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# An important new fossil genus of Berothinae (Neuroptera: Berothidae) from Baltic amber

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## Abstract

*Elektroberotha groehni* **gen. et sp. nov.** (Neuroptera: Berothidae) is described from Baltic amber. The genus is assigned to Berothinae based on female terminalia that have the following characteristics: long hypocaudae on gonocoxite 9; sternite 7 that is medially divided into a pair of lateral sclerites; and gonocoxite 8 with a medial process that is very similar to that of some extant berothine genera. The new genus is the first described fossil genus of the subfamily Berothinae. It is noteworthy for the possession of a fully-developed CuP in the hind wing, a vein that is strongly reduced in all other species of the subfamily. The genus *Spiroberotha* is considered to belong to the Berothinae.

**Key words:** Baltic amber, Eocene, Berothidae, Berothinae

## Introduction

The Berothidae is a small family (approximately 130 extant species, including Rhachiberothinae) that occurs in most warm-temperate to tropical regions of the world, and very rarely in temperate regions (Oswald 2013). Fossil berothids are numerous (45 named species in 31 genera, excluding *Mesithone* Panfilov, 1980), known from the Middle Jurassic to late Eocene (Makarkin *et al.* 2011, 2012; Azar & Nel 2013; Khramov 2015; Makarkin 2015; Shi *et al*. 2015).

Baltic amber berothids are currently known from only one named species, the rhachiberothine *Whalfera wiszniewskii* Makarkin et Kupryjanowicz, 2010, although five described larvae are thought to belong to at least two (maybe more) species of two different subfamilies (Wedmann *et al.* 2013). *Proberotha prisca* Krüger, 1923 was considered for a long time as a berothid, but recently it was reasonably assumed to be a nevrorthid (Wedmann *et al.* 2013; Wichard 2014).

In this paper, a remarkable new berothid genus and species from Baltic amber is described, based on two specimens. The new genus is assigned to the subfamily Berothinae based on female terminalia, although it possesses a fully-developed CuP in the hind wing, a vein that is strongly reduced in all other species of the subfamily.

## Material and methods

This study is based on two specimens from Baltic amber. The amber piece containing the holotype is nearly square, ca. 15 by 14 mm. The piece containing the paratype is broadly rectangular, about 27 by 45 mm.

The photographs of the holotype were taken by Carsten Gröhn using a Zeiss stereomicroscope (modified with variable objectives: Nikon M Plan 5x, 10x, 20x, 40x; Luminar 18 mm, 25 mm, 40 mm) and an attached Canon EOS 450D digital camera. The photographs of the paratype were taken by Lukas Kirschey using a Leica DFC420 digital camera on a Leica MZ95 dissecting microscope. Line drawings were prepared by the first author using Adobe Photoshop CS3.

The venational terminology in general follows Kukalová-Peck & Lawrence (2004) as interpreted by Yang *et al*. (2012b, 2014). Terminology of wing spaces and details of venation (e.g., spaces, veinlets) follow Oswald (1993).

Abbreviations: AA1 to AA3, first to third branches of anterior anal vein; CuA, anterior cubitus; CuP, posterior cubitus; hp, humeral plate; MA and MP, anterior and posterior branches of media; RA, anterior radius; RP, posterior sector; RP1, proximal-most branch of RP; ScP, subcosta posterior.

## Systematic paleontology

### Order Neuroptera Linnaeus, 1758

### Family Berothidae Handlirsch, 1906

### Subfamily Berothinae Handlirsch, 1906

### Genus *Elektroberotha* gen. nov.

**Type and only species.** *Elektroberotha groehni* **sp. nov.**

**Diagnosis.** May be easily distinguished from other genera of Berothinae by a combination of the following character states: scapus relatively short, approximately twice as long as wide; sternite 7 of female divided medially into pair of large lateral sclerites; gonocoxite 8 of female with long narrow medial process directed anteriorly; hypocaudae long; pseudohypocaudae of female long, not separated from tergite 9 + ectoproct; in forewing, 2r-m connects RP, MA; three crossveins between RA, RP before termination of ScP; in hind wing, CuP fully developed.

**Etymology.** From the Greek *elektro*, amber and *Berotha*, a genus-group name, in reference to the occurrence of the genus in Baltic amber. Gender feminine.

**Remarks.** *Elektroberotha* **gen. nov.** is the first described fossil genus in the subfamily Berothinae, the largest berothid subfamily comprising 85 extant species in eleven genera (Oswald 2013).

### *Elektroberotha groehni* sp. nov.

Figs 1–5

*Proberotha prisca* (non Krüger, 1923): Scheven 2004: Fig. on p. 7.

**Type material.** Holotype GPIH Typ. Kat. Nr. 4550 (*ex* collection of C. Gröhn, Nr. 7069), deposited in the Geological-Paleontological Institute and Museum of the University of Hamburg [Geologisch-Paläontologisches Institut und Museum der Universität Hamburg]. An incomplete female specimen: body complete, with both coxae of forelegs, fragments of left mid-leg, complete right hind leg, and femur of left hind leg preserved (apical parts of antennae, other segments of legs missing); an almost complete right forewing; a proximal part of left forewing; and an incomplete, damaged right hind wing (left hind wing missing).

Paratype MB I.6021 (*ex* collection of J. Velten), deposited in the Museum für Naturkunde, Berlin. A nearly complete female specimen.

**Etymology.** After the surname of Carsten Gröhn, recognizing his help in examination of the holotype.

**Description.** *Holotype* (Figs 1–6). Length of body 8.3 mm as preserved. Head poorly preserved. Eyes large; postocular lobe neither expanded, nor inflated. Antennae rather long; scapus relatively short, approximately twice as long as wide, covered with short setae; pedicellus slightly longer that first flagellomeres; flagellum consists of ca.70 preserved segments (antennae possibly incomplete).

Pronotum narrowed toward anterior margin, rounded at anterior margin; nearly as long as wide in posterior part; covered with long setae; with two transverse furrows (proximal furrow interrupted medially, distal complete, deeper). Mesonotum almost bare (setae possibly lost post mortem); single scale preserved on left mesopleuron.

Metanotum not clearly visible. Legs incompletely preserved. Procoxa long, covered with long setae. Metatibia without terminal spurs; metatarsus with basal tarsomere longer than remaining tarsus (relative length of tarsomeres 8.5–2.5–1.5–1–1.6); first (basal) to fourth tarsomeres each with pair of apical inner (ventral) spine-like setae; claws thin, curved.


**FIGURE 1**. *Elektroberotha groehni* **gen. et sp. nov.**, holotype GPIH Typ. Kat. Nr. 4550. A, specimen as preserved, dorsal view. B, left forewing (ventral view) showing basal crossvein 1r-m. Scale bar = 1 mm.

No dorsal scales on abdomen detected. Tergite 6, Sternite 6 long, unspecialized. Tergite 7 rather long, unspecialized. Sternite 7 medially dividing into pair of large lateral sclerites. Tergite 8 narrower than tergite 7. Gonocoxites 8 fused, narrow; strongly chitinized anteriorly, with margin distinctly visible; posterior margin indiscernible, probably weakly chitinized; long median process directed forward, markedly dilated and round apically (Fig. 5B). Tergite 9 probably fused with ectoprocts, kidney-shaped in ventral view; one preserved ventral pseudohypocauda poorly visible, long, slender in ventral view, covered with dense very long setae apically. Gonocoxites 9 deeply excised anteriorly (in ventral view), with dense long setae; one preserved hypocauda rather long (very probably, its apical part broken off), with scarce long setae.

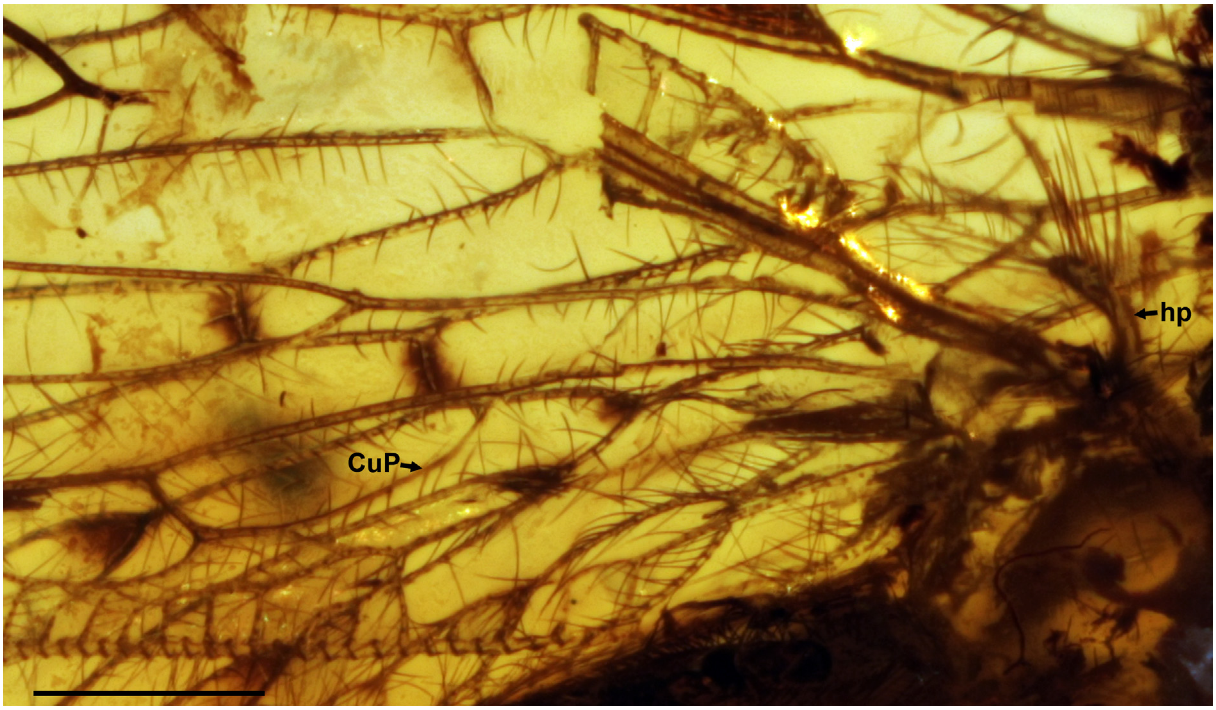



**FIGURE 2**. *Elektroberotha groehni* **gen. et sp. nov.**, holotype GPIH Typ. Kat. Nr. 4550. Proximal part of right hind wing (ventral view) showing CuP and humeral plate (hp). Scale bar = 0.5 mm.

Forewing 10.7 mm long as preserved (estimated complete length ca. 11.5 mm), ca. 5 mm wide. Costal space moderately broad, strongly narrowed basally. Humeral veinlet slightly recurrent, with two simple short branches. All subcostal veinlets 1–3 times forked; weakly bent to wing apex, two central veinlets perpendicular to ScP. ScP relatively short, distally connected with RA by short distal crossvein. Subcostal space relatively broad, with two crossveins: basal, located much proximad origin RP, and distal. RA enters margin well before wing apex, apically dichotomously branched, with five long veinlets (branches): four dichotomously branched in similar manner as stem of ScP, one once forked. RA space (between RA, RP) slightly wider than subcostal space, with four crossveins: three proximad distal subcostal crossvein, one distad. RP origins rather near wing base, with eight branches. RP1 relatively deeply forked, in general dichotomous. RP2 forked shallower than RP1, but much deeper than other branches which shallowly forked. Crossvein 1r-m very short, connecting R, M (discernible in left forewing; Fig. 1B); 2r-m long, connecting RP, MA rather far from fork of M; strongly thinner towards MA in right forewing. Other ten radial crossveins arranged in one nearly complete gradate outer series from ScP+RA to CuA (crossvein between stem of RP, RP8 absent); one additional crossvein between RP7, RP8 located basad crossvein of outer series. M not fused basally with R, thinning and adjoining R basad 1m-cu; forked at level of origin of RP. MA branched similarly to RP1 branching. MP deeply dichotomously branched; its basal-most fork proximad crossvein between MA, MP. Crossvein 1m-cu (‘M5’) long, oblique, connecting M, CuA; 2m-cu located much distad fork of M. Cu dividing into CuA, CuP rather close to wing base. CuA deeply dichotomously branched (alternatively, pectinately forked with three branches; proximal-most branch deeply dichotomously forked). CuP configured similarly to CuA but with more oblique branches. One crossvein between CuA, CuP (1icu) located proximad 2m-cu. AA1 dichotomously branched distally. AA2 forked distally into two branches; anterior branch pectinately forked (with four short simple branches); posterior branch only with terminal fork. AA3 rather short, with at least three very short, pectinate branches. Terminal fork of all branches of RP to AA2 very shallow; sometimes these ‘forks’ have three branches. Two crossveins posterior to CuP: cup-aa1, aa1-aa2. Trichosores prominent along entire wing margin. Macrotrichia on veins, wing margins rather long, dense. Wing membrane probably hyaline with majority of crossveins narrowly margined with dark brown, and majority of forks (inside) dark brown.

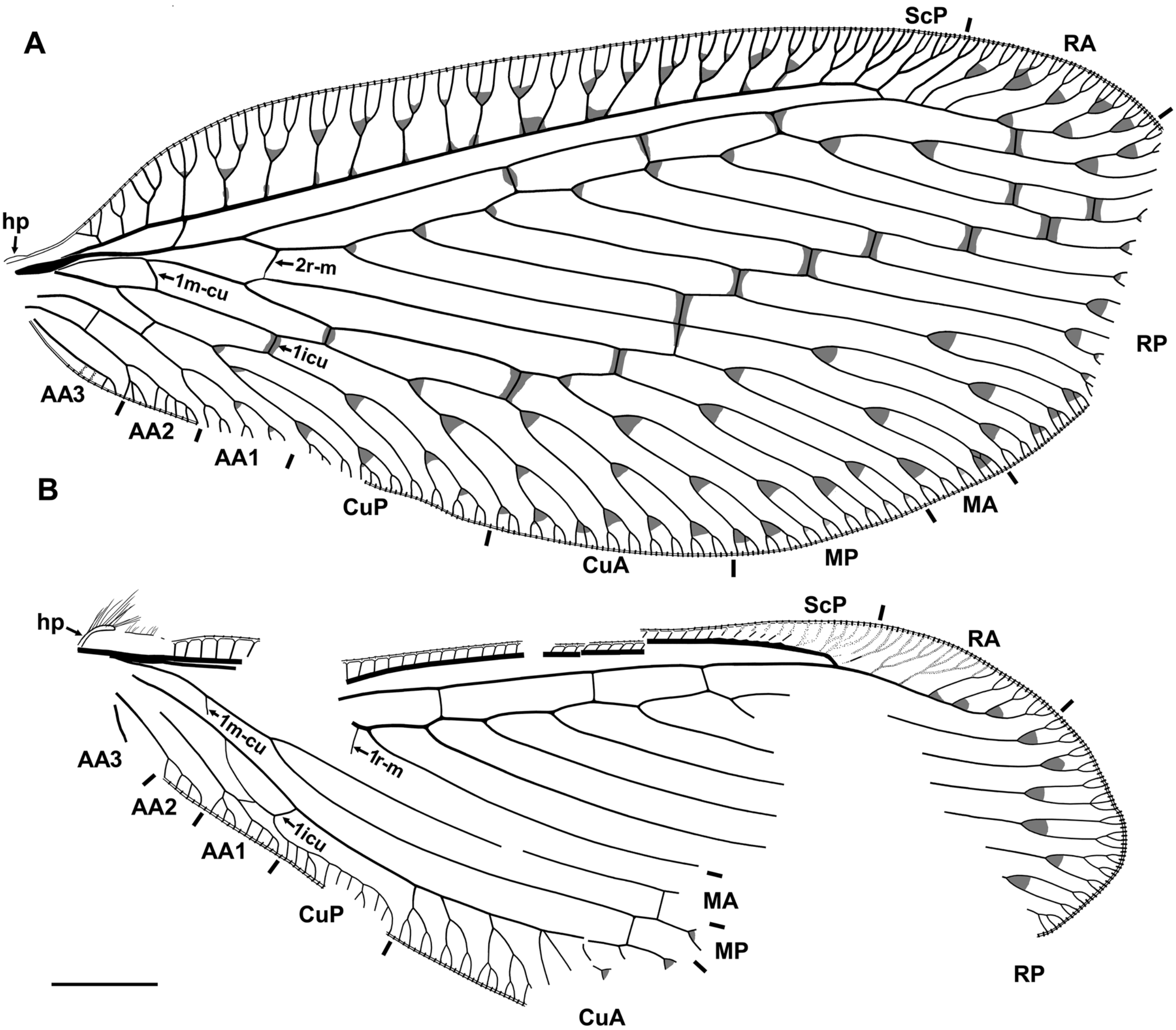



**FIGURE 3**. Wing venation of *Elektroberotha groehni* **gen. et sp. nov.**, holotype GPIH Typ. Kat. Nr. 4550. A, right forewing (veins in the apical-most preserved portion are probably optically distorted by irregularities in the amber). B, right hind wing. Macrotrichia are omitted except in the humeral area of the hind wing. Scale bar = 1 mm (both to scale).

Hind wing 9.8 mm long, 3.7 mm wide as preserved (estimated complete width ca. 4 mm). Humeral plate long, curved, covered with dense long setae. Costal space very narrow medially, slightly dilated basad, markedly dilated distad. Subcostal veinlets closely spaced, short, simple except three distal deeply forked. ScP stout, relatively short, distally connects with RA by distal crossvein. Subcostal space relatively broad, with one distal crossvein detected. RA enters margin well before wing apex, with six long veinlets (branches): four veinlets once forked, two veinlets forked three times. RA space (between RA, RP) distinctly wider than subcostal space, with three preserved crossveins proximad distal subcostal crossvein. RP with six branches; all of these shallowly dichotomously branched. Crossvein 1r-m incompletely preserved: long, straight, nearly perpendicular to MA, connecting stem of RP, MA. Radial crossveins not preserved. M not fused basally with R, forked rather far from wing base. MA, MP parallel to each other; branching not preserved. Crossvein 1m-cu ('M5') rather short, oblique, connecting M, Cu. Cu divided into CuA, CuP very far from wing base. CuA long, incurved; its distal part and posterior wing margin slightly divergent; pectinately branched with eight preserved branches (three proximal-most branches deeply dichotomously forked; other branches incompletely preserved). CuP pectinately branched, with nine short branches. Two distal crossveins (between MA, MP and MP, CuA) represent posterior-most crossveins of outer gradate series. Between CuA, CuP one long crossvein (1icu). AA1 forked distally; anterior branch pectinately forked (with three short simple branches); posterior branch with two short branches. AA2 pectinately forked, with at least three short simple branches. AA3 incompletely preserved, rather stout. Terminal fork of all preserved branches of RP to AA2 shallow; sometimes these 'forks' have three branches. Between CuP, AA1 one crossvein proximad 1icu. Trichosores prominent, except basally in costal margin where these indistinct. Macrotrichia on veins, wing margins rather long, dense. Wing membrane hyaline with forks (inside) in apical wing portion dark brown.

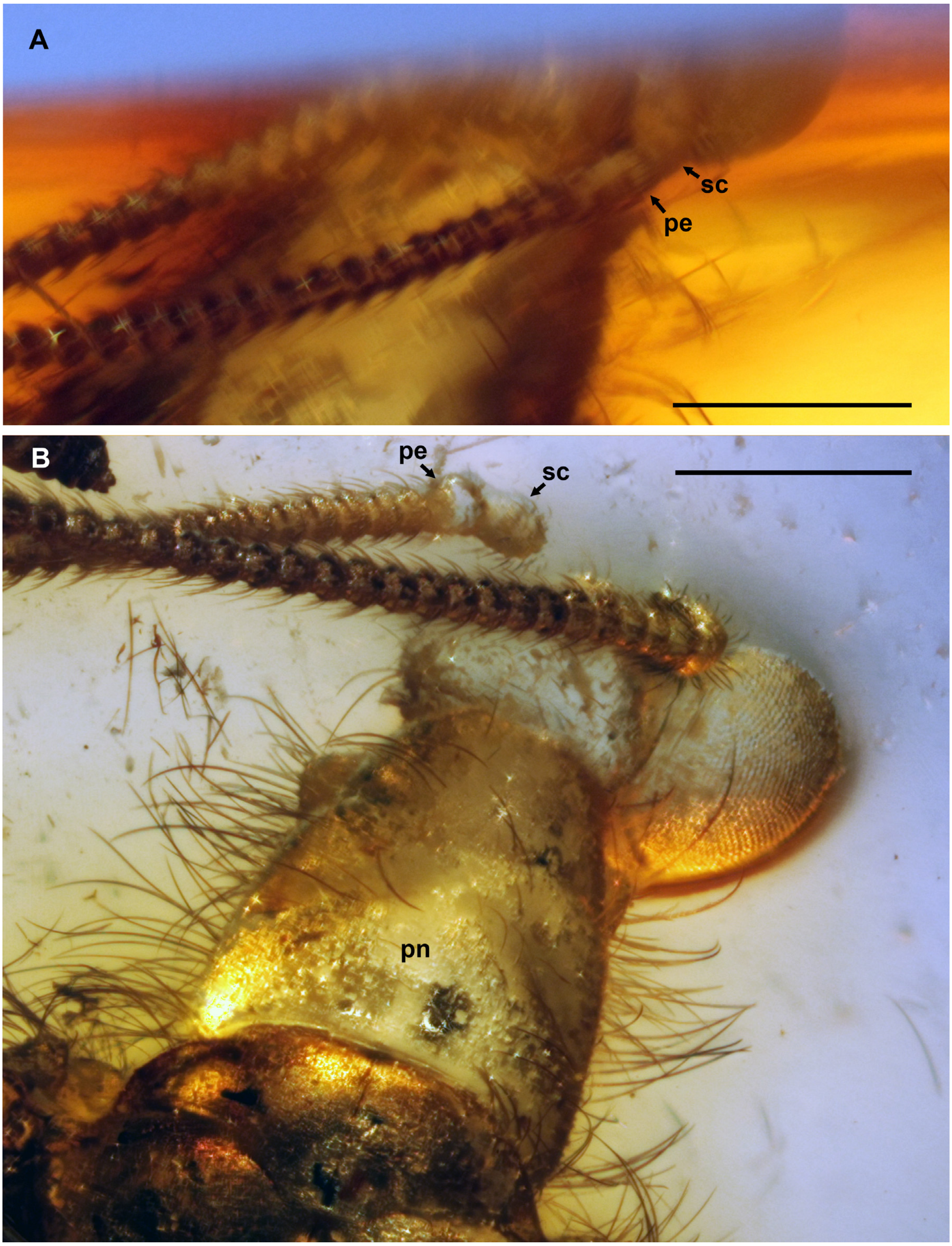
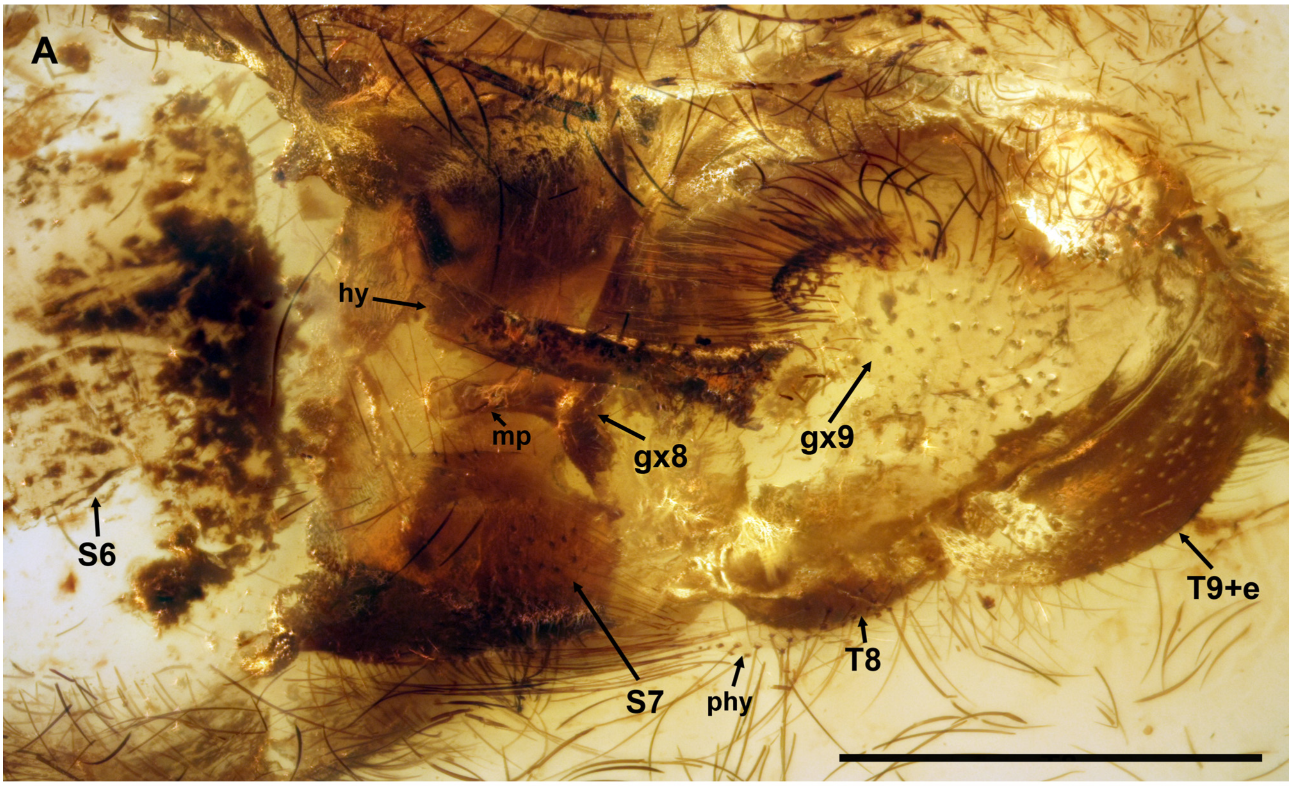



**FIGURE 4**. *Elektroberotha groehni* **gen. et sp. nov.**, holotype GPIH Typ. Kat. Nr. 4550. A, photograph showing scapus (sc) and pedicellus (pe) of right antenna, almost anterior view. B, head and pronotum (pn), dorsal view. Scale bar = 0.5 mm.



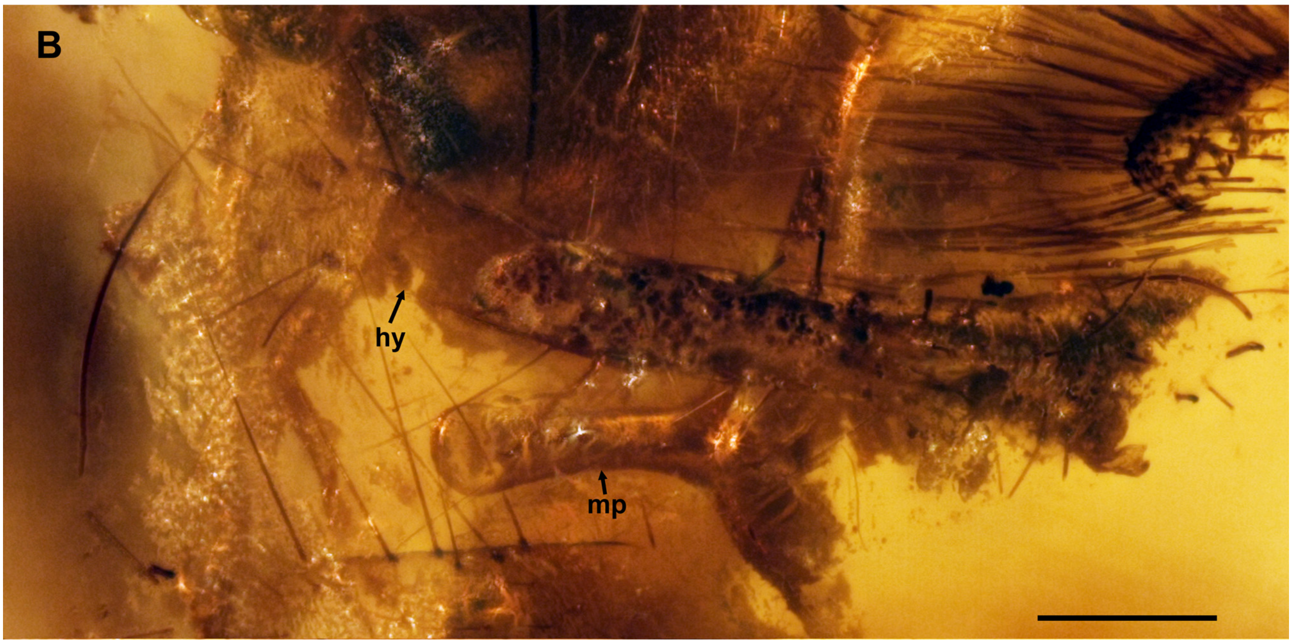




**FIGURE 5**. *Elektroberotha groehni* **gen. et sp. nov.**, holotype GPIH Typ. Kat. Nr. 4550. A, apical segments of female abdomen, ventral view. B, hypocauda (hy) and medial process (mp) of gonocoxites 8 (gx8). e, ectoproct; gx9, gonocoxite 9; phy, pseudohypocauda; S6, S7, 6th and 7th sternites; T8, T9, 8th and 9th tergites. Scale bars = 0.5 mm (A), 0.1 mm (B).

*Paratype* (Fig. 7). Length of body 12.4 mm. Head with large eyes, short face. Vertex covered with rather short setae. Postocular lobe neither especially expanded nor inflated. Antennae rather long; scapus short, approximately twice as long as wide, covered with relatively short setae; pedicellus only slightly longer that first flagellomeres; flagellum of right (complete) antenna consists of 82 segments. Terminal segments of maxillary, labial palpi narrow, elongate, acutely pointed.

Thorax dorsally covered with rather scarce long setae. No thoracic scales detected. Anterior lateral cervical sclerite covered with dense very long setae.

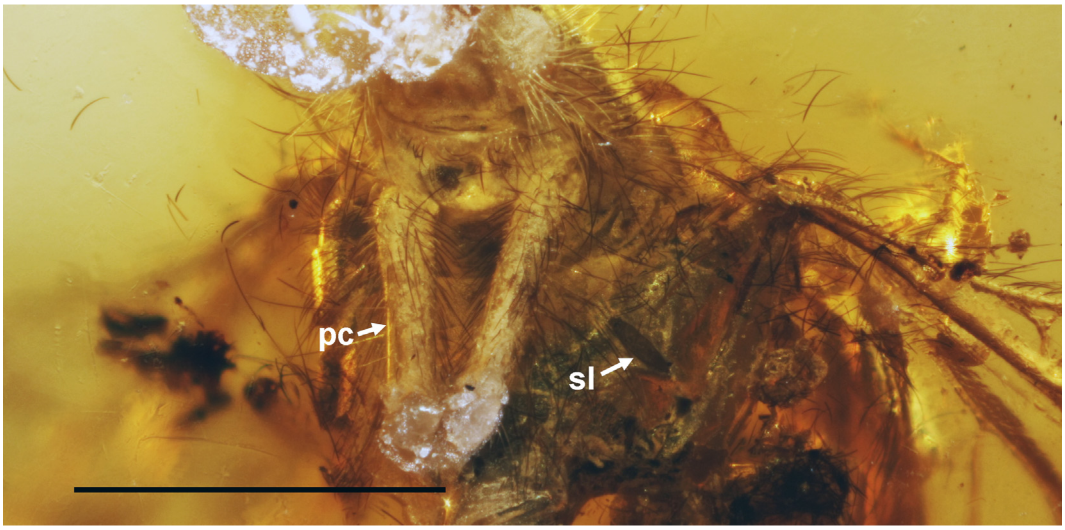



**FIGURE 6**. *Elektroberotha groehni* **gen. et sp. nov.**, holotype GPIH Typ. Kat. Nr. 4550. Thorax showing thoracic scale (sl) and coxa of fore legs (procoxa, pc), ventro-lateral view. Scale bar = 1 mm.

Procoxa, profemur covered with long dense setae; protibia covered with shorter setae, without terminal spurs; protarsus with basal tarsomere longer than remanding tarsus.

Sternite 7 medially divided into pair of large lateral sclerites. Gonocoxites 8 fused, narrow, strongly chitinized; its margins rather distinctly visible; long median process directed forward, somewhat dilated apically. Tergite 9 probably fused with ectoprocts; its ventral pseudohypocaudae well visible, long, covered with dense very long setae, especially apically, not separated from tergite 9 + ectoproct. Gonocoxites 9 rather small, with dense long setae; hypocaudae very long, with rather scarce long setae.

Forewing ca. 13.1 mm long as preserved (estimated complete length ca. 14 mm), 6.8 mm wide. Venation very similar to that of holotype, differing only in details of branching, location of crossveins. Outer gradate series of crossveins complete, including crossvein between stem of RP, RP8; additional (more basal) crossveins between RP7, RP8 absent.

Hind wing 11.6 mm long as preserved (estimated complete length ca. 12.5 mm), 5.6 mm wide. Venation very similar to that of holotype differing only in small details. Additional data not preserved in holotype as follows: six preserved crossveins in outer gradate series (from RP4 to CuA); no inner gradate series of crossveins present; 1r-m straight, connecting RP, MA just after fork; 1m-cu short, oblique.

**Remarks.** The holotype specimen was most probably trapped in resin *post mortem* as it has lost many body parts and its wings are damaged.

The conspecificity of specimen MB I.6021 and the holotype is based on a strong similarity of their wing venation and maculation, and of their visible body structures. These specimens differ in small details of their genital segments structure as preserved; however, these differences appear to be due to the holotype being partly damaged and incomplete. The rather big size difference between the holotype and paratype (estimated complete forewing length 11.5 mm and 14 mm, respectively) is not exceptional in the family. Such size differences between conspecific individual specimens are known in the large Australian species *Trichoma gracilipenne* Tillyard, 1916 and *Trichoberotha ferruginea* Handschin, 1935: the forewing length of the male in the former species ranges from 9.5 mm to 14.5 mm, and that of the female in the latter species ranges from 12.5 mm to 15 mm (Aspöck & Aspöck 1985).

Two other undescribed berothid specimens also reported from Baltic amber (i.e., Bachofen-Echt 1949: Fig. 122; Weitschat & Wichard 1998: Pl. 55a,b). These differ from *Elektroberotha groehni* **sp. nov.** in their reduced number of RP branches (six versus eight respectively), but they might belong to this species. The latter specimen has otherwise very similar venation and its wing maculation is identical with that of the holotype and the paratype.

A further undescribed female from Baltic amber which “has long hypocaudae” (MacLeod & Adams 1968: p. 258) may also be conspecific with *Elektroberotha groehni* **sp. nov.**, but it is not illustrated.

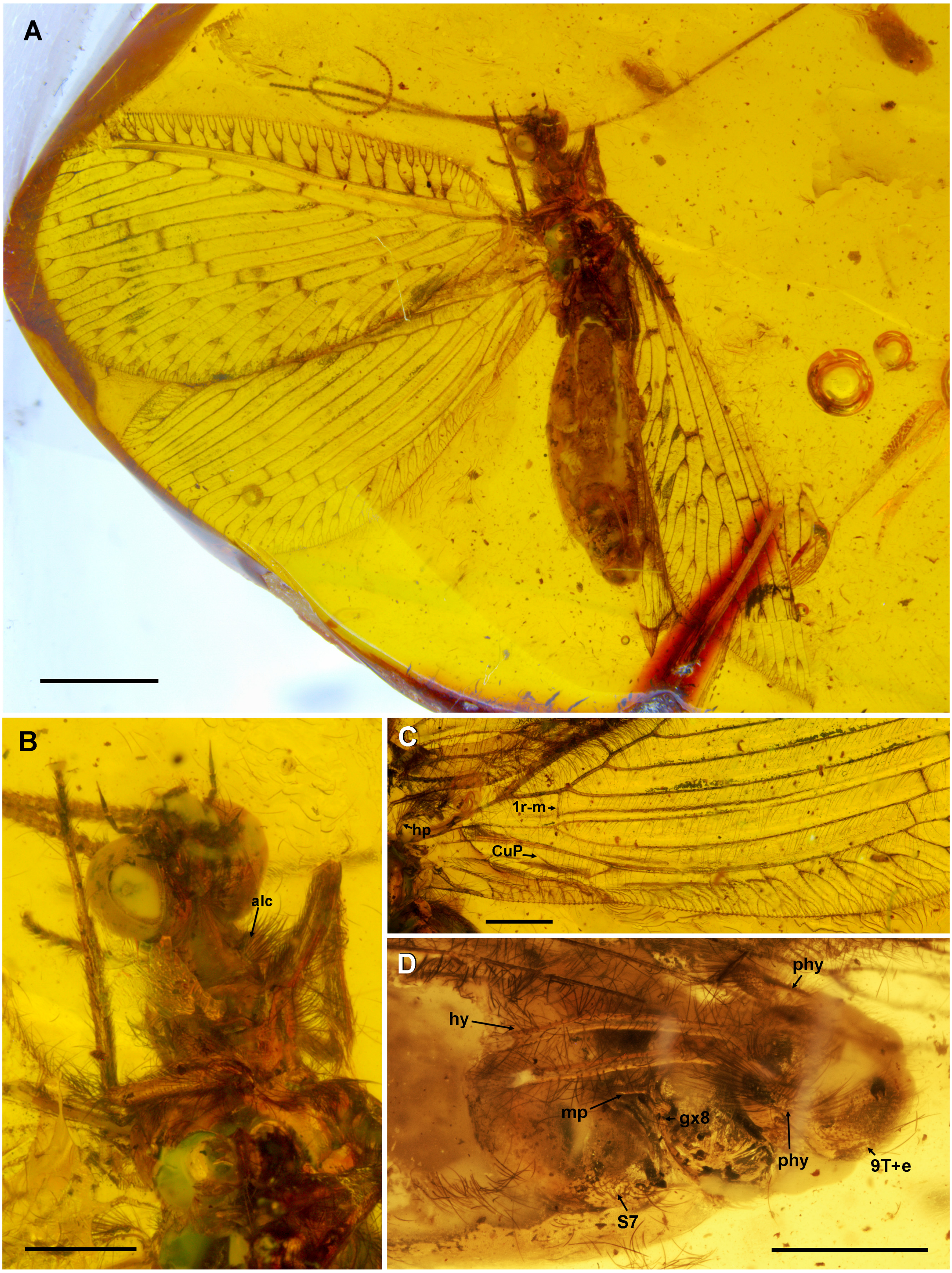



**FIGURE 7**. *Elektroberotha groehni* **gen. et sp. nov.**, paratype MB I.6021. A, specimen as preserved, ventral view. B, head and thorax, ventral view. C, proximal part of right hind wing (dorsal view) showing CuP, basal crossvein between Rs and M (1r-m) and humeral plate (hp). D, apical segments of female abdomen, ventral view. alc, anterior lateral cervical sclerite; e, ectoproct; gx8, gonocoxite 8; hy, hypocauda; mp, medial process; phy, pseudohypocauda; S7, 7th sternite; T9, 9th tergite. Scale bars = 3 mm (A), 1 mm (B–D).

### Distinctive features of *Elektroberotha* gen. nov.

**Scales (squamae) on the thorax.** Modified setae resembling scales of Lepidoptera occur on the thorax in three berothine genera: *Podallea* Navás, 1936, *Spermophorella* Tillyard, 1916, and *Spiroberotha* Adams, 1990 (Aspöck & Nemeschkal 1998). However, these scales occur only on the pronotum, at least in *Podallea* and *Spermophorella* (Aspöck & Aspöck 1986b, 1996), whereas one thoracic scale is detected on the mesopleuron of the holotype of *Elektroberotha* **gen. nov.** (Fig. 6), and none are detected in the paratype. This and the following character state are obviously apomorphic in the family.

**Scales (squamae) on the wings.** These scales occur only in the female, where they are on one (fore- or hind wing) or both wings of many, but not all species of most genera of Berothinae (Aspöck & Nemeschkal 1998). The absence of scales on the wings of *Elektroberotha* **gen. nov.** indicates that this condition might not have evolved yet in Berothinae at that time.

**Scapus.** The relatively short scapus as found in *Elektroberotha* **gen. nov.** is plesiomorphic in the family (Aspöck & Nemeschkal 1998). Among Berothinae, a similar length of the scapus occurs in the Australian *Spermophorella* and *Quasispermophorella* Aspöck et Aspöck, 1986b, and some *Nodalla* Navás, 1926 (e.g., *N. vartianella* (Aspöck et Aspöck, 1984) from Afghanistan). Other genera of Berothinae have a long to extremely long scapus (at least four times the length of the pedicellus).

**Humeral veinlet in the forewing.** The presence of the recurrent humeral veinlet with one or two short branches (i.e., similar to that of the new genus) is a plesiomorphic condition at the family level, and occurs in some extant genera and species (e.g., *Cyrenoberotha* MacLeod et Adams, 1968, *Manselliberotha* Aspöck et Aspöck, 1988a, *Trichoma* Tillyard, 1916, *Naizema* Navás, 1919, *Spiroberotha*). In Berothinae, it is found in *Lekrugeria koenigi* (Esben-Petersen, 1915).

**Crossveins between RA and RP in the forewing.** The majority of extant berothids possess two of ra-rp crossveins proximad the distal subcostal crossvein (or the fusion of ScP and RA). Three ra-rp crossveins as found in *Elektroberotha* **gen. nov.** occur rarely in the family, only in a few genera, e.g., *Mucroberotha*, *Isoscelipteron* Costa, 1863, *Trichoma* Tillyard, 1916. However, a few extant species have many ra-rp crossveins either normally (e.g., *Ormiscocerus nitidipennis* Blanchard in Gay, 1851: Penny & Winterton 2007: Figs 3, 4), or abnormally (e.g., *Trichoma gracillipenne* Tillyard, 1916: Aspöck & Aspöck 1985: Fig. 5). One to two of these crossveins are present in all fossil Berothidae, and three only in *Banoberotha enigmatica* Whalley, 1980 and one specimen of *Mesithone proberotha* Makarkin, 1999 (Whalley 1980: Fig. 4; Makarkin, 1999: Fig. 2c). One crossvein occurs in smaller species with reduced venation (e.g., Engel & Grimaldi 2008: Figs. 31, 35). Therefore, the presence of two crossveins proximad the distal subcostal crossvein (or the fusion of ScP and RA) is most probably a plesiomorphic condition, and their increase to three (or more) or decrease to one is derived. The vast majority of Mantispidae also possess two of these crossveins; some (i.e., Symphrasinae) have one crossvein, an apomorphic character state (Wedmann & Makarkin 2007).

**Crossvein 2r-m in the forewing.** In all Mesozoic berothids, 2r-m (if preserved) connects RP and MA, a state found in Mesithoninae and Paraberothinae as well as in *Elektroberotha* **gen. nov.** This condition is certainly plesiomorphic in the family, as it is present in all other members of the mantispoid clade (both fossil and extant), i.e., Mantispidae and Dipteromantispidae (except some extant mantispid Symphrasinae, in which this crossvein connects RP and M near the fork). In extant berothid taxa, this plesiomorphic condition is retained in more basal groups of Berothidae (i.e., Rhachiberothinae, Cyrenoberothinae, Nyrminae, and Protobiellinae), and very rarely in 'higher' Berothidae, i.e., in Berothinae (only *Lomamyia* Banks, 1905) and Nosybinae (only *Spiroberotha*). The crossvein 2r-m connects R and MA in *Nosybus* Navás, 1910, and RP and M in *Naizema* and *Trichoma*. In the remaining genera of Berothidae, 2r-m is shifted basad and connects R and M.

**CuP in the hind wing.** The presence of the fully-developed CuP in *Elektroberotha* **gen. nov.** is extraordinary for the Berothinae. In extant Berothidae, the fully-developed CuP in the hind wing is present in the small subfamilies Nyrminae (Aspöck 1989: Fig. 1) and Berothimerobiinae (Monserrat & Deretsky 1999: Figs 32, 33; Penny & Winterton 2007: Figs 3, 4). In Rhachiberothinae, the distal part of CuP is reduced, but its proximal part is present (Aspöck & Mansell 1994: Figs 18, 30, 43; Aspöck & Aspöck 1997: Fig. 36). In other berothids, CuP is reduced from its origin to the crossvein 1icu, and represented by only its distal (branching) part. Rarely, the distal part of CuP is slightly longer, extending basad the crossvein 1icu (e.g., *Ausroberothella* Aspöck et Aspöck, 1985: Fig. 25; *Spiroberotha* Adams, 1990: Fig. 1; Ardila-Camacho 2013: Fig. 1e). The hind wings of fossil berothids are usually poorly preserved; at least, their CuP is often difficult to identify with certainly. CuP is clearly detected as a whole vein (a plesiomorphic condition) at least in two fossil species: the Cretaceous paraberothine *Scoloberotha necatrix* Engel et Grimaldi (2008: Fig. 46), and a specimen determined as "near *Jersiberotha luzzii* Grimaldi, 2000" from the Turonian New Jersey amber (Berothidae *incertae sedis*) (Grimaldi 2000: Fig. 19c).

In those genera whose hind wings normally lack CuP, some specimens may occasionally possess it as an abnormality, e.g., in at least one hind wing of *Lomamyia trombenensis* Penny, 1985 from Brazil (see Faulkner 1992: Fig. 38). A similar situation occurs in Mesochrysopidae, where CuP in the hind wing is also reduced. However, in one of the hind wings of *Kareninoides lii* Yang *et al*., 2012 CuP is fully developed and absent in the other (see Yang *et al*. 2012a: Fig. 7). The presence of CuP in *Elektroberotha groehni* **sp. nov.** is probably normal, as CuP is detected in both known specimens of this species.

**Hypocaudae of gonocoxites 9 (gonapophyses laterales).** Long to extremely long hypocaudae are present in all genera of Berothinae (except small in some species of *Stenobiella* Tillyard, 1916) and *Spiroberotha*. In other genera of Berothidae, the hypocaudae are absent or very short.

**Pseudohypocaudae of tergite 9 + ectoproct.** Well-developed pseudohypocaudae are present in all Protobiellinae (i.e., *Austroberothella* Aspöck et Aspöck, 1985 and *Protobiella* Tillyard, 1923) and Rhachiberothinae. This structure is clearly separated from tergite 9 in Rhachiberothinae (Aspöck & Mansell 1994: Figs. 13, 33; Aspöck & Aspöck 1997: Fig. 39), whereas they appear not fully separated in *Protobiella* (Aspöck & Aspöck 1985: Fig. 21), and clearly fused in *Austroberothella* and *Spiroberotha* (Aspöck & Aspöck 1985: Fig. 28; Adams 1989: Fig. 7). It is believed that all other berothids lack pseudohypocaudae (Aspöck & Nemeschkal 1998). However, the pseudohypocauda of *Spiroberotha* fused with tergite 9 + ectoproct is not longer than the protruding ventral part of tergite 9 + ectoproct in some *Lomamyia* species (e.g., MacLeod & Adams 1968: Fig. 18). Therefore, it is hard to distinguish such a fused pseudohypocauda from such a protruding ventral part, and the pseudohypocauda of *Elektroberotha* **gen. nov.** may also be interpreted as a long protruding ventral apex of the tergite 9 + ectoproct. This protruding structure in some berothine genera (especially in *Nodalla* and *Lekrugeria*) is covered with long dense setae similar to those of the new genus (Aspock & Aspock 1986a: Figs. 15, 23; 1998b: Figs. 15, 24, 27).

**Gonocoxites 8 (8th sternite, subgenitale)**. This structure strongly varies throughout the family. It is entirely absent or weakly developed in some basal genera (i.e., *Mucroberotha* Tjeder, 1959, *Hoelzeliella* Aspöck et Aspöck, 1997, *Cyrenoberotha*, and *Manselliberotha*). The genera possessing it are divided into three groups: (1) processes are absent or very unclear; (2) one unpaired medial process; and (3) two processes are present (Aspöck & Nemeschkal 1998). The shape of the unpaired medial process of *Elektroberotha groehni* **sp. nov.** is most similar to that found in the following genera (all Berothinae): *Asadeteva* Aspöck et Aspöck, 1981, some *Podallea* (e.g., *P. tansanica* Aspöck et Aspöck, 1996: Fig. 15), and especially *Nodalla* (e.g., Aspöck & Aspöck 1984: Figs 9, 18; Aspock & Aspock 1998b: Figs 9, 25, 28).

**Sternite 7.** The condition of sternite 7 (i.e., divided medially into a pair of large lateral sclerites) is characteristic of most genera of Berothinae and the rhachiberothine *Rhachiberotha* Tjeder, 1959 and *Hoelzeliella.* This sternite in other berothid genera is unspecialized or at most excided postero-medially.

## Subfamily affinity of *Elektroberotha* gen. nov.

Despite the small number of its known species, the family Berothidae is currently divided into ten subfamilies: the Mesozoic Mesithoninae and Paraberothinae, the Eocene to Recent Rhachiberothinae and Berothinae, and the exclusively extant Cyrenoberothinae, Berothimerobiinae, Nyrminae, Protobiellinae, Trichomatinae and Nosybinae (Wedmann *et al*. 2013). Recently, Berothimerobiinae and Nyrminae were synonymized (Aspöck & Randolf 2014), but this question requires more detailed examination.

The morphology of the *Elektroberotha* **gen. nov.** female terminalia (i.e., long hypocaudae of gonocoxites 9; the medially divided sternite 7; and the structure of gonocoxites 8, especially of the median process) and the presence of at least one thoracic scale clearly indicate that the genus belongs to the subfamily Berothinae. A similar structure of the female terminalia is present in the South American genus *Spiroberotha*, which is currently considered to belong to the Nosybinae, although it superficially most resembles the American berothine genus *Lomamyia*. This putative nosybine affinity is in need of confirmation. *Spiroberotha* was originally assigned to Berothinae by Adams

(1990), and transferred to Nosybinae by Aspöck & Nemeschkal (1998). The latter authors note, however, that this genus "eidonomically looks very similar to some berothine taxa and shares many characters with this subfamily", and that *Spiroberotha* is a "conflicting element within the Nosybinae" (p. 61). The females of *Spiroberotha* can hardly be distinguished from those of Berothinae (especially from *Lomamyia*); only male internal genitalia are similar to those of the Nosybinae. The basic structure of the female internal genitalia is rather conservative in Neuroptera (Szíraki 1996). It is quite possible that this may pertain also to female external structures, at least at the subfamily level within the Berothidae. Recently, Aspöck & Randolf (2014) concluded that *Spiroberotha* "might belong to the Berothinae" (p. 169) based on these female structures, although they still considered the genus to belong to the Nosybinae in their cladogram (Aspöck & Randolf 2014: Fig. 56). Therefore, *Elektroberotha* **gen. nov.** might be better considered as a conflicting element within the Berothinae rather than within the Nosybinae.

Superficially, *Elektroberotha* **gen. nov.** most resembles the berothine genus *Lekrugeria*, especially the African species *L. koenigi*, by its general venation, shape (i.e., outer wing margin not excised), and size (see Aspöck & Aspöck 1986a: Fig. 19). However, the new genus easily differs from *Lekrugeria* by its complete hind wing CuP, short scapus, and female terminalia (especially by the structure of gonocoxites 8). In general, its fully-developed hind wing CuP distinguishes *Elektroberotha* **gen. nov.** from all other Berothinae genera.

The female terminalia of *Elektroberotha* **gen. nov.** appear to be most similar to those of the northern African to southern Asian berothine genus *Nodalla*. The scapus and wing shape in these genera are also configured similarly. However, specimens of *Elektroberotha* **gen. nov.** are larger and have richer venation with some character states differing from those of *Nodalla* (e.g., the crossvein 2r-m connecting RP and MA; three crossveins between RA and RP proximad the distal crossvein scp-ra). Well-developed pseudohypocaudae are absent in *Nodalla*, but the long, dense setae at the elongated ventral part of its tergite 9 + ectoproct are similar to those on the pseudohypocaudae of *Elektroberotha* **gen. nov.**

Interestingly, another Baltic amber berothid genus, *Whalfera* Engel, 2004, is also most similar to an extant African genus, i.e., *Mucroberotha* (Makarkin & Kupryjanowicz 2010).

Two first instar larvae of Berothinae recently described from Baltic amber as "Berothidae indet., larva A" and "Berothidae indet., larva B" (Wedmann *et al*. 2013) may belong to this species.

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