Palaeoentomology 002 (5): 453–464
https://www.mapress.com/j/pe/

Article

ISSN 2624-2826 (print edition)
PALAEOENTOMOLOGY
ISSN 2624-2834 (online edition)

https://doi.org/10.11646/palaeoentomology.2.5.9
http://zoobank.org/urn:lsid:zoobank.org:pub:60B1EA12-9999-4A99-ABEF-4258D3642653

An unusual new genus and species of beaded lacewings (Neuroptera: Berothidae) from the mid-Cretaceous Burmese amber

YIJUAN SHI[1], WEIWEI ZHANG[2], BO WANG[3] & XINGYUE LIU[1,*]
[1]*Department of Entomology, China Agricultural University, Beijing 100193, China*
[2]*Three Gorges Entomological Museum, P.O. Box 4680, Chongqing 400015, China*
[3]*State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China*
[*]*Corresponding author. E-mail: liuxingyue@cau.edu.cn*

Abstract

A new genus and species of the neuropteran family Berothidae from the mid-Cretaceous Burmese amber, namely *Xiaoberotha bipunctata* **gen. et sp. nov.**, is described. In addition, an undetermined species of this new genus is also described. This new genus greatly differs from most known berothids by the presence of forewing ScA and the configuration of hind wing Cu that is not approximating posterior wing margin. The new genus superficially resembles Hemerobiidae by having the distinct, posteriorly curved forewing ScA and the two forewing cua-cup crossveins that are shared by many brown lacewing genera. However, no autapomorphy of Hemerobiidae could be confirmed to be present in the new species. Here we tentatively place this new genus in Berothidae by the configuration of the female gonocoxites 8, which is conspicuous and dorsoventrally extended. This unusual beaded lacewing genus highlights the morphological diversity of the extinct Berothidae.

Keywords: Mantispoidea, Hemerobiidae, taxonomy, Mesozoic, Myanmar

Introduction

The family Berothidae (beaded lacewings) is a small group of Neuroptera, comprising less than 120 described extant species in 25 genera worldwide, presently assigned to six subfamilies (Aspöck & Randolf, 2014). Rhachiberothidae (thorny lacewings), which was considered as a subfamily of Berothidae, is a separate family being as the sister group of Mantispidae (Liu *et al.*, 2015; Wang *et al.*, 2017). The adult berothids are characterized by the scale-like setae on the wings and/or thorax and coxae of many species, the long scape of antenna, the frequently falcate forewings, and the CuA approximating posterior margin of hind wing. Berothidae has a cosmopolitan distribution, occurring in all zoogeographical regions, yet restricted to warmer temperate, subtropical and tropical regions.

The oldest definite fossils of Berothidae are known from the Middle Jurassic of China (Makarkin *et al.*, 2011). The oldest fossil Berothidae (without however counting the Rhachiberothinae considered by some authors as a separate family) in amber are from the Lebanese amber: *Banoberotha enigmatica* Whalley, 1980 and *Sibelliberotha rihanensis* Azar & Nel, 2013. Hitherto, there are 25 genera and ca. 36 species of fossil berothids described from Eurasia, North and South America (Makarkin *et al.*, 2011; Yang *et al.*, 2019). The richest palaeodiversity of Berothidae is known from the Upper Cretaceous of Myanmar, currently with 11 genera and 14 species described based on the Burmese amber specimens (Engel & Grimaldi, 2008; Yuan *et al.*, 2016; Makarkin, 2018; Huang *et al.*, 2019; Yang *et al.*, 2019). Among the Burmese amber lacewing families, Berothidae is the most specie-rich group, being one of the major lineages of Neuroptera from the Upper Cretaceous of Myanmar.

Here we describe a new genus and species from the Burmese amber, namely *Xiaoberotha bipunctata* **gen. et sp. nov.**, together with another undetermined species of this genus. This new genus differs greatly from most known berothids by the presence of forewing ScA and the configuration of hind wing Cu that is not approximating posterior wing margin. The new finding highlights the morphological diversity in the fossil Berothidae.

Material and methods

The amber specimens herein described are from the Hukawng Valley in Tanai Township, Myitkyina District of Kachin State, Myanmar (Kania *et al.*, 2015: fig. 1). The age of this deposit has been investigated and dated to be

Accepted by D.-Y. Huang: 17 Sep. 2019; published: 31 Oct. 2019

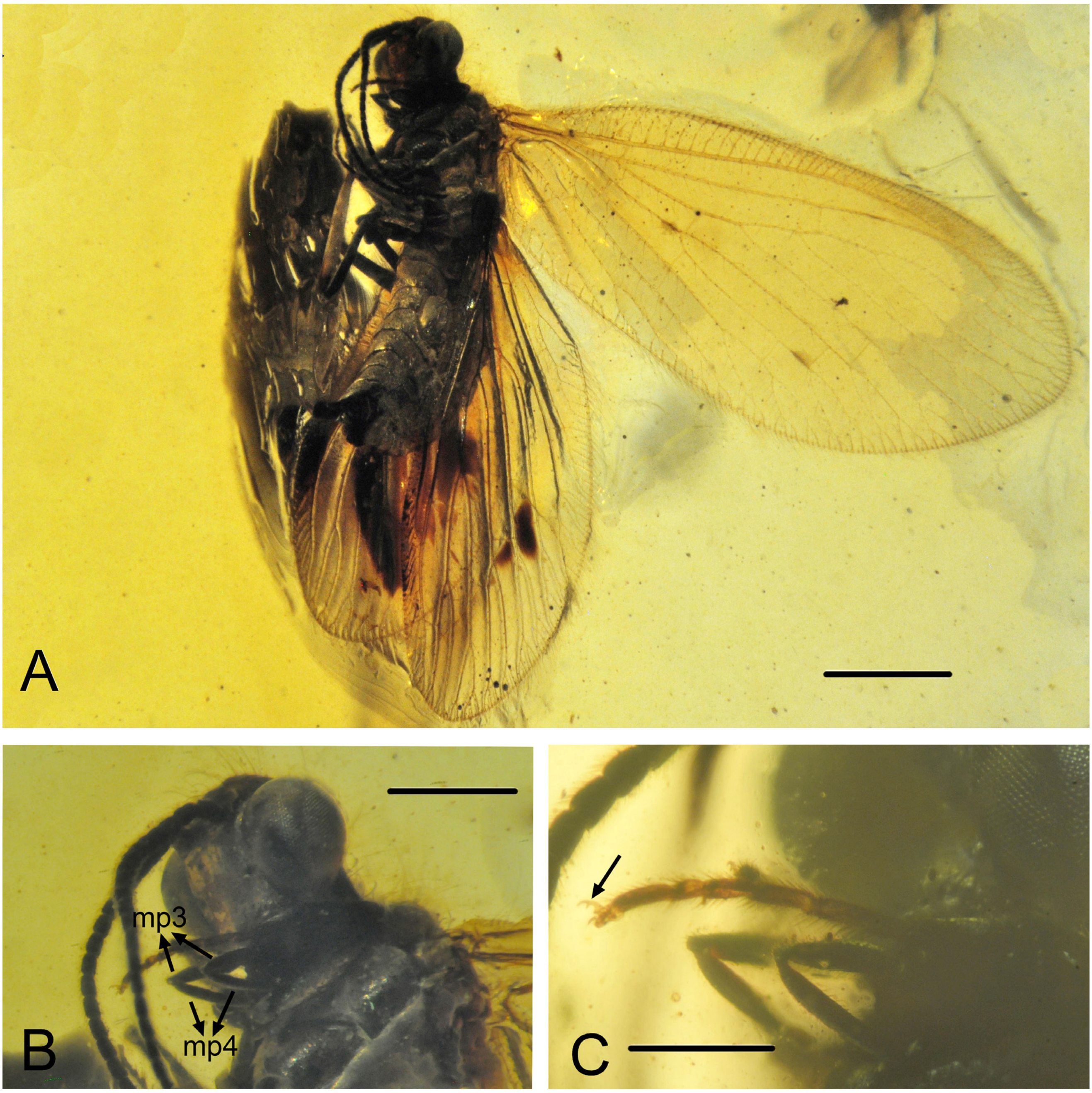

FIGURE 1. *Xiaoberotha bipunctata* **gen. et sp. nov.**, holotype EMTG BU-001590, male. **A**, Habitus photo in ventral view. **B**, Photo of maxillary palpus, anterolateral view. **C**, Photo of protarsus, lateral view. mp, maxillary palpomere. Arrow in **C** showing the additional process on pretarsal claw. (Scale bars represent 1.0 mm in **A**; 0.5 mm in **B**; 0.25 mm in **C**.)

98.8 ± 0.6 million years by U-Pb dating of zircons from the volcanoclastic matrix of the amber (Shi *et al.*, 2012).

The studied specimens are deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing; the Century Amber Museum (CAM), Shenzhen; and the Three Gorges Entomological Museum (EMTG), Chongqing.

Photographs and drawings were taken and made by using a Zeiss SteREO Discovery V12 stereo microscope system and a Leica DM 2000 optical microscope with Nikon D90 digital camera. The figures were prepared with Adobe Photoshop CS4®. Terminology of wing venation generally follows Aspöck *et al.* (1980). Terminology of genitalia follows Aspöck & Aspöck (2008).

Abbreviations used for wing veins are as following: A, anal vein; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; h, humeral veinlet; M, media; MA, media anterior; MP, media posterior; R, radius; RA, radius anterior; RP, radius posterior; ScA, subcosta anterior; ScP, subcosta posterior.

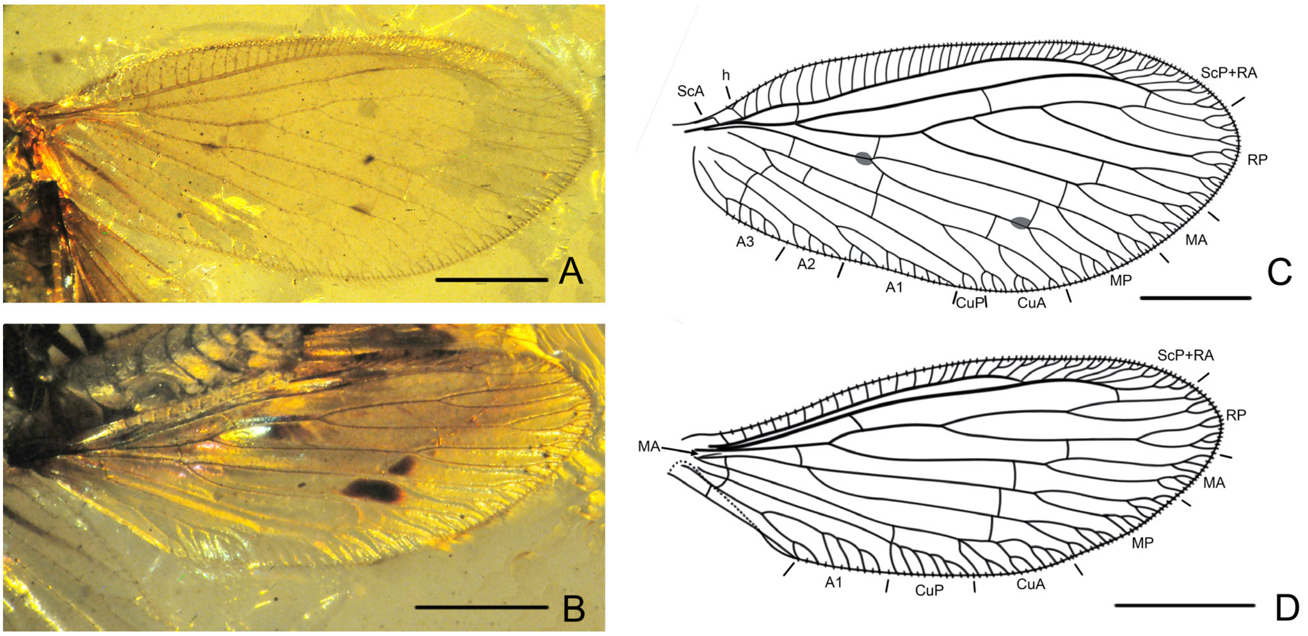

FIGURE 2. *Xiaoberotha bipunctata* **gen. et sp. nov.**, holotype EMTG BU-001590, male. **A**, Photo of forewing. **B**, Photo of hind wing. **C**, Line drawing of forewing. **D**, Line drawing of hind wing. (Scale bars represent 1.0 mm.)

Systematic palaeontology

Class Insecta Linnaeus, 1758
Order Neuroptera Linnaeus, 1758
Family Berothidae Handlirsch, 1906

***Xiaoberotha* gen. nov.**

Type species. *Xiaoberotha bipunctata* **sp. nov.**
(Figs 1–6)

Diagnosis. Small-sized beaded lacewings, with forewing length 3.7–5.7 mm. Antenna short, with 29–32 flagellomeres; scape about twice as long as wide. Forewing ovoid, about 2.0–2.5 times as long as wide; ScA present and distally curved posteriad nearly in right angle; humeral veinlet recurrent and bifurcated; costal crossveins mostly simple except for those forked in pterostigmal area; ScP and RA fused distally; two ra-rp crossveins respectively present at midpoint of wing and a position distad of fusing point of ScP and RA; RP+MA with five main branches; an inner gradate series of crossveins present at proximal 1/3 of wing, incorporating three crossveins respectively between RP+MA and MP1, MP2 and CuA, and CuA and CuP; an outer gradate series of crossveins present, incorporating four or six crossveins respectively between branches of RP+MA, RP+MA and MP1, MP1 and MP2, and MP2 and CuA; two cua-cup crossveins present. Hind wing with indistinct, oblique, straight stem of MA; CuA and CuP long and pectinately branched near wing margin, but not parallel for a long distance to posterior wing margin. Genitalia: Tergum 9 and ectoprocts not fused together in both male and female. Female fused gonocoxites 8 broad; gonocoxites 9 without hypocaudae.

Etymology. The generic name is a combination of *Xiao* (the given name of Mrs. Xiao Jia who kindly provided the paratype of the following new species for our study) and *Berotha* (the type genus name of Berothidae). Gender: Feminine.

***Xiaoberotha bipunctata* sp. nov.**

Diagnosis. Same as for the genus. In addition, forewing with two dark spots respectively at initial branching point of MP and initial branching point of MP2.

Description. Male (Figs 1, 2). Total body length 3.9 mm; forewing length 5.1 mm, width 2.2 mm; hind wing length 4.0 mm, width 1.6 mm. Body and wings with many moderate-lengthened setae. Head subtriangular; vertex moderately domed, medially with a longitudinal suture. Compound eyes large and semi-globular. Antennae short; scape not greatly elongated, about 2–3 times as long as wide; flagellum with 29 flagellomeres, terminal flagellomere acutely pointed at tip. Mouthparts chewing-mandibulate; maxillary palpus (Fig. 1B) with distal four segments visible, palpomere 2 very short, palpomere 3 and 4 longest, terminal palpomere about one third of palpomere 4 and distally pointed. Prothorax short, slightly longer than wide. Meso- and metathorax robust, mesothorax much longer than prothorax. Legs slender; foreleg much shorter than mid and hind legs; meso- and

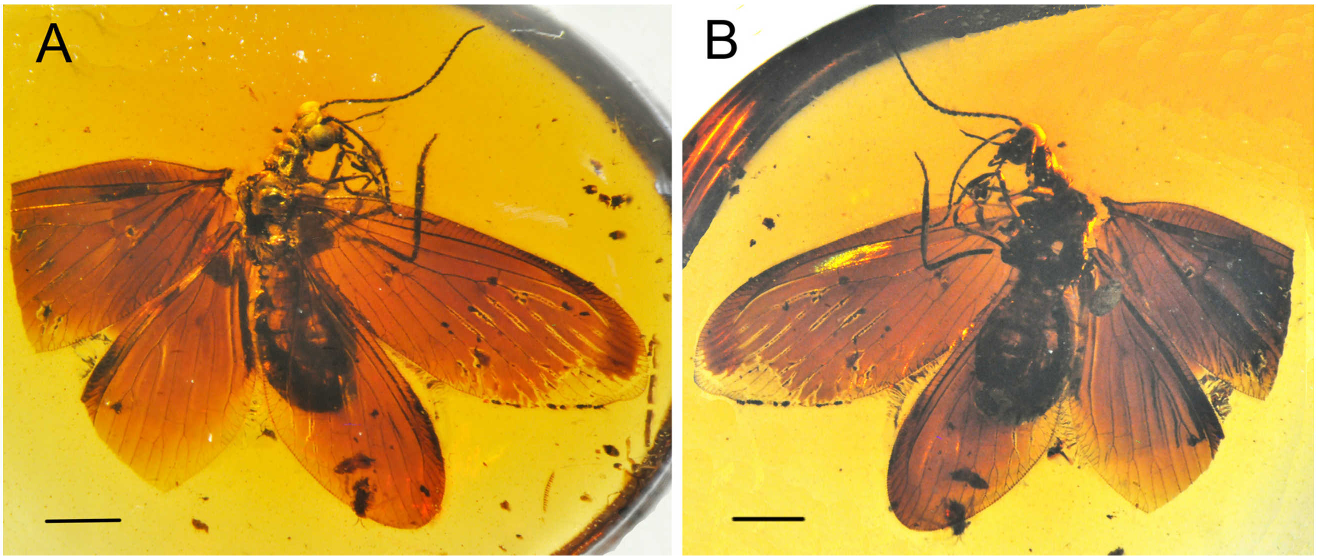

FIGURE 3. *Xiaoberotha bipunctata* **gen. et sp. nov.**, paratype CAM BA-0014, female. **A**, Habitus photo, dorsal view. **B**, Habitus photo, ventral view. (Scale bars represent 1.0 mm.)

metafemora slightly thinner and shorter than meso- and metatibiae; femora with dense long setae; tibia with dense short setae except for apex ventrally with some stiff setae, tibial spur absent; tarsus with tarsomere 1 nearly as long as combined tarsomeres 2–4, tarsomere 5 slightly shorter than tarsomere 1; tarsomeres 1–4 ventrodistally with some stiff setae; pretarsal claws (Fig. 1C) distinctly curved, each claw subdistally forked; arolium present.

Forewing (Fig. 2A, C): Ovoid, about twice as long as wide. Entirely transparent, with two ovoid dark spots present respectively at initial branching point of MP and initial branching point of MP2. Trichosors present along entire wing margin. ScA present and distally curved posteriad nearly in right angle; humeral veinlet recurrent and bifurcated; costal space proximally broadened; costal crossveins mostly simple except for those forked in pterostigmal area; ScP and RA fused distally, pectinately branched, with four branches, each marginally forked; subcostal space broad, a single scp-ra present proximally; two ra-rp crossveins respectively present at midpoint of wing and a position distad of fusing point of ScP and RA; RP+MA separating from R near wing base, with five main branches, posterior two of them secondarily branched, all branches marginally forked; two crossveins present between RP+MA and MP; MP initially branched slightly proximad of branching point between RP and MA, with two main branches, each with secondary and marginal forks; one mp1-mp2 present; three crossveins present between MP and Cu; Cu initially branched near wing base, with two main branches; CuA distally with three branches, each marginally forked; CuP with only a marginal fork; two cua-cup; A1 distally with two branches, anterior branch pectinately branched with six short simple branches, posterior branch with three short simple branches; A2 distally with four pectinate, short, simple branches; A3 pectinately branched distally, with five short, simple branches; three aligned crossveins present proximally between CuA and A1, A1 and A2, and A2 and A3; an inner gradate series of crossveins present at proximal 1/3, incorporating three crossveins respectively between RP+MA and MP1, MP2 and CuA, and CuA and CuP; an outer gradate series of crossveins present, incorporating four crossveins respectively between branches of RP+MA, RP+MA and MP1, MP1 and MP2, and MP2 and CuA.

Hind wing (Fig. 2B, D): Ovoid, slightly narrower than forewing, about 2.5 times as long as wide. Transparent and immaculate. Trichosors present along entire wing margin. Costal space narrow; costal crossveins mostly simple except for those forked in pterostigmal area; ScP and RA fused distally, pectinately branched, with six branches, each marginally forked; subcostal space narrow, scp-ra absent; two ra-rp crossveins respectively present proximad midpoint of wing and distad fusing point of ScP and RA; RP+MA separating from R near wing base, with four main branches, posterior two of them secondarily branched, all branches marginally forked; an indistinct, straight MA stem present; two crossveins present between RP+MA and MP; MP initially branched slightly proximad of branching point between RP and MA, with two main branches, each with secondary and marginal forks; one mp1-mp2 present; two crossveins present between MP and Cu; Cu initially branched near wing base, with two main branches; CuA distally pectinately branched, most branches marginally forked; CuP distally with six pectinate simple branches; two cua-cup; A1 distally with

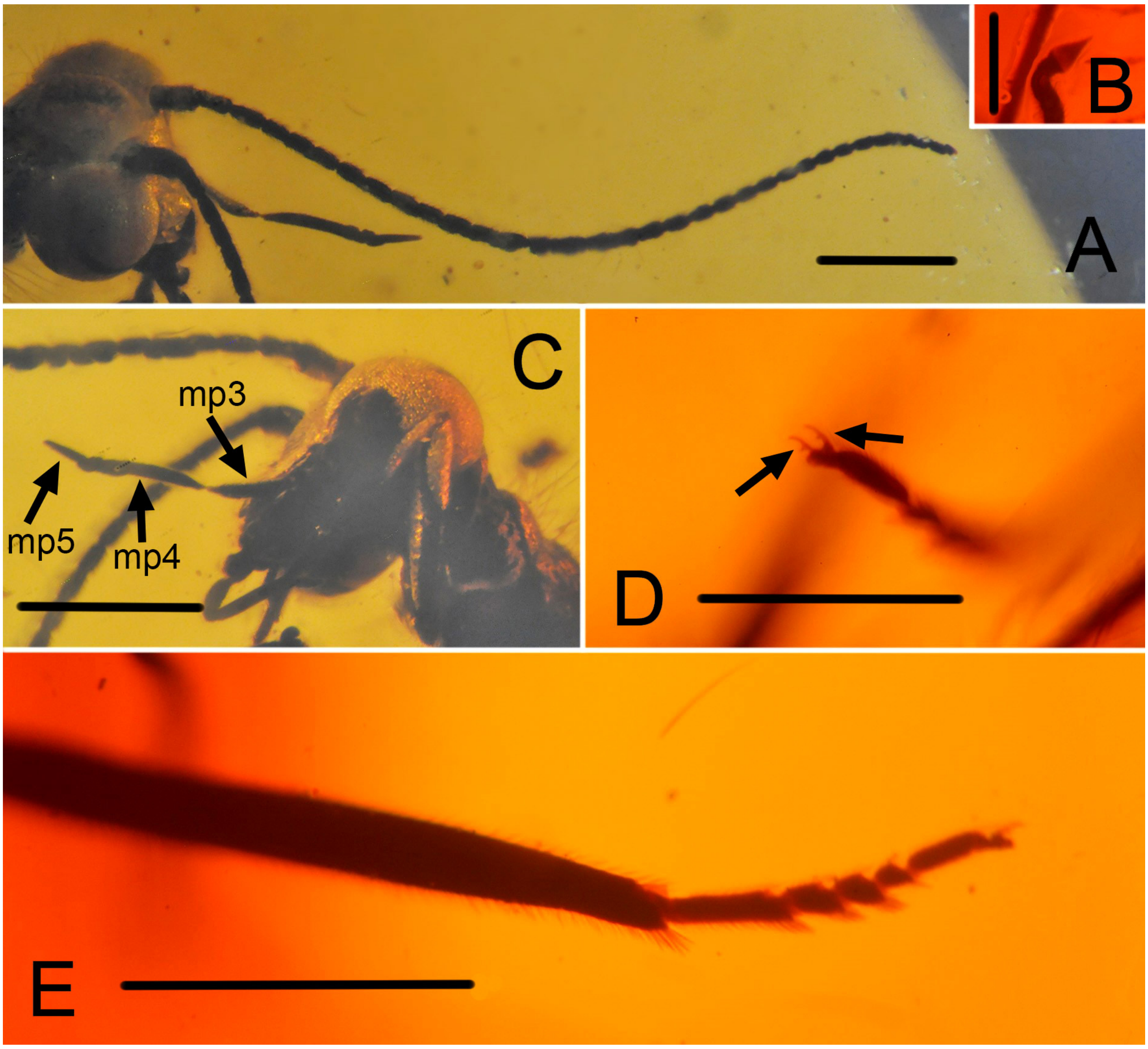

FIGURE 4. *Xiaoberotha bipunctata* **gen. et sp. nov.**, paratype CAM BA-0014, female. **A**, Photo of head, dorsal view. **B**, Photo of terminal flagellomere. **C**, Photo of maxillary palpus. **D**, Photo of pretarsal claws. **E**, Photo of distal part of tibia and tarsus in hind leg, lateral view. mp, maxillary palpomere. Arrow in **D** showing the additional process on pretarsal claw. (Scale bars represent 1.0 mm in **E**; 0.25 mm in **A**, **C** and **D**; 0.1 mm in **B**.)

two branches, anterior branch pectinately branched with four short simple branches, posterior branch bifurcated; A2 and A3 poorly preserved; a1–a2 and a2–a3 present and closely spaced; an outer gradate series of crossveins present, incorporating four crossveins respectively between branches of RP+MA, RP+MA and MP1, MP1 and MP2, and MP2 and CuA.

Genitalia (Fig. 6A, C): Tergum 9 short, nearly half length of tergum 8, distinctly extending ventrad. Sternum 9 much longer than tergum 9, posterior margin nearly truncate. A pair of putative gonocoxites 9 present, broad, acutely pointed at tip. Ectoproct slightly longer than tergum 9, posterior margin in lateral view slightly arcuately convex; an ovoid callus cercus visible on posterodorsal portion, barely prominent.

Female (Figs 3–5). Total body length 5.1 mm; forewing length 5.7 mm, width 2.3 mm; hind wing length 5.0 mm, width 2.1 mm.

External morphological characters mostly same to those in male. Additional description: Antenna with 32 flagellomeres (Fig. 4A, B). Labial palpus (Fig. 4C) with distal two palpomeres longest, terminal palpomere distally pointed. Wing membrane largely dark, but probably due to preservation because apex of right forewing transparent as in male. Forewing (Fig. 5A, B): Humeral veinlet in left forewing trifurcated (Fig. 5E); outer gradate series of crossveins present, incorporating six crossveins respectively between branches of RP+MA, RP+MA and MP1, MP1 and MP2, and MP2 and CuA; A2 and A3 both distally trifurcated.

Genitalia (Fig. 6B, D): A pair of broad sclerites (putative gonocoxites 8) present anteriad segment 9, nearly

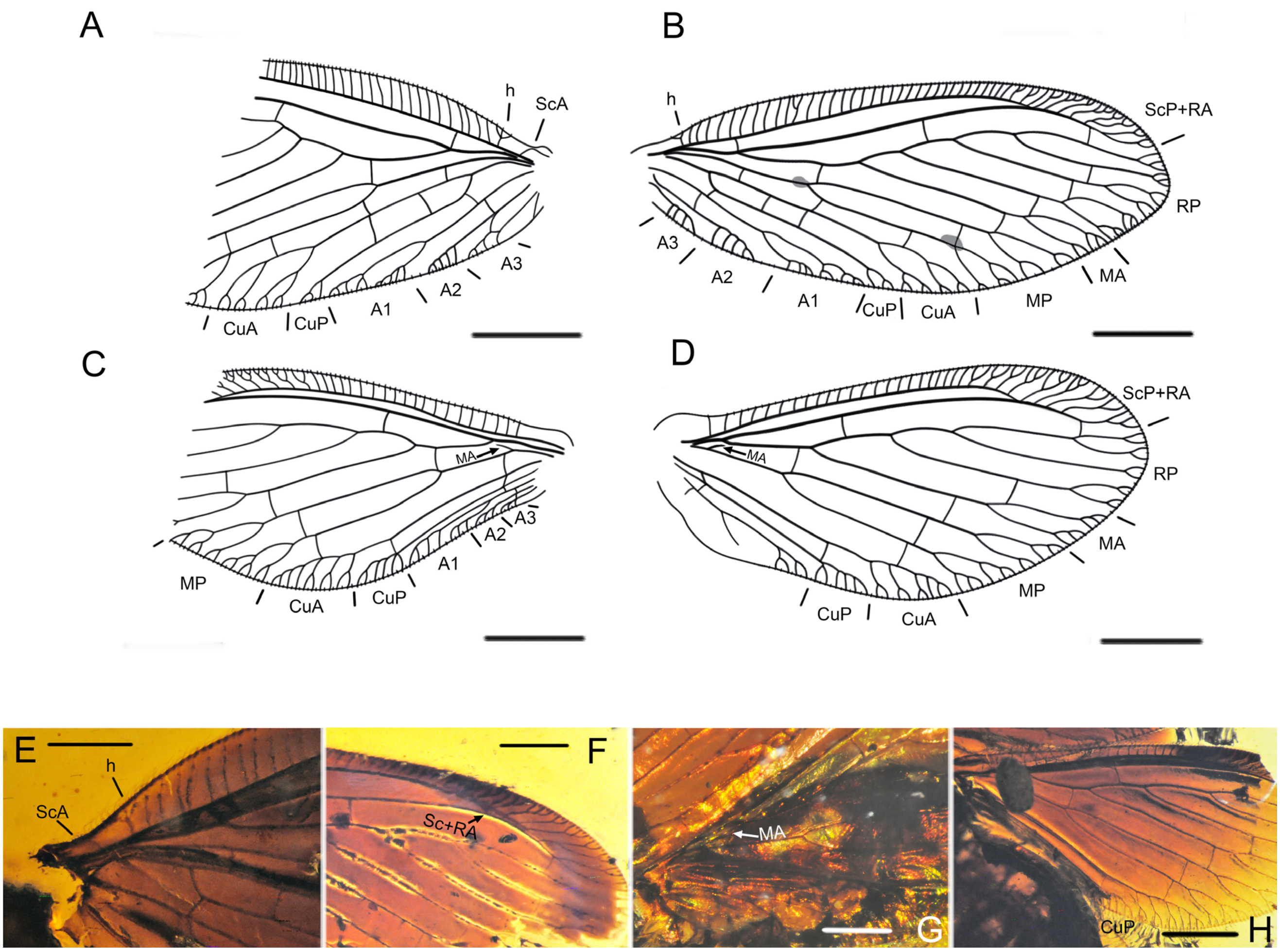

FIGURE 5. *Xiaoberotha bipunctata* **gen. et sp. nov.**, paratype CAM BA-0014, female. **A**, Line drawing of left forewing. **B**, Line drawing of right forewing. **C**, Line drawing of left hind wing. **D**, Line drawing of right hind wing. **E**, Photo of left forewing base, showing ScA and humeral veinlet. **F**, Photo of right forewing distal, showing fusion of ScP and RA. **G**, Photo of right hind wing base, showing the indistinct, straight MA stem. **H**, Photo of left hind wing, showing the configuration of CuP. (Scale bars represent 1.0 mm in **A**–**D** and **H**; 0.5 mm in **E**–**G**)

vertically extending ventrad. Tergum 9 dorsally short, but strongly extending and broadened ventrad. Gonocoxites 9 paired, unclear due to preservation, but anteriorly without distinct hypocaudae. Ectoprocts unpaired, much longer than tergum 9, with arched posterior margin.

Etymology. The specific epithet "*bipunctata*" refers to the presence of two dark spots on the forewing in the new species.

Type material. Holotype EMTG BU-001590, a complete male. Paratype CAM BA-0014, a nearly complete female specimen, with distal parts of left fore- and hind wings lost.

***Xiaoberotha* sp.**
(Figs 7–8)

Description. Total body length 2.9 mm; forewing length 3.7 mm, width 1.5 mm; hind wing length 3.3 mm, width 1.3 mm. Body and wings with many moderate-lengthened setae. Vertex moderately domed, medially with a longitudinal suture. Compound eyes large and semi-globular. Antennae incomplete; scape about twice as long as wide; preserved part of flagellum with 21 flagellomeres. Prothorax slender, about twice as long as wide. Meso- and metathorax robust, mesothorax slightly longer than prothorax.

Forewing (Fig. 8A, B): Ovoid, about twice as long as wide. Wing membrane largely dark, but probably due to preservation because distal parts of both forewings transparent; dark spots absent. Trichosors present along entire wing margin. ScA present and distally curved posteriad, nearly at right angle; humeral veinlet recurrent and bifurcated; costal space proximally broadened; costal crossveins mostly simple except for those forked in

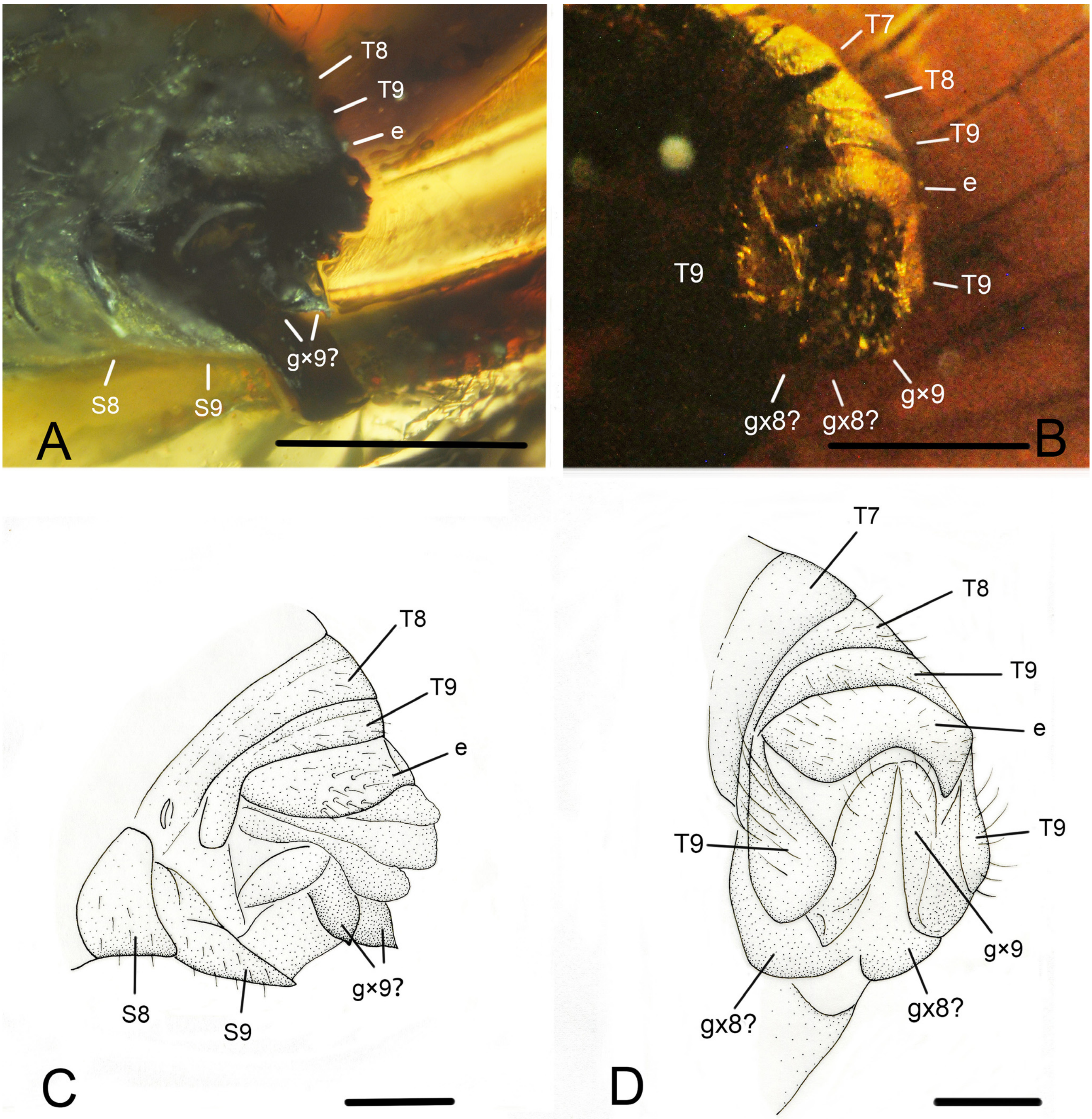

FIGURE 6. Genitalia of *Xiaoberotha bipunctata* **gen. et sp. nov.**. **A** and **C**. Holotype EMTG BU-001590, male. **A**, Photo of genitalia, lateral view. **C**, Line drawing of genitalia, lateral view. **B** and **D**. Paratype CAM BA-0014, female. **B**, Photo of female abdomen, caudal view. **D**, Line drawing of female genitalia, caudal view. e, ectoproct; gx, gonocoxite; pd, pudiculum; S, sternum; T, tergum. (Scale bars represent 1.0 mm in **A** and **B**; 0.1 mm in **C** and **D**)

pterostigmal area; ScP and RA fused distally, pectinately branched, with six branches, most of them marginally forked; subcostal space broad, a single scp-ra present proximally; two ra-rp crossveins respectively present at midpoint of wing and a position distad of fusion point of ScP and RA; RP+MA separating from R near wing base, with five main branches, posterior two of them secondarily branched, all branches marginally forked; two crossveins present between RP+MA and MP; MP initially branched slightly proximad branching point between RP and MA, with two main branches, each with secondary and marginal forks; one mp1-mp2 present; three crossveins present between MP and Cu; cubital and anal veins in left forewing aberrant; in right forewing Cu initially branched near wing base, with two main branches; two cua-cup; A1 distally with two branches, anterior branch pectinately branched with six short simple branches, posterior branch with three short simple branches; A2 pectinately branched

FIGURE 7. *Xiaoberotha* **sp.**, NIGP171262, sex unknown. Habitus photo in dorsal view. (Scale bar represent 1.0 mm.)

distally, with four short, simple branches; A3 pectinately branched distally, with four short, simple branches; three aligned crossveins present proximally between CuA and A1, A1 and A2, and A2 and A3; inner gradate series of crossveins reduced; an outer gradate series of crossveins present, incorporating six crossveins respectively between branches of RP+MA, RP+MA and MP1, MP1 and MP2, and MP2 and CuA.

Hind wing (Fig. 8C): Ovoid, slightly narrower than forewing, about 2.5 times as long as wide. Wing membrane largely dark, but probably due to preservation because distal parts of both hind wings transparent; immaculate. Trichosors present along entire wing margin. Costal space narrow; costal crossveins mostly simple; ScP and RA fused distally, pectinately branched, with five branches, each marginally forked; subcostal space narrow, scp-ra absent; two ra-rp crossveins respectively present proximad of midpoint of wing and distad of fusion point of ScP and RA; RP+MA separating from R near wing base, with four main branches, posterior two of them secondarily branched, all branches marginally forked; an indistinct, straight MA stem present; two crossveins present between RP+MA and MP; MP initially branched slightly proximad of branching point between RP and MA, with two main branches, each with secondary and marginal forks; one mp1-mp2 present; cubital and anal veins largely poorly preserved.

Abdomen poorly preserved.

Material examined. NIGP171262, a nearly complete specimen, but only visible in dorsal view.

Remarks. The morphological characters of this species are almost same to those in *X. bipunctata* **sp. nov.** except for the relatively small body size and the immaculate forewings. The intraspecific variation of body size is common, while the variation, particularly the presence/absence of the pigmented wing markings, is relatively rare within same species in Neuroptera. Nevertheless, we refrain here to describe another new species of *Xiaoberotha* **gen. nov.** based solely on one specimen. Ascertaining its specific status requires more specimens, especially those without forewing markings, are available.

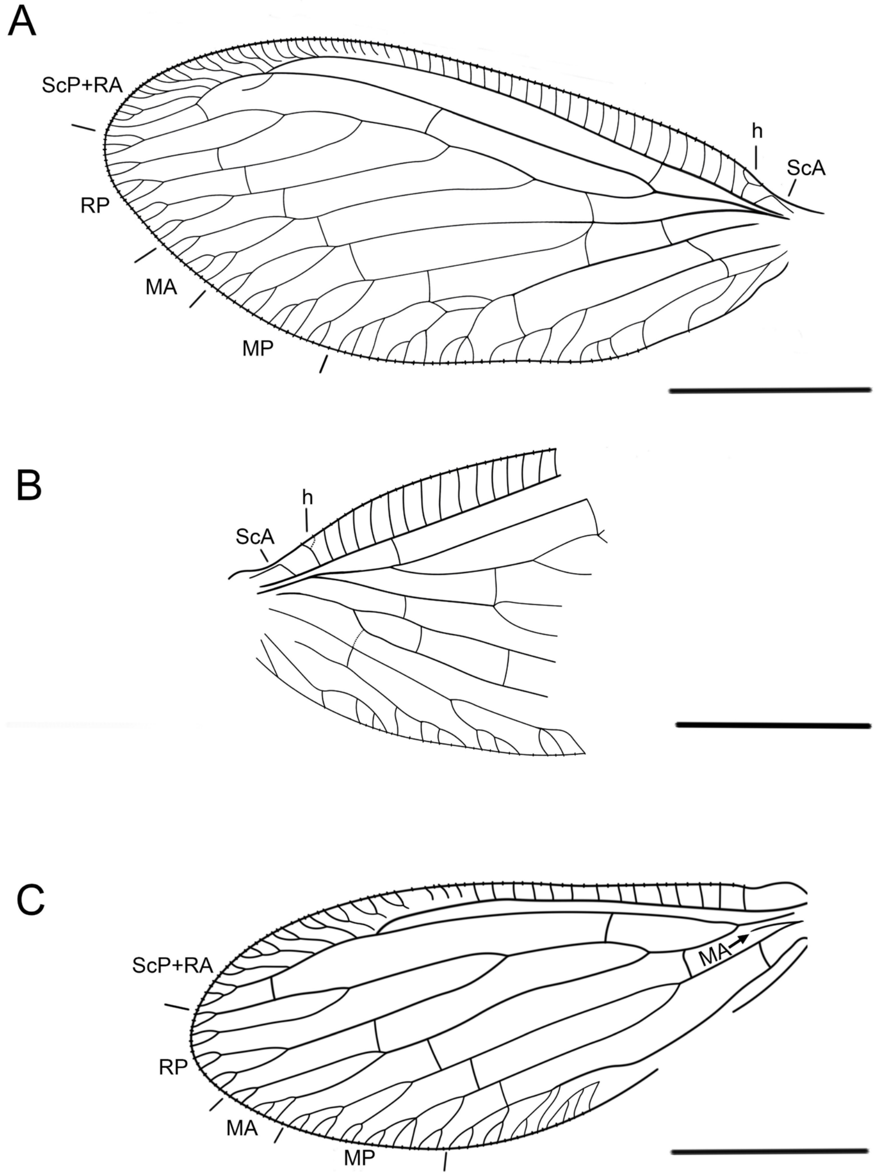

FIGURE 8. *Xiaoberotha* **sp.**, NIGP171262, sex unknown. **A**, Line drawing of left forewing. **B**, Line drawing of right forewing. **C**, Line drawing of left hind wing. (Scale bars represent 1.0 mm.)

Discussion

Xiaoberotha **gen. nov.** lacks many typical characters of Berothidae and differs from the other fossil and extant beaded lacewing genera by the presence of forewing ScA [absent in all the other known berothid genera], the presence of two forewing cua-cup crossveins [forewing cua-cup absent or only one present in all the other known berothid genera], and the hind wing Cu not approximate to posterior wing margin but with well developed CuP [shared by some species of *Sinosmylites* (see Khramov, 2015: fig. 5b); hind wing CuA approximate to the posterior wing margin in a parallel feature with many short branches while CuP more or less reduced in most berothid genera]. It is noteworthy that the distinct, posteriorly curved forewing ScA and the presence of two forewing cua-cup crossveins are shared by many genera of Hemerobiidae (see Makarkin *et al.*, 2016: fig. 8). However, no autapomorphy of Hemerobiidae proposed in Garzón-Orduña *et al.* (2016) could be confirmed to be present in the new genus (see discussion below). In addition, the presence of two forewing cua-cup crossveins is also shared by the Triassic fossil genus *Mesoberotha* Carpenter, 1991 (see Riek, 1955: fig. 18), which is currently placed in an extinct mantispoid family Mesoberothidae. Nevertheless, the new genus can be distinguished from *Mesoberotha* by the presence of many simple forewing costal crossveins [forewing costal crossveins mostly forked in the latter genus].

To further investigate the familial affinity of *Xiaoberotha* **gen. nov.**, we also compared the new genus with the other lacewing families with comparable wing shape and venations, *i.e.*, Nevrorthidae, Sisyridae, Dilaridae, and Hemerobiidae. First, the new genus differs from Nevrorthidae by the absence of nygmata [present in the latter family], the absence of median gradate series of crossveins in the forewing [present in the latter family], the hind wing CuA not approximating to posterior wing margin [hind wing CuA approximating to posterior wing margin in a parallel feature with many short branches in the latter family], the hind wing CuP with multiple branches [simple in the latter family], and the male genitalia without large external gonocoxites 9 [a pair of large external gonocoxites 9 in males of the latter family] (see Aspöck *et al.*, 2017).

Second, the new genus can be distinguished from Sisyridae (excluding the fossil subfamily Paradoxosisyrinae Makarkin, 2016 with uncertain familial status), which has a close phylogenetic relationship with Nevrorthidae (Wang *et al.*, 2017; Winterton *et al.*, 2018), by the maxillary and labial palpi each with its terminal segment not dilated [maxillary and labial palpi with their terminal segments dilated in Sisyridae] (see Makarkin, 2016: fig. 6), the forewing A1 with multiple branches [simple, or rarely with a bifurcate marginal fork in Sisyridae], the hind wing CuP with multiple branches [simple in Sisyridae], and the male genitalia without large external gonocoxites 9 [a pair of large external male gonocoxites 9 in Sisyridae] (see Assmar *et al.*, 2017). Moreover, the new genus is obviously different from Paradoxosisyrinae, which could be a separate family rather than a subfamily of Sisyridae as considered in Khramov *et al.* (2019), by the chewing mandibulate mouthparts [mouthparts specialized into a proboscid type in the latter taxon] and the thinner body setation [body densely setose in the latter taxon] (see Makarkin, 2016; Khramov *et al.*, 2019).

Third, the new genus differs from Dilaridae [excluding the fossil subfamily Cretadilarinae, which should be treated as a junior synonym of Paradoxosisyrinae based on the same female genital characters (see Makarkin, 2017: fig. 3; Khramov *et al.*, 2019: fig. 6E)] by the head without three ocellus-like tubercles [head with three ocellus-like tubercles in the latter family], the antennae not sexually dimorphic [sexually dimorphic antennae present in the latter family], the absence of nygmata [present in the latter family], and the female gonocoxites 9 not strongly elongate [long female gonocoxites 9 (ovipositor) present in the latter family] (see Liu *et al.*, 2017).

Lastly, the new genus cannot be assigned into Hemerobiidae due to its absence of tibial spurs [well developed in the latter family], the single origin of forewing RP+MA on R [two or more origins on R in most brown lacewing genera except the Cretaceous fossil genera *Hemeroberotha* Makarkin & Gröhn, 2019 and *Plesiorobius* Klimaszewski & Kevan, 1986], the indistinct hind wing humeral plate [well developed in the latter family], and the hind wing CuP with multiple branches [simple or with only a small marginal fork, sometimes absent in the latter family] (see Oswald, 1993). Unfortunately, we could not confirm the presence/absence of the apomorphic characters on the head of hemerobiids (*e.g.*, the setation on clypeus and the sensillae on galeae of maxillae) in the new genus due to its preservation condition. Basing on a comprehensive phylogenetic analysis, Garzón-Orduña *et al.* (2016) confirmed that the presence of two or more branches of RP+MA originated from R in the forewing is an autapomorphy of Hemerobiidae. However, Makarkin & Gröhn (2019) considered that the single origin of forewing RP+MA as a plesiomorphic condition is present in some fossil hemerobiids (*i.e.*, *Hemeroberotha* and *Plesiorobius*). This latter hypothesis is certainly reasonable, but the positive evidence known so far is still not sufficient. At least the hemerobiid affinity of *Hemeroberotha* needs further clarification as this genus greatly differs from all the other hemerobiids as noted in Makarkin & Gröhn (2019).

According to above discussion, *Xiaoberotha* **gen. nov.** definitely does not belong to the Nevrorthidae, Sisyridae, or Dilaridae, and it might also not belong to the Hemerobiidae. Here we tentatively place this new genus in Berothidae by the configuration of the female gonocoxites 8. In the female of *Xiaoberotha* **gen. nov.** there is a broad sclerite anteriad the segment 9 and extended dorsoventrally. This sclerite is herein interpreted as putative female gonocoxites 8. It is conspicuous and dorsoventrally extended in the crown-group of Berothidae (see Huang *et al.*, 2019). However, the female gonocoxites 8 are strongly reduced or absent in Hemerobiidae (see Aspöck & Aspöck, 2008).

The adult autapomorphies of Berothidae are very few. Based on a morphology-based phylogenetic analysis, Aspöck & Nemeschkal (1998) proposed three autapomorphies in the adults of Berothidae, *i.e.*, the crossvein-like hind wing MA stem, the absence of the basal part of hind wing CuP, and the presence of female pudiculum (= gonapophyses 8). In *Xiaoberotha* **gen. nov.** the hind wing MA stem is reduced into a straight, oblique veinlet but not sinuate (a plesiomorphic condition), and the very base of hind wing CuP is very weak and hardly discernible although a long stem of hind wing CuP is well developed. It is difficult to clearly confirm these two character states to be homologous with the aforementioned two hind wing autapomorphies in Berothidae, but the possibility still exists. The presence/absence of pudiculum is unknown in *Xiaoberotha* **gen. nov.** due to preservation.

In conclusion, *Xiaoberotha* **gen. nov.** represents an unusual neuropteran lineage, which probably belongs to Berothidae. However, a possible hemerobiid affinity of this new genus cannot be excluded. The Mesozoic fossils of Hemerobiidae are very scarce, and definite brown lacewings with two or more origins of forewing RP+MA on R have not been reported from the Upper Cretaceous of Myanmar. More material of species with intermediate characters of Berothidae and Hemerobiidae are needed to clarify the above question.

Acknowledgements

We are very grateful to Mrs. Xiao Jia for kindly providing the amber specimen for this study. The first author thanks Mr. Hongyu Li and Ms. Ying Yang for help with photography. We also thank Dr. Dany Azar and an anonymous reviewer for kindly reading and improving the manuscript. This research was supported by the National Natural Science Foundation of China (Nos. 31972871 and 41688103), and the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000 and XDA19050101)

References

Aspöck, H., Aspöck, U. & Hölzel, H. (1980) *Die Neuropteren Europas: eine zusammenfassende Darstellung der Systematik, Ökologie und Chorologie der Neuropteroidea (Megaloptera, Raphidioptera, Planipennia) Europas, 2 vols*. Goecke & Evers, Krefeld, 495; 355 pp.

Aspöck, U. & Aspöck, H. (2008) Phylogenetic relevance of the genital sclerites of Neuropterida (Insecta: Holometabola). *Systematic Entomology*, 33, 97–127. https://doi.org/10.1111/j.1365-3113.2007.00396.x

Aspöck, U. & Nemeschkal, H.L. (1998) A cladistic analysis of the Berothidae (Neuroptera). *Acta Zoologica Fennica*, 209, 45–63.

Aspöck, U. & Randolf, S. (2014) Beaded lacewings—a pictorial identification key to the genera, their biogeographics and a phylogenetic analysis (Insecta: Neuroptera: Berothidae). *Deutsche Entomologische Zeitschrift*, 61, 155–172. https://doi.org/10.3897/dez.61.8850

Aspöck, U., Aspöck, H. & Liu, X.Y. (2017) The Nevrorthidae, mistaken at all times: phylogeny and review of present knowledge (Holometabola, Neuropterida, Neuroptera). *Deutsche Entomologische Zeitschrift*, 64, 77–110. https://doi.org/10.3897/dez.64.13028

Assmar, A.C. & Salles, F.F. (2017) Taxonomic and distributional notes on spongilla-flies (Neuroptera: Sisyridae) from southeastern Brazil with first interactive key to the species of the country. *Zootaxa*, 4273, 80–92. https://doi.org/10.3897/dez.64.13028

Engel, M.S. & Grimaldi, D.A. (2008) Diverse Neuropterida in Cretaceous amber, with particular reference to the paleofauna of Myanmar (Insecta). *Nova Supplementa Entomologica*, 20, 1–86.

Garzón-Orduña, I.J., Menchaca-Armenta, I., Contreras Ramos, A., Liu, X.Y. & Winterton, S.L. (2016) The phylogeny of brown lacewings (Neuroptera: Hemerobiidae) reveals multiple reductions in wing venation. *BMC Evolutionary Biology*, 16 (192), [19 pp]. https://doi.org/10.1186/s12862-016-0746-5

Huang, S., Ren, D. & Wang, Y.J. (2019) A new basal beaded lacewing (Neuroptera: Berothidae) from mid-Cretaceous Myanmar amber. *Cretaceous Research*, 95, 1–7. https://doi.org/10.1016/j.cretres.2018.10.025

Kania, I., Wang, B. & Szwedo, J. (2015) *Dicranoptycha* Osten Sacken, 1860 (Diptera, Limoniidae) from the earliest Cenomanian Burmese amber. *Cretaceous Research*, 52, 522–530. https://doi.org/10.1016/j.cretres.2014.03.002

Khramov, A.V. (2015) Jurassic beaded lacewings (Insecta: Neuroptera: Berothidae) from Kazakhstan and Mongolia. *Paleontologicheskii Zhurnal*, 2015, 26–34. https://doi.org/10.1134/S0031030115010062

Khramov, A.V., Yan, E. & Kopylov, D.S. (2019) Nature's failed experiment: Long-proboscid Neuroptera (Sisyridae: Paradoxosisyrinae) from Upper Cretaceous amber of northern Myanmar. *Cretaceous Research*, 104, 1–12. https://doi.org/10.1016/j.cretres.2019.07.010

Liu, X.Y., Aspöck, H., Winterton, S.L., Zhang, W.W. & Aspöck, U. (2017) Phylogeny of pleasing lacewings (Neuroptera: Dilaridae) with a revised generic classification and description of a new subfamily. *Systematic Entomology*, 42, 448–471. https://doi.org/10.1111/syen.12225

Makarkin, V.N. (2016) Enormously long, siphonate mouthparts of a new, oldest known spongillafly (Neuroptera, Sisyridae) from Burmese amber imply nectarivory or hematophagy. *Cretaceous Research*, 65, 126–137. https://doi.org/10.1016/j.cretres.2016.04.007

Makarkin, V.N. (2017) New taxa of unusual Dilaridae (Neuroptera) with siphonate mouthparts from the mid-Cretaceous Burmese amber. *Cretaceous Research*, 74, 11–22. https://doi.org/10.1016/j.cretres.2016.12.019

Makarkin, V.N. (2018) A new species of *Haploberotha* (Neuroptera: Berothidae) from mid-Cretaceous Burmese amber. *Cretaceous Research*, 90, 375–381. https://doi.org/10.1016/j.cretres.2018.06.011

Makarkin, V.N. & Gröhn, C. (2019) The first unusual Hemerobiidae (Neuroptera) from mid-Cretaceous Burmese amber.

Cretaceous Research, in press. https://doi.org/10.1016/j.cretres.2019.104206

Makarkin, V.N., Wedmann, S. & Weiterschan, T. (2016) A new genus of Hemerobiidae (Neuroptera) from Baltic amber, with a critical review of the Cenozoic *Megalomus*-like taxa and remarks on the wing venation variability of the family. *Zootaxa*, 4179, 345–370. https://doi.org/10.11646/zootaxa.4179.3.2

Makarkin, V.N., Yang, Q. & Ren, D. (2011) Two new species of *Sinosmylites* Hong (Neuroptera, Berothidae) from the Middle Jurassic of China, with notes on Mesoberothidae. *ZooKeys*, 130, 199–215. https://doi.org/10.3897/zookeys.130.1418

Oswald, J.D. (1993) Revision and cladistic analysis of the world genera of the family Hemerobiidae (Insecta: Neuroptera). *Journal of the New York Entomological Society*, 101, 143–299.

Riek, E.F. (1955) Fossil insects from the Triassic beds at Mt. Crosby, Queensland. *Australian Journal of Zoology*, 3, 654–691. https://doi.org/10.1071/ZO9550654

Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q. & Li, X. (2012) Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research*, 37, 155–163. https://doi.org/10.1016/j.cretres.2012.03.014

Wang, Y.Y., Liu, X.Y., Garzón-Orduña, I.J., Winterton, S.L., Yan, Y., Aspöck, U., Aspöck, H. & Yang, D. (2017) Mitochondrial phylogenomics illuminates the evolutionary history of Neuropterida. *Cladistics*, 33, 617–636. https://doi.org/10.1111/cla.12186

Winterton, S.L., Lemmon, A.R., Gillung, J.P., Garzon, I.J., Badano, D., Bakkes, D.K., Breitkreuz, L.C.V., Engel, M.S., Lemmon, E.M., Liu, X.Y., Machado, R.J.P., Skevington, J.H. & Oswald, J.D. (2017) Evolution of lacewings and allied orders using anchored phylogenomics (Neuroptera, Megaloptera, Raphidioptera). *Systematic Entomology*, 43, 330–354. https://doi.org/10.1111/syen.12278

Yang, Q., Shi, C.F. & Ren, D. (2019) A new genus and species of berothids (Insecta, Neuroptera) from the Late Cretaceous Myanmar amber. *ZooKeys*, 864, 99–109. https://doi.org/10.3897/zookeys.864.35271

Yuan, D.D., Ren, D. & Wang, Y.J. (2016) New beaded lacewings (Neuroptera: Berothidae) from Upper Cretaceous Myanmar amber. *Cretaceous Research*, 68, 40–48. https://doi.org/10.1016/j.cretres.2016.08.007