

Short communication

A new species of *Haploberotha* (Neuroptera: Berothidae) from mid-Cretaceous Burmese amber

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ARTICLE INFO

Article history:

Received 7 April 2018

Received in revised form

7 June 2018

Accepted in revised form 16 June 2018

Available online 20 June 2018

Keywords:

Neuroptera

Berothidae

New species

Burmese amber

ABSTRACT

Haploberotha carsteni sp. nov. (Neuroptera: Berothidae) is described from mid-Cretaceous Burmese amber. It has a very similar venation to *H. persephone* Engel and Grimaldi, 2008, but clearly differs by the male genitalia. The simplification of the venation (as found in *H. carsteni* sp. nov.) likely occurred independently many times in berothids during the Mesozoic. There are at least two character states in the male genitalia of some Cretaceous berothids, which are not found in extant taxa, i.e., the presence of extremely long gonocoxites 9, which extend far beyond the ectoprocts, and the long slender ventral process of T9+ectoproct.

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1. Introduction

Berothidae is a relatively small family today, comprising approximately 130 extant species (including Rhachiberothinae) (Oswald, 2018). Nine subfamilies are currently recognized in the family: Mesithoninae and Paraberothinae from the Mesozoic (see Makarkin et al., 2012; Makarkin, 2015a); Rhachiberothinae and Berothinae known from the Eocene to Recent (see Makarkin and Kupryjanowicz, 2010; Makarkin, 2017), and Cyrenoberothinae, Nyrminae, Protobiellinae, Trichomatinae and Nosybinae, which include only extant species (Aspöck and Nemeschkal, 1998; Aspöck and Randolph, 2014). The Rhachiberothinae is often considered as a distinct family.

There are numerous fossil taxa: 49 species in 35 genera have been described from the Middle Jurassic to late Eocene (pers. data). In particular, berothids dominate the neuropteran assemblage in the mid-Cretaceous Burmese amber, both in number of specimens and species, with 15 described species (Engel, 2004; Engel and Grimaldi, 2008; Makarkin, 2015a; b; Yuan et al., 2016). Of these, four species belong to Paraberothinae, which have raptorial forelegs; the subfamily affinities of others with walking (cursorial) forelegs are unclear.

The only known species of the genus *Haploberotha* Engel and Grimaldi, 2008, *H. persephone* Engel and Grimaldi, 2008, is

abundant in Burmese amber. It was described from 23 specimens (Engel and Grimaldi, 2008), and subsequently reported by Yuan et al. (2016). Additionally, there are specimens in private collections. Herein, a new species of *Haploberotha* is described from Burmese amber, whose venation is very similar to that of *H. persephone*, but their male genitalia are different. The structure of male genitalia in the Cretaceous berothids, and the simplification of their venation are discussed.

2. Material and methods

This study is based on single specimen of Berothidae embedded in a small piece of Burmese amber (about 9 mm long), with two specimens of Psychodidae (Diptera) and parts of another berothid as sininclusions. The precise mine from which this piece originated cannot be determined, as it was acquired from a fossil trader. Burmese amber originates from the Hukawng Valley in the state of Kachin in northern Myanmar. A map of this valley is given by Grimaldi et al (2002, fig. 1). The age is currently considered to be earliest Cenomanian (Shi et al., 2012; Smith and Ross, 2018).

The 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.

The venational terminology in general follows Kukulová-Peck and Lawrence (2004) as interpreted by Yang et al. (2012, 2014).

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Terminology of wing spaces and details of venation (e.g., spaces, veinlets) follows [Oswald \(1993\)](#). The crossveins designation follows [Makarkin \(2015a\)](#). Crossveins are designated after the longitudinal veins which they connect and are numbered in sequence from the wing base, e.g., 1scp-r, first (proximal-most) crossvein connecting ScP and R/RA; 2m-cu, second crossvein between M/MP and Cu/CuA. Terminology of genitalia follows [Aspöck and Aspöck \(2008\)](#).

All taxonomic acts established in the present work have been registered in ZooBank LSID (see below), together with the electronic publication urn:lsid:zoobank.org:pub:499C8085-92B5-453F-88CC-91F7B091872D.

Abbreviations: AA1–AA3, first to third anterior Analis; CuA, anterior Cubitus; CuP, posterior Cubitus; MA and MP, anterior and posterior branches of the Media; RA, anterior Radius; RP, posterior Radius; RP1, proximal-most branch of RP; RP2, branch of RP distad RP1; ScP, posterior Subcosta.

3. Systematic palaeontology

Order Neuroptera [Linnaeus, 1758](#)

Family Berothidae [Handlirsch, 1906](#)

Genus *Haploberotha* [Engel and Grimaldi, 2008](#)

Type species. *Haploberotha persephone* [Engel and Grimaldi, 2008](#), by original designation.

Revised diagnosis. T9+ectoproct of male bears elongate, slender ventral process; in both wings, no gradate series of crossveins present; in forewing, one crossvein between RA, RP (3ra-rp); two branches of RP proximad 3ra-rp; in hind wing, basal crossvein 1r-m lost.

Species included. *H. persephone* and *H. carsteni* sp. nov. from Burmese amber.

Remarks. The genus easily differs from other berothid genera by the male genitalia and simplified venation (see discussion below).

Haploberotha carsteni sp. nov.

(urn:lsid:zoobank.org:act:35385D77-CC0C-4804-BF81-920BA920DDD2)

[Figs. 1–3](#)

Derivation of name. After the first name of Carsten Gröhn, in recognition of for his help in the examination of the holotype.

Type material. Holotype GPIH Typ. Kat. Nr. 4936 (collection of C. Gröhn, no. 11220), deposited in Centrum of Natural History [Centrum für Naturkunde] (formerly Geological-Paleontological Institute and Museum of the University of Hamburg [Geologisch-Paläontologisches Institut und Museum der Universität Hamburg]). A complete well-preserved male specimen.

Type locality and horizon. Burmese amber (Northern Myanmar: Kachin State: Myitkyina District: Tanai Township: Hukaung Valley). Lowermost Cenomanian.

Diagnosis. Forewing maculation (see description) distinct [absent or poorly-developed in *H. persephone*: see [Engel and Grimaldi, 2008](#), figs. 26, 31; [Yuan et al., 2016](#), fig. 8C]; gonocoxites 9 not visible (not extruding beyond abdomen segments) [far extruding beyond abdomen segments in *H. persephone*]; ventral process of T9+ectoproct not curved inward and bifid terminally [curled inward and acute terminally in *H. persephone*].

Description. Male. Body length 1.85 mm long as preserved. Head with large eyes. Face anterior eyes short. Vertex probably with two lateral setigerous calluses (? ocular pulvinae) (poorly discernible). Postocular lobe well-developed, inflated. Third and fourth segments of maxillary palpus relatively short, approximately twice as long as wide; terminal segment elongated, very acute distally. Terminal segment of labial palpus similar to that of terminal

segment of maxillary palpus. Antennae: scapus elongate (approximately two times as long as maximum wide); pedicellus only slightly longer than maximum wide, which slightly broader than flagellomeres; flagellum with 22 segments covered by relatively long setae; basal flagellomeres transverse, distal flagellomeres slightly elongate; terminal segment conical.

Pronotum elongate, narrow (in lateral view); dorsally covered with long, dense setae. Structure of mesonotum, metanotum unclear.

Legs. Tibiae without terminal spurs. Structure of tarsi similar in all legs.

Foreleg. Procoxa long (ca. 0.30 mm) covered by scarce, short setae. Protrochanter elongate (nearly two times as long as wide), slightly curved. Profemur relatively short (ca. 0.33 mm), slender; covered with long setae on inner (ventral) and dense, much shorter setae on outer (dorsal) edge. Protibia slender, nearly as long as profemur; covered with very long setae on inner edge, and shorter setae on outer edge. Protarsus: probasitarsus longest, fourth protarsomere shortest (relative length of tarsomeres 3.3–1.7–1.3–1–1.7).

Mid-leg poorly preserved. Mesofemur and mesotibia appear relatively short, covered with dense relatively short setae.

Hind leg. Metacoxa stout, conical, rather short. Metatrochanter short. Metafemur long, slender; covered with relatively short fine setae. Metatibia long, slender; covered with dense elongate fine setae, and with several longer and stronger setae erected at more obtuse angle.

Forewing broadly-oval, ca. 2.10 mm long, 0.85 mm wide. Costal space relatively narrow, slightly dilated proximally. All subcostal veinlets simple, moderately widely spaced. Humeral veinlet crossvein-like. Subcostal space broad; proximal crossvein (1scp-r) located proximad origin of RP. ScP, RA fused apically. ScP+RA with two forked veinlets, entering wing margin before apex. RA space slightly wider than subcostal space, with one crossvein proximad fusion of ScP, RA, none distad. RP originates relatively far from wing base (at 0.23 of complete wing length), with two long branches originated proximad 3ra-rp, and one short branch distad 3ra-rp (in both wings). RP1 dichotomously branched distally; stem of RP, RP2, RP3 shallowly forked (in both wings). No crossveins between branches of RP. One crossvein between RP, M (2r-m) connecting stem of RP, MA. M basally approaching R; forked distad origin of RP. MA, MP dichotomously branched. No crossveins between MA, MP. Two crossveins between M, Cu: 1m-cu ('M5') connecting M, Cu proximad origin of CuP; 2m-cu connecting MP, CuA. Cu divided into CuA, CuP rather far from wing base. CuA, CuP dichotomously branched. No intracubital crossveins. One crossvein (1cu-aa1) between Cu, AA1 connecting CuP, AA1 much proximad their branching. AA1, AA2 pectinately branched, with two short branches. AA3 short, simple. One crossvein (1aa1-aa2) between AA1, AA2 located much proximad 1cu-aa1. Setae on veins rather long. Marginal setae arranged in bunches at end of veins and trichosors, long to very long. Trichosors prominent along entire wing margin. Wing membrane hyaline, with following dark brown maculation: narrowly margined crossvein 3ra-rp; widely margined crossvein 2m-cu; spots at origin (inside) of RP1, RP3 and at primary forks of RP1, MA, MP, CuA.

Hind wing narrowed proximally, broadened distally, ca. 1.60 mm long, 0.65 mm wide. Costal space strongly narrowed medially, slightly dilated proximally and strongly dilated distad fusion of ScP, RA. Subcostal veinlets simple, rather widely spaced. Subcostal space rather broad, basally appears narrowed; no crossveins detected. ScP, RA fused apically. ScP+RA entering wing margin before apex, with five simple veinlets. RA space clearly wider than subcostal space, with one crossvein proximad fusion of ScP, RA,



Fig. 1. *Haploberotha carsteni* sp. nov., holotype GPIH Typ. Kat. Nr. 4936 as preserved. Scale bar represents 0.2 mm.

none distad. RP originates rather far from wing base, with two branches originated proximad 3ra-rp, none distad. Stem of RP, RP2 shallowly forked (in right wing; stem of RP twice forked in left wing); RP1 dichotomously branched distally. No crossveins between branches of RA and RP, M; basal 1r-m not detected, most probably absent. M basally not fused with R; forked distad origin of RP and slightly proximad 2icu. MA, MP nearly parallel for most length; MA dichotomously branched; MP pectinately branched, with two short simple branches. No intramedian crossveins. One poorly-discernible crossvein between M, Cu (1m-cu) connecting these veins far proximad fork of M. CuA long, running close to hind margin distally, pectinately branched with six simple short branches (right wing; five branches in left wing). Basal part of CuP not discernible; CuP distally with one poorly-discernible simple branch. One crossvein (2icu) between CuA, CuP. No crossveins between Cu, AA1 detected. AA1 pectinately branched, with two short branches. AA2, AA3 short, simple. Crossveins between anal veins not detected. Setae on veins rather long. Marginal setae arranged in bunches at end of veins and trichosors; long to very long, especially along hind margin. Trichosors prominent along entire wing margin. Wing membrane hyaline, without maculation.

Abdomen oval, stout. All segments clearly visible except terminal-most, with broad membranous space between sternites and tergites (Fig. 2A). First tergite and sternite relatively long, only slightly shorter than two to six tergites and sternites. Seventh tergite well developed, dorsally broader than laterally. Seventh sternite narrow. Eighth tergite not clearly identified, probably short. Eighth sternite well developed, rather narrow ventrally, slightly dilated laterally. Ninth tergite appears fused with ectoprocts forming paired separate structures (T9+ectoprocts); T9+ectoprocts nearly ovoid in lateral view, with long, slender, slightly curved, terminally bifid ventral process (clearly discernible only on right T9+ectoproct); distal part of ectoproct somewhat

bent inward, deckle-edged in ventral part and armed with small finger-like process. Ninth sternite not clearly identified; probably very short. All tergites and sternites covered with dense, long fine setae.

Remarks. The venation of *Haploberotha carsteni* sp. nov. is very similar to that of *H. persephone*, but the new species differs from the latter by the presence of rather well-developed maculation on the forewing. Also, the crossvein 1m-cu is located much proximad the origin of CuP in *H. carsteni* sp. nov., whereas it is distad the origin of CuP in the reported specimens of *H. persephone* (see Engel and Grimaldi, 2008, figs. 26, 31; Yuan et al., 2016, fig. 8C) and unpublished specimens (pers. obs.). However, in at least one unpublished male of *H. persephone* this crossvein is located slightly distad the origin of CuP, and there is poorly-developed maculation (pers. obs.). So, these species may be confidently differentiated from each other mainly by male genitalia.

4. Discussion

4.1. Simplification of the venation in *Haploberotha*

The venation of *Haploberotha* is simplified in comparison with the vast majority of other berothid genera. By the complete loss of the outer gradate series of crossveins in the radial to medio-cudital spaces (hereinafter, the gradate series) and generally by similar simplified crossvenation, its forewing venation is most similar to that of three fossil species, e.g., *Pseudosysira minima* Makarkin, 1999 (? Mesithoninae) from the Barremian of Baissa (Russia: Transbaikalia), *Spinoberotha mickaelacrai* Nel et al., 2005 (Paraberothinae) from the late Barremian of Lebanese amber (Mdeirij/Hammana locality), and *Microberotha macculloughi* Archibald and

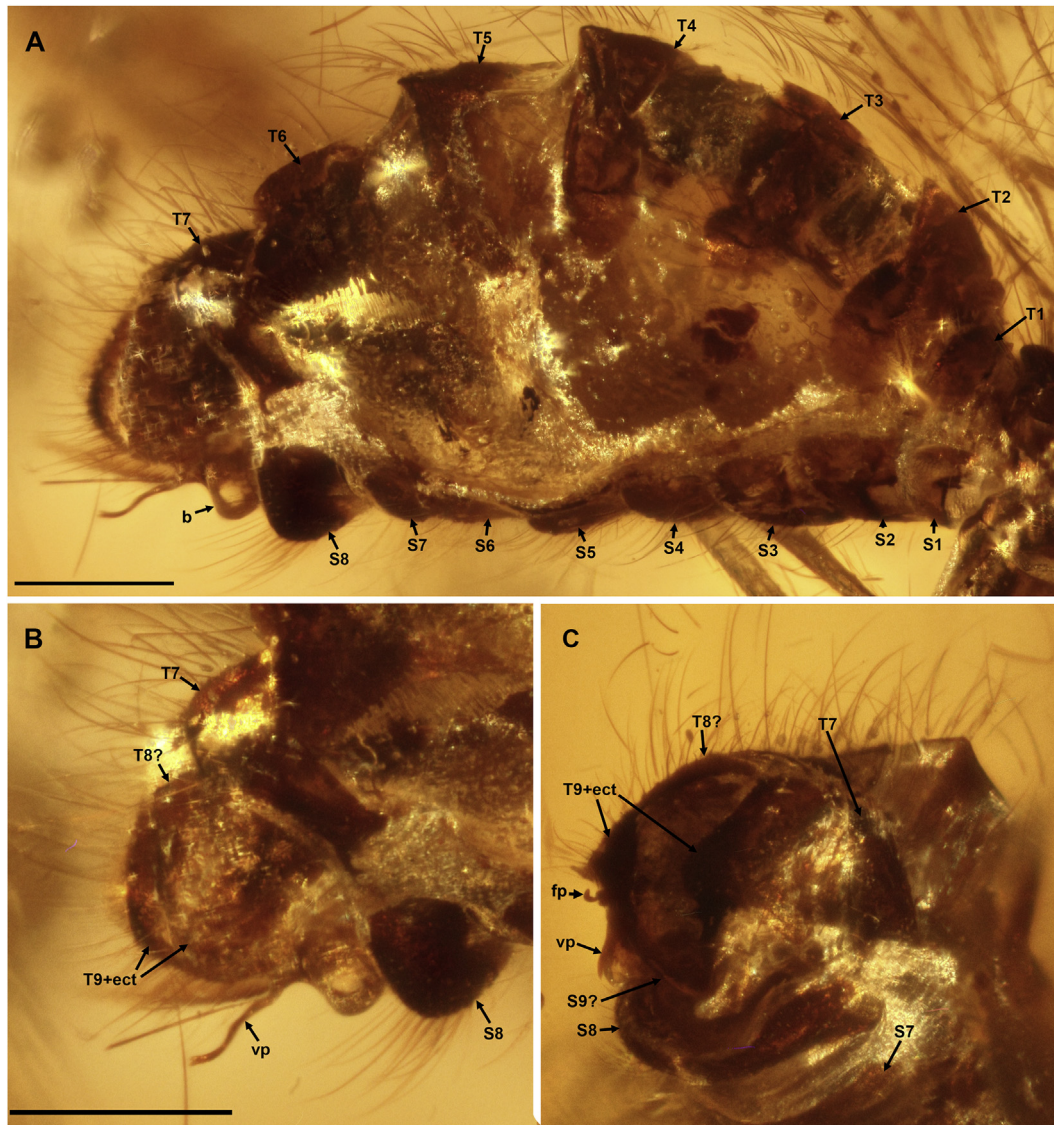


Fig. 2. *Haploberotha carsteni* sp. nov., abdomen of the holotype GPIH Typ. Kat. Nr. 4936. A, whole abdomen, lateral view; B, terminal segments, lateral view; C, terminal segments, ventro-latero-caudal view. b, air bubble; ect, ectoproct; fp, finger-like process of ectoproct; S1–S9, 1st to 9th sternite; T1–T9, 1st to 9th tergite; vp, ventral process of T9+ectoproct. Scale bars represent 0.2 mm (B, C to scale).

Makarkin, 2004 (uncertain subfamily but genitally is similar to Cyrenoberothinae) from the early Eocene of Hat Creek amber (Canada: British Columbia). The gradate series is also not figured in *Krokhathone tristis* Khrakov, 2015 (? Mesithoninae) from the Late Jurassic of Karatau (Kazakhstan), however this needs confirmation as the specimen is poorly preserved (Khrakov, 2015, pl. 5, fig. 65), and in other species (*Krokhathone parvas* Khrakov, 2015) from the same locality this series appears to be present (Khrakov, 2015, pl. 5, fig. 5). A similar situation is present in some other berothids from Burmese amber (e.g., *Iceloberotha simulatrix* Engel and Grimaldi, 2008 and *Jersiberotha tauberorum* Engel and Grimaldi, 2008), in which the gradate series is absent, but these species possess additional crossveins and other species in these genera have the gradate series. It is noteworthy, that these genera belong to several (at least three) quite different lines of the family. The loss of the gradate series is not found in extant berothids.

The loss of the basal crossvein 1r-m in the *Haploberotha* hind wing is also noteworthy. This condition occurs rarely in the family, and is obviously apomorphic. This crossvein is probably absent only

in some Cretaceous species: in Paraberothinae (i.e., *Spinoberotha mickaelacrai* from the late Barremian of Lebanese amber; *Scoloberotha necatrix* Engel and Grimaldi, 2008 and *Creagroparaberotho groehni* Makarkin, 2015a from Burmese amber), and in two species with cursorial forelegs (i.e., *Jersiberotha similis* Grimaldi, 2000 from the Turonian of New Jersey; *Iceloberotha simulatrix* Engel and Grimaldi, 2008 from Burmese amber). However, other species of *Jersiberotha* possess this crossvein, so its absence in *J. similis* needs confirmation. The crossvein is present in all extant berothids.

All berothid species with simplified venation are small or minute; their forewing length ranges from 2.1 mm (*Haploberotha carsteni* sp. nov.) to 4.2 mm (*Krokhathone tristis*). However, the venation is more complete (including the presence of the gradate series of crossveins and the hind wing 1r-m) in many other minute fossil berothids. In general, all Cretaceous berothids (except Mesithoninae) are small with a maximum forewing length of 5 mm in *Araripeberotha fairchildi* Martins-Neto and Vulcano, 1990 from the upper Aptian of the Crato Formation (Brazil). The smallest extant berothid species *Nyrma kervillea* Navás, 1933 has a minimum

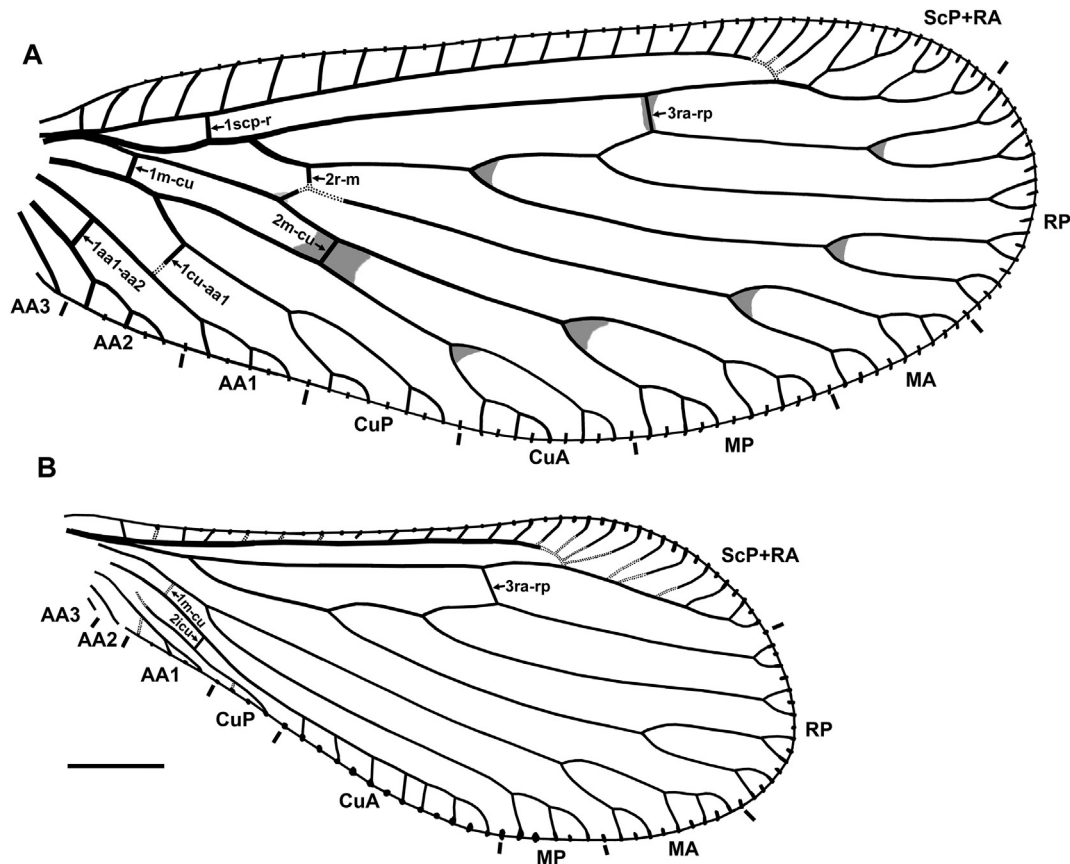


Fig. 3. Wing venation of *Haploberotha carsteni* sp. nov., the holotype GPIH Typ. Kat. Nr. 4936. A, right forewing; B, right hind wing (this is not actual wing shape as the wing is viewed at an angle). Poorly-discernible veins are shown by dotted lines. Scale bar represents 0.2 mm (both to scale).

forewing length of 3.8 mm (see Aspöck, 1989), but its forewing venation is more complicated than in many larger species. Therefore, the miniaturization and the simplification of the venation are not strongly correlated. The simplification of the venation probably occurred independently many times in small berothids, oddly enough mainly in the Cretaceous.

4.2. Male genitalia in the Cretaceous berothids compared with those of Haploberotha

The male genitalia are poorly studied in Cretaceous Berothidae. Among berothids with raptorial forelegs (i.e., the Mesozoic subfamilies Mesithoninae and Paraberthinae), the genitalia are only known in Paraberthinae.

Two species of the subfamily Paraberthinae are represented by males, i.e., *Raptorapax terribilissima* Petrulevičius et al., 2010 from the late Barremian of Lebanese amber (Bouarj locality) and *Albertoberotha leuckorum* McKellar and Engel, 2009 from the Campanian of Canadian amber. The structure of the terminal segments of *A. leuckorum* is unclear as the abdomen is crumpled and covered with fine bubbles (McKellar and Engel, 2009, fig. 1); the only definite structures are “protrusion of two talon-shaped paramere-mediunci” (p. 119). However, it is hard to find these ‘paramere-mediunci’ in the photograph and drawing, so it is impossible to homologize them. At least, any long processes are absent in this species.

Terminal segments of *R. terribilissima* are better preserved. The presumed 9th sternite is long and unspecialized (Petrulevičius et al., 2010, pl. 2, fig. 4, designated as “gonapophysis lateralis?”); the presumed 8th sternite is short, dilated laterally (ibidem, designated as “pseudohypocauda”). Terminal tergites are poorly visible due to

the position of the specimen, but 9th tergite and ectoproct appear large. A heavy-sclerotized finger-like structure, which is bifid terminally, is located between ectoprocts (probably gonostyli 10), which likely does not especially extend beyond the ectoprocts.

Male genitalia are known in four-five Cretaceous species with cursorial legs. Terminal segments are poorly preserved in *Banoberotha enigmatica* Whalley, 1980 from the late Barremian of Lebanese amber (Jezzire locality), but its inner genitalia are fully extruding beyond abdomen (likely post-mortem), with the presumable gonocoxites 9 long and strongly curved inwards (see Whalley, 1980, fig. 5). Other details cannot be definitely interpreted.

The structure of the terminal segments of the Burmese amber species *Jersiberotha myanmarensis* Engel and Grimaldi, 2008 is not described, but the presumable gonocoxites 9 (= ‘mediunci’ of the authors) are extending beyond ectoprocts, exceedingly long, thin with pointed apex, terminally curved and crossing (Engel and Grimaldi, 2008, figs. 17, 18). The presumed male holotype of *Jersiberotha similis* has completely different genitalia (Grimaldi, 2000, fig. 20). It does not possess any processes, and its 8th (or 7th) sternite has paired appendages like pseudohypocaudae. So, this specimen may be actually a female.

The terminal segments of *Haploberotha persephone* is not described, but provided with photographs (see Engel and Grimaldi, 2008, figs. 29, 30). Examination of these photographs and those of undescribed specimens in private collections allows the male genitalia in this species to be understood. The structure of the terminal segments (i.e., 8th, 9th and ectoproct) cannot definitely be interpreted, but the ventral process of T9+ectoproct (or ectoproct) and the presumable gonocoxites 9 are easily discernible, curved inward and acute terminally. Gonocoxites 9 are extending beyond the ectoprocts, slender, very long and straight.

The abdomen and genitalia of *Haploberotha carsteni* sp. nov. are the best preserved among the reported fossil berothids (see their description above). Its eighth tergite and ninth sternite appear very short in contrast with those of extant taxa; the ventral process of T9+ectoproct is shaped differently than in *H. persephone*. In contrast with that species, gonocoxites 9 are not detected; probably these are short and hidden within abdomen. Therefore, there are clear difference in male genitalia, while these species are very similar in the venation.

There are at least two character states in male genitalia of some Cretaceous berothids, not found in extant taxa.

First, the presence of extremely long gonocoxites 9, found in *Jersiberotha myanmarensis* and *Haploberotha persephone*, both from Burmese amber. Similar long gonocoxites 9 occur in the extant dilarid genus *Nallachus* Navás, 1909 (see Aspöck and Aspöck, 2008, figs. 31, 32). Among extant berothids, fairly long gonocoxites 9 is present in *Manselliberotha* (see Aspöck and Aspöck, 1988b, figs. 10, 11), but these are partly hidden within abdomen.

Second, the presence of the long slender ventral process of T9+ectoproct, found only in *Haploberotha*. It resembles a ventral process of the ectoproct in some extant hemerobiids, especially species of *Micromus* Rambur, 1842 (see e.g., Oswald, 1993, fig. 222). A ventral process of the ectoproct is also present in a few extant berothids, e.g., *Manselliberotha neuropterologorum* Aspöck and Aspöck, 1988b and some species of *Podallea* Navás, 1936 (see Aspöck and Aspöck, 1988a, fig. 11; 1988b, figs. 10, 11; 1996, fig. 6). However, this process is shorter and not like the structure observed in both species of *Haploberotha*; these are probably not homologous. Other berothids do not bear such a process.

5. Conclusion

The discovery of the new species of *Haploberotha* allows better understanding of the structure of male genitalia in Cretaceous berothids. It is now clear that Cretaceous genera closely related to it (e.g., *Jersiberotha* Grimaldi, 2000; *Iceloberotha* Engel and Grimaldi, 2008) do not belong to known subfamilies. In particular, they are characterised by the miniaturization and the simplification of their venation. However, it is currently difficult to classify these Cretaceous genera with cursorial forelegs due to their male and female genitalia being poorly known or unknown. Only after detailed examination of these structures in Cretaceous berothids, will we be able to interpret their taxonomic affinities.

Acknowledgements

I thank Carsten Gröhn (Glinde, Germany) for allowing this research on the specimen, performing photography, and answering my questions; James E. Jepson (University College Cork, Ireland) for editing of the English; and anonymous reviewers for providing valuable suggestions to improve this manuscript. The study is supported by Grant No. 16-04-00053 of the Russian Foundation for Basic Research.

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