylidae, Dilaridae, Hemerobiidae, and Ithonidae (Carpenter, 1940; Tjeder, 1957; Aspöck et al., 1980). A similar condition to a sinuous rp-m crossvein, however, appears to occur in the recently described genus *Xiaoberotha* Shi, Zhang, Wang, and Liu, 2019, where the crossvein (treated as the base of MA by the authors) is equally oblique but incomplete (Shi et al., 2019).

Even though the mouthparts of the specimen are not complete, the possibility that these could have been elongate, forming an assemblable proboscis as in the Paradoxosisyrinae (this group possessing wing venation closely resembling that of Berothidae), is ruled out due to the size of the preserved labial palpomeres and the allegedly preserved basalmost maxillary palpomere. In all of the known paradoxosisyrines, maxillary and labial palpi are, at least, equally enlarged as the elements forming the proboscis, with the basalmost palpomeres at least 4–5 times longer than thick (Makarkin, 2016; Khramov et al., 2019). Other characters of the antennae, wing venation and genitalia allow to distinguish the known paradoxosisyrine diversity from that of berothids, although a detailed account on these exceeds the aim of the present contribution. A work describing the known paradoxosisyrine diversity from Spanish amber is currently in development.

Cantabroberotha soplaensis sp. nov.
Figs 2–3
Berothidae indet.: Najarro et al. (2010), p. 972, fig. 8.
--- Zoobank ID to be inserted upon acceptance ---

Etymology. The specific epithet is based on "El Soplao", the amber outcrop where the specimen was found.

Locality and horizon. El Soplao amber outcrop, near the village of Rábago, Cantabria, northern Spain (Fig. 1); Albian, Early Cretaceous.

Holotype. CES 004. The specimen is relatively well-preserved and almost complete, although most of the abdomen is badly preserved. A fracture removed the anterior part of the right compound eye, apparently most of the clypeus, the distal region of the mouthparts, and distal podites from all legs, specifically the tibiae and tarsi. Other missing parts include areas of the right fore- and hind wings, which are folded upon the partially-crushed abdomen.

Diagnosis. As for the genus (*vide supra*).

Description. Female. Total body length about 4.00. *Head*. Oval when viewed from above, 0.52 long, maximum width 0.51 (between outer compound eye margins). Compound eyes prominent, ovoid, relatively small, 0.26 long, about half as long as head; post-ocular lobes not expanded (Fig. 2E). Vertex prominently raised in a single dome, with sparse long setae, up to 0.23 long (Fig. 2D, E). Antennae moderately elongate, ca. 2.30 long, widely separated (space between scapes 0.16 mm), antennal insertion closer to compound eye margin than between them; scape elongate, flattened laterally, about 3× longer than high, 0.18 long, 0.03 wide, 0.06 high; pedicel relatively elongate, about ¾× scape length; flagellum with 27 flagellomeres; flagellomeres elongate, about 2× as long as wide; last flagellomere distinctly longer than preceding ones (about 1.5×), without a tubular distal projection. Mouthparts largely incomplete as preserved. Maxillary stipes prominent as preserved. Basal maxillary palpomere (distal end of stipes?) apparently fully preserved, cylindrical, 0.08 long, 0.03 thick. Basal portion of labial palpus preserved, 0.18 long, left labial palpomere likely with two to three preserved palpomeres, thinner than maxillary palpomeres. Other mouthparts barely discernible. *Thorax*. Prothorax elongate, 0.43 long, narrower than meso- and metathorax; pro- and mesothorax each with a pair of tubercles bearing long setae beneath head on prothorax and slightly before wing insertion on mesothorax. At least mesothorax with additional pair of rather joined, flat tubercles bearing long setae on mesonotum. Forelegs not raptorial. Procoxa inserted on posterior side of prothorax, elongate and thin, 0.64 long, with a dense field of short, bristle-like setae along its ventral half, up to 0.08 long. Profemur with short setae dorsally and longer setae ventrally. Protibia not preserved. Mesocoxa 0.52 long, with densely-packed, apically curved bristle-like setae. *Wings*. Oval; membrane hyaline, with no indication of maculation; trichosors present along entire wing margin, single between forks; setae along entire wing margin, slightly longer on posterior margins; outer and inner gradate series of crossveins absent. *Forewing*. Length

4.22, maximum estimated width ca. 1.8; apex rounded. Humeral vein recurrent, simple (not branched). Area between C and Sc moderately broad, broadest point along proximal third of wing, with 26 simple costal veinlets. Sc and RA meeting slightly before distal third of wing, at 2.73 from wing base, running apparently fused for a long stretch following wing margin. Area between C and Sc+RA with eight poorly defined costal veinlets, likely all simple except apicalmost one forked. Sc+RA ending at 0.55 from wing apex. Area between Sc and RA as wide as narrowest point of area between C and Sc, with one proximal sc-r crossvein located before forking of RP. RP originating relatively far from base of wing, at 1.08. RP with seven posterior branches. Two ra-rp crossveins slightly oblique, distal one shorter than proximal one, separated by two branches of RP. Crossvein between Sc+RA and RP absent. M forking into MA and MP beyond origin of RP (at 1.30 from wing base). Crossvein rp-m absent, instead proximal crossvein rp-ma likely present, located slightly distad forking of M. Cu forking into CuA and CuP basally (0.60 from wing base). Crossvein cua-cup in rather proximal position, almost at level of RP base. A1 pectinate, with five distal branches; A2 very distally forked; A3 simple, convex distally (Fig. 2B). *Hind wing*. Length 3.63 as preserved; maximum width about 1.50; apex not preserved. Humeral vein not conspicuous, likely indistinguishable from a costal veinlet. Area between C and Sc narrow, with 17 preserved simple costal veinlets. Sc and RA meeting at distal third of wing, at 2.40 from wing base, running apparently fused for a long stretch following wing margin. Area between C and Sc+RA with nine costal veinlets, all simple except apicalmost one forked. Sc+RA virtually ending close to wing apex. Area between Sc and RA as wide as narrowest point of area between C and Sc, without visible crossveins. RP originating at 0.88 from wing base. RP with five posterior branches. Only one ra-rp crossvein present, oblique, between last two posterior branches. Crossveins between Sc+RA and RP absent. M running closely parallel to R for a stretch before rp-m crossvein. M forking into MA and MP at origin of RP. Crossvein rp-m present, elongate and sigmoidal (Fig. 2C). CuA elongate, parallel to wing margin, pectinate, with at least eight simple posterior branches. CuP and anal veins not visible. *Abdomen.* Genitalia with moderately long setae. Subgenitale bearing two triangular processes arranged transversally. Gonocoxites IX bearing moderately sized, relatively sturdy hypocaudae that are cephalically directed at a ca. 45° angle, about 0.15 long (Fig. 2F). Further details not assessable due to insufficient preservation.

Berothidae indeterminate 1

Figs 4–5

Material. MCNA 10033, from Peñacerrada I amber. Partially preserved specimen. The body is almost complete and in good condition but only the basalmost part of wings is preserved, with the exception of the costal area plus the distal branching of RP from the right forewing.

Descriptive notes. Female. Total body length about 2.5. *Head*. Head oval when viewed from above, about as wide as long; 0.35 long (vertex to tip of clypeus), 0.20 maximum width between compound eyes, 0.13 minimum width between compound eyes. Compound eyes prominent, ovoid, large, 0.21 long, 0.6× as long as head; post-ocular lobes not expanded. Vertex moderately raised in a single dome, with sparse long setae. Antenna relatively short, 0.99 long; widely separated (antennal foramen 0.06 apart); antennal insertions closer to compound eye margin than to each other. Scape rather short, length about 3× width; pedicel short, about three quarters as long as scape; flagellum with 21 flagellomeres, each flagellomere subquadrate, slightly longer than wide; last flagellomere distinctly longer than preceding flagellomeres (about 1.5×), with a tubular distal projection. Clypeus 0.07 long, 0.17 wide at base. Labrum rounded, 0.04 long, 0.08 wide at base. Mouthparts short. Right mandible visible, distal region concealed by labrum. Maxillary palpus pentamerous, 0.17 long, last maxillary palpomere brush-shaped, with a distal finger-like projection. Galea 0.08 long, 0.03 wide, with inner microsetae, basigalea visible. Lacinia 0.05 long, 0.02 wide, with three inner visible bristles. Labial palpus 0.12 long; last labial palpomere brush-shaped, with a tubular distal projection. *Thorax*. Prothorax rather short, 0.11 long, tubercles not visible. Forelegs not raptorial. Procoxa elongate and thin, 0.30 long, 0.06 thick; protrochanter 0.12 long; profemur 0.30 long, with short setae dorsally and long setae ventrally; protibia 0.35 long. Meso- and metatibiae with particularly elongate setae, up to 0.22 long. Probasitarsus 0.09 long, apicalmost protarsomere 0.07 long, as long as protarsomere II. Tarsomeres I–IV without distoventral, paired, strong spine-like setae. All pretarsal claws simple, at least those from meso- and metathoracic legs without arolium. *Forewing*. Membrane hyaline, with no indication of maculation; trichosors present along entire costal margin, single between forks; setae along entire costal margin. Length 3.15 as preserved, width not measurable; apex not preserved. Humeral vein present, recurrent, not pectinate but likely simply branched. Area between C and Sc rather narrow (broadest point along proximal quarter of wing), with 23 visible simple costal veinlets. Sc and R likely not meeting distally, instead with a transverse vein between them at 2.38 from wing base (Fig. 4C). Area between C and RA with two costal veinlets, poorly defined, basal costal veinlet triple branched (with distalmost branch forked), and distal costal veinlet forked. Area between Sc and RA wider than narrowest point of area between C and Sc, without visible crossveins. RP origin not preserved. RP with three visible posterior branches. Two ra-rp crossveins, slightly oblique, subequal in length, separated by one branch of RP. Crossvein between RA and RP absent. M forking and radiomedial crossveins not visible. CuA and CuP forking basally (0.43 mm from wing base). A1 not visible distally. A2 pectinate, with two posterior branches. A3 simple. *Abdomen.* Length about 1.15 long. Segment VIII reduced, with tergite VIII about half the height of previous tergites, 0.05 long, 0.06 high. Sternite VIII elements not discernible, probably reduced. Tergite IX + ectoproct transverse when seen laterally, anteriorly (tergite IX part) as high as tergite VIII, then increasing in height, 0.14 long, 0.10 high posteriorly. Gonocoxites IX elongate, fully vertical, directed ventrally, slightly divergent, shaped like rabbit ears, i.e., similar to a cylinder cut by an oblique longitudinal plane and thus with an elliptical cross section, with ventral (ental) side concave, expanding in width subdistally, and with distal end rounded (see Fig. 5B).

Comments. The preserved parts, although apparently distinctive from the other known extinct berothids, are not deemed complete enough as to erect a new taxon. The most distinctive character of the preserved forewing fragment is the lack of contact and apparent fusion between Sc and RA. Although this character appears to be quite distinctive (Fig. 4C), it is likely enhanced by preservation, although not fully attributed to it. Although we herein consider that Sc and RA do not meet and run independently towards the wing margin, the option that these two veins indeed meet in a rather cross-vein like appearance should not be ruled out. In any case, the lack of “fusion” between Sc and RA, yet uncommon within Berothidae, can be found in some extant genera such as *Berlekrumyia* Aspöck and Aspöck, 1988, *Cyrenoberotha* MacLeod and Adams, 1967, *Lekrugeria*, or *Nosybus* Navás, 1910 (MacLeod and Adams, 1967; Aspöck and Aspöck, 1982, 1985, 1988), and also the extinct species *Microberotha macculloughi* Archibald and Makarkin, 2004 from Eocene Canadian amber (Archibald and Makarkin, 2004), although it is also present in the hind wing of *Protoberotha minuta* Huang, Ren, and Wang, 2019 from Burmese amber (Huang et al., 2019). The genitalia of MCNA 10033, with the tergite IX + ectoproct transverse and the gonocoxites IX elongate, vertical, directed ventrally, bears a certain resemblance to that of the extinct species *Ansoberotha jiewenae* Yang, Shi, and Ren, 2019 (see Yang et al., 2019), and it is reminiscent of the condition otherwise occurring in the extant genus *Nosybus* (Aspöck and Aspöck, 1982; Huang et al., 2019).

Berothidae indeterminate 2

Figs 6–7

Material. MCNA 9902, from Peñacerrada I amber. A virtually complete specimen, but highly obscured due to abundant debris (particularly the head), folded body parts, and amber fractures. The anterior margin of the left compound eye is crushed. Syninclusions include a phorid fly and a psocopteran.

Descriptive notes. Male. Total body length about 2.5 (from vertex to end of abdomen). *Head*. Head oval when viewed from above, slightly transverse, ca. 0.52 long (from vertex to tip of clypeus), maximum width of ca. 0.60 (maximum between compound eyes). Compound eyes prominent, ovoid, about 0.22 long, 0.4× as long as head; post-ocular lobes apparently not expanded. Vertex slightly raised in apparently a single dome, with sparse long setae. Antenna 1.55 long; insertion not visible. Scape elongate, expanding distally, 0.13 long, 0.04 high proximally, 0.06 high distally, about 3.5× longer than high proximally, bearing a 0.05 long projection dorsodistally oriented forwards and two whorls of setae. Pedicel slightly larger than flagellomeres, 0.06 long. Flagellum with 25 elongate flagellomeres, each flagellomere dorso-ventrally flattened (as preserved), about 0.05 long, 2× longer than high; last flagellomere distinctly longer than preceding flagellomeres (more than 1.5×), with a tubular distal projection. Mouthparts short; mandibles not visible; galea 0.08 long; labial palpus 0.12 long; maxillary palpus with four visible palpomeres, >0.18 long. Further details not discernible. *Thorax*. Prothorax rather short, ca. 0.30 long, apparently narrower than meso- and metathorax; no tubercles visible. Foreleg not raptorial. Procoxa elongate and thin; profemur with elongate setae ventrally, up to 0.20 long. At least meso- and metatarsomeres I–IV with distoventral, paired, strong spine-like setae, ca. 0.03 long (Fig. 6B). All pretarsal claws simple; at least metathoracic legs with arolium between pretarsal claws (Fig. 6B). *Wings*. Oval; membrane mostly hyaline, with no indication of maculation; trichosors present along entire wing margin, single between forks; setae slightly longer on posterior margins. *Forewing*. Length ca. 3.20 as preserved, maximum width not measurable; apex not preserved. Humeral vein not visible. Area between C and Sc moderately broad as preserved (broadest point not visible), with 11 preserved costal veinlets, all simple. Sc and RA meeting at about distal third of wing (at 2.09 from wing base), running apparently fused for a long stretch following wing margin. Area between C and Sc+RA with eight costal veinlets poorly defined, all simple. Area between Sc and RA about as wide as narrowest point of area between C and Sc, with one sc-r crossvein located beyond virtual origin of RP, latter not visible. RP with four posterior branches. Three ra-rp crossveins in total: two slightly oblique, distal one shorter than proximal one, separated by one branch of RP, and an additional ra-rp crossvein present proximally, right below sc-ra crossvein.

Crossvein between Sc+RA and RP absent. M forking not visible. Radiomedial crossveins not visible. Cubital veins barely visible. Anal veins not visible. *Hind wing*. Length ca. 2.8; maximum width ca. 1.20; apex rounded. Humeral vein not visible. Area between C and Sc narrow, costal veinlets not visible. Sc and RA meeting at about distal third of wing (at about 1.80 from wing base), running apparently fused for a long stretch following wing margin. Area between C and Sc+RA with eight visible simple costal veinlets. Sc+RA ending at 0.20 from wing apex. Area between Sc and RA without visible crossvein distally. RP originating at about 0.7 from wing base. RP with three posterior branches. One ra-rp crossvein present, oblique. Crossvein between Sc+RA and RP absent. M forked slightly beyond branching of R. Radiomedial crossveins not visible. CuA long, pectinate, subparallel to wing margin, with at least three posterior branches forked. CuP and anal veins barely visible. *Abdomen.* Tergite IX and ectoproct fusion not visible, if present. Sternite IX with produced ventroposterior margin when seen laterally, probably scoop-shaped. Gonocoxites IX large, flap-shaped, laterally flattened, with ventral side evenly rounded. Complex of fused gonocoxites, gonapophyses and gonostyli X (=paramere-mediuncus complex) unpaired, with free portion significantly elongate, bent dorsally, reaching up to about midheight of tergite IX + ectoproct, slightly recurved distally towards cephalic direction. Elements of gonocoxites XI (=gonarcus) detected (see Fig. 7E), likely paired and obliterated/incorporated into gonocoxites IX.

Comments. Although some features of the present fossil specimen, such as the characteristic shape of the genitalia, are highly distinctive, the obscured head and incomplete wing venation preclude formally naming the present material for the sake of prudence. The visible characters of the present berothid bear a certain resemblance with the preserved parts of berothid indeterminate 3, MCNA 13379.1, being altogether similar to species from Burmese and New Jersey ambers classified in the genus *Jersiberotha* Grimaldi, 2000 (see Remarks of this specimen below).

Most distinctively, the genitalia of MCNA 9902 possesses a complex of fused gonocoxites, gonapophyses and gonostyli X with an elongate free portion that is bent dorsally and slightly recurved distally (Fig. 6E, 7E). A similar condition within Berothidae is found in *Cyrenoberotha* (MacLeod and Adams, 1967), but had not been described up to now from a fossil beaded lacewing. The complex of fused gonocoxites, gonapophyses and gonostyli X bearing highly recurved distal portions (typically hypercoiled) are more commonly known among the Rhachiberothidae and the Mantispidae, such as in *Mucroberotha* Tjeder, 1959 and *Plega* Navás, 1928 (Aspöck and Mansell, 1994; Ardila-Camacho et al., 2019), and this condition was considered plesiomorphic within Berothidae (Aspöck, 1986). Aside from that, the overall external genitalic configuration of this specimen, particularly the gonocoxites IX, bear resemblance with those of some species classified within the genera *Podallea* Navás, 1936 or *Trichoma* Tillyard, 1916 (Aspöck and Aspöck, 1984; Aspöck and Aspöck, 1996).

Berothidae indeterminate 3

Figs 8–9

Material. MCNA 13379.1, from Peñacerrada I amber. Partially preserved specimen. Part of the thorax, the abdomen, and one set of wings (right fore- and hind wings) are preserved, but basal portions of the latter are not visible. No last tarsomeres or pretarsi, including the claws, are preserved. The distal four flagellomeres of one antenna are preserved. An undetermined, badly preserved mesostigmatan mite, MCNA 13379.2 (Fig. 8B) (see Discussion), is grasping the setae from the costal vein of the preserved hind wing. Other syninclusions: a cephalothoracic portion including three partial, greatly elongate legs from a relatively large arthropod, likely a spider (MCNA 13379.3).

Descriptive notes. Female. *Head.* Four distalmost flagellomeres of one antenna preserved, ovoid to subspherical. Terminal flagellomere elongate, with a tubular distal projection. *Thorax.* Forelegs not raptorial. Profemur and protibia with particularly elongate setae, up to ca. 0.25 long. Mesotibia with a few elongate, curved spine-like setae distoventrally, 0.18 long. Tarsomeres I–IV without distoventral, paired, strong spine-like setae. *Wings*. Oval; membrane hyaline, with no indication of maculation; trichosors present along entire wing margin, single between forks; setae slightly longer on posterior margins. *Forewing*. Estimated length 2.70, maximum width as preserved 1.10; apex rounded. Humeral vein not visible. Area between C and Sc relatively narrow (broadest point before proximal quarter of wing, 0.14 wide, 0.10 at narrowest point), with 24 simple costal veinlets preserved. Sc and RA meeting at about distal third of wing (at ca. 1.86 from wing base, as estimated), running apparently fused for a long stretch following wing margin. Area between C and Sc+RA with six costal veinlets poorly defined, shape as follows (towards wing apex): two simple, two forked, and two simple. Sc+RA ending 0.18 from wing apex. Area between Sc and RA slightly wider than narrowest point of area between C and Sc, without visible crossveins. RP origin not visible. RP most likely with three posterior branches. Crossveins between Sc+RA and RP absent. *Hind wing*. Length 2.31; maximum width 0.94; apex rounded. Humeral vein not visible. Area between C and Sc narrow, 0.03 minimum width, with 12 preserved simple costal veinlets (those from basal third of wing not preserved). Sc and RA meeting at about distal third of wing (at 1.51 from wing base), running apparently fused for a long stretch following wing margin. Area between C and Sc+RA with five costal veinlets, shape as follows (towards wing apex): two simple, two forked, and one simple. Sc+RA ending 0.18 from wing apex. Area between Sc and RA wider than narrowest point of area between C and Sc, without visible crossveins. RP origin ca. 0.45 from wing base. RP with three posterior branches. One oblique ra-rp crossvein present beyond distalmost RP branch. Crossvein between Sc+RA and RP absent. MP forked slightly beyond origin of RP. Radiomedial crossveins not visible. *Abdomen.* Length 1.65, poorly preserved. Abdominal segments VIII and IX narrower than remainder of abdominal segments, with tergite VIII particularly narrow. No genitalic sclerites or processes visible.

Comments. The preserved hind wing fragment bears a great resemblance to some species classified within the genus *Jersiberotha*, i.e., *J. luzzi* Grimaldi, 2000 from New Jersey amber (Turonian) and *J. tauberorum* Engel and Grimaldi, 2008, from Burmese amber (earliest Cenomanian), with some forked costal veinlets in the area between C and Sc+R, three branches of RP and an oblique ra-rp crossvein subdistally. Some minor differences exist between the forewings of these two species of *Jersiberotha* and the preserved portion of MCNA 13379.1: there are no forked costal veinlets in the costal region unlike in the holotype of *J. luzzi*, and the alleged last branch of RP is forked twice unlike in the holotype of *J. tauberorum*. Although there are other taxa showing an oblique ra-rp crossvein subdistally in the hind wing, the RP bears a different number of branches in these, i.e., two in *Iceloberotha simulatrix* Engel and Grimaldi, 2008 and *Haploberotha* Engel and Grimaldi, 2008 (in *H. persephone* Engel and Grimaldi, 2008 and *H. carsteni* Makarkin, 2018) (Engel and Grimaldi, 2008; Makarkin, 2018), and five in *C. soplaensis* (*vide supra*). The genitalia appears to be similar to that of female *Haploberotha* (Yuan et al., 2016), with both segments VIII and IX reduced in diameter, but lacking visible ventrally-directed processes such as hypocaudae or pseudohypocaudae.

Berothidae indeterminate 4

Figs 10–11

Material. MCNA 12590, from Peñacerrada I amber; impressions of two sets of wings (namely the hind wings) upon a rounded, even surface from a flow-like, opaque amber piece, plus likely darkened cuticular remains inside the amber (visible in section) associated to the wings preserved as an inclusion. Hind wing venation almost fully virtually preserved, except the most proximal region. Setation is not apparent.

Descriptive notes. Sex unknown. *Forewing.* Area between C and Sc moderately broad, with several costal veinlets visible, all simple but one forked rather proximally. Other characters not visible. *Hind wing*. Length 2.73 as preserved; maximum width ca. 1.50; apex rounded. Humeral vein not visible. Area between C and Sc narrow, costal veinlets not discernible. Sc and RA meeting much before distal third of wing (distance from wing base not measurable), running apparently fused for a long stretch following wing margin. Area between C and Sc+R with abundant costal veinlets, 12 simple veinlets visible, around 20 estimated. Sc+RA ending 0.30 from wing apex. Area between Sc and RA wider than narrowest point of area between C and Sc. Distance of RP origin from wing base not measurable. RP with four posterior branches. Only one ra-rp crossvein present, oblique. Crossvein between Sc+RA and RP likely absent. Radiomedial crossveins not visible. M forked slightly beyond the origin of RP. CuA elongate, parallel to wing margin, pectinate. Crossvein cua-cup at level of M forking. CuP and anal veins not visible.

Remarks. The specimen is considered a berothid despite that it could also represent a rhachiberothid based on the preserved remains, as the wings of the Cretaceous fauna of these two closely related groups can be virtually indistinguishable (e.g., see Nel et al., 2005). As thorny lacewings have not been found up to now in Spanish amber, it would appear more parsimonious to attribute the present fossil, at least for the time being, to Berothidae. Within the latter, MCNA 12590's preserved hind wing venation is most reminiscent of that of *Maculaberotha nervosa* Yuan, Ren, and Wang, 2016 due to their similar size and four posterior branches of RP (Yuan et al., 2016), although it differs from the latter in some proportions such as Sc and RA meeting relatively further away from the wing tip (therefore with a longer Sc+RA).

5. Discussion

The specimen MCNA 12590 possesses taphonomic significance, as it is one of the few reported instances in which an amber fossil, rather than as a full inclusion, is also and most conspicuously preserved as an impression. Amber impressions are unfortunately not often reported as they can be difficult to detect and interpret. Nonetheless, they can sometimes represent important sources of information, such as impressions of ferns from Eocene Baltic amber (Sadowski et al., 2019), an alleged dipterocarp leaf in Upper Miocene Borneo amber (Kocsis et al., 2020), or even partial vertebrate dentary material (Kosmowska-Ceranowicz and Kulicka, 1995; McKellar et al., 2019). The lacewing impression is composed of the two sets of wings on a concave surface from a brownish to greyish, opaque amber piece representing the subterminal portion of a resin flow (Fig. 10). Whereas the hind wings are almost fully imprinted, only the areas surrounding the costa and the tip of the forewings are evident. Fore- and hind wing venation overlap distally in the right set of wings, which suggests that one of the wings slightly penetrated into the resin, upon which the other wing left its imprint. Moreover, some darkened remains in immediately close association with the impressed wings, probably cuticular in nature, appear to be present beneath the wing impressions, visible in the transverse, fractured section of the flow-like amber piece (Fig. 10). The flat arrangement between the two sets of wings and their preservation on a single plane along the concave surface of the amber piece allows to ascertain that the impression resulted from the contact of the insect wings with a sticky surface of resin. The lacewing was not fully included into the resin when making first contact, most likely because the latter had a relatively low fluidity. The insect partially penetrated into the resin either by its ventral or its dorsal side, i.e., with its legs fully in or out of the resin. Regardless, the lacewing likely remained stuck to the resin surface until its exposed parts decayed and/or were consumed, but the impressions of its wings eventually remained on the resin surface. The resulting fossil most likely represents a highly altered, partial inclusion in which the wings are preserved as an impression. The preservation of this delicate imprint on an amber piece surface allows us to infer that a very low grade transport of, at least, some of the resin pieces must have taken place during the biostratinomic phase of the genesis of the Peñacerrada I amber deposit, i.e., from the resin's primary gathering location on the forest floor to their allegedly definitive burial site downstream after being transported by water currents such as runoff or floods (Martínez-Delclòs et al., 2004). Therefore, we conclude that at least some of the resin that originated the Peñacerrada I amber deposit accumulated in para-autochthonous conditions. This circumstance had been previously inferred for the El Soplao outcrop based on much more conclusive evidence, that is the abundant preservation of similarly delicate amber pieces and macroscopic plant remains in anatomical connection, which would not have endured a prolonged transport either, and the existence of levels of roots *in situ* (Najarro et al., 2009, 2010; Pérez-de la Fuente, 2012). Other interpretations that could explain how the wing impressions were formed are deemed as less plausible. Namely, the resin surface trapping the insect wings could have been covered by a second resin flow and, after fossilisation and during the excavation of the resulting flow-like amber piece, the amber could have split along the desiccation surface between the two flows, exposing the apparent impression. However, in that case, we would expect the relatively freshly-split surface to be more irregular in shape, smoother in texture and have a different aspect than that from the flat side of the amber piece (see Fig. 10A), the latter probably resulting from resin in contact with the tree bark. But the concave side of the amber piece is uniformly rounded and both surfaces of the piece (the concave and the flat) have the same rough texture, indicating that these two preserved surfaces of the resin flow/amber piece most likely remained exposed during all the taphonomic phases.

The likely immature mite MCNA 13379.2, preserved grasping the setae from the hind wing costa of berothid indeterminate 3 (MCNA 13379.1), possesses characters suggesting that it represents a mesostigmatan. These traits are gnathosoma with chelicerae slightly longer than palpi; idiosoma oval in outline, truncate posteriorly; all legs relatively short and inserted on anterior half of idiosoma, with L4 oriented backwards and remaining pairs forwards; legs L2 and L4 particularly sturdy, L1 clearly thinner; and anal aperture relatively small, composed of two valves situated on an small anal plate (likely corresponding to the whole anal shield rather than its innermost plate preserved differentially) in subterminal position and which is shaped like an inverted isosceles subtrapezoid with anterior margin rounded (Fig. 8B). An exact systematic assessment is not possible due to the lack of diagnostic characters owing to poor preservation and visibility, but possible mesostigmatan families to which the mite could belong to are Macrochelidae, Parasitidae, Ascidae, or Laelapidae (Lindquist et al., 2009). These groups possess forms that are often associated with other arthropods, namely as phoretic or parasitic instars (Lindquist et al., 2009). Both behaviours could explain the presence of the mite on the berothid, rather than a fortuitous accidental coming together, although both its attachment mode and site is more consistent with phoresy. Phoretic mites are often known to target areas that are more challenging to reach by the host’s grooming. Some phoretic mites are known to attach to exposed insect wings, including their bases (Eickwort, 1994). Instances of phoretic organisms attached to wing costal margins in the fossil record have been reported in springtails on a mayfly and a termite preserved in Dominican amber (Penney et al., 2012; Robin et al., 2019), while cases of phoresy involving attachment elsewhere on the body are relatively common. In any case, it is important to note that the fossilization position of the mite MCNA 13379.2 probably resulted to a lesser or greater degree from the drag and post-entombment agony while the resin was still fresh, as the setae from the costal vein would appear to provide a weak attachment per se to a phoretic organism. On the other hand, records of phoresy involving Neuroptera are rare. A phoretic behaviour was inferred for heterostigmatic mites reported adjacent to a mantidfly from Burmese amber (Khaustov and Poinar Jr, 2011; Poinar Jr and Buckley, 2011). Although extant Neuroptera have been scarcely reported as carriers, extant records exist for phoretic pseudoscorpions (Aguiar and Bührnheim, 1998).

6. Conclusions

Based on the findings presented in this work, the diversity of beaded lacewings recovered from Spanish amber, yet modest, appears to be promising, and has the potential to become as substantial as that already unearthed from the highly excavated, slightly younger Cretaceous amber deposits from Myanmar. Although the resolved structures of some of the unnamed specimens described herein, including the genitalia, would be enough to distinguish them from the rest of currently known fossil berothid diversity, we refrain from establishing new taxa for these specimens following good practice and hoping that more complete and better preserved conspecific material is recovered in the future.

The preservation of delicate wing impressions on an opaque amber piece from the Peñacerrada I outcrop allows to infer a low grade pre-burial transport for, at least, part of the resin that formed this Spanish amber deposit, matching interpretations obtained from other Basque-Cantabrian Basin deposits such as the El Soplao outcrop. Lastly, an occurrence of a mesostigmatan mite preserved grasping the wing setae of a berothid specimen possibly represents an instance of phoresy or, less likely, parasitism.

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FIGURE CAPTIONS

Fig. 1. Map of the Iberian Peninsula during the late Aptian–early Albian (Early Cretaceous) showing the location and geological context of the El Soplao and Peñacerrada I amber localities (black dots). Modified from Mas et al. (2004).

Fig. 2. Photomicrographs of *Cantabroberotha soplaensis* gen. et sp. nov. (Neuroptera: Berothidae), CES 004, from El Soplao amber. **A**, ventrolateral habitus. **B**, anal region of left forewing, with anal veins tagged. **C**, left crossvein rp-m from hind wing (arrows). **D**, head in frontal oblique view, distally missing due to a general fracture (mouthparts only preserved proximally). **E**, head in lateral view. **F**, female genitalia in lateral view. Scale bars: A, 0.5 mm; B, C, D, E, 0.2 mm; F, 0.1 mm.

Fig. 3. Camera lucida drawings of *Cantabroberotha soplaensis* gen. et sp. nov. (Neuroptera: Berothidae), CES 004, from El Soplao amber. **A**, ventrolateral habitus. **B**, head and antennae. **C**, female genitalia in lateral view. **D**, left forewing. **E**, left hind wing. Scale bars: A, D, E, 1 mm (D and E share the scale); B, 0.5 mm; C, 0.2 mm.

Fig. 4. Photomicrographs of Berothidae indeterminate 1, MCNA 10033, from Peñacerrada I amber. **A**, frontolateral habitus. **B**, detail of head in frontolateral view. **C**, detail of subcostal-radial anterior crossvein (sc-ra) in forewing. **D**, base of left forewing and hind wing. **E**, female genitalia in right lateral view. **F**, genitalia in left lateral view. Scale bars: A, 0.5 mm; B, D, 0.2 mm; C, E, F, 0.1 mm.

Fig. 5. Camera lucida drawings of Berothidae indeterminate 1, MCNA 10033, from Peñacerrada I amber. **A**, left antenna and head in frontolateral view. **B**, female genitalia in lateral view (left), and idealised (not observable) caudal view (right). **C**, preserved right forewing portion. Costal space wider than depicted due to the angle of drawing. Setae have not been depicted. Scale bars: A, B, 0.2 mm; C, 0.5 mm.

Fig. 6. Photomicrographs of Berothidae indeterminate 2, MCNA 9902, from Peñacerrada I amber. **A**, lateral habitus. **B**, detail of base of left antenna, with arrow pointing to scape. **C**, detail of metatarsus in ventrolateral view; arrow points out to the arolium. **D**, head in ventrolateral view, note the anteriorly crushed left eye (arrow). **E**, male genitalia in lateral view. Scale bars: A, 0.5 mm; B, 0.1 mm; C, 50 µm; D, E, 0.2 mm.

Fig. 7. Camera lucida drawings of Berothidae indeterminate 2, MCNA 9902, from Peñacerrada I amber. Wings are depicted with their biostratinomic foldings, marked with asterisks (*). **A**, head and base of left antenna in lateral view. **B**, visible portion of right forewing. **C**, visible portion of left hind wing. **D**, visible portion (posterior half) of right hind wing. **E**, male genitalia in lateral view. Scale bars: A–D, 0.5 mm (B, C and D share the scale); E, 0.2 mm.

Fig. 8. Photomicrographs of Berothidae indeterminate 3, MCNA 13379.1, and associated mesostigmatan mite from Peñacerrada I amber. **A**, lateral habitus; mesostigmatan mite grasping at setae from the costal vein of the hind wing (above) and genitalia (below) are framed. **B**, detail of mesostigmantan mite, MCNA 13379.2. in dorsal view; inset magnifies the anal region, which is visible by transparency of the dorsal cuticle of the idiosoma. **C**, detail of abdominal segments VIII and IX in lateral view (ventral is at the top of the image). **D**, detail of preserved legs portions in frontal view. Scale bars: A, D, 0.5 mm; B, 50 µm; C, 0.2 mm.

Fig. 9. Camera lucida drawings of Berothidae indeterminate 3, MCNA 13379.1, from Peñacerrada I amber. **A**, visible portion of left/right forewing. **B**, visible portion of left/right hind wing. **C**, preserved terminal portion of antenna. Scale bars: A, B, 0.5 mm (both at the same scale); C, 0.1 mm.

Fig. 10. Photographs of Berothidae indeterminate 4, MCNA 12590, a partial inclusion, with wings preserved as an impression, from Peñacerrada I amber. **A**, frontal (left) and lateral (right) views of the opaque, flow-shaped amber fragment preserving the lacewing as a visible imprint (arrows). **B**, complete view of the impression, mostly representing the hind wings and only parts of the forewings. Scale bars: A, 5 mm; B, 1 mm.

Fig. 11. Camera lucida drawings of Berothidae indeterminate 4, MCNA 12590, from Peñacerrada I amber. Relative thickness of veins not depicted due to the difficulty to assess this trait from the fossil. **A**, left hind wing. **B**, right hind wing. Scale bars: A, B, 1 mm (both to the same scale).