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A New Mantispid-Like Species of Rhachiberothinae (Neuroptera: Berothidae) from Baltic Amber, with a Critical Review of the Fossil Record of the Subfamily

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Abstract: *Whalfera wiszniewskii* sp. nov . is described from the Late Eocene Baltic amber. The genus *Whalfera* is considered as the only fossil genus confidently assigned to the Rhachiberothinae. Others previously placed in this subfamily belong to Paraberothinae (except perhaps for *Oisea*). The Late Eocene/present Rhachiberothinae and the Cretaceous Paraberothinae are considered to be the subfamilies of Berothidae.

Key words: Neuroptera, Berothidae, Rhachiberothinae, Paraberothinae, Mantispidae, Symphrasinae

1 Introduction

The Rhachiberothinae today constitutes a small taxon comprising three genera and 13 species restricted to Africa (Aspöck and Mansell, 1994; Aspöck and Aspöck, 1997). Its taxonomic status remains uncertain, and has been recently discussed as a subfamily of Berothidae (Tjeder, 1959; MacLeod and Adams, 1968; Grimaldi, 2000; Archibald and Makarkin, 2004; Monserrat, 2006), a separate family (Aspöck and Mansell, 1994; Aspöck and Aspöck, 1997; Engel, 2004; Grimaldi and Engel, 2005; Nel et al., 2005b; Wedmann and Makarkin, 2007; Engel and Grimaldi, 2008; McKellar and Engel, 2009), and even as a subfamily of Mantispidae (Willmann, 1990, 1994). This uncertainty stems from their appearance, which superficially resembles mantispids, specifically Symphrasinae in a similar specialized structure of the raptorial foreleg, and is distinguished from those genera confidently assigned to the Berothidae. In this paper, we provide reasons to consider this taxon as a subfamily of Berothidae, and describe a new fossil species of *Whalfera* Engel based on a beautifully-preserved male specimen from Baltic amber. We consider *Whalfera* to be the only known fossil genus confidently belonging to the Rhachiberothinae, and herein, exclude the previous Cretaceous “Rhachiberothinae” genera from this subfamily (Schlüter, 1978; Whalley, 1980; Grimaldi, 2000; Engel, 2004; Nel et al., 2005b; Engel and Grimaldi, 2008; McKellar and Engel, 2009).

2 Materials and Methods

The specimen described in this paper is preserved in a small, thin, clear piece of amber (11×14×4 mm). The right side of the neuropteran is obscured by a milky covering. This piece also includes air bubbles, wood debris, and stellate hairs of oak. It was prepared by Janusz Kupryjanowicz in Bialystok, Poland.

All measurements were made using an ocular graticule. Drawings were done with a camera lucida attached to a Zeiss Stemi SV 11 stereomicroscope, and photographs were taken with a Camedia attached to an Olympus S2X9 stereomicroscope.

Wing venation terminology follows that of Wedmann and Makarkin (2007). Principal cross-veins in the basal part of wing are designated after the longitudinal veins to which they connect, and are numbered in sequence from the wing base, for example, 1sc-r1, 2sc-r1, 3sc-r1, basal, intermediate, and distal subcostal cross-veins; 1r-m, basal cross-vein between radius (R) (or radial sector (Rs)) and media (M) (or anterior branch of media (MA)).

Venation abbreviations used are as follow: anal veins (1A–3A); cubitus (Cu); anterior cubitus (CuA); posterior cubitus (CuP); posterior branch of media (MP); first branch of radius (R1); and subcosta (Sc).

3 Systematic Paleontology

Order Neuroptera Linnaeus, 1758
Family Berothidae Handlirsch, 1906
Subfamily Rhachiberothinae Tjeder, 1959

Diagnosis: Berothids of medium size (forewing 6.2–8.8 mm long); foreleg raptorial (character 1); tarsus of male 4 segmented with basitarsus apically pointed (character 2). In forewing, M and R not fused basally (or fused proximal to basal cross-vein 1m-cu) (character 3); intermediate subcostal cross-vein (2sc-r1) present (character 4); Sc and R1 widely separated distally (character 5); 2A and 3A having a tendency to fuse distally, forming closed cell (character 6). In hindwing, basal cross-vein r-m long and sinuate (character 7); at least proximal part of CuP present (character 8).

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Included genera: *Whalfera* Engel 2004 from the Late Eocene of English and Baltic ambers; *Rhachiberotha* Tjeder 1959; *Mucroberotha* Tjeder 1959; and *Hoelzeliella* Aspöck et Aspöck 1997; all three are extant, distributed in South and East Africa.

The genus *Hoelzeliella* is only tentatively assigned to this subfamily, as they are known only from females, and its rhachiberothine affinity is indicated mainly by plesiomorphic character states of the venation, for example, the characters 4, 7, and 8. Although their forelegs are raptorial, their structure is strongly different from that of *Rhachiberotha*, *Mucroberotha*, and *Whalfera*. *Hoelzeliella* resembles some other berothine subfamilies by the presence of a well-developed epicranial suture (though this is also plesiomorphic), absent in other rhachiberothine genera. Therefore, it is quite possible that this genus might not belong to Rhachiberothinae.

Comments on characters:

Character 1. Raptorial forelegs of Rhachiberothinae were considered homoplastic, with regards to Mantispidae by Aspöck and Mansell (1994), but later as a synapomorphy of them (Aspöck and Nemeschkal, 1998). Besides the Berothidae and Mantispidae, raptorial forelegs occur in single genera of other groups (Coniopterygidae, Mesochrysopidae, Myrmeleontoidea: Aspöck and Nemeschkal, 1998; Nel et al., 2005a). We believe that the former opinion is more reasonable (Aspöck and Mansell, 1994).

Character 2. The structure of the male foretarsus in the berothid subfamily Rhachiberothinae and the mantispid subfamily Symphrasinae is very similar: the tarsus is 4 segmented, the basitarsus is pointed apically, and next tarsal segment joins far from the apex of the basitarsus. This modification of the foretarsus in males in Rhachiberothinae was first considered homoplastic with Symphrasinae (Aspöck and Mansell, 1994), and later as a synapomorphy of rhachiberothine and symphrasine genera (Aspöck and Nemeschkal, 1998). We believe that the earlier view is correct.

Character 3. This state is plesiomorphic, occurring in the majority of Berothidae genera. All Symphrasinae are characterized by R and M fused for a considerable distance (far distal to the cross-vein 1m-cu).

Character 4. The presence of cross-vein 2sc-r1 in the forewing of Rhachiberothinae is here considered plesiomorphic. This cross-vein does not occur in other Berothidae (extant and fossil), except *Hoelzeliella* and *Oisea* Nel et al. 2005c, whose subfamily position is rather unclear. The presence of this cross-vein in the Hemerobiidae could also be plesiomorphic (Makarkin et al., 2003).

Character 5. Sc and R1 being widely separated distally in the forewing is most probably a plesiomorphic character state in Berothidae. In the majority of other Berothidae, these veins are free as well (although they sometimes closely approach apically), but in the Cretaceous Paraberothinae, they are fused (probably an apomorphic condition). The apical fusion of Sc and R1 is usually considered as a derived state in various groups (e.g. Hemerobiidae: Makarkin et al., 2003; Polystoechotidae: Archibald and Makarkin, 2006).

Character 6. In the forewing, 2A and 3A have a tendency to fuse distally, forming a closed cell. *Rhachiberotha* and *Mucroberotha* are polymorphic for this character, but we treat this as a synapomorphy of rhachiberothine genera, rather than as homoplasious.

Character 7. In the hindwing, basal cross-vein 1r-m is long and sinuate (plesiomorphic for the order), which occurs in the mantispid subfamily Symphrasinae. In all other extant Mantispidae and Berothidae, it is straight, rarely inclined, or lost (apomorphic states). In fossil taxa, 1r-m is long and sinuate in *Whalfera fera* Whalley (Willmann, 1994, fig. 6) and the Early Cretaceous berothid *Oloberotha sinica* Ren et Guo (V. Makarkin, pers. observation, 2009), and straight in the Ablian/Cenomanian *Systenoberotha magillae* Engel et Grimaldi and *Rhachibermissa phenax* Engel et Grimaldi (Engel and Grimaldi, 2008, figs. 37, 48), the Turonian *Rhachibermissa splendida* Grimaldi (Grimaldi, 2000, figs. 15, 16), and the Early Eocene *Microberotha macculloughi* Archibald et Makarkin (Archibald and Makarkin, 2004, fig. 5b).

Character 8. CuP in the hindwing is usually well-developed proximally (plesiomorphic state). In other Berothidae (except Paraberothinae) and Mantispidae (except Symphrasinae), this vein is completely lost or at least proximally (apomorphic state).

We consider the following character states of Rhachiberothinae to be important along with those listed in the diagnosis.

Character 9. Vesicae (vesicular wing structures) are present in males of all extant *Rhachiberotha* and *Mucroberotha* (see Tjeder, 1968, figs. 3–5; Aspöck and Mansell, 1994, figs. 6, 20; Aspöck and Aspöck, 1997, figs. 10, 12). Their position on the wings in the species of these genera is different, and can vary in size and shape in at least one species (vesicae in the forewing of some specimens of *Mucroberotha vesicaria* Tjeder are even absent, but present in the hindwings: Aspöck and Aspöck, 1997, figs. 19–24). It is unknown yet if the absence of vesicae observed in the only known specimen of a *Whalfera wiszniewskii* male is a case of such intraspecific variability, or if it is characteristic of the species. The presence of vesicae in males is considered as an autapomorphy of the Rhachiberothinae (Aspöck and Mansell, 1994).

Character 10. The eggs of Rhachiberothinae are sessile, which is certainly plesiomorphic. This occurs in two berothid subfamilies, not only in the Rhachiberothinae (*Mucroberotha vesicaria* Tjeder: Minter, 1990), but also the Berothimerobinae (*Berothimerobius reticulatus* Monserrat et Deretsky: Monserrat, 2006). Stalked eggs are thought to occur in all other berothid taxa, and are described in Berothinae (*Spermophorella disseminata* Tillyard: Tillyard, 1916; *Lomamyia latipennis* Carpenter: Toschi, 1964; *Lomamyia hamata* (Walker): Tauber & Tauber, 1968; Brushwein, 1987; *Podallea* sp.: Minter, 1990), and in ?Cyrenoberothinae (*Manselliberotha neuropterologorum* Aspöck et Aspöck: Aspöck and Aspöck, 1988). Nothing is known of eggs of the mantispid subfamilies Symphrasinae, Drepanicinae, and Calomantispinae. However, the eggs of Symphrasinae are probably not stalked, judging by adult morphology (the female has a long ovipositor), and their biology and reproductive behavior (the females of *Trichoscelia santareni*

Navás penetrate the nests of wasps to oviposit; Dejean and Canard, 1990). The eggs of Mantispinae, the most morphologically-derived mantispid group, have a short stalk. The egg stalk of Berothinae and *Manselliberotha* is long, similar to that of Chrysopidae and unlike that of Mantispinae. Stalked eggs are probably an example of parallel evolution; they appeared independently in more derived taxa of Berothidae, Mantispidae, and Chrysopidae (see also Duelli, 1986; Aspöck and Aspöck, 2007).

Character 11. The head vertex of *Rhachiberotha* possesses three tubercles: two lateral and one median; all other genera of Rhachiberothinae have none. The feature found in *Rhachiberotha* also occurs in Dilaridae, Ithonidae, some Psychopsidae, and in at least one genus of Berothidae: Nosybinae (i.e. *Tanzanberotha* Aspöck and Hynd, 1995), and appears to be plesiomorphic in the order. These tubercles are placed in the same position where the ocelli occur in Osmylidae, which is the only extant neuropteran family with ocelli. In the Early Eocene *Oisea*, the vertex is rather pronounced posteriorly, with two flat lateral tubercles and one median tubercle (Nel et al, 2005b). Two lateral tubercles are detected in many Cretaceous Paraberothinae (Grimaldi, 2000; Nel et al., 2005b), and the Early Eocene *Microberotha* Archibald et Makarkin (Archibald and Makarkin 2004, fig. 4b), as well as in many extant Berothidae. They are fused into a dome in *Mucroberotha*, which is considered an autapomorphy (Aspöck and Mansell, 1994).

Character 12. The postocular lobe is more or less expanded in all genera of Rhachiberothinae (see Tjeder, 1959, figs. 222, 253D; Aspöck and Aspöck, 1997, fig. 33). In other berothid species, its condition varies from very expanded and inflated (e.g. *Nosybus* Navás, *Lekrugeria* Navás: Aspöck and Aspöck, 1983, fig. 1; Aspöck and Aspöck, 1986, fig. 20) to reduced (e.g. *Mansellíberotha*: Aspöck and Aspöck, 1988); in the Cretaceous Paraberothinae, it is more or less reduced (see Nel et al., 2005b). The postocular lobe in Mantispidae varies from expanded (many Drepanicinae, Symphrasinae, and Calomantispinae) to very narrow (Mantispinae) (e.g. see Lambkin, 1986, figs. 11–16). It seems that the state "postocular lobe moderately expanded" is plesiomorphic for the taxon Berothidae+Mantispinae, and the states "postocular lobe very inflated" and "postocular lobe reduced" are apomorphic.

The character states 1, 2, 9, and 10 are considered by Aspöck and Mansell (1994) to be autapomorphies of the extant Rhachiberothinae. Nel et al. (2005b) diagnosed Rhachiberothinae by five character states: 4, 12, "absence of spines on inner edge of fore tibia", 5, and the presence of cross-vein r1-rs distal to 3sc-r1 (the latter two are not present in the Eocene *Oisea*), that is, by only plesiomorphic conditions. In our opinion, only two character states can be identified as synapomorphies of rhachiberothine genera: the modification of the foretarsus in the male (homoplastic with the mantispid Symphrasinae), and 2A and 3A having a tendency to fuse distally, forming a closed cell in the forewing. Other apomorphic character states found within the Rhachiberothinae are not present in all genera, and are therefore not diagnostic for the subfamily (e.g. character 9) or occur in other subfamilies of Berothidae and/or in the clade Berothidae+Mantispidae (e.g. characters 1, 12), or are plesiomorphic (e.g. characters 3–5, 7, 8, 10).

Comments on the systematic position of Rhachiberothinae: The Rhachiberothinae were established as a subfamily of Berothidae to include the extant genera *Rhachiberotha* and *Mucroberotha* (Tjeder, 1959). Aspöck and Mansell (1994) elevated it to a family level. Later, Aspöck and Aspöck (1997) added the genus *Hoelzeliella* to it. In recent years, it is usually treated at family rank: Rhachiberothidae (Grimaldi and Engel, 2005; Nel et al., 2005b; Aspöck and Aspöck, 2007; McKellar and Engel, 2009).

In general, we agree to a considerable degree with Engel (2004, p.137) that "it is merely a matter of semantics and preference whether (Berothidae and Rhachiberothidae) are accorded familial or subfamilial rank"; however, it seems to us preferable to consider it as a subfamily of Berothidae for the following reasons: a precedent is set in Mantispidae, where exactly same situation occurs, and we believe that there should be consistency in the treatment of this taxon and the Rhachiberothinae. Symphrasinae and Rhachiberothinae are considered sister groups of other Mantispidae and other Berothidae, respectively (Lambkin, 1986; Aspöck et al., 2001). Symphrasinae, which closely resembles Rhachiberothinae by similar foreleg morphology, and to a lesser extent, in the structure of the pronotum and its wing venation, are confidently treated as belonging to Mantispidae. Although the adults of this subfamily are rather strongly different from those of other mantispids by some features (e.g. the presence of a long ovipositor in the female, absent in other mantispids), their larvae have a strong similarity to those of other Mantispidae. In particular, the larvae of both Symphrasinae and Mantispinae have no trace of a tentorium; "this condition occurs nowhere else among any of the larvae of Neuroptera" (MacLeod, 1964, p.287). In addition, the adults of Mantispidae have an important synapomorphy: the pronotum is elongated posterior to the forelegs.

The larvae of Rhachiberothinae (known only in *Mucroberotha vesicaria* Tjeder, 1968: Minter, 1990) are very similar to those of other Berothidae (known in Berothimerobiinae and Berothinae: Gurney, 1947; Toschi, 1964; Tauber and Tauber, 1968; Riek, 1970; Minter, 1990; Monserrat, 2006). The only known significant difference of the larvae of *Mucroberotha* from the berothine genera *Lomamyia* Banks and *Podallea* Navás was the presence of five stemmata in the former instead of 0–2 in the latter; however, the recently-described larva of the Chilean berothid *Berothimerobius reticulatus* Monserrat and Deretsky has six (Monserrat, 2006). This species is also notable because of its "raptorial" forelegs in the male, as its coxae are much enlarged. Based on a single female, it was previously assigned to the Hemerobiidae and placed in the monotypic subfamily Berothimerobiinae (Monserrat and Deretsky, 1999), but the subsequent discovery of males and larvae allowed confident assignment to the Berothidae (Monserrat, 2006). Recently, Penny and Winterton (2007) redescribed another Chilean monotypic genus *Ormiscocerus* Blanchard and found that these two genera are closely related (in particular, both have a similar enlarged coxa and wing venation). A fossil larva described from the Early

Cretaceous amber of Lebanon (Whalley, 1980, figs. 9, 10) belongs to "non-rhachiberothine" Berothidae, judging from the structure of its mouthparts and antennae; however, it possesses five stemmata like rhachiberothine larvae. These larvae (both fossil and berothimerobiine) share other character states, including a rounded head (elongated in other berothids) and a very hairy body. So the presence of 5–6 stemmata in the larvae of the Rhachiberothinae and Berothimerobiinae is a plesiomorphic condition, and their reduction to 0–2 in Berothinae is an apomorphy. This is in good concordance with the phylogeny of the family (Aspöck and Nemeschkal, 1998).

Both Rhachiberothinae and Symphrasinae are "side" taxa, with regards to other taxa of their families; they are alike in the combination of most plesiomorphic conditions, compared to other subfamilies of their families, and many autapomorphies. Both possess the plesiomorphic character states 7 and 8, while all other Berothidae and Mantispidae have apomorphic states of these (except the Cretaceous Paraberothinae); in Rhachiberothinae and Symphrasinae, the anterior part of the pronotum is not closed ventrally (i.e. not tubular, a plesiomorphic state), while in other Mantispidae, the pronotum is entirely tubular. Both groups possess a number of striking autapomorphies consistent with early branching.

Whalfera Engel 2004.

Whalfera Engel 2004: 140 (nomen novum pro *Fera* Whalley 1983); Wedmann and Makarkin 2007: 709 (systematic position).

Fera Whalley 1983: 230 (nomen praeoccupatum, nec *Fera* Hong, 1983: Diptera: Pleciofungivoridae); Willmann 1994: 178–201 (redescription, systematic position).

Type species: *Fera venatrix* Whalley 1983, by original designation.

Diagnosis: Two to three trichosors between tips of each vein/veinlet in basal portion of forewing (one trichosor between tips of each vein/veinlet in other genera).

Composition: Two species from the Late Eocene amber of northern Europe: *Whalfera venatrix* (English amber: Norfolk, the coast of eastern England), *Whalfera wiszniewskii* sp. nov. (Baltic amber: Sambian Peninsula, the Polish coast). The English amber is considered contemporarily with Baltic amber (Jarzembowski, 1999).

Comments: The genus *Whalfera* was initially considered a member of Mantispidae, belonging (or closely related) to Symphrasinae (Whalley, 1983; Grimaldi, 2000). Willmann (1994) considered it to be the sister group of Mantispidae, which he treated in the broadest sense, as Mantispidae+Rhachiberothidae. Aspöck and Mansell (1994), Engel (2004), and Grimaldi and Engel (2005) tentatively treated *Whalfera* as belonging to Rhachiberothidae, whereas Nel et al. (2005b) did not mention this genus among the genera of this family. Wedmann and Makarkin (2007) analyzed the taxonomic position of *Whalfera* based on *Whalfera venatrix*, and concluded that it had the greatest possibility of belonging to Rhachiberothidae than to a stem group of Mantispidae.

The discovery of *Whalfera wiszniewskii* helps to determine the position of the genus. This species superficially resembles those of the mantispid subfamily Symphrasinae, particularly of the genus *Trichoscelia*. However, an analysis of the characters shows that *Whalfera* should be assigned to the berothid subfamily Rhachiberothinae. The following character states found in *Whalfera* are characteristic of Rhachiberothinae and absent in Symphrasinae: the pronotum is prolonged before forelegs (synapomorphy of Berothidae, including Rhachiberothinae according to Aspöck and Mansell, 1994); in the forewing, M and R are not fused basally (or fused for short distance, proximal to basal cross-vein 1m-cu; fused for longer distance, far distal to basal cross-vein 1m-cu in Symphrasinae); basal subcostal cross-vein 1sc-r1 is present (absent in Symphrasinae); 2A and 3A are fused distally (free in Symphrasinae); humeral veinlet is simple and cross-vein-like (recurrent and branched in Symphrasinae).

Whalfera is most closely related to *Mucroberotha*, based on the presence of a very long penisfilum (cf. Tjeder, 1968, figs. 9, 11; Aspöck and Mansell, 1994, figs. 22, 24, 25). The arrangement and size of the forefemur teeth in these genera are also very similar.

Whalfera wiszniewskii sp. nov. (Figs. 1–4)

Etymology: Species epithet is formed from the surname of Andrzej Wiszniewski, jeweler and collector of amber, who has generously donated numerous amber pieces with inclusions to the Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland.

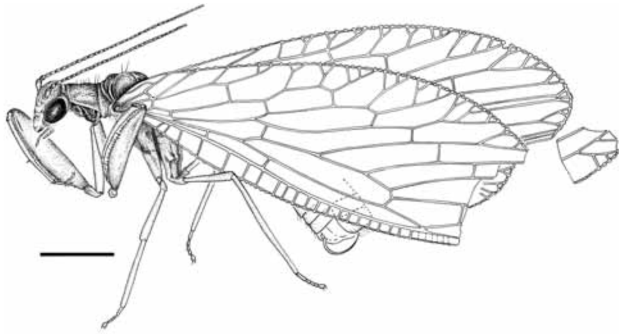

Fig. 1. *Whalfera wiszniewskii* sp. nov.
Holotype MZ 24203. Drawing of the specimen, lateral left view. Scale bar=1 mm.

Holotype: Specimen MZ 24203, deposited in the Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland, and labeled "HOLOTYPE *Whalfera wiszniewskii* Makarkin et Kupryjanowicz, Baltic amber, Sambian Peninsula, No. inw. MZ 24203, coll. J. Kupryjanowicz". A beautifully-preserved, almost complete male specimen lacking the tips of the left forewing and antennae.

Type locality and horizon: Sambian Peninsula, the Polish coast of the Baltic Sea. Late Eocene, Baltic amber.

Diagnosis: The new species can be easily distinguished from *Whalfera venatrix* by the absence of basal cross-vein between R1 and Rs.

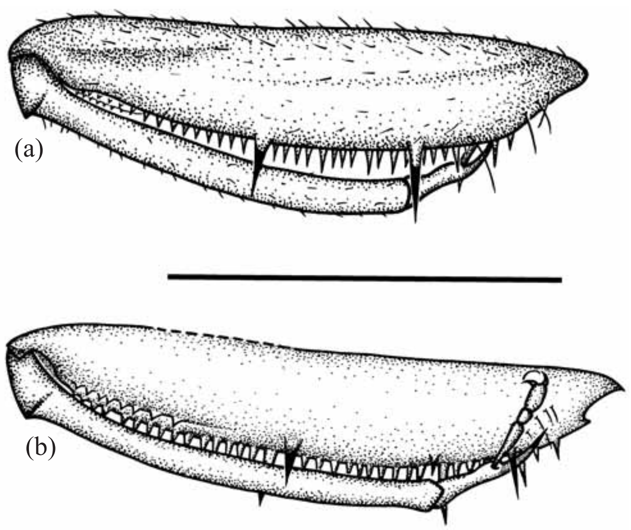

Fig. 2. *Whalfera wiszniewskii* sp. nov.
Holotype MZ 24203, drawings of the forelegs (femora, tibiae, and tarsi). (a) Right foreleg (inner view); (b) left foreleg (outer view). Scale bar=1 mm.

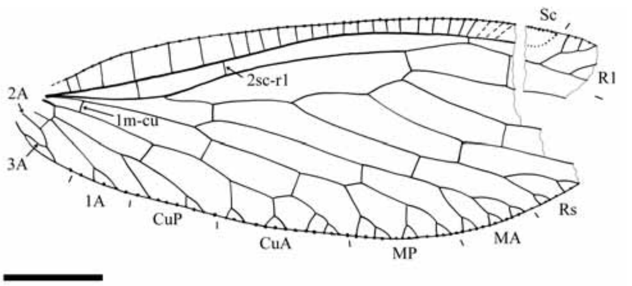

Fig. 3. *Whalfera wiszniewskii* sp. nov.
Holotype MZ 24203. Forewing venation of the left wing. Scale bar=1 mm.

Description: Head moderately prolonged (lateral view), with prominent eyes. Face (between antennae and clypeus) rather short, slightly convex (lateral view); genae darkish, extending ventral to eyes as bulbous structure. Vertex moderately raised, without visible tubercles. Postocular lobe moderately extended. Antennae widely separated, moniliform; scapus enlarged, relatively short, less than twice as long as wide; pedicellus larger than any segment of flagellum; flagellum with 29 (left antenna) and 34 (right antenna) segments (tips of antennae missing). Mouthparts poorly visible, quite short; maxillary and labial palps (clearly visible) moderately long with acute apical joints.

Pronotum moderately elongated, 1.5 times as wide as long (dorsal view), narrowed towards anterior margin (lateral view); part anterior to forecoxa without distinct furrows, simple, open ventrally; part posterior to forecoxa short, apparently open ventrally (poorly discernible). These two parts separated by distinct transverse furrow (Fig. 4b). Pronotum and mesonotum covered with scarce long hairs. Metanotum mostly obscured. Forelegs raptorial, slightly different in size (right leg longer that left); coxa long, rather slender; trochanter rather long; femur large with two rows of teeth (spine-like specialized hairs): outer row complete with numerous moderately long teeth and two very long teeth; inner row incomplete with several very short teeth distally and three long teeth basally (Fig. 2); tarsus four segmented; basitarsus long, pointed apically like spine; second tarsal segment slender and prolonged, joints at nearly middle of basitarsus; third segment very short; apical segment larger with short claws. Middle and hindlegs rather pale, slender, covered with fine hairs; tibial spurs not detected; four proximal segments of middle and hindtarsi ventrally with bristles. Length of leg joints: forelegs coxa 1.25 mm, trochanter 0.3 mm, femur 1.6 mm in right leg (1.5 mm in left leg), tibia 1.2 mm in right leg (1.1 mm in left leg), tarsus 0.35, claws 0.17; left mid-leg trochanter 0.2 mm, femur 0.8 mm, tibia 1.1 mm, tarsus 0.5 mm; left hindleg trochanter 0.1 mm, femur 0.95 mm, tibia 1.7 mm, tarsus 0.45 mm.

Forewing (Fig. 3) elongated, ovoid, 6.2 mm long, 2.2 mm wide. Trichosors prominent along entire wing margin; anterocostal and anal margins with 2–3 trichosors between each vein. Costal space relatively narrow, dilated maximally at proximal one-quarter of length, narrowed basally. Humeral vein cross-vein-like, not branched. All subcostal veinlets simple; prestigmal veinlets perpendicular to Sc, stigmal veinlets oblique, with their tips directed towards wing apex. Subcostal space broad, with two rather long prestigmal cross-veins (1sc-r1 and 2sc-r1) located proximal and distal to origin of Rs, respectively, and one short pterostigmal cross-vein (3sc-r1). Pterostigma inconspicuous. Sc and R1 not fused distally; distal-most portion of Sc poorly visible. R1 not completely preserved, with several distal forked branches (two preserved). Origin of Rs located far from base of wing. Two cross-veins detected in R1 space (between R1 and Rs): prestigmal shorter, poststigmal longer. Rs with three branches in proximal two-thirds of forewing (apical portion of forewing not preserved). R and M appear fused proximally to basal cross-vein 1m-cu. Cross-vein 1r-m connects Rs and MA. M forked at level of origin of Rs. MA not branched, dichotomously forked distally. MP with one branch dichotomously forked distally. Cross-vein 2m-cu distal to fork of M. Cu forked near wing base; CuA shallowly forked, with three branches, two of which are shallowly forked. CuP originating at nearly a right angle to Cu, then shortly bent at nearly a right angle, deeply forked distally; anterior branch of this fork shallowly forked, posterior branch simple. One cross-vein cua-cup, distal to fork of CuP. 1A rather long, with shallow marginal fork. 2A short, simple. 3A short, sinuate, fused, with 2A distally. Basal cross-vein 1cu-a1 short; cross-vein 1a1-a2 long, opposite 1cu-a1; cross-veins between 2A and 3A absent. Single gradate series of cross-veins, of which five cross-veins preserved. All veins appear rather pale. Margins of wing, longitudinal veins with very short, sparse hairs. Membrane of forewings colorless, hyaline.

Hindwing venation poorly visible. CuA parallel to hind margin, with at least nine branches: one forked, others simple; one trichosor between tips of each next branches of CuA.

Abdomen: 5th–7th segments well developed, of unspecialized morphology. Ninth tergite narrow, slightly expanded ventrally, covered dorsally with hairs of medium size, not fused with ectoproct (10th tergite). Ectoproct large, more or less rounded, without caudal or ventral projections, dorsally covered with long

Fig. 4. *Whalfera wiszniewskii* sp. nov**.**
(a) Holotype MZ 24203. Photograph of the specimen, lateral left view; (b) photograph of the prothorax showing a transverse suture (arrow), lateral view; (c) photograph of the abdominal apex, lateral/slightly caudal view. e, ectoproct; pf, penisfilum; S9, ninth sternite. Scale bar = 0.2 mm.

setae; callus cerci not detected. Eighth and ninth sternites appear not fused; both similar in shape, short; ninth sternite not prolonged. Of inner genitalia, portion of penisfilum of paramere–mediuncus complex (free portion of mediuncus of MacLeod and Adams, 1968), portion of fused ninth gonocoxite and gonarcus (gonarcus of Tjeder, 1968) clearly visible. Penisfilum very long, relatively thick; apical portion not visible, hidden between parts of ectoprocts (Fig. 4c).

Remarks: We assign this species to *Whalfera* by its wing venation, which is similar to that of the type species *Whalfera venatrix*, and its possession of at least one character state shared with *Whalfera venatrix*, a synapomorphy of this genus: the presence of 2–3 trichosors between the tips of each two veins/veinlets in the basal portion of the wing margin. Additionally, these two species have very similar foreleg morphologies (particularly of their tarsi and the arrangement of tibial spines). Unfortunately, some important characters in the type species are not discernible (e.g. the relationships of their anal veins and prothorax morphology) or missing (e.g. distal portion of the forewing, male terminalia). Together, these factors tentatively render the assignment of *Whalfera wiszniewskii* to the genus *Whalfera*.

4 Fossil Record of Rhachiberothinae

Thirteen species (one unnamed) of 11 genera were previously ascribed to this taxon, treating it either as a family or a subfamily of Berothidae or Mantispidae (Schlüter, 1978; Whalley, 1980; Grimaldi, 2000; Engel, 2004; Nel et al., 2005b; Wedmann and Makarkin, 2007; Engel and Grimaldi, 2008; McKellar and Engel, 2009). However, according to the above diagnosis, only the fossil genus *Whalfera* can be assigned to this subfamily with confidence (see above). The position of *Oisea* is not clear (see below); other fossil genera confidently do not belong to it and are treated here as belonging to the berothid subfamily Paraberothinae.

Nel et al. (2005b) created Paraberothinae as a subfamily of Rhachiberothidae, including six Cretaceous genera: *Paraberotha* Whalley 1980, *Rhachibermissa* Grimaldi 2000, *Chimerhachiberotha* Nel et al. 2005b, *Alboberotha* Nel et al. 2005b, *Retinoberotha* Schlüter 1978, *Spinoberotha* Nel et al. 2005b (the latter two provisionally). Subsequently, three other Cretaceous genera were described in the Rhachiberothidae: *Eorhachiberotha* Engel 2004, *Albertoberotha* McKellar et Engel 2009, and *Scoloberotha* Engel et Grimaldi, 2008. All of these are similar enough to form a monophyletic Cretaceous (Neocomian–Campanian) taxon.

Nel et al. (2005b) characterized Paraberothinae by possession of numerous spines (teeth) on the inner edge of the foretibia; reduced postocular lobe; absence of intermediate cross-vein sc-r2 in the forewing; absence of a cross-vein "in distal part of area between R and Rs, opposite pterostigmal zone in fore and hind wings", and R1 and Sc distally fused (p. 53) (the latter two characters are also present in *Oisea*).

In our opinion, Paraberothinae can be diagnosed by the following: small berothids (forewing 2.9–4.0 mm long); postocular lobe reduced (character A); scapus long to very long (up to 10 times longer than pedicel) (character B); forelegs raptorial (character C); tarsus of male five segmented (character D); tibia with numerous spine-like setae on inner edge (character E); Sc and R1 fused distally in both wings (character F); intermediate subcostal cross-veins 2sc-r1 absent in the forewing (character G); basal cross-vein 1r-m is straight in the hindwing (sinuate in some genera; not confirmed yet, see below) (character I), and CuP present (character J).

Character states E and F are possible synapomorphies of paraberothinae genera; and the characters A, B, G, and I can be synapomorphic of these plus other berothid subfamilies with walking forelegs (but also possibly homoplasious between them). Paraberothinae and Rhachiberothinae share the characters C and J; it is possible that they are sister groups.

The structure of the foreleg femora is very diverse in Paraberothinae, from almost non-raptorial in *Spinoberotha* to true raptorial in *Scoloberotha*, resembling those found in Rhachiberothidae. Paraberothinae can be polymorphic for the structure of basal cross-vein 1r-m. This cross-vein is straight in *Rhachibermissa splendida* Grimaldi (Grimaldi, 2000, figs. 15, 16) and *Rhachibermissa phenax* Engel et Grimaldi (Engel and Grimaldi, 2008, figs. 37, 48). Nel et al. (2005b) mentioned that in *Paraberotha*, "sigmoidal vein MA (=1r-m) between M and (are) Rs present" (p.58) and in *Spinoberotha* "sigmoidal vein MA (=1r-m) between M and Rs present, but not well visible" (p.76). However, the sinuate 1r-m is not visible in the photos and drawings of these genera (Nel et al. 2005b, figs. 1, 4, 15–18), so this remains unconfirmed.

These genera are discussed below based on their geological age, beginning with the oldest, and only the most important species characters are mentioned.

Three monotypic genera are known from Early Cretaceous (Neocomian) Lebanese amber: *Paraberotha*, *Spinoberotha*, and *Chimerhachiberotha* (Nel et al., 2005b).

Paraberotha acra Whalley 1980 is represented by a single incomplete crumpled specimen, whose forewing is 3.7 mm long. The original description was incomplete (Whalley, 1980, figs. 6, 11, 12). Recently, the species was redescribed by Nel et al. (2005b); however, this was ambiguous in its treatment of some important characters, for example, "tarsus of male four-segmented" (Nel et al. 2005b, p. 53). This should, however, be considered only hypothetical: their figs. 1, 4, 5 clearly show that the apex of the abdomen and terminal segment(s) of the foretarsus are missing, and the authors state "genital appendages missing" (p. 58); therefore, it is impossible to determine the sex of the specimen and the number of tarsomeres in the forelegs.

Spinoberotha mickaelacrai Nel et al., 2005 is known from an incomplete female (Nel et al., 2005b, figs. 15–20). Forewing length is 3.1 mm. The profemur is almost not enlarged, and its forelegs are the simplest in the subfamily. The forewing venation of *Paraberotha acra* and *Spinoberotha mickaelacrai* is very similar to that of *Pseudosisyra minima* Makarkin, described as a member of the Mesithonidae from the Early Cretaceous locality of Baissa, Transbaikalian Russia. This species is known by an isolated, well-preserved forewing 4.1 mm long (Makarkin, 1999, figs. 4, 7). *Pseudosisyra minima* differs from the former genera by the presence of a branched recurrent vein. It is quite possible that *Pseudosisyra minima* belongs to Paraberothinae.

Chimerhachiberotha acrasarii Nel et al., 2005b is represented by an incomplete crumpled specimen, and characterized by its peculiar forelegs (Nel et al., 2005b, fig. 11) and the longest scapus in the subfamily. The forewing is approximately 4 mm long.

The monotypic genus *Alboberotha* (with *Alboberotha petrulevicii* Nel et al., 2005b) is known only from a poorly-preserved, almost complete specimen from the Early Cretaceous (late Albian) amber of southwestern France (Archingeay locality). It appears to most resemble *Retinoberotha stuermeri* Schlüter 1978. The scapus in this species is the shortest known in the subfamily; the forewing is 3.33 mm long.

Two genera are known from the Early Cretaceous (Cenomanian or Late Albian) Burmese amber: *Eorhachiberotha* and *Scoloberotha*. *Eorhachiberotha* includes two species: *Eorhachiberotha burmitica* Engel 2004 and an unnamed species tentatively assigned to this genus (Engel, 2004). *Eorhachiberotha burmitica* is represented by a male specimen; its tarsus is simply constructed, probably five segmented (this is difficult to determine in the specimen with certainty), basitarsus certainly not pointed apically, and second tarsomere joins to its apex. Its forewing is approximately 3 mm long (estimated).

In the female of *Scoloberotha necatrix* Engel et Grimaldi 2008, the only known specimen, hindwing 1r-m is lacking. The forewing is 3.62 mm long.

Retinoberotha (with *Retinoberotha stuermeri*) is represented by a poorly-preserved, very incomplete and crumpled specimen from the Late Cretaceous (Cenomanian) amber of northwestern France. This specimen was subsequently studied intensively, in particular with X-ray imaging (Schlüter and Stürmer, 1982, 1984; Schlüter, 1989; Willmann, 1994). Estimated forewing length is approximately 4 mm (based on 3.7 mm hindwing length).

The genus *Rhachibermissa* is known from two species from Late Cretaceous (Turonian) New Jersey amber: *Rhachibermissa splendida* Grimaldi 2000 and *Rhachibermissa phenax* Engel et Grimaldi 2008. *Rhachibermissa splendida* is the smallest paraberothine species (forewing 2.84–2.95 mm long), and is known from seven specimens. Although the description is in general adequate and complete, it lacks some important details, such as sex of either specimen, including those shown in drawings (Grimaldi, 2000, figs. 16, 17). In the hindwing, the basal cross-vein 1r-m is “apparently not sinuate (but also hardly observable)” (Grimaldi, 2000, p. 271). The foreleg tarsus is five segmented; the basal two tarsomeres each with a hook-shaped spine.

Rhachibermissa phenax is a well-preserved female, with 3.21 mm forewing length. Cross-vein 1r-m in the hindwing is long and straight (Engel and Grimaldi, 2008, fig. 48).

Albertoberotha leuckorum McKellar et Engel was recently described by McKellar and Engel (2009) from the Late Cretaceous (Campanian) Canadian amber (Grassy Lake locality in Alberta). This species was mentioned as a Neuroptera by Pike (1994). The holotype is a male; the forelegs have a five-segmented tarsus, and the basitarsus is not pointed apically; the forewing is 3.25 mm long.

The genus *Oisea* (=*Eorhachiberotha* Nel et al., 2005b, nomen praeoccupatum) is monotypic, with *Oisea celinea* Nel et al. 2005c described from the earliest Eocene amber of the Oise Department, northern France. The holotype is an almost complete, relatively large female (forewing estimated length is approximately 6 mm, the hindwing approximately 5.6 mm). Although this genus “has none of the known apomorphies proper to any of the modern genera” (Nel et al., 2005b, p.76), it was considered by these authors to be the single fossil member of Rhachiberothinae. The description and figures do not allow confident determination of its affinity. Cross-vein 2sc-r is present as in Rhachiberothinae; however, Sc and R1 are fused distally as Paraberothinae, so its subfamily position remains undetermined.

5 Conclusions

We assign the Late Eocene species described here to the genus *Whalfera*, and agree with Engel (2004), Grimaldi and Engel (2005), and Wedmann and Makarkin (2007) that it belongs to Rhachiberothinae. We find that this is the only fossil genus confidently known in this subfamily, and that others previously assigned to it belong to Paraberothinae (except perhaps for *Oisea*). We treat Rhachiberothinae and the Cretaceous Paraberothinae as subfamilies of Berothidae. The morphological similarity between Rhachiberothinae and Symphrasinae (Mantispidae) are convergent.

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