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A new species of Paraberothinae (Neuroptera: Berothidae) from mid-Cretaceous Kachin amber, with discussion of family affinity of the subfamily

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Abstract

Stygioberotha groehni **sp. nov.** (Neuroptera: Berothidae: Paraberothinae) is described from mid-Cretaceous Kachin amber. Its foreleg setation is very similar to that of *S. siculifera* Nakamine *et al*., 2020, but it is easily distinguished from that species by the presence of five spines on the ventral edge of the protibia (four in *S. siculifera*), forewing maculation (absent in *S. siculifera*), and a much shorter scapus. Analysis of wing venation, scapus and prothoracic structure, and female genitalia support the Paraberothinae as being a subfamily of Berothidae rather than of Rhachiberothidae.

Keywords: Neuroptera, Berothidae, Paraberothinae, new species, Kachin amber

Introduction

The Paraberothinae constitute a taxon of small Neuroptera with raptorial forelegs restricted to the Cretaceous. Twenty-three species in 18 genera have been described (Schlüter, 1978; Whalley, 1980; Grimaldi, 2000; Engel, 2004; Nel *et al*., 2005; Engel & Grimaldi, 2008; McKellar & Engel, 2009; Petrulevičius *et al*., 2010; Makarkin, 2015; Shi *et al*., 2015; Nakamine & Yamamoto, 2018; Nakamine *et al*., 2020; Jouault, 2022; Li *et al*., 2023). Its systematic position is controversial, having been assigned to both the Rhachiberothidae (*e.g*., Nel *et al*., 2005) and Berothidae (*e.g*., Makarkin, 2015).

Paraberothines were especially diverse and numerous in mid-Cretaceous Kachin amber of Myanmar. Here, a new species of *Stygioberotha* Nakamine *et al*., 2020 is described from Kachin amber, and the family affinity of Paraberothinae is discussed.

Material and methods

This study is based on a single specimen of Paraberothinae embedded in an oval piece of Kachin amber about 27 × 16 × 5 mm, with two small specimens of Diptera (Psychodidae: Sycoracinae and Tanyderidae), one small Coleoptera (Bostrichidae) and a mite as syninclusions. It was collected from the Hukawng Valley in the state of Kachin in northern Myanmar. The amber is currently considered early Cenomanian (Shi *et al*., 2012; Smith & Ross, 2018). The type specimen is deposited in the Leibniz-Institut zur Analyse des Biodiversitätswandels (Hamburg, Germany).

Photographs were taken by Carsten Gröhn using a Zeiss stereomicroscope (modified with variable objectives: Nikon M Plan 5×, 10×, 20×, 40×; Luminar 18 mm, 25 mm, 40 mm) and an attached Canon EOS 450D digital camera. Line drawings were prepared by the author using Adobe Photoshop CS3.

Venational terminology follows Breitkreuz *et al*. (2017). Crossveins are designated after the longitudinal veins with which they connect and are numbered in sequence from the wing base, *e.g*., 1sc-r, first (proximal-most) crossvein connecting Sc and R/RA; 2m-cu, second crossvein between M/MP and Cu/CuA. Terminology of genitalia follows Aspöck and Aspöck (2008).

Abbreviations: A1–A3, first to third anal veins; CuA, anterior cubitus; CuP, posterior cubitus; jv, jugal vein; M, media; MA, anterior media; MP, posterior media; RA, anterior radius; RP, posterior radius; RP1, proximal-most branch of RP; Sc, subcosta.

Systematic palaeontology

Order Neuroptera Linnaeus, 1758
Family Berothidae Handlirsch, 1906–1908 [1906]
Subfamily Paraberothinae Nel *et al*., 2005

Genus *Stygioberotha* Nakamine *et al*., 2020

Type species. *Stygioberotha siculifera* Nakamine *et al*., 2020, by original designation.

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Revised diagnosis. It may be easily distinguished from other genera of Paraberothinae by very long probasitarsus lacking spine-like setae.

Species included. *S. siculifera*, *S. groehni* **sp. nov.** from Kachin amber.

Stygioberotha groehni **sp. nov.**
(Figs 1–5)

Type material. Holotype GPIH Typ. Kat. Nr. 5221 (CCGG 240461), deposited in the Geological-Paleontological Museum of Nature Hamburg (Das Museum der Natur Hamburg—Geologie-Paläontologie) in the Leibniz Institute for the Analysis of Biodiversity Change (Leibniz-Institut zur Analyse des Biodiversitätswandels), Hamburg, Germany. The Carsten Gröhn collection is separately deposited in the museum with the abbreviation CCGG.

Etymology. After the surname of Carsten Gröhn, a collector and examiner of amber.

Diagnosis. Three crossveins in forewing (3ra-rp, 4im, 2m-cu) with fuscous margins (maculation absent in *S. siculifera*); five spines on ventral edge of protibia (four in *S. siculifera*); scapus *ca*. 3.2 times as long as maximum wide (*ca*. 10 times in *S. siculifera*).

Locality and horizon. Kachin amber (Tanai Township, Myitkyina District, Hukawng Valley, Kachin State, Northern Myanmar); latest Albian/earliest Cenomanian.

Description. Female. Body length 4.3 mm long as preserved. Head with large eyes. Face strongly narrowed towards anterior (in frontal view). Postocular lobe poorly-developed. Maxillary palpus very slender; second to fifth segments relatively long; terminal segment longest, very acute distally. Terminal segment of labial palpus much broader than that of terminal segment of maxillary palpus. Antennae: scapus dark, stout, elongate, approximately 0.25 mm long (*ca*. 3.2 times as long as maximum wide); pedicellus dark, elongate (2.2 times as long as maximum width), pear-shaped, markedly broader that flagellomeres; flagellum pale, with 46 slightly elongate segments covered by relatively long fine setae; terminal segment conical.

Pronotum elongate, much narrower than mesonotum (in dorsal view); dorsally covered with long setae. Structure of mesonotum, metanotum unclear.

Foreleg. Procoxa long (as long as tibia) covered by dense, long fine setae. Protrochanter elongate (nearly two times as long as wide), pear-shaped. Profemur long (0.95 mm), relatively slender; covered with dense fine setae on outer (dorsal) edge, and numerous spines variable lengths forming two rows on inner (ventral) edge (mostly acute, but blunt in distal portion of profemur); one proximal spine longest (Fig. 2C). Protibia slender, shorter than profemur (0.80 mm); with two protrusions in proximal part and five thorn-shape setae in distal part on inner (ventral) edge; fine setae on outer (dorsal) edge. Protarsus covered only with fine setae; probasitarsus longest, second to fourth protarsomere shortest (relative length of tarsomeres 4.8-1-1-1-1.5).

Mid- and hind legs similar, with elongate slender femora, tibiae and tarsi. Metafemur covered with dense, relatively short fine setae and scarce long, stronger setae. Metatibia covered with dense, relatively short fine setae, and with several long, stronger setae at apex forming

FIGURE 1. *Stygioberotha groehni* **sp. nov.**, the holotype GPIH Typ. Kat. Nr. 5221 as preserved. Scale bar = 1 mm.

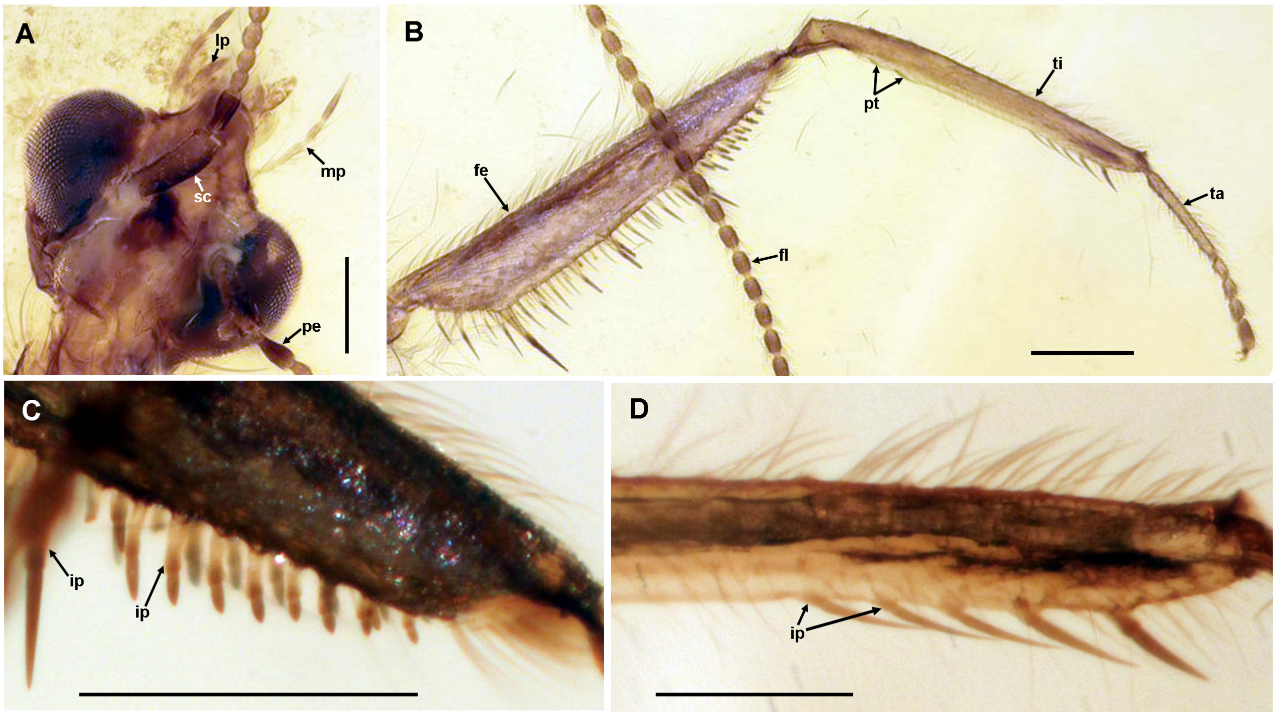

FIGURE 2. *Stygioberotha groehni* **sp. nov.**, the holotype GPIH Typ. Kat. Nr. 5221, head and foreleg. **A**, Head (dorsal view). **B**, Foreleg. **C**, Distal portion of femur. **D**, Distal portion of tibia. Abbreviations: fe, femur; fl, flagellum; ip, integumentary process (peritheca); lp, labial palpus; mp, maxillary palpus; pe, pedicellus; pt, protrusion; ta, tarsus; ti, tibia. Scale bars = 0.2 mm (**A**–**C**), 0.1 mm (**D**).

apical collar. Metatarsus covered with short, fine setae (relative length of tarsomeres 10-2.2-1.4-1-1.2).

Abdomen oval, stout. Boundaries between segments not clearly visible. Presumed eighth tergite long; presumed ninth tergite shorter. These tergites well discernible only in dorsal view. In lateral view, presumable small ectoproct and presumable elongate gonocoxite 9 poorly discernible.

Forewing oval, 4.1 mm long, 1.4 mm wide. Costal space relatively broad, clearly dilated in proximal part. Four subcostal veinlets forked in proximal part of wing, one forked in distal part of Sc (left wing), other simple, moderately widely spaced. Humeral veinlet crossvein-like. Subcostal space broad; basal crossvein (1sc-r) located far proximad origin of RP. Sc, RA fused apically. Sc+RA entering wing margin before apex, apically forked, with two (left wing) to four (right wing) forked veinlets. RA space approximately equal in width to subcostal space, with two crossveins proximad fusion of Sc, RA, none distad. RP originating relatively far from wing base (at 0.25–0.30 complete wing length), zigzagged, with three branches proximad 3ra-rp, and one branch distad 3ra-rp (in both wings). Stem of RP, RP1, RP2, RP3 dichotomously branched distally; RP4 shallowly forked (in both wings). No crossveins between branches of RP. Two crossveins between RP, M: 2r-m connecting stem of RP and probably M before fork (incompletely preserved); 4r-m belonging to outer gradate series. M basally not fused with R; forked slightly distad origin of RP. MA, MP both dichotomously branched distally. One crossvein between MA, MP belonging to outer gradate series. Three crossveins between M, Cu: 1m-cu (‘M5’) connecting M, Cu distad origin of CuP; 2m-cu connecting MP, CuA; 4m-cu belonging to outer gradate series. Cu divided into CuA, CuP rather far from wing base. CuA pectinately branched, with two forked branches. CuP deeply forked; its anterior branch dichotomously forked; its posterior branch pectinately forked with two short branches. One intracubital crossveins. One crossvein (1cu-a1) connecting CuP, A1 much proximad fork of CuP. A1, A2 pectinately branched, with four short branches each. A3 short, with one short branch. Vein-like dark membrane formation between A3 and jugal vein (possibly A4), jugal vein very short, simple; both lack setae. One crossvein (1a1-a2) between anal veins, located much proximad 1cu-a1. Setae on veins long, scarce. Marginal setae arranged in bunches at end of veins and trichosors, moderately long to long (in basal portion). Trichosors prominent along entire wing margin. Wing membrane hyaline, with brown maculation narrowly margined on crossvein 3ra-rp, 4im; widely margined on crossvein 2m-cu.

Hind wing narrowed proximally, broadened distally, *ca*. 3.4 mm long, 1.3 mm wide. Costal space strongly narrowed medially, slightly dilated proximally and strongly dilated distad fusion of Sc, RA. Subcostal veinlets simple, rather widely spaced. Subcostal space rather broad, appears narrowed basally; no crossveins detected. Sc, RA fused apically. Sc+RA ending on wing margin before apex, with six veinlets (two simple, four forked once). RA space (between RA, PR) slightly wider than maximum width of subcostal space, with two crossveins proximad fusion of Sc, RA, none distad. RP originating rather far from wing base (at 0.22 complete wing length), with four branches originating proximad 3ra-rp, none distad. Stem of RP (right wing) shallowly forked twice; RP1–RP3, stem of RP (left wing) dichotomously branched distally; RP4 shallowly forked once. Basal 1r-m long, straight, connected to RP and M at its fork (left wing; possibly incomplete in right wing). M basally probably not fused with R; forked distad origin of RP and at level of 2icu. MA, MP parallel for most of length; MA, MP dichotomously shallowly forked. Outer (fourth) gradate series includes three crossveins from RP1 to CuA. CuA long, running close to hind margin distally, pectinately branched with ten simple short branches. CuP rather long, running very close to hind margin distally, with fire-six very short simple branches. One crossvein (2icu) between CuA, CuP long. No crossveins between Cu, A1 detected. A1 pectinately branched, with two short branches. A2 pectinately branched, with three branches. A3 short, stout, simple. Crossveins between anal veins not detected. Setae on veins rather long, sparsely spaced. Marginal setae arranged in bunches at end of veins and trichosors; long, especially along hind margin. Trichosors prominent along almost entire wing margin (basally poorly discernible). Wing membrane hyaline, without maculation.

Discussion

Generic affinity of the new species

Eight genera (11 species) of Paraberothinae have been described from Kachin amber (Engel, 2004; Engel & Grimaldi, 2008; Makarkin, 2015; Shi *et al*., 2015; Nakamine *et al*., 2020; Jouault, 2022; Li *et al*., 2023). The venation of *Paradoxoberotha* Nakamine *et al*., 2022 and *Dicranoberotha* Li *et al*., 2023 are also very similar to that of Paraberothinae; and its scapus is long, as is characteristic of the subfamily. Its protibia lacks spines on the ventral edge, however, which is diagnostic of Paraberothinae. In any case, these genera appear more closely related to Paraberothinae than Rhachiberothinae; the absence of protibial spines may be a secondary loss or a plesiomorphic state. I would agree with Li *et al*. (2023) that these two genera may represent a specialized group within Paraberothinae

All genera of Kachin amber Paraberothinae have very similar venation, but they may be distinguished by foreleg spines, forewing maculation, and scapus length.

Four genera possess five or less protibial spines: *Scoloberotha* Engel & Grimaldi, 2008 (three), *Micromantispa* Shi *et al*., 2015 (two to three), *Astioberotha* Nakamine *et al*., 2020 (two and five), and *Stygioberotha* Nakamine *et al*., 2020 (four). Other genera have more protibial spines. In *Scoloberotha*, the outer gradate series of crossveins is absent in both fore- and hind wings, but it is present in the new species, and the basitarsus of *Micromantispa* and *Astioberotha* bear two spine-like setae. The new species has a protarsus structure very similar to that of the monotypic genus *Stygioberotha*: its basitarsus is also very long and lacks any spine-like setae. The structure of profemur and protibia are also similar in the two species.

Family affinity of the subfamily Paraberothinae

The taxon was established as a subfamily of Rhachiberothidae by Nel *et al*. (2005) and most authors follow this treatment (*e.g*., Aspöck *et al*., 2020; Nakamine *et al*., 2020, 2022) based exclusively on the raptorial forelegs shared by both taxa. Recently, paraberothine genera were considered to nest within Rhachiberothidae (Li *et al*., 2024). Moreover, Ardila-Camacho *et al*. (2021) considered it to be sister of Symphrasinae in Rhachiberothidae. According to Ardila-Camacho *et al*. (2021), this sister relationship is supported mainly by a unique character state, *i.e*., the presence of the foretarsal Stitz organ situated at the apex of a lanceolate process on the basitarsus, occurring in Paraberothinae, Rhachiberothinae and Symphrasinae that the authors considered to be a synapomorphy of these taxa. In the new species, the absence of the foretarsal spine-like setae could be considered a secondary loss. However, there is significant doubt that the distal part of the lanceolate process ('dorsal spine-like seta' of Makarkin, 2015) of Paraberothinae and the Stitz organ of Symphrasinae are the same character states, although they are surely homologous. The Stitz organ is a specialized sensory receptor that is a highly modified seta, *i.e*., a modified sensilla trichoidea (see Pérez-de la Fuente & Peñalver, 2019) or more likely a modified sensilla chaetica as sensilla trichoidea differs from sensilla chaetica by a weakly developed peritheca (= integumentary process). The Stitz organs are small structures that are situated at the apex on profemoral spines in Symphrasinae (and other Mantispidae) and on the pronotum of some Drepanicinae (Poivre, 1974, 1978; Lambkin, 1986). Poivre (1974) examined these organs in detail. However, spine-like setae on forelegs of Paraberothinae are most probably normal socketed (movable) spines, which are similar in general structure and external morphology to ordinary sensilla chaetica, but thicker. Sensilla chaetica occur on legs of all Neuroptera (Vshivkova & Makarkin, 2010). These sensilla in extant Neuroptera are straight or slightly curved and sit in openings surrounded by a more or less developed bulb-like or pitcher-like base (= socket of Tjeder, 1959, = peritheca of Vshivkova & Makarkin, 2010, = integumentary process of Pérez-de la Fuente & Peñalver, 2019) formed by a joint membrane, and longitudinally grooved with weakly or well-developed ridges, from 6–16 in number (*e.g.*, Vshivkova & Makarkin, 2010: figs 21, 23). The peritheca in Paraberothinae varies from short (Fig. 2D) to very long, tube-like (Fig. 2C).

Therefore, foreleg spines of Paraberothinae are unspecialized relative to the specialized Stitz organs of Symphrasinae, *i.e*., states of these characters are certainly different. In general, these subfamilies are very dissimilar by many characters (*e.g*., the different structure of the prothorax; the absence prostrate setae and sabre-like ovipositor in Paraberothinae; and many others).

The Rhachiberothidae (*s. str*.) and Berothidae are the only taxa to which Paraberothinae may be closely related. Previously, it was argued that Paraberothinae are more correctly considered to be a subfamily of Berothidae, not Rhachiberothidae (see Makarkin & Kupryjanowicz, 2010; Makarkin, 2015). New specimens published after 2015 (*e.g*., Nakamine *et al*., 2020; Yang *et al*., 2020; Li *et al*., 2023; Chen *et al*., 2024) support this idea. In Neuroptera, the extremely long scapus occurs only in some Berothidae with cursorial forelegs and most Paraberothinae (the scapus of Rhachiberothidae is maximum 2.5 times as long as wide). Their wing venation (especially of fossil species) is often very similar, particularly that of the hind wing (*cf*. Fig. 4; Makarkin, 2015: fig. 3B; Makarkin & Ohl, 2015: fig. 4B). The structure of the prothorax of Paraberothinae is similar to that of Berothidae (*cf.* Li *et al*., 2023: fig. 8F and Aspöck & Aspöck, 1986: fig. 26): they lack the posterior postcoxal sclerite, which is separated from other parts of the prothorax by a furrow, whereas such a structure is present in all Rhachiberothidae and Symphrasinae (Aspöck & Aspöck, 1997: fig. 33; Makarkin & Kupryjanowicz, 2010: fig. 4b; Aspöck *et al*., 2020: fig. 7; Ardila-Camado *et al*., 2021: fig. 20a–d). This sclerite has had various names or is not referred to by name. It is located posterior (Fig. 6) or dorsal (in Symphrasinae, see Ardila-Camacho *et al*., 2021: fig. 20d) to the postfurcasternum, and was called "the posterior piece [of the prothorax]" by Lambkin (1986), is probably the "basal sclerite behind the coxae" of Aspöck & Aspöck (1997), is the "part [of the prothorax] posterior to forecoxa" of Makarkin & Kupryjanowicz (2010), was unnamed by Ardila-Camacho *et al*. (2021), and is not mentioned by Tjeder (1959), Aspöck & Mansell (1994), and Aspöck *et al*. (2020). The structure of the female genitalia also does not contradict this assignment. The three most important characters of venation and female genitalia are analysed below in more detail.

All Paraberothinae have only one basal subcostal crossvein in the forewing. The vast majority of extant Berothidae possess a maximum of two subcostal crossveins (basal and distal if Sc and RA are separate distally), except for three extant genera, *i.e*., *Nyrma* Navás, 1933, *Ormiscocerus* Blanchard, 1851, and *Berothimerobius* Monserrat & Deretsky, 1999, which have numerous irregular subcostal crossveins (see Aspöck & Aspöck, 1980: fig. 7; Monserrat & Deretsky, 1999: fig. 32; Monserrat, 2006: fig. 7; Penny & Winterton, 2007: figs 3, 4). The venation of these genera is probably a result of secondary proliferation of crossvenation as crossveins

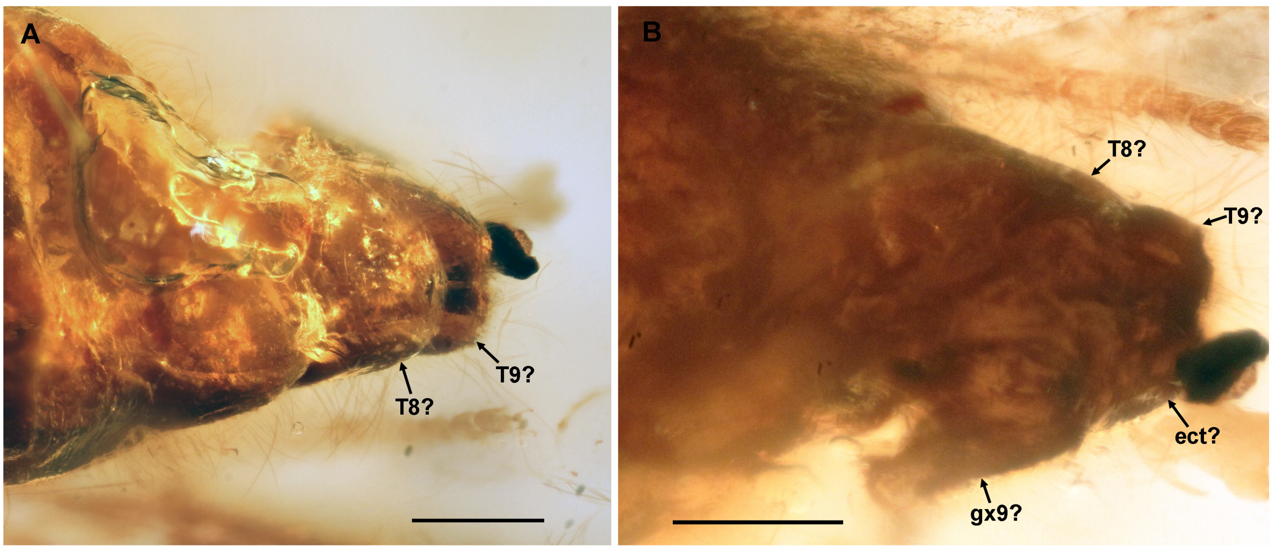

FIGURE 3. *Stygioberotha groehni* **sp. nov.**, the holotype GPIH Typ. Kat. Nr. 5221, abdomen. **A**, Dorsal view. **B**, Ventro-lateral view. Abbreviations: ect, ectoproct, gx9, gonocoxite 9; T8, T9, 8th to 9th tergites. Scale bars = 0.2 mm.

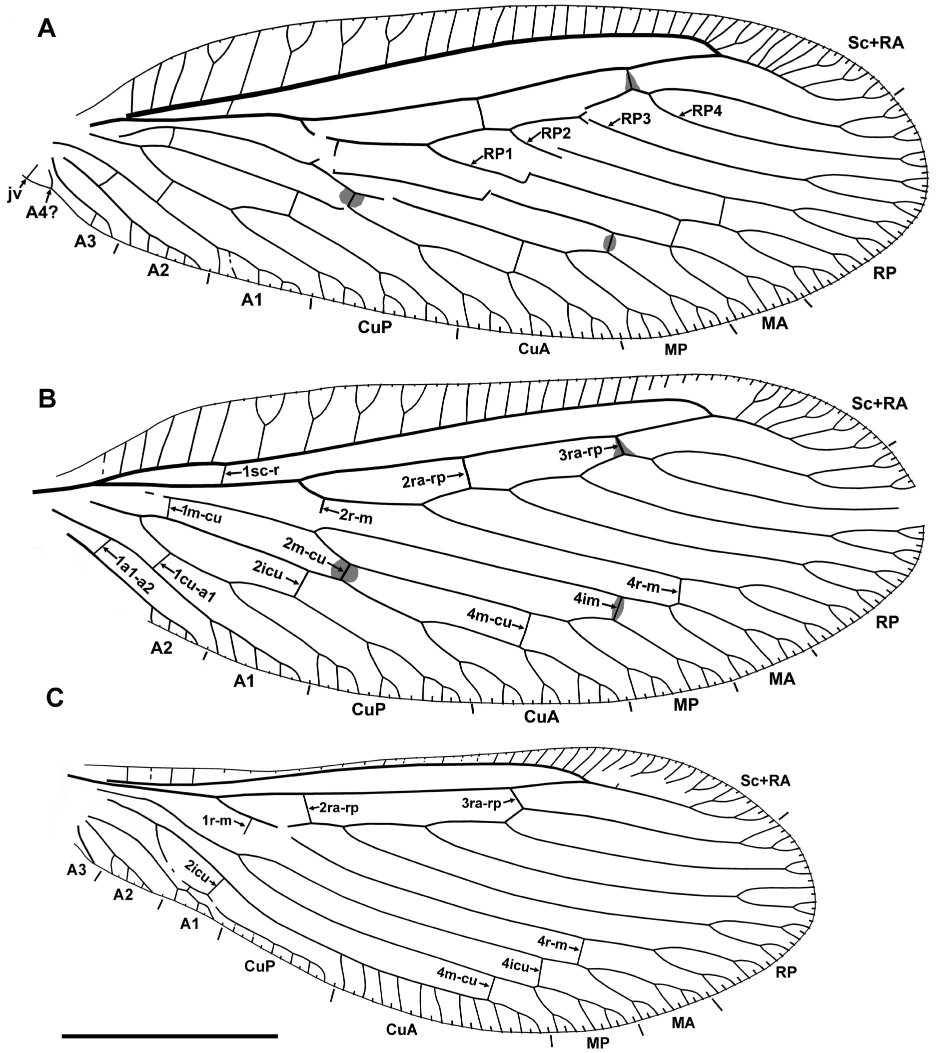

FIGURE 4. Wing venation of *Stygioberotha groehni* **sp. nov.**, the holotype GPIH Typ. Kat. Nr. 5221. **A**, Left forewing (converted to standard dorsal view). **B**, Right forewing. **C**, Right hind wing. Scale bar = 1 mm (all to same scale).

are numerous and irregular also in the radial to medio-cubital spaces. Only one fossil species of Berothidae with cursorial legs possessing an intermediate subcostal crossvein belongs to the unusual Kachin amber genus *Osmyloberotha* Khramov, 2021 (see Li *et al*., 2023). On the other hand, an intermediate subcostal crossvein is present in all Rhachiberothinae (*e.g*., Aspöck & Mansell, 1994: figs 6, 43; Makarkin & Kupryjanowicz, 2010: fig. 3), and the Mesozoic Mesithoninae (*e.g*., Makarkin, 1999: fig. 1; Khramov, 2015: fig. 1).

The fully-developed CuP in the hind wing is present in all Paraberothinae in which hind wings are well preserved (*e.g*., Makarkin, 2015: fig. 4; Nakamine *et al*., 2020: fig. 1). The condition of the hind wing CuP in Berothidae was discussed earlier (see Makarkin & Ohl, 2015). Of extant taxa, the fully-developed CuP in the hind wing is present only in three genera, which have similar dense crossvenation and are treated as constituting the subfamily Nyrminae (Aspöck & Randolf, 2014): *Nyrma*, *Ormiscocerus*, and *Berothimerobius*. CuP is reduced proximally in other extant berothids, but present distally (*e.g*., Aspöck & Aspöck, 1991: fig. 1). However, in fossil berothids the fully-developed hind wing CuP appears to be a normal condition. In particular, this is characteristic of *Elektroberotha groehni* Makarkin & Ohl, 2015 from late Eocene Baltic amber, the only species of the subfamily Berothinae with such a character state. Most mid-Cretaceous species of Berothidae with cursorial legs possess a fully-developed hind wing CuP (*e.g*., Yang, 2020: figs 2B, 4B, 8B, 10B, 11D, 18B; Chen *et al*., 2024: fig. 8D). In all extant Rhachiberothinae, the CuP is present proximally but reduced distally, and CuP appears to be continuous with a long longitudinal crossvein between CuA and CuP (Tjeder, 1959: fig. 237; Aspöck & Mansell, 1994: figs 18, 30, 43; Aspöck & Aspöck, 1997: fig. 36).

The configuration of the hind wing basal crossvein between R and M (1r-m) in Paraberothinae is similar to that of Berothidae with cursorial legs, *i.e*., crossvein-

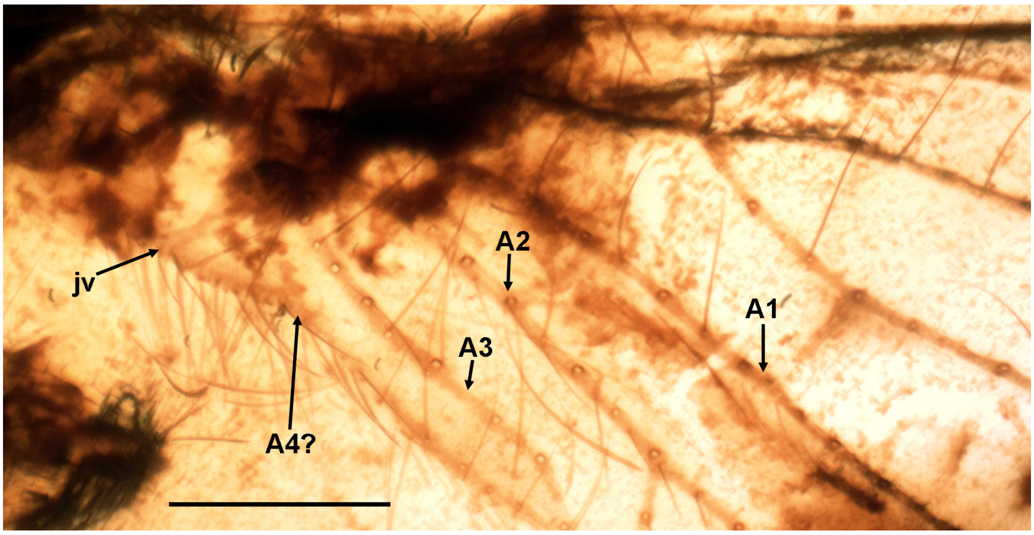

FIGURE 5. *Stygioberotha groehni* **sp. nov.**, the holotype GPIH Typ. Kat. Nr. 5221, the basal posterior portion of the left forewing. Scale bar = 0.2 mm.

like (upright) or absent. The only species of Berothidae with cursorial legs that possesses the long sinuous (sigmoid) 1r-m belongs to the unusual Kachin amber *Osmyloberotha* (see Li *et al*., 2023: fig. 2A, B). However, all Rhachiberothinae have a long sinuous 1r-m (*e.g.*, Aspöck & Mansell, 1994: figs 6, 18, 43). The crossvein 1r-m is also sinuous in one specimen of the rhachiberothine-like *Dicranoberotha liumohanae* Zhuo, Li & Liu in Li *et al*., 2023 (fig. 13H), but it is located far from the base of M and this curvature may well be secondary.

The correct interpretation of male and female genital structures in fossils is usually difficult, but they are clearly discernible in some amber species, and in females of the Kachin amber rhachiberothid-like genera *Paradoxoberotha* and *Dicranoberotha*, these are remarkable. Nakamine *et al*. (2022) and Li *et al*. (2023) described very long hypocaudae and pseudohypocaudae in these genera.

The hypocauda of *Paradoxoberotha chimaera* Nakamine *et al*., 2022 appears to be articulated with gonocoxite 9 (Nakamine *et al*., 2022: fig. 4), whereas in all extant species of Berothidae with cursorial forelegs and Rhachiberothinae it is a simple process of gonocoxite 9 without articulation (see *e.g*., Aspöck & Aspöck, 2008: figs 115, 116; Li *et al*., 2018: figs 15, 16, 21, 22, 31, 32). An extremely long, non-articulated hypocauda is also present in two species of *Dicranoberotha* (Li *et al*., 2023: figs 14, 16B–E). A similar long hypocauda is only found in extant Berothinae (*e.g*., Aspöck & Aspöck, 1991: figs 2, 9).

The pseudohypocauda of *Paradoxoberotha* and *Dicranoberotha* is very long and slender structure. Very similar structures are found in the Kachin amber berothids with cursorial forelegs *Jersiberotha myanmarensis* Engel & Grimaldi, 2008 and *Haploberotha persephone* Engel & Grimaldi, 2008. The pseudohypocauda of extant species of Berothidae with cursorial forelegs and Rhachiberothinae is a process of the 9th tergite (often articulated), but it is never so slender and long (Aspöck & Aspöck, 1985: figs 21, 28; Aspöck & Mansell, 1994: figs 13, 33, 44). On the other hand, the hypocauda and pseudohypocauda of the berothid with cursorial forelegs *Cornoberotha aspoeckae* Yang *et al*., 2020 (fig. 3D) from Kachin amber are very similar to those of extant Rhachiberothinae (*e.g*., Aspöck & Mansell, 1994: figs 13, 44). Females of Paraberothinae have an elongate structure which is usually interpreted as gonocoxite 9 (Fig. 3; Nakamine *et al*., 2020: figs 12, 14), whose ventral part is most probably homologous with the hypocauda.

These examples show that female genitalia of Berothidae with cursorial forelegs, Paraberothinae and Rhachiberothinae (especially those of fossils) are generally similar and may be confused. At this stage, we can only say that all three taxa are characterized by a tendency to form a ventral process of 9th tergite and ectoproct.

Ardila-Camacho *et al*. (2021) and Li *et al*. (2024) argue that raptorial forelegs originated only once in Mantispoidea, *i.e*., in the following taxa: Mantispidae, Rhachiberothidae, Dipteromantispidae, Paraberothinae, and Mesithoninae. I think, however, that this idea is only hypothetical. Judging from this, Paraberothinae cannot belong to Berothidae. The oldest members of Mantispoidea that possess raptorial forelegs are those from the late Middle/early Late Jurassic Daohugou locality (China). They are represented by three taxa: Mesomantispinae (Mantispidae), *Archarhachiberotha longitarsa* Wang

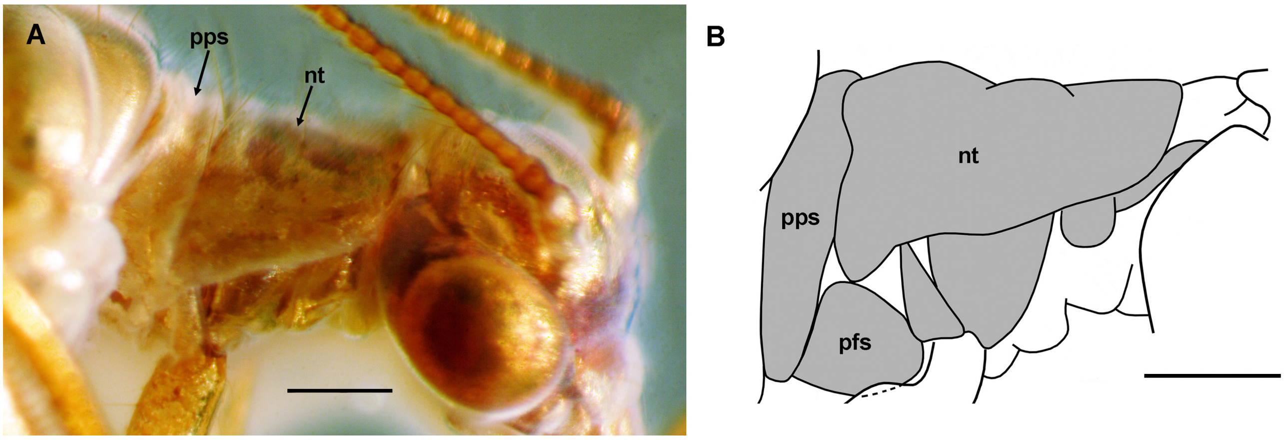

FIGURE 6. Prothorax of Rhachiberothidae (lateral view). **A**, *Whalfera wiszniewskii* Makarkin & Kupryjanowicz, 2010 from late Eocene Baltic amber (photograph of J. Kupryjanowicz). **B**, extant *Mucroberotha vesicaria* Tjeder, 1968 (re-drawn from Ardila-Camacho *et al*., 2021, simplified). Abbreviations: nt, pronotum; pfs, postfurcasternum; pps, posterior postcoxal sclerite. Scale bars = 0.2 mm.

et al., 2024 (stem-group lineage of Mantispoidea or Rhachiberothidae without assigning to a family), and an undescribed species of Mesithoninae (status and systematic position unclear) (Jepson *et al*., 2013; Wang *et al*., 2024; pers. obs.). *Archarhachiberotha longitarsa* and an undescribed mesithonine lack the prothoracic posterior postcoxal sclerite (which have Rhachiberothidae and Mantispidae) and prostate setae (the presence of which is an autapomorphy of Mantispidae). So, these mantispoids are berothid-like taxa, and do not belong to Mantispidae.

The raptorial forelegs in *Archarhachiberotha longitarsa* are very primitive. The only slightly thickened femur and tibia indicate its raptorial nature along with the absence of spines on the femur and tibia. The structure of the raptorial forelegs in Mesomantispinae and Mesithoninae from Daohugou is very different: the femur shape and its spination (small spines in two rows) of Mesomantispinae are similar to those of extant Symphrasinae, *i.e*., rather typical for Mantispidae, while the femoral spination of an undescribed mesithonine is represented by one row of homonomous long spine-like setae. Therefore, the raptorial forelegs are strongly dissimilar in the oldest known Mantispoidea, and they may well have originated independently in different groups of the superfamily, including Paraberothinae.

Conclusion

The discovery of *Stygioberotha groehni* **sp. nov.** highlights the diversity of Paraberothinae in Kachin amber. Its study allows a better understanding of the structure of the forelegs and wing venation in this subfamily. In particular, their profemoral, protibial and protarsal spines do not bear Stitz organs. Analysis of venation, antennal scapus and prothoracic structure, and female genitalia support the idea that it is more correct to consider Paraberothinae as a subfamily of Berothidae, not Rhachiberothidae.

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