New beaded lacewings (Neuroptera: Berothidae) from Upper Cretaceous Myanmar amber

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ABSTRACT

Two new genera with two new species in Berothidae, *Maculaberotha nervosa* gen. et sp. nov. and *Magniberotha recurrens* gen. et sp. nov., are described from Upper Cretaceous Myanmar (Burmese) amber. Based on the new specimens of the same species, we propose some venational characters as intraspecific variations, e.g., the markings on the wings and crossveins in the radial sector. We also study and compare the female genital sclerites from three genera of *Haploberotha*, *Dasyberotha*, and *Jersiberotha* to highlight the importance of using these characters preserved in amber for taxonomic and phylogenetic studies. Furthermore, an updated key to the berothid genera of Myanmar amber is provided.

Keywords: Cretaceous; Myanmar amber; new genus; genitalia

1. Introduction

Berothidae, as a relic group of Neuroptera, comprise about 110 extant species in 24 genera (Aspöck and Randolph, 2014). Due to the characteristic raptorial forelegs, this family is generally considered to be related to the other homologous family Rhachiberothidae, which were originally treated as a subfamily of Berothidae for sharing similar venational characters (Tjeder, 1959). Although both groups are easily identified by the specialization of the forelegs, the involvement of Mantispidae with the similar raptorial forelegs raised the question about the relationships of these three families (Willmann, 1990). Aspöck and Mansell firstly clarified the familial status of Rhachiberothidae, and suggested the sister relationships of Berothidae, Rhachiberothidae and Mantispidae (Aspöck and Mansell, 1994), which are supported by the morphological analyses (Aspöck et al., 2001; Beutel et al., 2010; Zimmermann et al., 2011; Randolph et al., 2013, 2014; Aspöck and Randolph, 2014). However, this taxonomy was challenged by the subsequent molecular phylogenetic analysis (Haring and Aspöck, 2004; Winterton, 2010). The Paraberothinae was first established as a subfamily of Rhachiberothidae for its typical raptorial forelegs (Nel et al., 2005). Makarkin et al. did not support the familial status of Rhachiberothidae and treated it as a subfamily (Rhachiberothinae) of the Berothidae and therefore, Paraberothinae was correspondingly regarded as a subfamily of

Berothidae (Makarkin and Kupryjanowicz, 2010; Makarkin, 2015). Herein, we tentatively follow the morphological results that regard Rhachiberothidae at the family rank (Aspöck and Randolph, 2014) and treat Paraberothinae as a subfamily of Rhachiberothidae.

The fossil record of Berothidae (excluding Rhachiberothidae) is scarce, comprising about 20 genera with about 31 species described from the Middle Jurassic to upper Eocene, they are distributed in Myanmar, Kazakhstan, China, Lebanon, America, Brazil, France, England, Mongolia, Columbia and the Baltic, including amber and compression (Krüger, 1923; Whalley, 1980; Klimaszewski and Kevan, 1986; Martins-Neto and Vulcano, 1990; Makarkin, 1994; Ren and Guo, 1996; Grimaldi, 2000; Engel, 2004; Makarkin, 2004; Engel and Grimaldi, 2008; Makarkin et al, 2011; Azar and Nel, 2013; Khramov, 2015; Makarkin and Ohl, 2015). The oldest convincing berothids were found from the uppermost Middle Jurassic of Daohugou, Inner Mongolia, China (Makarkin et al., 2011). Among various localities with documented berothid fossils, Myanmar amber preserve speciose berothids with high morphological diversity. Engel and Grimaldi have described the Myanmar amber berothids with seven genera and nine species (Engel, 2004; Engel and Grimaldi, 2008).

Up to date, we have collected nearly one hundred berothids from Myanmar amber, which allowed us to conduct a comprehensive study of

Myanmar amber berothids. In addition, we describe two new genera with two new species, *Maculaberotha nervosa* gen. et sp. nov. and *Magniberotha recurrens* gen. et sp. nov. Furthermore, we report the female genital structure of three genera, *Haploberotha*, *Dasyberotha*, and *Jersiberotha*. Meanwhile, some diagnostic characters are regarded as the intraspecific individual variations, e.g. the wing markings, and the crossveins in radial sector.

Based on our analyses, we propose the key diagnostic characters at generic level as followings: wing shape, hairs on the body and wings, the configuration of crossvein r1-rs (number and position), number of Rs branches. We set up a key to the genera from Myanmar amber.

2. Material and methods

The amber specimens studied in this paper are from Hukawng Valley in Tanai Village, Myitkyina District of Kachin State, Myanmar (Fig. 1)(Cruickshank and Ko, 2003; Dong et al., 2015). The amber-bearing deposits have been dated to the earliest Cenomanian, circa 98.8 ± 0.6 Ma, based on U-Pb radiometric dating of zircons from the volcanoclastic matrix (Shi et al., 2012).

All specimens are housed in the Key Lab of Insect Evolution & Environmental Changes, the College of Life Sciences, Capital Normal University, Beijing (CNUB; Dong Ren, Curator). The specimens are

examined using a Leica MZ12.5 dissecting microscope (Leica, Wetzlar, Germany) and illustrated with the aid of a drawing tube attachment. The photographs were taken with an attached Leica DFC500 digital camera system. And the figures were prepared with Adobe Photoshop CS6.

The venational and genital terminology in general follows the interpretation of Aspöck and Aspöck (1996). Venational abbreviations are as follows: C, costa; Sc, subcosta; R1, radius; Rs, radial sector; Rs1-5, first to fifth radial sector branches; Ma, anterior media; Mp, posterior media; Cu, cubitus; CuA, anterior cubitus; CuP, posterior cubitus; A, anal; A1-A3, first to third anal veins. Abdominal and genital abbreviations are as follows: T, Tergite; sgp, subgenitale; cc, callus cerci; gl, gonapophysis lateralis; T, Tergite; e, ectoproct; hc, hypocaustae; phc, pseudohypocaustae.

In addition, this work has been registered in Zoobank. The Zoobank LSIDs (Life Science Identifiers) for this work is: urn:lsid:zoobank.org:pub:B2C025D5-1356-4728-B7E7-8F4BE974E73B.

3. Systematic palaeontology

Key to genera of Berothidae from Myanmar amber.

1. Crossveins r1-rs present in forewing; forewing typically with sparse setae, rarely with dense setae.....2

- Crossveins r1-rs absent; forewing very densely covered with elongate setae.....*Ethiroberotha* Engel and Grimaldi, 2008
2. Only one r1-rs crossvein.....3
- More than one r1-rs crossvein (at least two)4
3. Vein Rs with only one branch, flagellum with 21-22 flagellomeres.....*Haploberotha* Engel and Grimaldi, 2008
- Vein Rs with four branches, flagellum with more than 70 flagellomeres.....*Maculaberotha* gen. nov.
4. Distalmost r1-rs crossvein present beyond Sc-R₁ fusion.....5
- Distalmost r1-rs crossvein present before Sc-R₁ fusion.....6
- 5 Forewing with numerous setae on margins, sparse over wing surface; not obscuring wing venation; apical rs-rs and rs-m crossveins absent.
- Body setae short and scattered.....
-*Telistoberotha* Engel and Grimaldi, 2008
- Forewing with dense setae on margins and over surface; apical rs-rs and rs-m present. Body setae dense and elongate.....*Dasyberotha* Engel and Grimaldi, 2008

- 6 Forewing narrowly elongate, apex acute; costal space considerably broader basally than apically at Sc-R1 fusion; scape short, as long as wide.....*Systemoberotha* Engel and Grimaldi, 2008
- Forewing ovoid, apex broadly round; costal space not broader basally than apically at Sc-R1 fusion; scape 2-3 times as long as wide.....7
- 7 Humeral vein simple, not recurrent; Rs with less than three branches.....8
- Humeral vein recurrent; Rs with four or five branches.....*Magniberotha* gen. nov.
8. Forewing with distinct areas of infuscation surrounding crossveins and vein forks, some or all crossveins simple prior to Sc-R1 fusion; one ma-mp crossvein and one cua-cup crossvein present (except *J. tauberorum*); veins stronger.....*Jersiberotha* Engel and Grimaldi, 2008
- Forewing lacking areas of infuscation; all c-sc crossveins simple prior to Sc-R1 fusion; ma-mp crossvein and cua-cup crossvein absent.....*Iceloberotha* Engel and Grimaldi, 2008

Class: Insecta Linnaeus, 1758

Order: Neuroptera Linnaeus, 1758

Family: Berothidae Handlirsh, 1906

Genus *Maculaberotha* gen. nov.

***Maculaberotha* gen. nov.** urn:lsid:zoobank.org:act:48C5D495-6083-4B4C-B8DF-2CFE493636C6.

Etymology. The generic name is from the Latin “*macula*” (meaning “maculate”), in reference of some scattered patches along veins. “*Berotha*”, a genus name of the family Berothidae. Gender feminine.

Type species: *Maculaberotha nervosa* sp. nov.

(Figs. 2-3).

Diagnosis. Body size small, but distinctly shorter than the forewing. Flagellum with 71 flagellomeres. Most veins irregularly mottled with fuscous markings. Costal crossveins simple, with a few distal forks. Humeral veinlet slightly recurrent. Single r1-rs crossvein. Rs with four branches, and a few crossveins throughout the radial sector.

Remarks. *Maculaberotha* gen. nov. is distinctly different from the other Myanmar berothid genera by having one r1-rs crossvein: *Ethiroberotha* (absence of r1-rs), *Jersiberotha*, *Iceloberotha*, *Telistoberotha* and *Dasyberotha* (with two r1-rs). Although *Haploberotha* has only a single r1-rs, but it is obviously different from the new genus: (1) the body size in the new genus (body length 3.0 mm and forewing length 4.3 mm) is larger than the body size in *Haploberotha* (body length

1.93 mm and forewing length 2.14 mm); (2) flagellum with 71 flagellomeres in the new genus vs. only 21-22 flagellomeres in *Haploberotha*; (3) Rs with four branches in the new genus vs. only one branch in *Haploberotha*; (4) veins irregularly mottled with fuscous markings in the new genus vs. veins with uniform coloration.

***Maculaberotha nervosa* gen. et sp. nov.** (Figs. 2-3).
urn:lsid:zoobank.org:act:44517EF5-D415-4BB6-8924-31235DEA2283.

Etymology. From the Latin “*nervosus*”, in reference of the multiple Rs branches.

Type material. Holotype, CNU-NEU-MA2016003, (Figs. 2-3).
Female, body preserved incompletely, but four wings spreading.

Locality and horizon. Hukawng Valley, Kachin State, Northern Myanmar; lowermost Cenomanian, Upper Cretaceous.

Diagnosis. As for genus.

Description. Female, total body length 3.0 mm. Head and body with numerous scattered, fine setae. Scape elongate, about 3 to 4 times as long as wide; flagellum with 71 flagellomeres; flagellomeres with a few, relatively long setae arranged in a circle. The maxillary palpus well preserved, and the apical segment elongated and acutely pointed (Fig. 2C). Pronotum narrow, a little longer than width; meso- and metanotum as long as wide. Legs slender and covered by numerous hairs. The first

six abdominal segments unmodified, and the other segments deformed. Tergite 9 probably fused with ectoproct (Fig. 2D).

Forewing: left forewing 4.3 mm in length, 1.7 mm in width; right forewing, 4.8 mm in length, 1.8 mm in width (the difference of both wings is likely due to preservation in amber). Membrane hyaline and some scattered patches along veins. Wing apex broadly rounded. Trichosors and microtrichia prominent along the entire wing margin. Veins covered by numerous long hairs. Humeral vein slightly recurrent. Costal crossveins simple, with occasional forks. Sc distally amalgamated with R1. One sc-r1 crossvein present between the points of Rs and Mp diverged from R1. Rs with four primary branches, and few crossveins present in the radial sector. Only one r1-rs crossvein distant from the base, located beyond the separation of Rs₄. Ma forming the simple distal bifurks. Single ma-mp crossvein situated before the divergence of Ma from Rs. Mp deeply forked, and Mp1 and Mp2 forming the distal dichotomous forks. Two crossveins (mp-cu) present between Mp2 and CuA. Cu deeply branched; CuA forming the distal dichotomous forks, and CuP deeply forked, and with three pectinate branches. A1 with four distal pectinate branches, and A2 with six pectinate branches, A3 not detected.

Hind wing: left hind wing 4.2 mm in length, 1.8 mm in width; right hind wing 4.5 mm in length, 1.8 mm in width. Trichosors well distributed

along the margin. Costal space narrow, and slightly dilated in distal. R₁ space broad, slightly wider than costal space. Costal crossveins simple. Single r1-rs distant from the wing base. Rs with three branches. Ma forked distantly. Mp with deep branches, Mp1 branched in one-third near the wing base. CuA almost parallel to hind margin, and pectinately branched.

***Magniberotha* gen. nov.** urn:lsid:zoobank.org:act:DC068DB6-4FBA-410E-9490-1077CA31793D.

Etymology. The generic name is from the Latin “*magnus*” (meaning “large”), in reference its large body size. “*Berotha*”, a genus name of the family Berothidae. Gender feminine.

Type species: *Magniberotha recurrens* sp. nov.

(Figs. 4-6)

Diagnosis. Small body size as long as the wing (> 4 mm); forewing elongate; humeral veinlet recurrent; Rs with four or five branches; two r1-rs crossveins, and proximal r1-rs present at wing midpoint, and slightly beyond the divergence of Rs₂ branch, distal r1-rs crossvein situated before Sc-R1 fusion; Ma separated from Rs at one third of the wing; Cu vein proximally branched; CuA dichotomously branched near the middle of wing, and CuP proximally branched and forming three further branches.

Remarks. *Magniberotha* gen. nov. has the body size > 4 mm in comparison with other berothids from Myanmar amber (not exceeding 3.2 mm). Notably, it is the first time to detect the recurrent humeral veinlet within the Myanmar amber berothids regardless of the relatives of Rhachiberothidae. In nature, the recurrent humeral veinlet is widely found in both extant and fossil (main in compression fossil) berothids, and it indicates the condition of recurrent veinlet is likely also common in the Myanmar amber berothids. Additionally, the new genus has two r1-rs crossveins in forewing, which is distinctly different with two other Myanmar berothids, *Ethiroberotha* (absence of r1-rs), and *Haploberotha* (only with a single r1-rs). Although *Telistoberotha* and *Dasyberotha* also have two r1-rs crossveins, the locations of r1-rs for both genera are conspicuously different from that of the new genus: distalmost r1-rs beyond Sc-R₁ fusion vs. distalmost r1-rs present before Sc-R₁ fusion (new species).

Magniberotha recurrens gen. et sp. nov. (Figs. 4-6)
urn:lsid:zoobank.org:act:8FC413EA-B3A8-45B8-9904-E1C594802851.

Etymology. From the Latin “*recurrens*”, in reference to its recurrent humeral veinlets.

Type material. Holotype, CNU-NEU-MA2016001, (Fig. 4). Female, body well preserved with incomplete antenna, wings and parts of legs.

Paratype, CNU-NEU-MA2016002, (Fig. 5). Amber with complete body and unilateral wings preserved.

Locality and horizon. Hukawng Valley, Kachin State, Northern Myanmar; lowermost Cenomanian, Upper Cretaceous.

Diagnosis. As for genus.

Description. Female. Length of body exceeding 4.0 mm. Head deformed due to preservation. Antennae moniliform, incompletely preserved; flagellum with 28 flagellomeres preserved and the apical tapered (Figs. 4A and 4B). Abdomen with nine segments, and the first seven tergites relatively small, and 8th tergite broad (Fig. 4C). Subgenitale (sgp) with a pair of ventral triangular ridges on both sides. 9th tergite and ectoproct incorporated as a large tergite. The possible callus cerci (cc) round and with many long hairs. The gonapophysis laterals (gl) simple and fingerlike, absence of hypocausta.

Forewing 4.3 mm in length, and 1.7 mm in width. Dense hairs and trichosors present along the margin. Membrane hyaline, without any markings. Costal space relatively broad, especially at proximal one third and distalmost Sc-R₁ fusion. Humeral veinlet recurrent. Costal crossveins simple, with some occasional distal forks. Sc and R₁ distally anastomosed and entering the margin before the apex. Single sc-r₁ crossvein located at the proximal of wing, just after origin of Rs (separated from Rs by less than crossvein length). Two r₁-rs crossveins,

and the proximal one present at the middle of wing, situated near the divergence of Rs_2 . Rs with four branches, and each branch shallowly forked. Ma separated from Rs one-third from wing base, and forming the simple distal dichotomous forks. Two crossveins present between Ma and Mp . Mp forking proximally, and Mp_1 and Mp_2 deeply dichotomously branched. Three crossveins present between Mp_2 and CuA . CuA and CuP diverged close to wing base. One $cua-cup$ just located after the second branching point of CuP . CuA dichotomously branched near the middle of wing, and CuP proximally deeply branched and forming three pectinate branches. One $cup-a_1$ present close to the wing base. A_1 , A_2 and A_3 well-preserved, A_2 pectinately branched, with 7 simple branches.

Hind wing length 3.5 mm, width 1.4 mm. Hind wing elongate. Costal space narrowed from the base to middle, and dilated distally, especially close to $Sc-R_1$ fusion. One r_1-rs situated before $Sc-R_1$ fusion, no other crossvein detected. Rs with four primary branches, and Rs_1 deeply branched. Mp proximally forking. CuA partly preserved, forming the pectinate branches.

4. Discussion

The Cretaceous Myanmar amber, as reported so far, show speciose berothids with high morphological diversity in comparison with those of berothids from other localities. As for most extinct winged insects, these

Myanmar berothids were also classified primarily according to the venational features, while the characters of genitalia were rarely used for classification mainly due to the lack of or limited preservation in the fossil insects. Nevertheless, it is quite likely that the genitalia of amber insects are better preserved and easier to be discerned in contrast to the compression fossils. Therefore, amber insects offer new insights on the identification, systematics, phylogeny to gain better understanding of the early development and evolution of extinct insects (Krivokhatsky, 2002; Lu et al, 2016).

As for the Cretaceous Myanmar amber berothids, a serious issue surfaced that the diagnosis and description of some taxa (particularly at species level) became obscure when more materials were examined. For instance, the genus *Jersiberotha* was firstly erected by Grimaldi from the New Jersey amber for sharing the wing characters: two adjacent r1-rs crossveins in the forewing, only one mp1-mp2 crossvein (Grimaldi, 2000). In 2008, Engel and Grimaldi described two other species (*J. myanmarensis* and *J. tauberorum*) and a related genus *Iceloberotha* from Myanmar amber based on the diagnostic characters of venation, i.e. speckless forewing in *Iceloberotha* vs distinctly spotted forewing in *Jersiberotha*; absence of crossvein ma-mp and cua-cup in *Iceloberotha* vs. presence of ma-mp and cua-cup in *Jersiberotha* (referring to the key to genera in Engel and Grimaldi, 2008). Nevertheless, it is evident that

these characters occurred mosaically in both genera, e.g. the Myanmar species *J. tauberorum* clearly loses the crossveins mp1-mp2 and cua-cup, while the type species of *Iceloberotha* has an evident mp1-mp2 crossvein in the original drawings (Engel and Grimaldi, 2008: figs. 21, 24). Additionally, the specimens in Fig. 7 are conspicuously related to *Jersiberotha* for the well-developed crossveins mp1-mp2 and cua-cup, however the speckless forewing in Figs. 7C, D indicates they also have the possible affinities to *Iceloberotha*. Consequently, it is difficult to identify the species of these two genera merely based on the venational characters. In Engel and Grimaldi (2008), a photo of male terminalia in *J. myanmarensis* was provided to show an elongated penisfilum out of the abdomen, but unfortunately it was not clearly visible in other related species to allow a comparison of the genitalia of these specimens. Therefore, future findings of new specimens with discernable genitalia will be a potential way to clarify the systematic status of these two genera.

To date, the genitalia of the Myanmar amber berothids (except for rhachiberothids) were not studied except for the recent works by Makarkin and Ohl (2015). Herein, we describe three types of structural homologous female genitalia based on our new materials, referring to three genera *Dasyberotha*, *Haploberotha* and *Jersiberotha* (Fig. 8), because the genitalia structures of these three genera are well preserved.

Figs. 8A, B show a female specimen of *Dasyberotha*, which possesses a pair of club-shape pseudohypocaudae (phc), fused tergite 9 and the stout gonapophyses laterales without hypocaudae. The terminalia of *Haploberotha* is slightly different from those of *Dasyberotha*. A pair of digitiform pseudohypocaudae protrudes ventrally from the tergite 9, while the gonapophyses laterales slightly elongate, with a short hypocaudae (Figs. 8C, D). But in *Jersiberotha* (Figs. 8E, F), the terminalia shape is different from *Dasyberotha* and *Haploberotha*. Pseudohypocaudae is very slender, gradually tapering to bluntly pointed top. The gonapophyses laterales are equipped with cephalically directed hypocaudae, slender and acute. Although their female genitalia show different shapes, the similar structure implies their close affiliations for sharing the well-developed pseudohypocaudae and absence of the hypocaudae. The pseudohypocaudae also exists in Rhachiberothidae which is characterized by their rapitorial forelegs (Aspöck and Aspöck, 2008). It seems the three genera are most similar to Protobiellinae for venation and female genitalia, e.g. round and broad wing apex, simple and unforked costal crossveins before Sc-R1 fusion, less Rs branches, well-developed pseudohypocaudae and absence of hypocaudae (Aspöck and Aspöck, 1985). While the female genitalia in the new genera *Magniberotha* and *Maculaberotha* seems to be more related to Berothinae, for absence of pseudohypocaudae and the well-developed

elongated hypocaustae. It is clear that the female genitalia in Myanmar amber berythids had been diversified in the Early Cretaceous. This work is just a preliminary analysis of the female genitalia in the Myanmar amber berythids, and it is hoped that more evidence of the genitalia of the amber berythids will be described in the future research.

Conclusion

Two new fossil genera and species, *Maculaberotha nervosa* gen. et sp. nov. and *Magniberotha recurrens* gen. et sp. nov., are described from the Upper Cretaceous Myanmar amber. An updated key to the known Myanmar amber berythids is provided. Additionally, the female genital structures of three genera are illustrated for the first time. In the previous research and taxonomy of fossil Berythidae, the classification of species was primarily based on venational features while the genital structures were rarely used. It is proposed that the genital character should not be overlooked, especially in the amber specimens.

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Figure captions

Fig. 1. Map of the amber locality near Tanai in Hukawng Valley (after Dong et al., 2015).

Fig. 2. Holotype of *Maculiberothera nervosa* gen. et sp. nov. (CNU-NEU-MA2016003). A. Photograph of the holotype. B. Details of forewing. C. Details of antenna. D. Details of abdomen. Scale bars = 1 mm.

Fig. 3. Drawing of the holotype of *Maculiberothera nervosa* gen. et sp. nov. Scale bar = 1 mm.

Fig. 4. Holotype of *Magniberothera recurrens* gen. et sp. nov. (CNU-NEU-MA2016001). A. Photograph of the holotype. B. Details of antenna. C. Details of abdomen. Scale bar = 1mm (A) and 0.5mm (B, C).

Fig. 5. Paratype of *Magniberothera recurrens* gen. et sp. nov. (CNU-NEU-MA2016002). A. Details of forewing. B. Details of antenna. Scale bar = 1mm (A) and 0.5mm (B).

Fig. 6. Fore (above) and hind (below) wing venation of *Magniberothera recurrens* gen. et sp. nov. Setation omitted. Scale bar = 1mm.

Fig. 7. Examined specimens of *Jersiberothera* and *Iceloberothera*. A. CNU-NEU-MA2016004. B. CNU-NEU-MA2016005. C. CNU-NEU-MA2016006. D. CNU-NEU-MA2016007. Scale bars = 1 mm.

Fig. 8. A. Examined specimen of *Dasyberothera eucharis*. CNU-NEU-MA2016008. B. Genital structure of *Dasyberothera eucharis*. C. Examined specimen of *Haploberothera persephone*. CNU-NEU-MA2016009. D. Genital structure of *Haploberothera persephone*. E. Examined specimen of *Jersiberothera myanmarensis*. CNU-NEU-MA2016010. F. Genital structure of *Jersiberothera myanmarensis*. Scale bars = 1 mm.

Figure 1

Figure 2

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Figure 8