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New beaded lacewings (Neuroptera: Berothidae) from the mid-Cretaceous of Myanmar with specialized cephalic structures

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Two new genera and five new spices of the lacewing family Berothidae from the mid-Cretaceous Burmese amber are described. Cornoberotha gen. nov. with three new species (C. anomala sp. nov., C. aspoeckae sp. nov., and C. monogona sp. nov.) and Dolichoberotha gen. nov. with two new species (D. burmana sp. nov. and D. bifurcata sp. nov.) are both closely related to Ansoberotha Yang, Shi & Ren, 2019 by having the strongly elongate antennae. Frontal horns are first found in Berothidae. The male genitalia in these "long antennae" berothids retain the separation of tergum 9 and ectoprocts and the absence of bristles on the gonocoxites 10 complex, which are plesiomorphic, while their female genitalia possess some apomorphic character states, such as the paired sternum 7 and the presence of hypocaudae, which are shared by the higher berothid subfamilies, e.g. Nosybinae and Berothinae. Accordingly, the presently described berothids probably represent the stem-group of higher groups of Berothidae.

1. Introduction

The family Berothidae (beaded lacewings), together with Mantispidae and Rhachiberothidae, belong to the superfamily Mantispoidea, which represents one of the major lineages in the crown-group of Neuroptera (Wang et al., 2017; Winterton et al., 2018; Engel et al., 2018). The extant Berothidae are distributed in all zoogeographical regions and currently comprise less than 120 described species of 25 genera in the world (Oswald, 2019). The adults of Berothidae are characterized by the scale-like setae on the wings and/or thorax and coxae in many species, the long scape of antenna, the frequently falcate forewings, and the CuA approximating posterior margin of hind wing.

The phylogenetic position of Berothidae within Mantispoidea has not been fully resolved. In recent phylogenomic studies, Berothidae was recovered to be either the sister group of Rhachiberothidae (Wang et al., 2017) or the sister group of Mantispidae excluding Symphrasinae (Winterton et al., 2018). Extant Berothidae are divided into six subfamilies: Berothinae, Cyrenoberothinae, Nyrminae, Protobiellinae, Trichomatinae, and Nosybinae (Aspöck & Randolf, 2014). However, the subfamilial division has only been tested by the morphology-based phylogenetic analyses (Aspöck and Nemeschkal, 1998; Aspöck and Randolf, 2014). Particularly, the relationship between Nyrminae and Berothimerobiinae (synonymized with the former subfamily in Aspöck and Randolf, 2014), as well as the relationship between Nosyninae and Trichomatinae, need further test (Aspöck and Randolf, 2014; Makarkin and Ohl, 2015).

Berothidae was estimated to be diverged during the Late Triassic based on molecular evidence (Wang et al., 2017). However, the fossil evidence only documents that the oldest definite fossils of Berothidae existed from the Middle Jurassic (Makarkin et al., 2011). Nevertheless, the extinct family Mesoberothidae (only known from the Late Triassic), which appears to be very similar to Berothidae based on wing venation (see Riek, 1955), could be the stem-group of Berothidae before the Jurassic. So far, 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 oldest fossil record of Berothidae refers to the species of Sinosmylites Hong

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(1983) from the Middle Jurassic of China (Makarkin et al., 2011). Most fossil berothids are not placed in any known subfamilies except two species from the Eocene (Elektroberotha groehni Makarkin & Ohl, 2015 and Xenoberotha angustialata Makarkin, 2017) belonging to Berothinae.

It is remarkable that the palaeodiversity of Berothidae is extraordinarily rich from the Upper Cretaceous of Myanmar, being one of the major lineages of Neuroptera in this deposit (see Ross, 2019), currently with 11 genera and 14 species described based on the Burmese amber specimens (Engel and Grimaldi, 2008; Yuan et al., 2016; Makarkin, 2018; Huang et al., 2019; Yang et al., 2019). These Burmese amber berothids show diverse morphological characters and are probably the members or as the stem-groups of different subfamilies (Huang et al., 2019).

Yang et al. (2019) reported a new genus and species of Berothidae from the Burmese amber, namely Ansoberotha jiewenae Yang et al. (2019). This species possesses strongly elongate antennae, including long scape and ca. 100 flagellomeres, which are unique in Berothidae. However, Yang et al. (2019) described this species based on only one specimen and did not provide any substantial discussion on its subfamilial placement in Berothidae.

Here we describe two new genera and five new species that are closely related to Ansoberotha based on nine amber specimens from the mid-Cretaceous of Myanmar. All of these species are characterized by the strongly elongate antennae similar as in Ansoberotha. We also provide additional description of A. jiewenae, especially that of its female genitalia. Notably, some of these species display spectacular morphological specialization on head, e.g. the frontal horns and strongly curved flagellomere 1, which have never been found in previously known beaded lacewings. Based on the female genital characters, these species appear to be closely related to Nosybinae and Berothinae. These interesting berothid fossils are important for understanding the morphology, phylogeny, and evolution of Berothidae.

2. Material and methods

The amber specimens for this study come from the Hukwang 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 98.8 ± 0.6 million years (the earliest Cenomanian) by U–Pb dating of zircons from the volcanoclastic matrix of the amber (Shi et al., 2012). The specimens are deposited in the Nanjing Institute of Geology and Palaeontology (NIPG), Nanjing and the Three Gorges Entomological Museum (EMTG), Chongqing.

Photographs were taken by using a Zeiss SteREO Discovery V12 stereo microscope system with Nikon D90 digital camera. Wing drawings were prepared by Zeiss SteREO Discovery V12 stereo microscope system and genital drawings were made by Nikon SMZ745 stereoscope. The figures were prepared with Adobe Photoshop CC 2018.

Terminology of wing venation generally follows Aspöck et al. (1980). Terminology of genitalia follows Aspöck and Aspöck (2008). Abbreviations used for wing veins are as following: A, anal vein; C, costa; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; M, media; MA, media anterior; MP, media posterior; R, radius; RA, radius anterior; RP, radius posterior; ScP, subcosta.

3. Systematic palaeontology

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

Genus Cornoberotha gen. nov.
(Figs. 1–8).
urn:lsid:zoobank.org:act:9E269DB4-4ABF-4088-959F-746B3161BB51.
Type species: Cornoberotha anomala sp. nov.

Diagnosis. Frons sometimes with horn-like projections; antenna with ca. 90-120 flagellomeres; scape elongate and slightly swollen distad, about 2.5–10.0 times as long as wide, sometimes with stiff setae distally. Forewing costal space proximally distinctly dilated; costal crossveins proximally simple, but forked from midpoint or distal portion of costal space; 3-5 ra-rp crossveins proximad fusing point of ScP and RA; one series of gradate crossveins (3-5) present between branches of RP+MA and MP; MP with two main branches, both pectinately branched distally, MP1 with less branches than that of MP2, most branches of MP1 and MP2 bifurcated or trifurcated; CuA with pectinate and forked branches; CuP branched dichotomously. Hind wing CuA with pectinate branches mostly forked or simple. Male tergum 9 and ectoprocts separated; gonocoxites 9 slender, acutely pointed at tip, and strongly curved ventrad; complex of gonocoxites 10 medially with a slenderly elongated sclerite, without bristles. Female tergum 9 with pseudohypocaudae; gonocoxites 9 with elongate and closed hypocaudae.
Etymology. The generic name is from “corn-”, horn, and Berotha, a genus name of the family Berothidae, in reference to horn-like projections sometimes existed on the frons of some species in this new genus. Gender: Feminine.

Cornoberotha anomala sp. nov.
(Figs. 1 and 2).

urn:lsid:zoobank.org:act:E836D51D-2AB9-4A7F-B151-E7FA9DAFC123.

Diagnosis. Frons with a pair of short horns anteriad antennal bases; antenna with ca. 90 flagellomeres; scape about 2.5 times as long as wide; flagellomere 1 proximally with a small projection directed medially. Forewing: Apex rounded, costal crossveins mostly simple but branched proximad fusing point of ScP and RA; 4-5 ra-rp crossveins present proximad fusing point of ScP and RA; one gradate series of five crossveins present between branches of RP+MA and MP. Hind wing: 3 ra-rp crossveins present proximad fusing point of ScP and RA; CuA with pectinate and simple branches.
Description. Female. Body length 5.2 mm, with scattered, fine setae; integument brown.
Head shorter than wide, with prominent compound eyes; frons with a pair short horns anteriad antennal bases. Antenna with scape elongate and slightly swollen distally, about 2.5 times as long as wide, covered by long, stiff setae dorsally; flagellomere 1 with a small subcylindrical projection that is directed medially; ca. 90 flagellomeres, each flagellomere with relatively long setae arranged in a circle; terminal flagellomere acutely pointed. Terminal maxillary palpomere slender, slightly longer than preceding two slender palpomeres respectively, pointed distad.
Prothorax slightly longer than wide; meso- and metathorax as long as wide. Legs slender; tibial spurs absent; tarsus 5-segmented; tarsomere 1 longest, nearly equal to combined length of tarsomeres 2-4; tarsomere 5 slightly swollen; pretarsal claws short, simple; arolium present.
Forewing: 6.1–6.7 mm long and 2.1–2.6 mm, membrane hyaline, immaculate, without scales; ovoid, apex rounded; trichosors present along entire wing margin; costal space dilated proximally; costal crossveins branched proximad fusing point of ScP and RA, with number of forked ones less than that of simple ones; ScP fused distally with RA; scp-ra present near wing base; 4 (right forewing) or 5 (left forewing) ra-rp crossveins proximad fusing point of ScP

Fig. 1. Cornoberotha anomala gen. et sp. nov., holotype, EMTG BU001249, female. A. Photograph of head, frontal view; B. Habitus photograph, ventral view. fa1: flagellomere 1; sc: scape. Arrows indicate a pair of frontal horns. Scale bar = 1.0 mm.

and RA; RP+MA with six main branches, posterior three RP branches secondarily branched from its base or midpoint, and all branches marginally forked; one gradate series of five crossveins present between branches of RP+MA and MP; one crossvein (or distally shifted MA stem) present between RP+MA and MP1; MP1 with three branches, MP2 with five pectinate branches, most branches of MP1 and MP2 bifurcated or trifurcated; mp1-mp2 present; two mp-cua present; CuA with six pectinate branches, all of them marginally forked; CuP branched dichotomously.

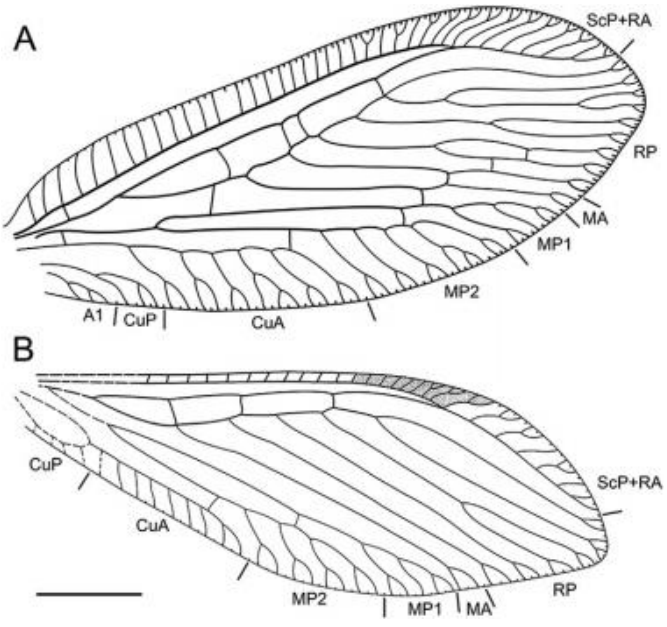

Fig. 2. Cornoberotha anomala gen. et sp. nov., holotype, EMTG BU001249, female. A. Drawing of forewing; B. Drawing of hind wing. Scale bar = 1.0 mm.

Hind wing: 5.8 mm long and 2.1 mm wide, narrower than forewing, immaculate; apex slightly pointed; trichosors present along entire wing margin; costal space narrow; costal crossveins mostly simple; a pigmented pterostigma present; scp-ra absent; three ra-rp crossveins present proximad fusing point of ScP and RA; gradate series of crossveins absent; RP+MA with six main branches, third RP branch bifurcated near midpoint, all branches marginally forked; MP with similar branching condition to that of forewing; CuA with eight pectinate and simple branches; CuP short, branched pectinately; one cua-cup present.

Abdomen obscure.

Male. Unknown.

Type material. Holotype, EMTG BU001249 amber piece preserving a complete and clear female of C. anomala sp. nov.; it is polished in the form of nearly quadrangle, transparent cabochon, with length × width about 22.3 × 23.8 mm, height about 6.1 mm.

Etymology. The specific epithet “anomala” refers to its peculiar cephalic structures, including the flagellomere 1 with a projection and the presence of a pair of frontal horns, in the new species.

Cornoberotha aspoeckae sp. nov.
(Figs. 3e6).

urn:lsid:zoobank.org:act:96816860-9846-4131-938A-C8F2AD746661.

Diagnosis. Frons without horn; antenna with ca. 120 flagellomeres; scape about 9.0 times as long as wide. Forewing: Costal crossveins branched from midpoint of costal space proximad fusing point of ScP and RA; 3 or 5 ra-rp crossveins present proximad fusing point of ScP+RA; one gradate series of three or four crossveins present between branches of RP+MA and MP. Hind wing: 3 ra-rp crossveins

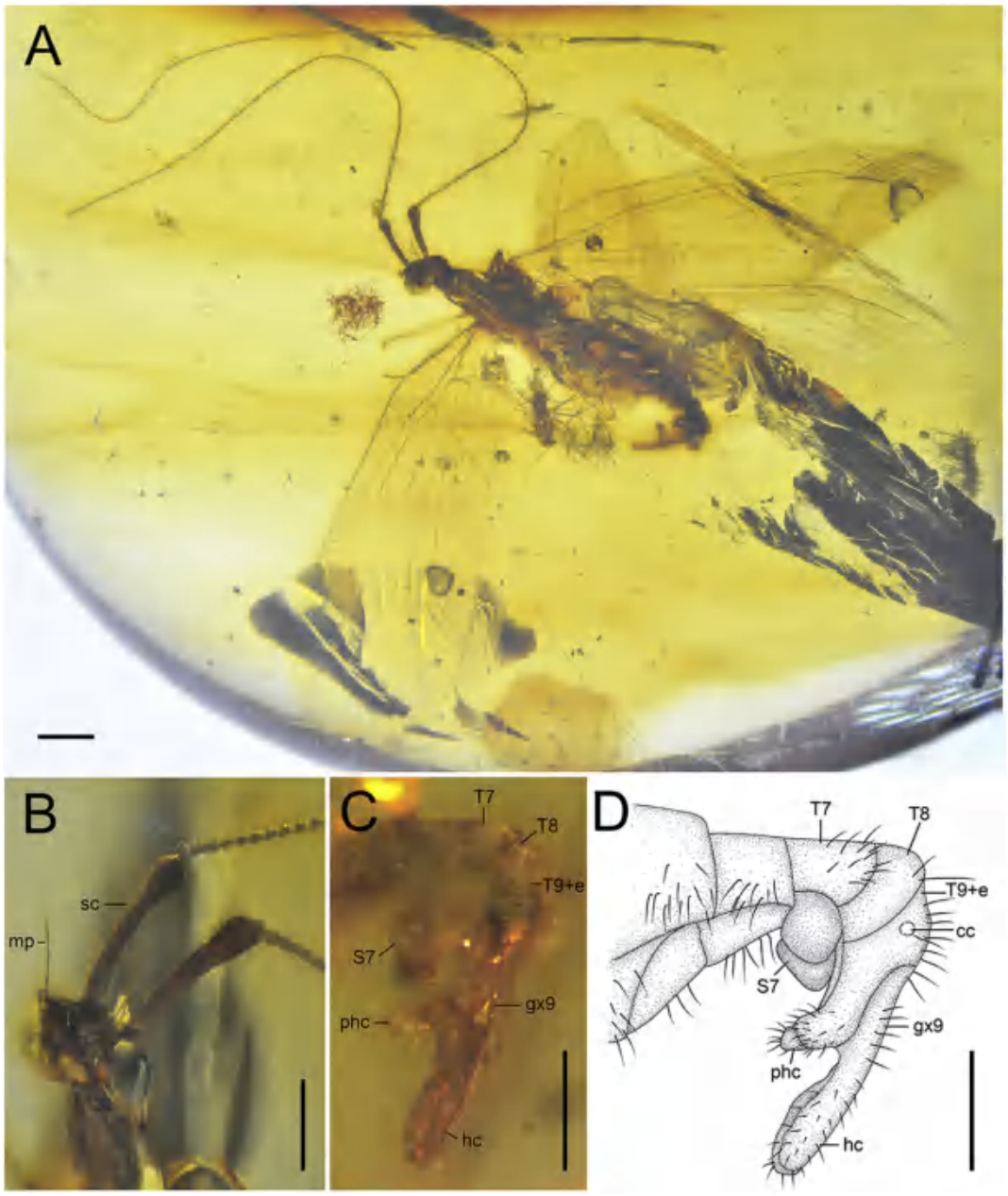

Fig. 3. Cornoberotha aspoeckae gen. et sp. nov., holotype, NIGP171707, female. A. Habitus photograph, lateral view; B. Photograph of head, ventrofrontal view; C. Photograph of genitalia, lateral view; D. Drawing of genitalia, lateral view. e: ectoproct; gx9: gonocoxite 9; hc: hypocauda; mp: maxillary palpus; phc: pseudohypocauda; sc: scape; S: sternum; T: tergum;. Scale bar = 1.0 mm (A); 0.5 mm (B, C, D).

present proximad fusing point of ScP and RA; CuA with pectinate and simple branches.

Description. Female. Body length 6.0 mm, with scattered, fine setae; integument brown.

Head slightly shorter than wide, with prominent compound eyes; frons without any horn. Antenna with scape elongate and swollen distally, about 9 times as long as wide, covered by long, thick, setae dorsally; ca. 120 flagellomeres, flagellomere 1 slightly broader than others, each flagellomere with relatively long setae arranged in a circle. Terminal maxillary palpomere slender, slightly longer than preceding two slender palpomeres respectively, acutely pointed distad.

Prothorax slightly longer than wide; meso- and metathorax as long as wide. Legs slender; procoxa about 4.0 times as long as meso- and metacoxa; metatibia longer than metafemora; tibial spurs absent; tarsus 5-segmented; tarsomere 1 longest, nearly equal to combined length of tarsomeres 2-3; tarsomere 5 slightly swollen; pretarsal claws short, simple; arolium present.

Forewing: 7.6 mm long and 2.7 wide; membrane hyaline, immaculate, without scales; apex rounded; trichosors present along entire wing margin; costal space dilated proximally; costal crossveins branched from midpoint of costal space, number of forked ones nearly equal to that of simple ones; ScP fused distally with RA; scp-ra present near wing base; 3 (right forewing) or 5 (left forewing) ra-rp crossveins proximad fusing point of ScP and RA; RP+MA with five main branches, third RP branch pectinately branched from its base, all branches marginally forked; one gradate series of three crossveins between branches of RP+MA and MP; one crossvein (or distally shifted MA stem) present between RP+MA and MP1; MP1 with less branches than that of MP2, most branches

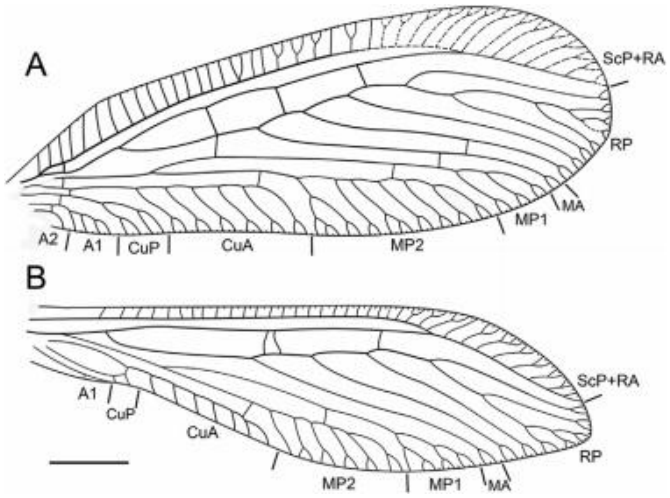

Fig. 4. Cornoberotha aspoeckae gen. et sp. nov., holotype, NIGP171707, female. A. Drawing of forewing; B. Drawing of hind wing. Scale bar = 1.0 mm.

of MP1 and MP2 bifurcated or trifurcated; one mp1-mp2 present; two mp-cua present; CuA with six pectinate branches, all of them marginally forked; CuP branched dichotomously; one cua-cup present; cup-a1 present; A1 short, with four pectinate simple branches; a1-a2 present; A2 and A3 simple.

Hind wing: 2.7 mm long and 1.9 mm wide; narrower than forewing, immaculate; apex slightly pointed; trichosors present along entire wing margin; costal space narrow; costal crossveins mostly simple; scp-ra absent; three ra-rp crossveins present proximad fusing point of ScP and RA; gradate series of crossveins absent; RP+MA with five main branches, third RP branch secondarily branched near its base, all branches marginally forked; MP with similar branching condition to that of forewing; CuA with seven pectinate and simple branches; CuP bifurcated; one cua-cup present.

Genitalia: Sternum 7 medially separated into a pair of broad sclerites. Tergum 9 + ectoprocts fused together, ventrally with putative pseudohypocaudae, which are slightly curved anteriad on apex. Gonocoxites 9 paired, anteriorly with long and closed hypocaudae, which terminally extend to abdominal segment 5.

Male. Body length 5.4 mm. Antenna with scape elongate and swollen proximally, about 4.0 times as long as wide (Note that the scape is preserved in frontal view, so the natural condition of scape could be much longer). Forewing 8.1 mm long and 2.2 mm wide; costal crossveins branched from midpoint of costal space on right forewing or slightly proximad fusing point of ScP and RA on left forewing; one gradate series of four crossveins present between branches of RP+MA and MP. Hind wing 6.8 mm long and 2.2 mm wide; one gradate series of three crossveins present between RP+MA branches and MP.

Genitalia: Tergum 9 and ectoproct separated. Sternum 9 tongue-shaped. Gonocoxites 9 slenderly elongate, acutely pointed at tip, and slightly curved laterally. Complex of gonocoxites 10 (= paramere-mediuncus complex) medially with a slenderly elongate sclerite, without bristles.

Type material. Holotype, NIGP171707, amber piece preserving a complete and clear female of C. aspoeckae sp. nov., a leafhopper, four midges, and a parasitoid wasp; it is polished in the form of nearly elliptical, transparent cabochon, with length × width about 32.3 × 23.5 mm, height about 10.0 mm. Paratype, EMTG BU001214, amber piece preserving a complete and clear male of C. aspoeckae sp. nov. and a true bug; it is polished in the form of nearly elliptical, transparent cabochon, with length × width about 21.8 × 22.2 mm, height about 6.2 mm.

Etymology. The new species is dedicated to Dr. Ulrike Aspöck for her tremendous contributions to the systematics of Berothidae.

Remarks. The assignment between male and female of this new species is based on the absence of cephalic horns and the presence of forked costal crossveins on distal half of forewing costal space. In the other species of Cornoberotha gen. nov. the cephalic horns are present and the forked costal crossveins on the forewing are present more distad.

Cornoberotha monogona sp. nov.
(Figs. 7 and 8).

urn:lsid:zoobank.org:act:A433F388-E724-493B-A8B4-927820118F09.

Diagnosis. Frons with one median horn; scape about 10.0 times as long as wide. Forewing: Apex pointed, distal margin slightly falcate; five ra-rp crossveins proximad fusing point of ScP and RA; one gradate series of five crossveins present between branches of RP+MA and MP. Hind wing: Pigmented pterostigma present; 4-5 ra-rp crossveins present proximad fusing point of ScP and RA; CuA with nine pectinate short branches, distal five branches forked.

Description. Female. Body length 5.6 mm, with scattered, fine setae; integument brown.

Head obviously longer than wide, with prominent compound eyes; frons with one median horn, which is pointed distad and slightly curved dorsad. Antenna with scape elongate and slightly swollen distad, about 10.0 times as long as wide, covered by long, thick setae dorsally; flagellomere 1 slightly broader than other flagellomeres, each flagellomere with relatively long setae arranged in a circle. Terminal maxillary palpomere slender, acutely pointed distally.

Prothorax slightly longer than wide; meso- and metathorax also longer than wide. Legs slender; procoxa longer than meso- and metacoxa; metatibia slightly longer than metafemora; tibial spurs absent; tarsus 5-segmented; tarsomere 1 longest, nearly equal to combined length of tarsomeres 2-4; tarsomere 5 slightly swollen; pretarsal claws short, simple; arolium present.

Forewing: 8.5 mm long and 2.3 mm wide; membrane hyaline, immaculate, without scales; apex pointed, distal margin slightly falcate; trichosors present along entire wing margin; costal space dilated proximally; costal crossveins branched proximad fusing point of ScP and RA, with number of forked ones less than that of simple ones; ScP fused distally with RA; one scp-ra present near wing base; five ra-rp crossveins proximad fusing point of ScP and RA; RP+MA with seven main branches, fourth RP branch pectinately branched from its base, all branches marginally forked; one gradate series of five crossveins between branches of RP+MA and MP; one crossvein (or distally shifted MA stem) present between RP+MA and MP1; MP with two main branches, both pectinately branched distally; MP1 with less branches than that of MP2, most branches of MP1 and MP2 bifurcated or trifurcated; one mp-cua present; CuA with six pectinate and distally forked branches; CuP branched dichotomously.

Hind wing: 7.6 mm long and 1.8 mm wide; narrower than forewing, immaculate; apex distinctly pointed and distal margin slightly falcate; trichosors present along entire wing margin; costal space narrow; costal crossveins mostly simple; a pigmented pterostigma present; 4 (left hind wing) or 5 (right hind wing) ra-rp crossveins present proximad fusing point of ScP and RA; RP+MA with seven main branches, fourth RP branch pectinately branched from its base, all branches marginally forked; MP with similar branching condition to that of forewing; two crossveins present

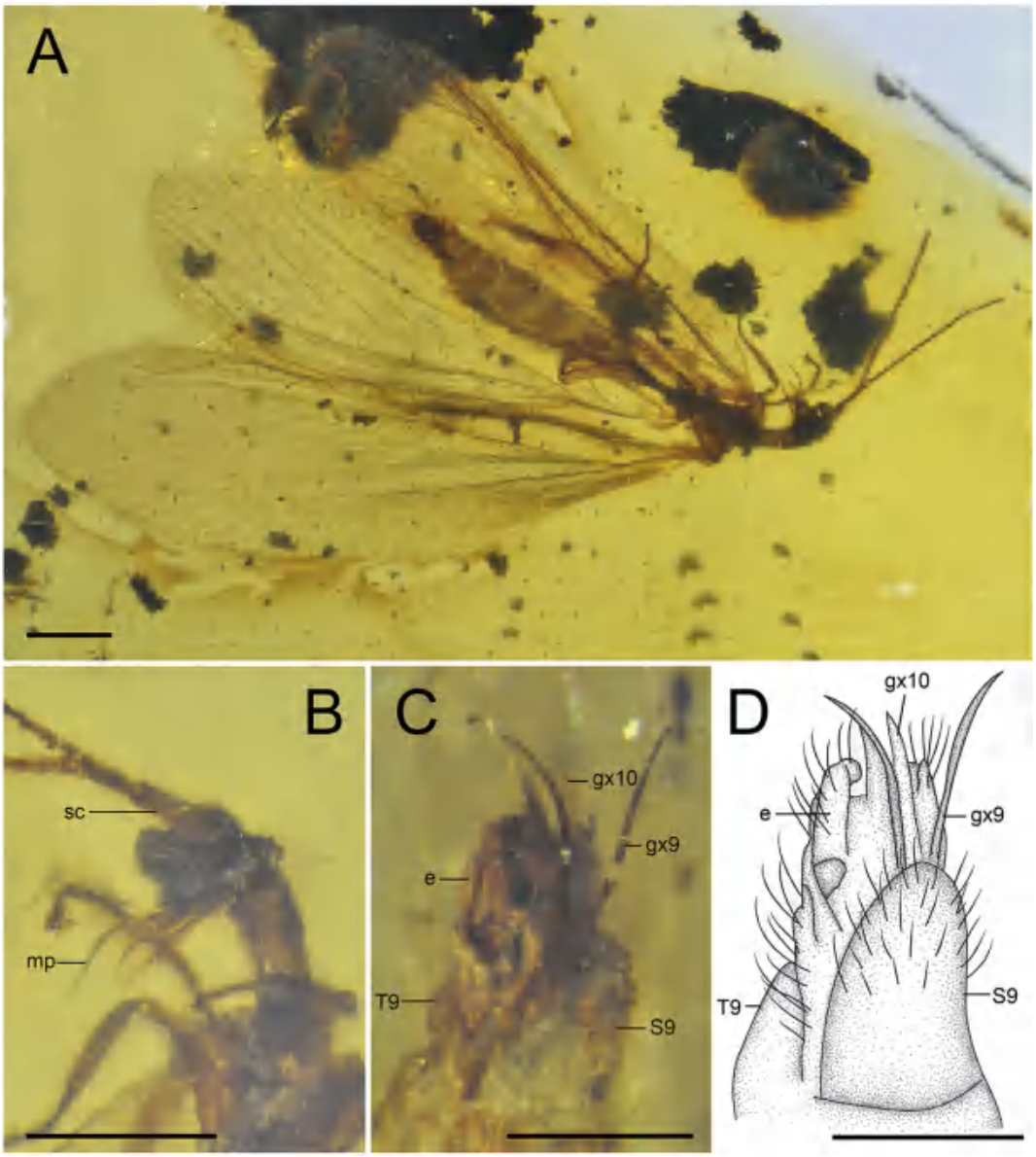

Fig. 5. Cornoberotha aspoeckae gen. et sp. nov., paratype, EMTG BU001214, male. A. Habitus photograph, ventral view; B. Photograph of head, frontal view; C. Photograph of genitalia, ventral view; D. Drawing of genitalia, ventral view. e: ectoproct; gx9: gonocoxite 9; gx10: complex of fused gonocoxites, gonapophyses and gonostyli 10 (= paramere-mediuncus complex); mp: maxillary palpus; sc: scape; S: sternum; T: tergum. Scale bar = 1.0 mm (A); 0.5 mm (B, C, D).

between branches of RP+MA and MP; CuA with nine pectinate short branches, distal five of them forked; CuP with three pectinate short and simple branches; one cua-cup present.

Genitalia: Only visible in ventral view. Ventral parts of abdominal segments 7 and 8 unclear. Pseudohypocaudae present. Gonocoxites 9 with long and closed hypocaudae, which extends to abdominal segment 5.

Male. Unknown.

Type material. Holotype, NIGP171708, amber piece preserving a complete and clear female of C. monogona sp. nov., and three hymenopterans; it is polished in the form of nearly rectangular, transparent cabochon, with length × width about 34.5 × 10.5 mm, height about 9.0 mm.

Etymology. The specific epithet "monogona" refers to the present of a single horn-like projection on the frons of the new species.

Remarks. The placement of the above three new species in a same genus is based on the similar forewing costal space distinctly dilated proximally with most crossveins simple and the female genitalia with pseudohypocaudae on tergum 9 (discernible in C. aspoeckae sp. nov. and C. monogona sp. nov.). However, the head characters greatly differ among these three species. In C. anomala sp. nov. there are a pair of short frontal horns anteriad the antennal bases, the scape is about 2.5 times as long as wide, distally bearing some stiff setae, and the flagellomere 1 proximally has a short process that is directed medially. In C. aspoeckae sp. nov. and C. monogona sp. nov. the scape is much longer, being 9.0e10.0 times as long as wide, distally without thickened setae, and the flagellomere 1 is of normal shape. However, C. monogona sp. nov. bears one median frontal horn, while there is no frontal horn in C. aspoeckae sp. nov. Besides, there is a pigmented pterostigma on the hind wing in C. monogona sp. nov., while this feature is not found in the other species of Cornoberotha gen. nov.

The derivation of specialized cephalic structures is rarely known in Neuroptera (see Discussion). The case known before the present

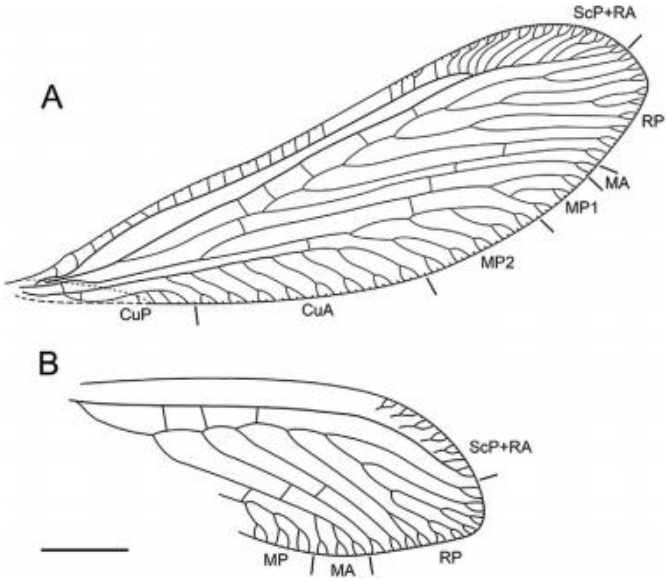

Fig. 6. Cornoberotha aspoeckae gen. et sp. nov., paratype, EMTG BU001214, male. A. Drawing of forewing; B. Drawing of hind wing. Scale bar = 1.0 mm.

finding refers to the dustywing species of the genus Neosemidalis Enderlein (1930) (Coniopterygidae) and the green lacewing species of the genus Ungla Navás (1914) (Chrysopidae). It is notable that the cephalic structures have diverse morphological modifications among different species of Neosemidalis (Meinander, 1972). Therefore, we tentatively consider that the disparate morphological characters on head of the species of Cornoberotha gen. nov. are attributed to interspecific differences within same genus. However, it needs further investigation with more materials.

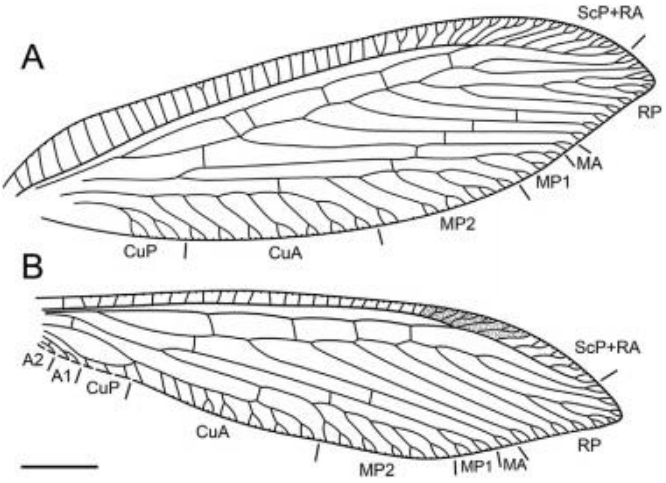

Fig. 8. Cornoberotha monogona gen. et sp. nov., holotype, NIGP171708, female. A. Drawing of forewing; B. Drawing of hind wing. Scale bar = 1.0 mm.

Genus Dolichoberotha gen. nov.
(Figs. 9e16).

urn:lsid:zoobank.org:act:6C4D0249-9F53-4281-A1FE-7A59EE0684AF.
Type species: Dolichoberotha burmana sp. nov.

Diagnosis. Antenna with ca. 80-120 flagellomeres; scape elongate and slightly swollen distad, about 4.5e6.0 times as long as wide. Forewing: Costal space proximally distinctly dilated; costal crossveins mostly forked; 2-3 ra-rp crossveins proximad fusing point of ScP and RA; one series of three to five gradate crossveins present

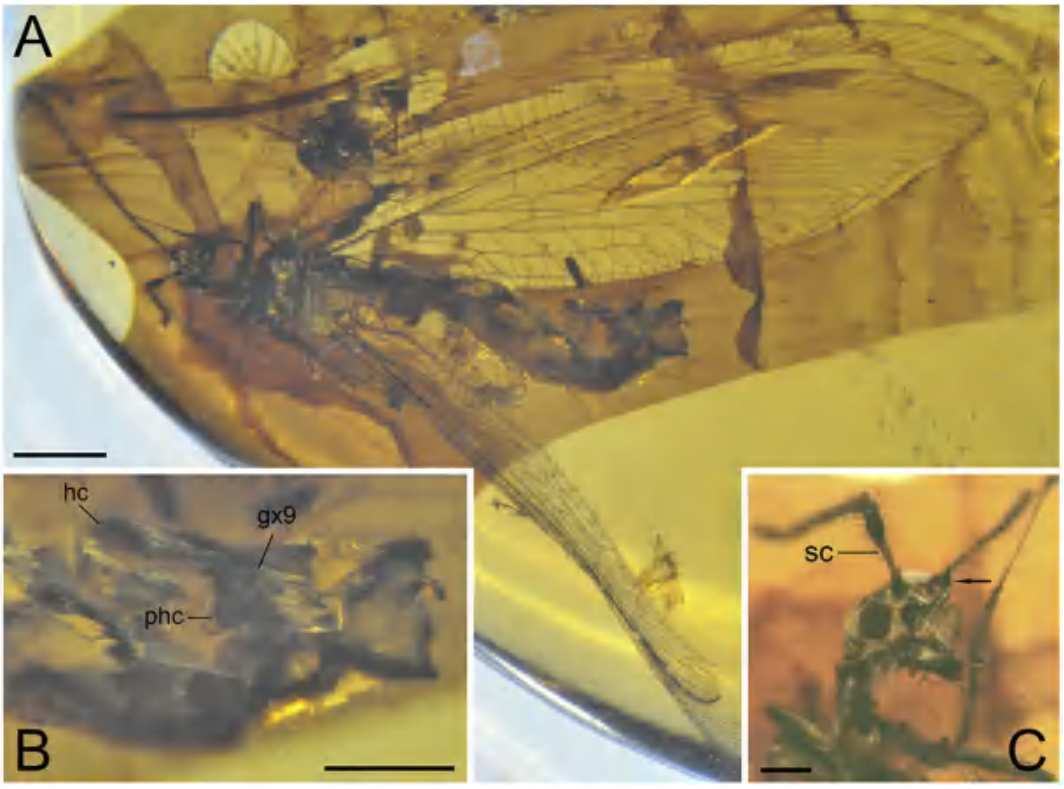

Fig. 7. Cornoberotha monogona gen. et sp. nov., holotype, NIGP171708, female. A. Habitus photograph, ventral view; B. Photograph of genitalia, ventral view; C. Photograph of head, frontal view. gx9: gonocoxite 9; hc: hypocauda; phc: pseudohypocauda; sc: scape. Arrow indicates frontal horn. Scale bar = 1.0 mm (A); 0.5 mm (B, C).

between branches of RP+MA and MP, or completely absent; MP with two main branches, both pectinately branched distally, MP1 with less branches than that of MP2, most branches of MP1 and MP2 bifurcated or trifurcated; CuA with pectinate and forked branches; CuP branched pectinately or dichotomously. Hind wing: CuA branches mostly forked and pectinate. Male tergum 9 and ectoprocts separated; gonocoxites 9 slender, strongly curved ventrad, and acutely pointed at tip; complex of gonocoxites 10 medially with a slenderly elongated sclerite, without bristles. Female gonocoxites 9 with elongate and closed hypocaudae.

Etymology. From “dolich-”, long and Berotha, a common genus-group name of Berothidae, it refers to the long antennae of the new genus. Gender: Feminine.

Dolichoberotha bifurcata sp. nov.
(Figs. 9e15).

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Diagnosis. Antenna with ca. 107 (male) or 121 (female) flagellomeres; scape about 4.5 times as long as wide. Forewing with 2e4 ra-rp crossveins proximad fusing point of ScP and RA; RP+MA with 6e7 main branches; one gradate series of crossveins (3 or 4) present between branches of RP+MA and MP. Hind wing with 2e3 ra-rp crossveins proximad fusing point of ScP and RA; one gradate series of crossveins (3-4) present between branches of RP+MA and MP.

Description. Male. Body length 4.3e5.5 mm, with scattered, fine setae; integument brown.

Head slightly shorter than wide, with prominent compound eyes. Antenna with scape elongate and slightly swollen distad, about 4.5 times as long as wide, covered by long setae; ca. 107

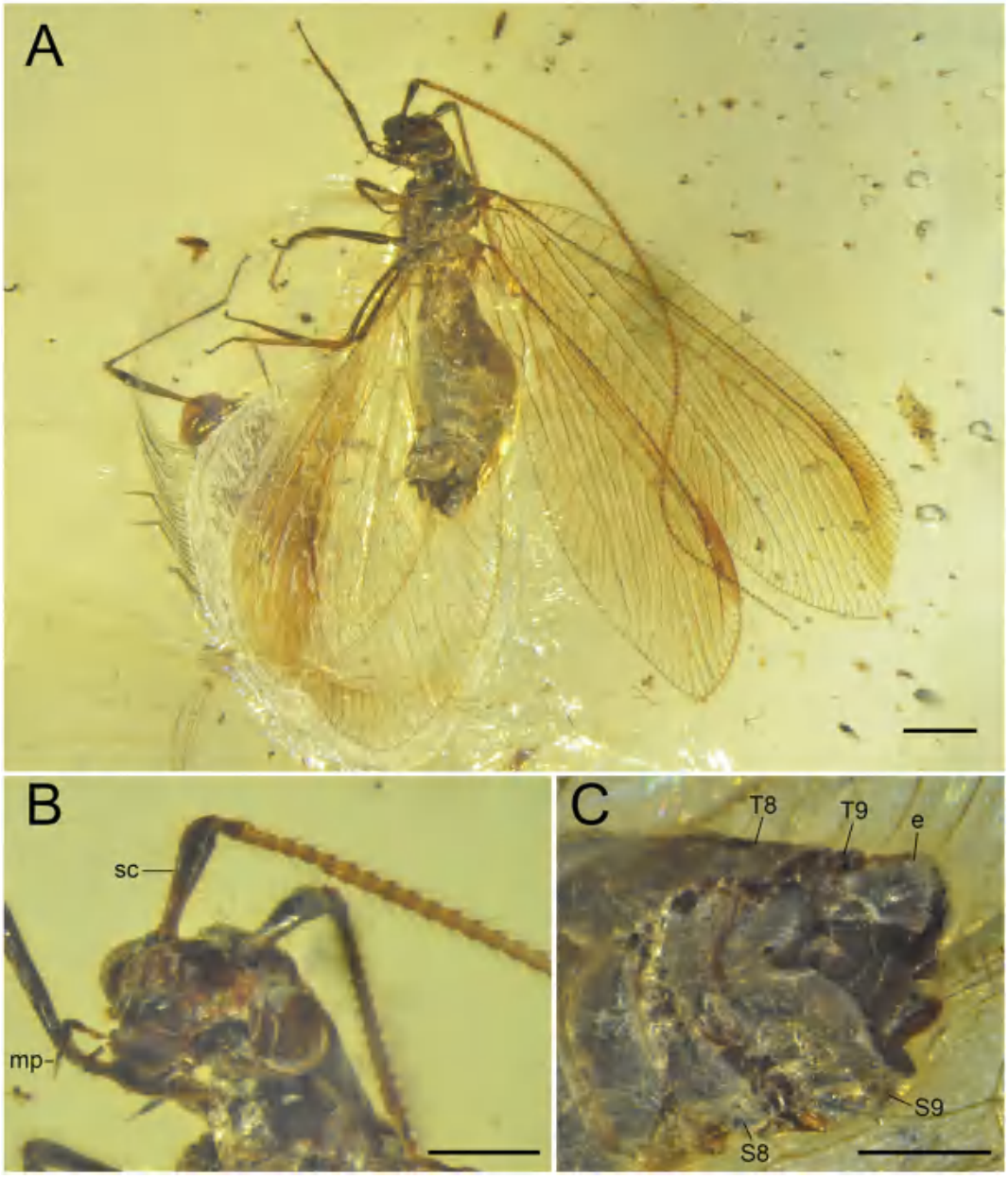

Fig. 9. Dolichoberotha bifurcata gen. et sp. nov., holotype, NIGP171709, male. A. Habitus photograph, ventral view; B. Photograph of head, frontal view; C. Photograph of genitalia, ventrolateral view. e: ectoproct; mp: maxillary palpus; sc: scape; S: sternum; T: tergum. Scale bar = 1.0 mm (A); 0.5 mm (B, C).

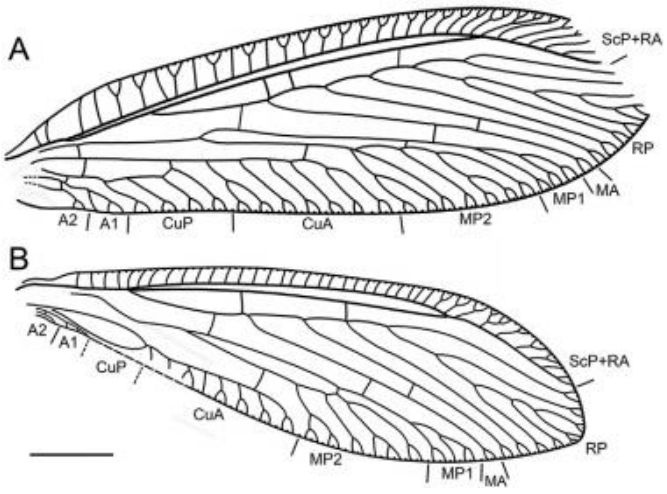

Fig. 10. Dolichoberotha bifurcata gen. et sp. nov., holotype, NIGP171709, male. A. Drawing of forewing; B. Drawing of hind wing. Scale bar = 1.0 mm.

flagellomeres, flagellomere 1 slightly broader than other flagellomeres, each flagellomere with relatively long setae arranged in a circle. Terminal maxillary palpomere about 1.5 times as long as preceding two palpomeres respectively, acutely pointed distad.

Prothorax slightly longer than wide; meso- and metathorax as long as wide. Legs slender; procoxa about 4.0 times longer than meso- and metacoxae; profemur slightly shorter than meta- and mesofemora; metatibia about twice as long as mesotibia and 3.0 times as long as protibia; tibial spurs absent; tarsus 5-segmented; tarsomere 1 longest, nearly equal to combined length of tarsomeres 2 and 3; pretarsal claws short, simple; arolium present.

Forewing: 7.6e8.1 mm long and 2.4e2.8 mm wide; membrane hyaline, immaculate, without scales; narrowly elliptical, apex rounded; trichosors present along entire wing margin; costal space proximally dilated; costal crossveins with more forked ones than simple ones; ScP distally fused with RA; one scp-ra present near wing base; 2-4 ra-rp crossveins proximad fusing point of ScP and RA; RP+MA with 6e7 main branches, all branches marginally forked, third or fourth RP branch pectinately branched from its base; one gradate series of crossveins (3 or 4) present between branches of RP+MA and MP; one crossvein (or distally shifted MA stem) present between RP+MA and MP1; MP with two main branches, both pectinately branched distally, MP1 with less branches than that of MP2, most branches of MP1 and MP2 bifurcated or trifurcated; two mp-cua crossveins present; CuA with 5e7 pectinate and distally forked branches; CuP with three pectinate and distally forked branches; two cua-cup crossveins present; A1 short and distally bifurcated; A2 simple.

Hind wing: 6.8e7.2 mm long and 2.0e2.4 mm wide; membrane hyaline, immaculate, without scales; narrower than forewing, apex slightly pointed; trichosors present along entire wing margin; costal space narrow and slightly dilated distally; costal crossveins mostly simple; scp-ra absent; 2 or 3 ra-rp crossveins proximad fusing point of RP and MA; RP+MA with 5e7 main branches, all of them marginally forked, third or fourth RP branch secondarily or pectinately branched from its base; MP with similar branching condition to that of forewing; CuA with seven pectinate short branches, most of them marginally forked; CuP with proximal part complete, distally approximating to CuA, with three simple or marginally forked branches; A1 distally bifurcated; A2 simple.

Genitalia: Tergum 9 and ectoprocts separated; tergum 9 much shorter than ectoproct; ectoprocts paired, callus cerci reduced; sternum 9 much longer than tergum 9; gonocoxites 9 paired, slender, strongly curved ventrad, and acutely pointed at tip; complex of gonocoxites 10 (= paramere-mediuncus complex) medially with a slenderly elongate rod-like sclerite, which is curved dorsad and obtuse at tip, without bristles.

Female. Body length 6.5 mm; forewing 8.9 mm long, 3.0 mm wide; hind wing 7.2 mm long, 2.5 mm wide. Morphology mostly similar to male, but antenna with 121 flagellomeres.

Genitalia: Only visible in ventral view; ventral parts of segment 7 and 8 unclear; tergum 9 and ectoprocts fused with each other, small ovoid callus cerci present; gonocoxites 9 paired, anteriorly with a pair of long and closed hypocaudae, which terminally extends to abdominal segment 5.

Type material. Holotype, NIGP171709, amber piece preserving a complete male of D. bifurcata sp. nov., a true bug and a thrips, it is polished in the form of nearly round, transparent cabochon, with length × width about 21.9 × 19.0 mm, height about 5.4 mm. Paratype, NIGP171710, amber piece preserving a complete male of D. bifurcata sp. nov., a fly and a hemipteran, it is polished in the form of nearly elliptical, transparent cabochon, with length × width about 26.0 × 15.3 mm, height about 7.2 mm. Paratype, EMTG BU002117, amber piece preserving a complete and slightly deformed male of D. bifurcata sp. nov. and a beetle, it is polished in the form of nearly elliptical, transparent cabochon, with length × width about 19.3 × 14.0 mm, height about 8.1 mm. Paratype, EMTG BU001991, amber piece preserving a complete female of D. bifurcata sp. nov., it is polished in the form of nearly rectangle, transparent cabochon, with length × width about 31.2 × 25.0 mm, height about 6.2 mm.
Etymology. The specific epithet “bifurcata” refers to the forewing costal crossveins, which are mostly bifurcated, in the new species.

Dolichoberotha burmana sp. nov.
(Fig. 16).

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Diagnosis. Scape about 6.0 times as long as wide. Forewing with two ra-rp crossveins proximad fusing point of ScP and RA; RP+MA with four main branches; gradate series of crossveins absent CuP branched dichotomously. Hind wing with only one ra-rp crossvein; crossvein (or distally shifted MA stem) between RP+MA and MP1 absent.
Description. Adult with sex unknown. Body length 4.0 mm, with scattered, fine setae; integument brown.
Head slightly shorter than wide, with prominent compound eyes. Antenna with scape elongate and slightly swollen distad, about 6.0 times as long as wide, covered by long setae; flagellum with distal part not preserved, ca. 88 flagellomeres preserved, flagellomere 1 slightly broader than other flagellomeres, each flagellomere with relatively long setae arranged in a circle. Terminal maxillary palpomere about 1.5 times as long as preceding two palpomeres respectively, acutely pointed distad.

Prothorax slightly longer than wide; meso- and metathorax as long as wide. Legs mostly not preserved.

Forewing: 5.4 mm long and 1.5 mm wide; membrane hyaline, immaculate, without scales; narrowly elliptical, apex slightly pointed; trichosors present along entire wing margin; costal space proximally distinctly dilated; costal crossveins with more forked ones than simple ones; ScP distally fused with RA; scp-ra invisible; two ra-rp crossveins present proximad fusing point of ScP and RA; RP+MA with four main branches, among which crossveins are absent; one crossvein (or distally shifted MA stem) present between RP+MA and MP1; MP with two main branches, both pectinately branched distally, MP1 with less branches than that of MP2, most branches of MP1 and MP2 bifurcated or trifurcated; two mp-cua crossveins; CuA with four pectinate and distally forked

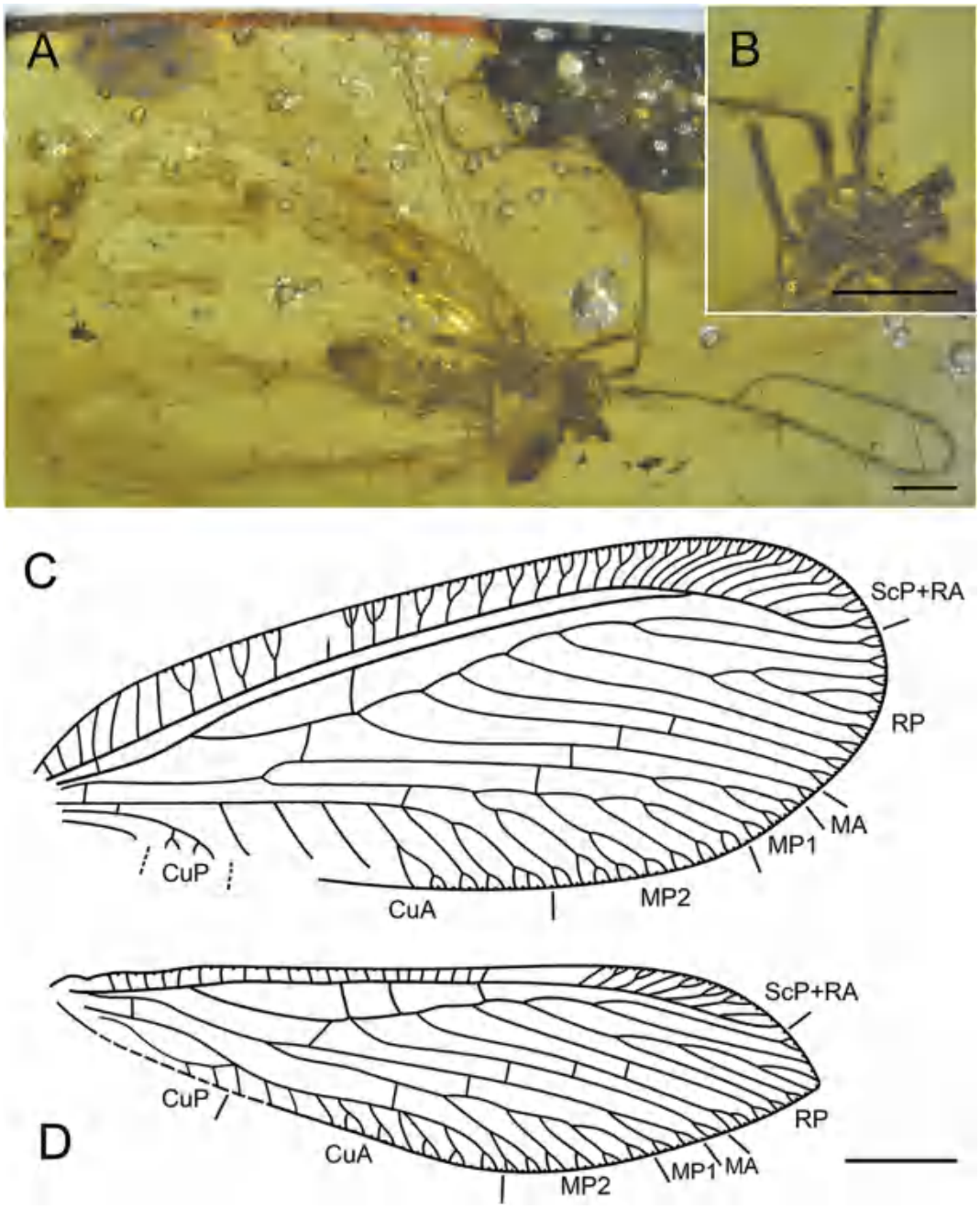

Fig. 11. Dolichoberotha bifurcata gen. et sp. nov., paratype, NIGP171710, male. A. Habitus photograph, ventral view; B. Photograph of head, frontal view; C. Drawing of forewing; D. Drawing of hind wing. Scale bar = 1.0 mm (A); 0.5 mm (B, C, D).

branches; CuP with one marginal fork; one cua-cup crossvein; A1 short and distally bifurcated; A2 simple.

Hind wing: 4.3 mm long and 1.0 mm wide; membrane hyaline, immaculate, without scales; narrower than forewing, apex distinctly pointed; trichosors present along entire wing margin; costal space narrow and slightly dilated distally; costal crossveins mostly simple; scp-ra absent; one ra-rp crossvein present proximad fusing point of ScP and RA; RP+MA with four main branches, all of them marginally forked; crossvein (or distally shifted MA stem) between RP+MA and MP1 absent; MP1 branched dichotomously distally, MP2 with four pectinate short branches, three of them marginally forked; remaining veins poorly preserved.

Abdomen damaged.

Type material. Holotype, NIGP171711, amber piece preserving a clear but incomplete adult of D. burmana sp. nov. and a fly; it is polished in the form of elliptical, transparent cabochon, with length × width about 31.5 × 31.0 mm, height about 11.0 mm.

Etymology. The specific epithet “burmana” refers to the occurrence of the new species from the mid-Cretaceous of Myanmar.

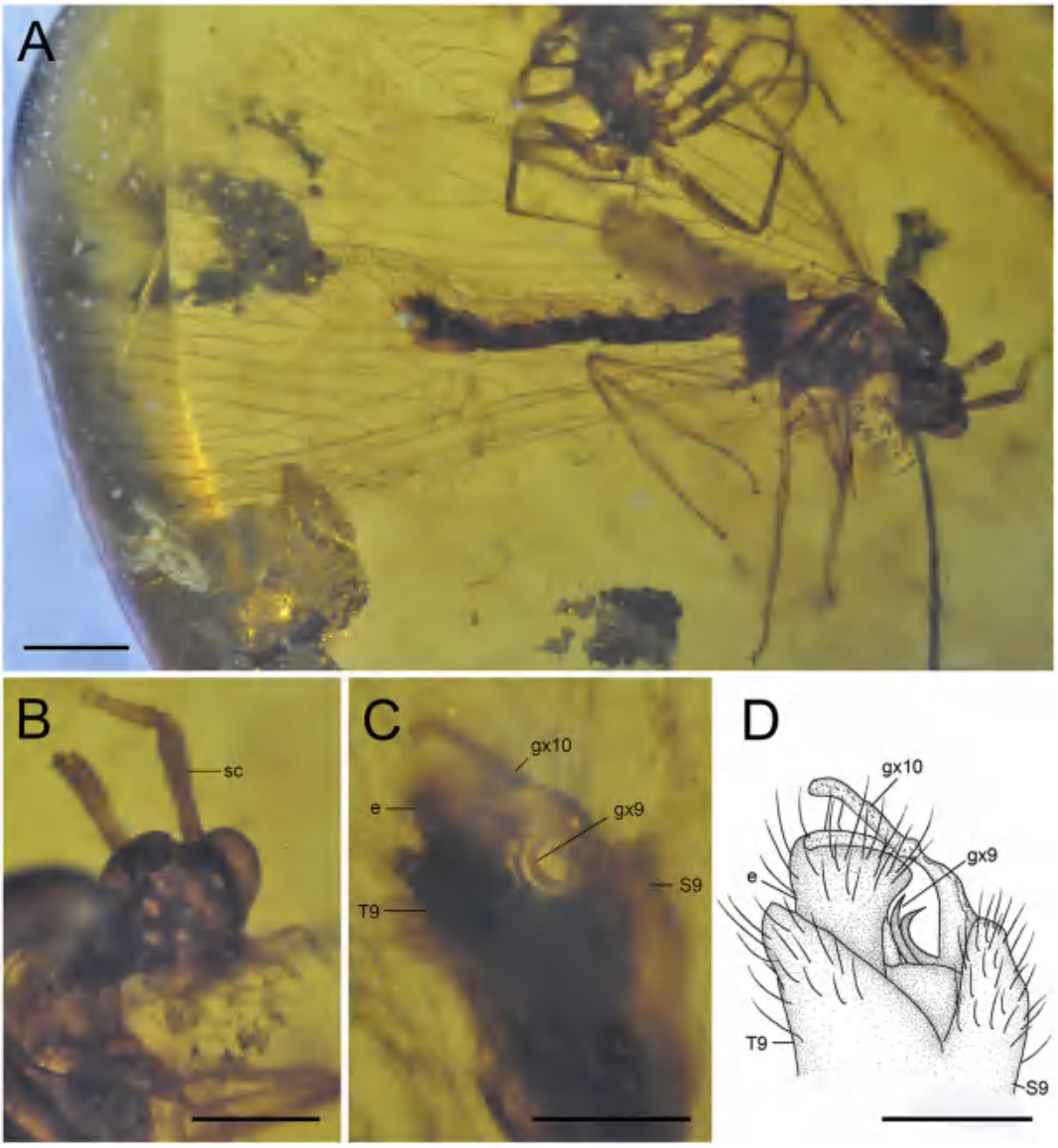

Fig. 12. Dolichoberotha bifurcata gen. et sp. nov., paratype, EMTG BU002117, male. A. Habitus photograph, lateral view; B. Photograph of head, frontal view; C. Photograph of genitalia, lateral view; D. Drawing of genitalia, lateral view. e: ectoproct; gx9: gonocoxite 9; gx10: complex of fused gonocoxites, gonapophyses and gonostyli 10 (= paramere-mediuncus complex); sc: scape; S: sternum; T: tergum. Scale bar = 1.0 mm (A, B); 0.5 mm (C, D).

Remarks. D. burmana sp. nov. can be distinguished from D. bifurcata sp. nov. by the smaller body size (forewing length 5.4 mm, but 7.6e8.1 mm in the latter species), the scape about 6.0 times (4.5 times in the latter species) as long as wide, the narrower forewing costal space, the fewer branches of RP+MA and CuA, and the absence of forewing gradate series of crossveins (present including 3-5 crossveins in the latter species). However, both species should belong to the same genus by having the generic diagnostic characters aforementioned.

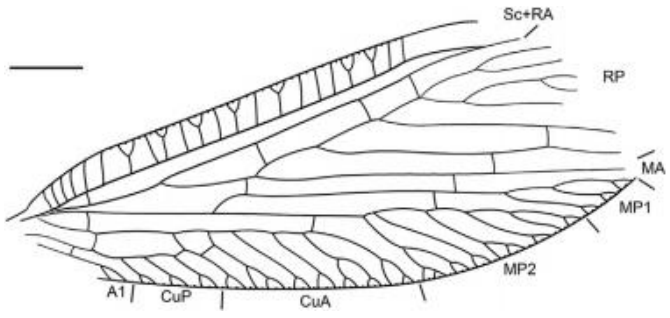

Fig. 13. Dolichoberotha bifurcata gen. et sp. nov., paratype, EMTG BU002117, male. Drawing of forewing. Scale bar = 1.0 mm.

Genus Ansoberotha Yang et al. (2019).
(Figs. 17e23).
Ansoberotha Yang et al. (2019): 102. Type species: Ansoberotha jiewenae Yang et al. (2019): 102.

Revised diagnosis. Antenna with ca. 83-109 flagellomeres; scape elongate and slightly swollen distad, about 10.0e12.0 times as long as wide. Forewing costal space proximally not dilated; costal crossveins mostly simple except for several forked ones near fusing point of ScP and RA; 3-4 ra-rp crossveins proximad fusing point of ScP and RA; two or three crossveins present between branches of RP+MA and MP2; MP with two main branches, both pectinately branched distally, MP1 with less branches than that of MP2, most branches of MP1 and MP2 bifurcated or trifurcated; CuA with

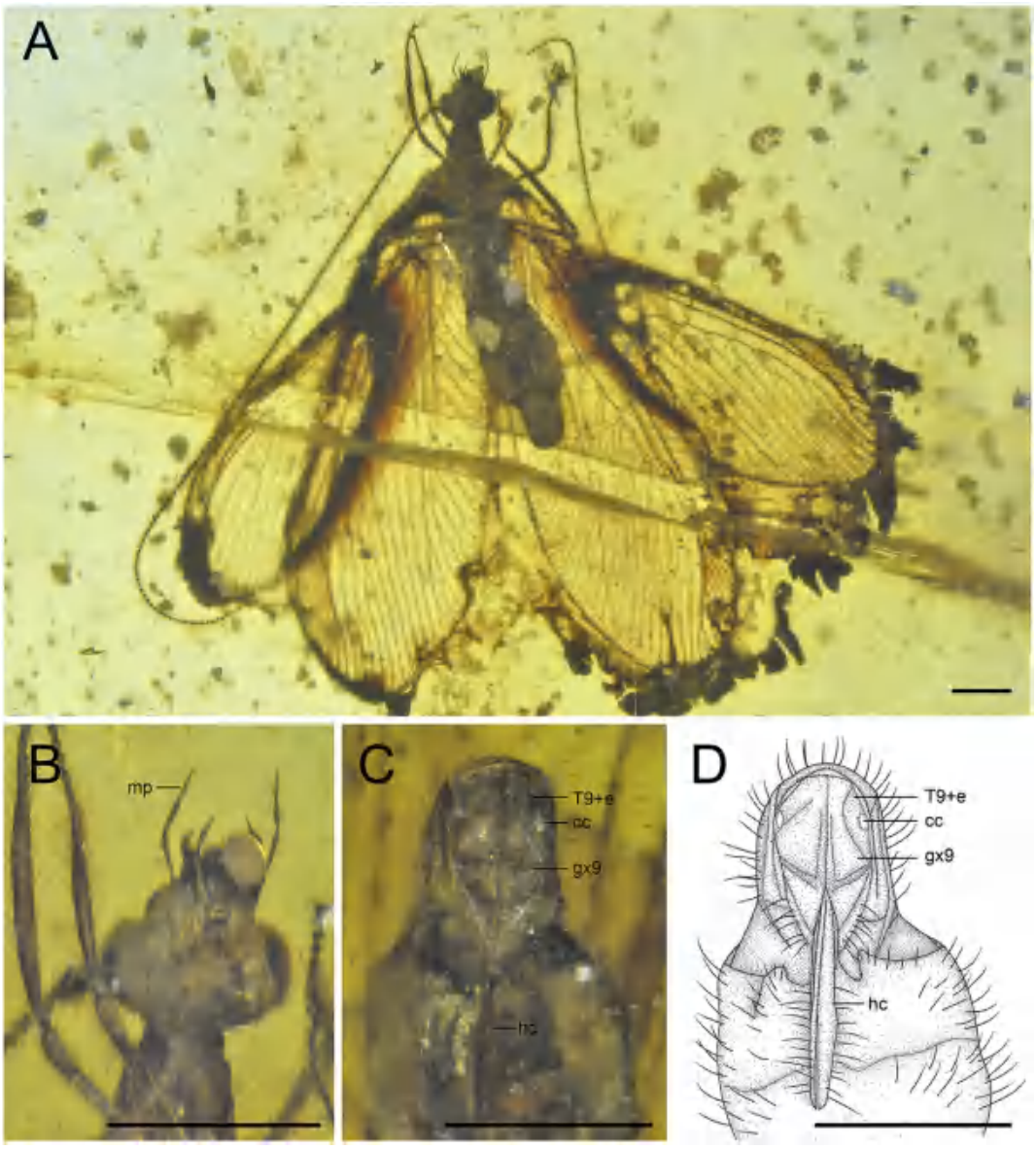

Fig. 14. Dolichoberotha bifurcata gen. et sp. nov., paratype, EMTG BU001991, female. A. Habitus photograph, ventral view; B. Photograph of head, ventral view; C. Photograph of genitalia, ventral view; D. Drawing of genitalia, ventral view. cc: callus cerci; gx9: gonocoxite 9; hc: hypocauda; mp: maxillary palpus; T: tergum. Scale bar = 1.0 mm (A), 0.5 mm (B, C, D).

pectinate and forked branches; CuP branched pectinately. Hind wing CuA with short, simple and pectinate branches. Female tergum 9 without pseudohypocaudae; gonocoxites 9 with elongate and closed hypocaudae.

Ansoberotha jiewenae Yang et al. (2019).
(Figs. 17e23).

Re-description. Female. Body length 3.2e4.5 mm, with scattered, fine setae; integument brown.

Head slightly shorter than wide, with prominent compound eyes. Antenna with scape elongate and slightly swollen distally, about 8.0e12.0 times as long as wide, covered by long setae; ca. 83-109 flagellomeres, flagellomere 1 slightly broader than other flagellomeres, each flagellomere with relatively long setae arranged in a circle. Prothorax longer than wide; meso- and metathorax as long as wide. Legs slender; tarsus 5-segmented; tarsomere 1 longest, nearly equal to combined length of tarsomeres 2-4; pretarsal claws short, simple; arolium present.

Forewing: 5.5e6.3 mm long and 1.3e2.2 mm wide; membrane hyaline, immaculate, without scales; wing shape narrowly elliptical, apex rounded; trichosors present along entire wing margin; costal space not dilated proximally; costal crossveins mostly simple, but forked near fusing point of ScP and RA; ScP distally fused with RA; 3-4 ra-rp crossveins present proximad fusing point of ScP and RA; RP with 4e5 main branches; MP with two main branches, both pectinately branched distally, MP1 with less branches than that of MP2, most branches of MP1 and MP2 bifurcated or trifurcated; one mp1-mp2 crossvein; two mp-cua crossveins; CuA with 4e6 pectinate and distally forked branches; CuP with three pectinate and distally forked branches; two cua-cup crossveins; two crossveins between MP and CuA; CuA branched pectinately with 4e6 long main branches; CuP dichotomously or pectinately branched; one cua-cup crossvein; A1 distally bifurcated; A2 simple.

Hind wing: 4.5e5.6 mm long and 1.0e1.7 mm wide; membrane hyaline, immaculate, without scales; narrower than forewing, apex

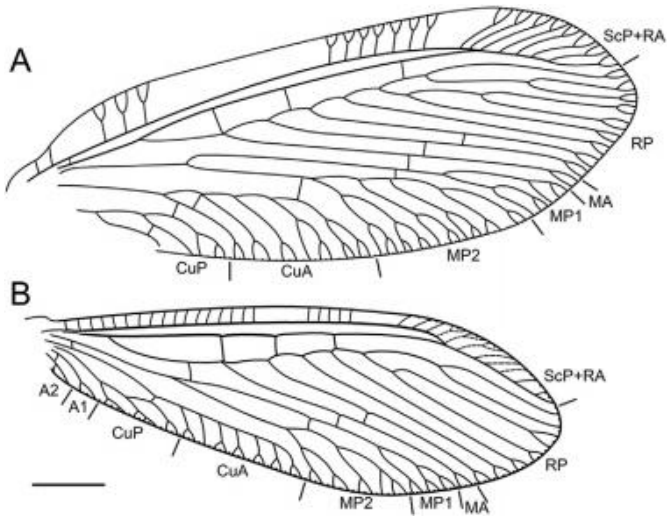

Fig. 15. Dolichoberotha bifurcata gen. et sp. nov., paratype, EMTG BU001991, female. A. Drawing of forewing; B. Drawing of hind wing. Scale bar = 1.0 mm.

distinctly pointed; trichosors present along entire wing margin; costal space narrow and slightly dilated distally; costal crossveins mostly simple; scp-ra absent; 2-3 ra-rp crossveins present proximad fusing point of ScP and RA; RP+MA with 4e6 main branches, all of them marginally forked; MP1 branched dichotomously or pectinately distally, MP2 with 4e6 pectinate short branches, all of them marginally forked; crossveins between branches of RP+MA and branches of MP absent; CuA with 7e10 pectinate simple branches; CuP with proximal part complete, distally with three pectinate simple branches; two cua-cup crossveins; A1 bifurcate distally; A2 simple.

Genitalia: Sternum 7 medially separated into a pair of broad sclerites. Tergum 9 + ectoprocts fused together, ventrally without pseudohypocaudae; small callus cerci present. Gonocoxites 9 paired, anteriorly with long and closed hypocaudae, which terminally extend to abdominal segment 6.

Male. Unknown.

Material examined. NIGP171713, amber piece preserving an incomplete adult of A. jiewenae and a beetle; it is polished in the form of nearly parallelogram, transparent cabochon, with length × width about 16.0 × 14.0 mm, height about 8.9 mm NIGP171712, amber piece preserving an incomplete adult of A. jiewenae, a beetle, and flies; it is polished in the form of nearly rectangular pyramid, transparent cabochon, with length × width about 27.5 × 23.0 mm, height about 20.8 mm NIGP171714, amber piece preserving a complete female of A. jiewenae and one beetle; it is polished in the form of nearly ovoid, transparent cabochon, with length × width about 37.8 × 30.1 mm, height about 14.2 mm NIGP171715, amber piece preserving a clear but incomplete adult of A. jiewenae; it is polished in the form of nearly ovoid, transparent cabochon, with length × width about 13.0 × 12.0 mm, height about 5.4 mm.

Remarks. The three "long-antennae" genera of Berothidae appear to be closely related by the presence of three or more ra-rp crossveins proximad the fusion of ScP and RA in the forewing, the presence of forewing MA stem (or proximal r-m crossvein) between RP+MA and MP1, the pectinately branched forewing MP2 and CuA, the complete hind wing CuP, and the flattened and closed hypocaudae. In addition, the monotypic genus Banoberotha Whalley (1980) from the Lower Cretaceous Lebanese amber resembles these "long-antennae" genera by the presence of the above forewing characters, but can be distinguished from them by the strongly dilated forewing costal space on proximal half. The three "long-antennae" genera can be distinguished from each other by the presence/absence of proximal dilation of the forewing costal space, the number of forked forewing costal crossveins, and the genital characters. Dolichoberotha gen. nov. differs from Ansoberotha and Cornoberotha gen. nov. by the forewing costal crossveins mostly forked (mostly simple in the latter two genera), and it further differs from Cornoberotha gen. nov. by the short and ventral curved male gonocoxites 9 (slenderly elongated and slightly curved dorsad in the latter genus). Cornoberotha gen. nov. is distinguished from Ansoberotha by the forewing costal space proximally distinctly dilated (barely dilated in the latter genus) and the presence of pseudohypocaudae in the female genitalia (absent in the latter genus).

4. Discussion

Distinctive characters of Ansoberotha, Cornoberotha gen. nov., and Dolichoberotha gen. nov.

Long antennae. The antennae in the Burmese amber berothids herein described are extremely elongated, with 80e120 flagellomeres. Moreover, the scapes in these species are also among the longest ones in Berothidae, being about 2.5e12.0 times as long as wide. However, in the other fossil berothids the number of flagellomeres is no more than 71 (see Yuan et al., 2016: fig. 2), and the scape is either short or elongated, but at most 4.0 times as long as wide (see Yuan et al., 2016: figs. 2, 3). Among the species of Burmese amber Neuropterida, similar long antennae are reported in several species of Mesoraphidiidae (Raphidioptera) and Osmylidae (Neuroptera) (see Liu et al., 2016: figs. 1, 3; Myskowiak et al., 2016: fig. 6). In extant Neuroptera there are a few species with such long antennae reported in Osmylidae and Chrysopidae (see Martins et al., 2016: fig. 2; Winterton and Brooks, 2002).

The number of flagellomeres is not greatly varied between conspecific males and females in D. bifurcata sp. nov., ranging from 107 to 120. The length and thickness of scape are variable not only among genera but also among congeneric species. In Cornoberotha gen. nov., the ratio of length and thickness of scape ranges from 2.5 (C. anomala sp. nov.) to 10.0 (C. monogona sp. nov.). In Dolichoberotha gen. nov. it ranges from 4.5 to 6.0, while in A. jiewenae it ranges from 8.0 to 12.0. Nevertheless, we only examined the specimens of two species with both sexes described, while the remaining species are only known as female or described based on only one specimen. Further materials are needed to investigate the variation of antennae in these "long-antenna" berothids.

Frontal horns. The development of one or a pair of frontal horns in C. anomala sp. nov. and C. monogona sp. nov. is surprising and unique in Berothidae. Cephalic horns are known in various insect groups, e.g. the rhinoceros beetles (Enrödi, 1985), fruit flies, etc. (Aluja and Norrbom, 2000), and in many species these structures are sexually dimorphic, with exaggerate development in males in relation to male-male combat during courtship (Eberhard, 1980). However, this character is rarely found in Neuroptera. The dustywing species of the genus Neosemidalis represent a case with similar cephalic structures in extant Neuroptera (Meinander, 1972: figs. 99e107). But, in the Neosemidalis species with elaborated cephalic structures, these morphological modifications are restricted to the vertex and the posterior part of frons, being present posteriad the antennal bases. In addition, these structures are only known in males of Neosemidalis. However, in C. anomala sp. nov. and C. monogona sp. nov. the cephalic horns are present on anterior part of frons, being anteriad the antennal bases. A similar feature was reported to be present in an extant green lacewing species Ungla bolivari (Banks, 1913) (see Tauber et al., 2017: fig. 18), while this frontal lobe has only been found in male of this species. In

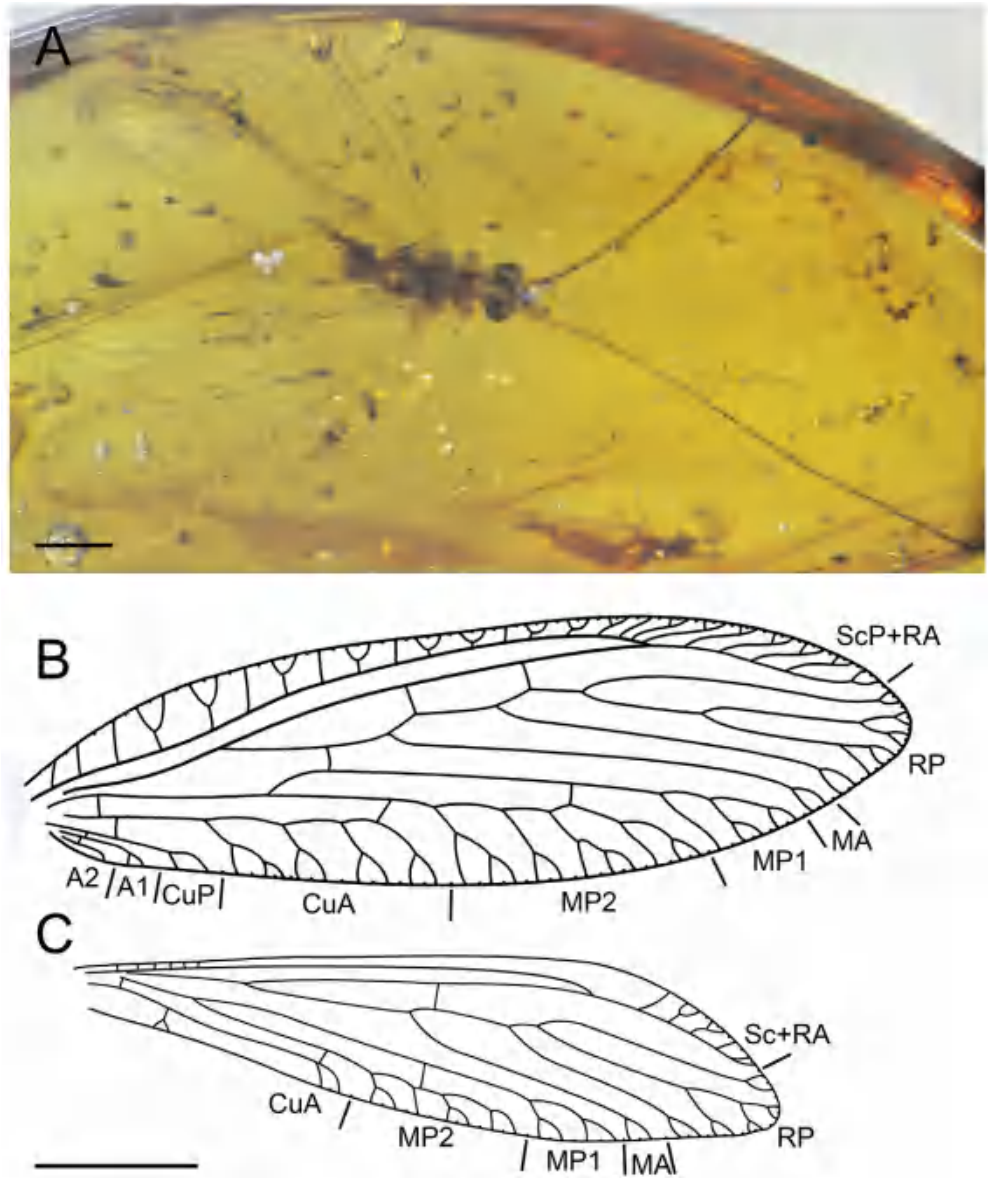

Fig. 16. Dolichoberotha burmana gen. et sp. nov., holotype NIGP171711. A. Habitus photograph, dorsal view; B. Drawing of forewing; C. Drawing of hind wing. Scale bar = 1.0 mm.

contrast, the frontal horns of the presently described berothids are present in females. Whether they are also present in males of these species is still unknown.

Wing apex. A falcate wing apex was assigned to be a synapomorphy of Trichomatinae, Nosybinae, and Berothinae (Aspöck and Nemeschkal, 1998). In C. monogona sp. nov. the wing apex is slightly falcate, and in A. jiewenae (see Yang et al., 2019: fig. 2) the apex of hind wing is slightly pointed. These modifications of wing apex could be homologous with the falcate wing apex in the crown group of Berothidae.

Forewing costal crossveins. In all extant species of Berothidae most costal crossveins in the forewings are forked. The presence of many simple forewing costal crossveins is more common in fossil berothids, probably being a plesiomorphic state. In the Mesozoic berothids, there is only one species, i.e. Maculaberotha nervosa Yuan et al. (2016) from the Burmese amber, with relatively more forked forewing costal crossveins, which, however, are confined to the proximal half of costal space. Considering the presence of many forked forewing costal crossveins in Dolichoberotha gen. nov. and the opposite condition in Ansoberotha and Cornoberotha gen. nov., such variation occurs in closely related berothid genera.

Forewing ra-rp crossveins. The number and position of the forewing ra-rp crossveins are important characters to distinguish some berothid genera from the Burmese amber (Engel and Grimaldi, 2008; Yuan et al., 2016). Makarkin and Ohl (2015) considered that the presence of two ra-rp crossveins proximad the distal subcostal crossvein (or the fusion of ScP and RA) is a plesiomorphic condition and occurs in most extant berothids, while the increase of these crossveins to three (or more) or decrease to one was considered to be apomorphic. In extant berothids, the presence of three ra-rp crossveins proximad the distal subcostal crossvein (or the fusion of ScP and RA) is found in a few genera of Nyrminae, Trichomatinae, and Berothinae. In fossil Berothidae this character state is present in Banoberotha Whalley (1980), Elektroberotha Makarkin and Ohl (2015), and the presently described species.

Forewing MA stem. The crossvein-like stem of forewing MA, or interpreted to be the proximal r-m crossvein (named as 2r-m in

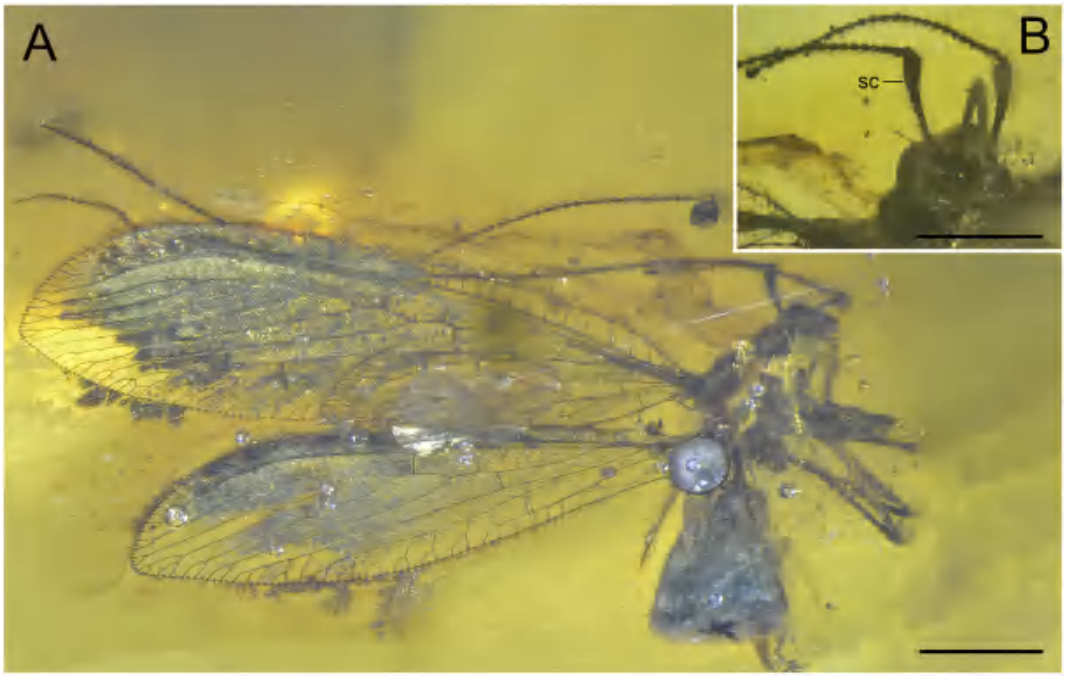

Fig. 17. Ansoberotha jiewenae Yang et al. (2019), NIGP171713. A. Habitus photograph, lateral view; B. Photograph of head, frontal view. sc: scape. Scale bar = 1.0 mm (A), 0.5 mm (B).

Makarkin and Ohl, 2015 and vein 'b' in Aspöck and Nemeschkal, 1998), is variable in position among berothid genera. Makarkin and Ohl (2015) deemed that the presence of this vein between RP (here termed as RP+MA) and MA (here termed as MP1) is plesiomorphic because it is present in all families of Mantispoidea. However, in some lacewing families relatively basal to Mantispoidea, e.g. Nevrorthidae, Osmylidae, etc., this veinlet is present between R and M (here termed as MP). Moreover, the presence of its homologous vein in the hind wing between RP (here termed as RP+MA) and M (here termed as MP) is universally developed in many groups of Megaloptera, Raphidioptera and Neuroptera (see Breitkreuz et al., 2017). Therefore, the presence of forewing MA stem between R (or RP+MA) and MP is probably plesiomorphic, while the presence of this veinlet between RP+MA and MP1 is apomophic and shared by most lineages of Mantispoidea, including the presently described fossil berothids.

Hind wing CuP. The proximal part of hind wing CuP is usually reduced in most extant berothids, while the fully-developed hind wing CuP is only known in Nyrminae and some fossil berothids (e.g. Elektroberotha and the presently described species; see Makarkin and Ohl, 2015). Interestingly, the reduction of proximal part of hind wing CuP, as an apomorphic condition, occurs in either basal or higher extant berothid subfamilies, while the complete hind wing CuP, as an plesiomorphic condition, remains in the fossil species (e.g. Elektroberotha of Berothinae) belonging to the higher berothid subfamilies.

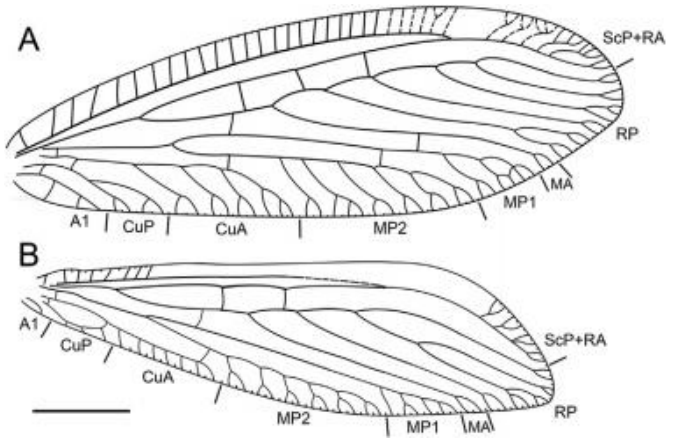

Fig. 18. Ansoberotha jiewenae Yang et al. (2019), NIGP171713. A. Drawing of forewing; B. Drawing of hind wing. Scale bar = 1.0 mm.

Male tergum 9 and ectoprocts. The fusion of male tergum 9 and ectoprocts is an apomorphic condition and present in the crown-group of Berothidae, i.e. Protobiellinae, Nosybinae, Trichomatinae, and Berothinae (Aspöck and Nemeschkal, 1998; Aspöck and Randolf, 2014). The separation of male tergum 9 and ectoprocts, being as the plesiomorphic condition, is present in the basal subfamilies Cyrenoberothinae and Nyrminae, although Nyrma Navás (1933) has a parallel derivation of fused male tergum 9 and ectoprocts (Aspöck and Nemeschkal, 1998). In fossil berothids, the fusion of male tergum 9 and ectoprocts is found in Haploberotha carsteni Makarkin (2018), while the separation of these sclerites remains in Cornoberotha gen. nov. and Dolichoberotha gen. nov.

Male gonocoxites 9. The male gonocoxites 9 are a separate pair of sclerites present between tergum 9 + ectoprocts and sternum 9 in Berothidae. This structure is posteriorly broadened in most extant berothids, while in Austroberothella Aspöck and Aspöck (1985) and Manselliberotha Aspöck and Aspöck (1988a, b) it is present as a pair of slenderly elongate sclerites with acutely pointed tip (Aspöck and Aspöck, 1988a, b). In all the fossil berothids with male gonocoxites 9 preserved, this structure is slender and either elongate or short but strongly curved ventrad (see Makarkin and Ohl, 2015: fig. 5). The characters of male gonocoxites 9 are very useful to distinguish the genera of Berothidae, but appear less useful to infer the subfamilial affinity of the genera.

Complex of male gonocoxites 10. The complex of male gonocoxites 10, also named as paramere-mediuncus complex (Aspöck and Nemeschkal, 1998), is highly specialized in most extant berothids, with few or a bundle of bristles, which is further modified by fusion into a ribbon or a long thread. In the basal subfamily

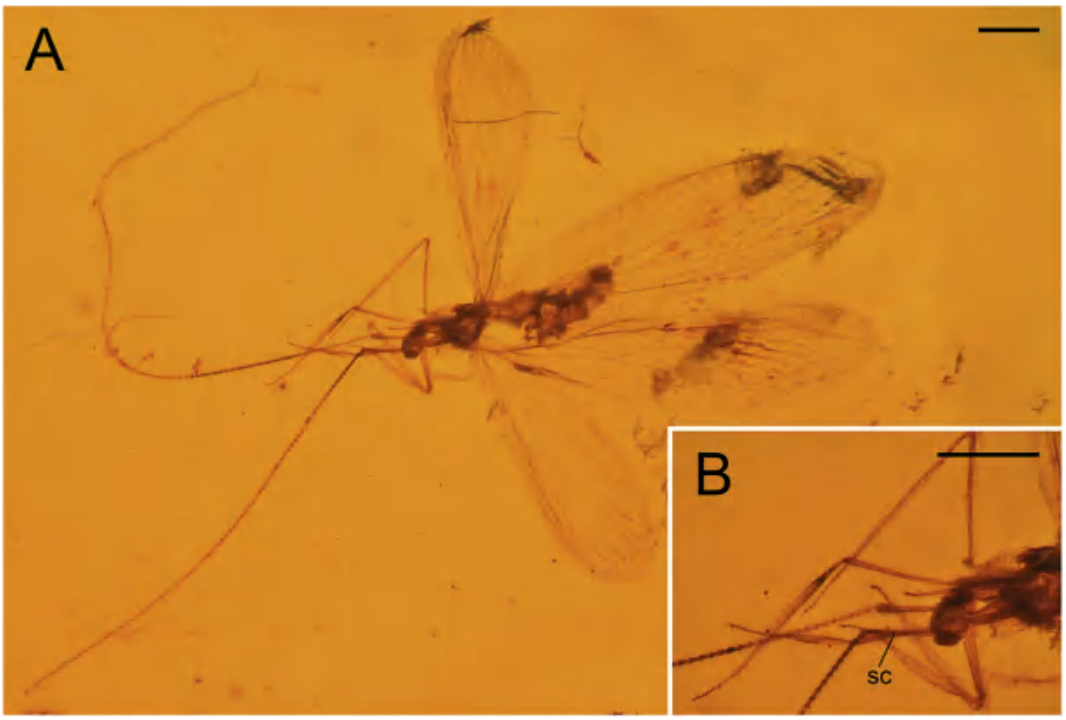

Fig. 19. Ansoberotha jiewenae Yang et al. (2019), NIGP171712. A. Habitus photograph, dorsal view; B. Photograph of head, dorsal view. sc: scape. Scale bar = 1.0 mm.

Cyrenoberothinae this structure is present as a slender sclerite, which is curved dorsad and acutely pointed at tip, without any bristles. The complex of male gonocoxites 10 is herein first described in fossil berothids. In both Cornoberotha gen. nov. and Dolichoberotha gen. nov. this structure is similar to that in Cyrenoberothinae, being a slender and dorsally curved sclerite without bristles (see MacLeod and Adams, 1967: figs. 7e12). However, in Cornoberotha gen. nov. the tip of this structure is obtuse but not acutely pointed.

Female sternum 7. The female sternum 7 in general is a complete and unpaired sclerite in Neuroptera, while in Berothinae it is medially separated into a pair of large lateral sclerites, which is an apomorphic condition (Aspöck and Nemeschkal, 1998). This character state is also present in Cornoberotha gen. nov. (Figs. 3, 7). In Ansoberotha and Dolichoberotha gen. nov. we could not confirm the presence of this character state due to preservation, but the sternum 7 in these two genera is at least not as same as in Cyrenoberothinae and Nyrminae.

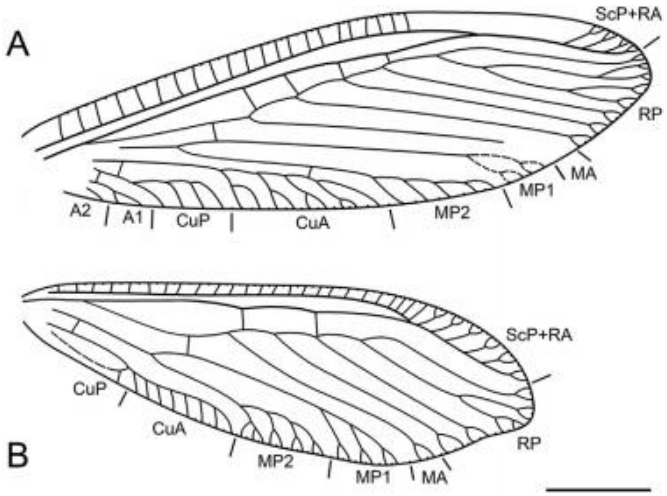

Fig. 20. Ansoberotha jiewenae Yang et al. (2019), NIGP171712. A. Drawing of forewing; B. Drawing of hind wing. Scale bar = 1.0 mm.

Pseudohypocaudae of female tergum 9. The pseudohypocaudae is a ventral protrusion of the female tergum 9, being an apomorphic condition (Aspöck and Nemeschkal, 1998). It is well developed in Protobiellinae and Spiroberotha Adams (1989) (a genus with unclear subfamilial placement either in Nosybinae or in Berothinae; see Makarkin and Ohl, 2015) but feebly or moderately developed in some genera of Berothinae. It is also present in some Burmese amber genera, i.e. Dasyberotha Engel and Grimaldi (2008), Jersiberotha, and Haploberotha. Here we found this structure in two species of Cornoberotha gen. nov., while it is absent in Ansoberotha. Whether this structure is present in Dolichoberotha gen. nov. could not be determined due to preservation condition. Nevertheless, it is obvious that the presence/absence of this structure is varied in closely related genera.

Hypocaudae of female gonocoxites 9. The anteroventral projection of the female gonocoxites 9, i.e. hypocaudae, is an apomorphic character state in Berothidae. Yuan et al. (2016) homologized this structure with the gonostyli 9, which, however, is incorrect because of the greatly differed position of these two structures. The presence of hypocaudae is shared by most genera of Trichomatinae, Nosybinae, and Berothinae in extant Berothidae, and assigned to be one of the synapomorphies of the clade including the latter two subfamilies (Aspöck and Nemeschkal, 1998). In fossil Berothidae, hypocaudae has been found in two genera of Berothinae, i.e. Elektroberotha and Xenoberotha Makarkin, 2017 (Makarkin and Ohl, 2015; Makarkin, 2017). Among the berothids with hypocaudae, it is noticeable that the paired anteroventral protrusions in Nosybus are flattened, very close to each other, and integrated together with posterodorsal part of gonocoxites 9 into a long, knife-shaped ovipositor. This feature is surprisingly found in Ansoberotha, Cornoberotha gen. nov., and

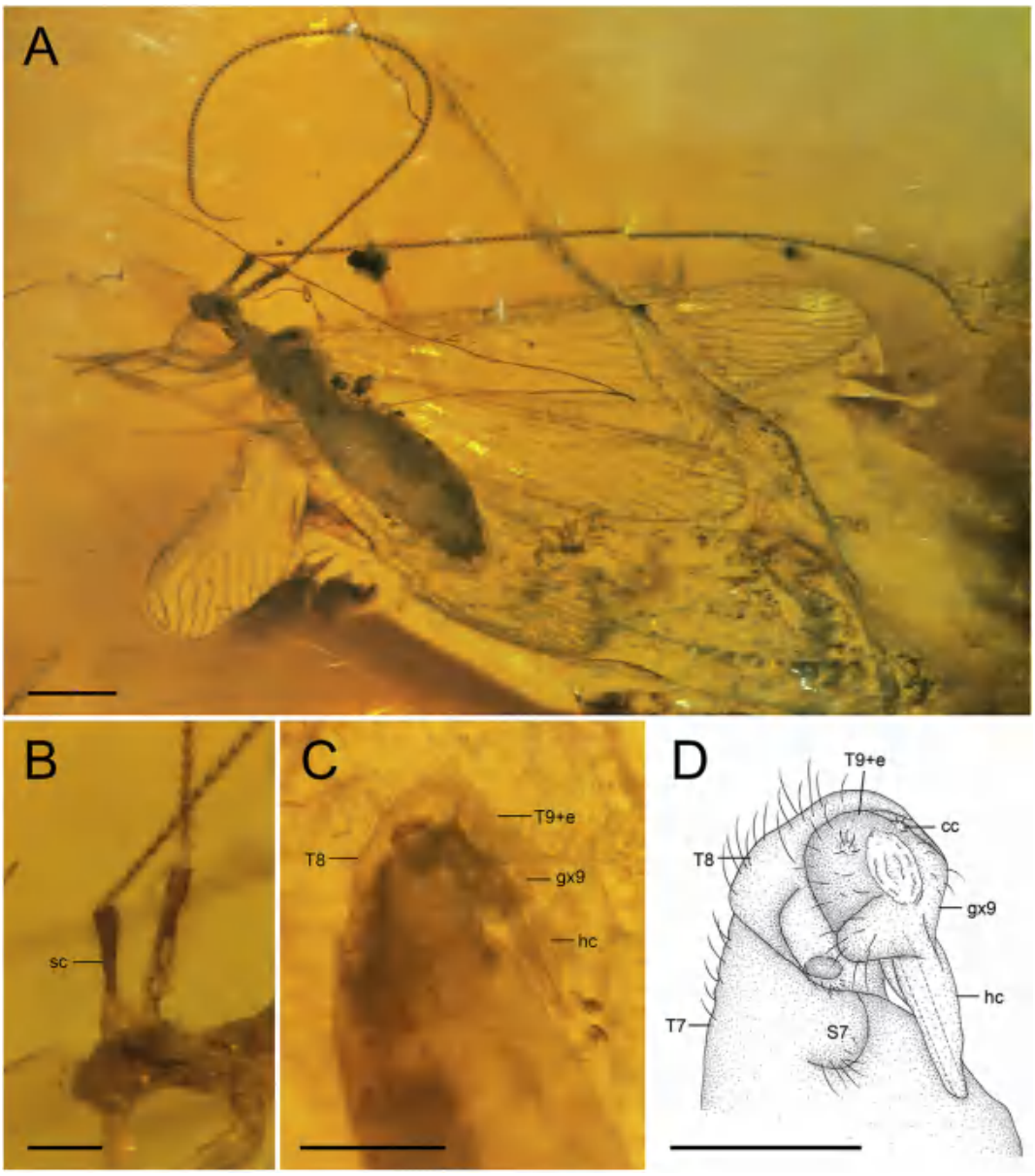

Fig. 21. Ansoberotha jiewenae Yang et al. (2019), NIGP171714, female. A. Habitus photograph, lateral view; B. Photograph of head, frontal view; C. Photograph of genitalia, ventrocaudal view; D. Drawing of genitalia, ventrocaudal view. cc: callus cerci; e: ectoproct; gx9: gonocoxite 9; hc: hypocauda; sc: scape; T: tergum. Scale bar = 1.0 mm (A); 0.5 mm (B, C, D).

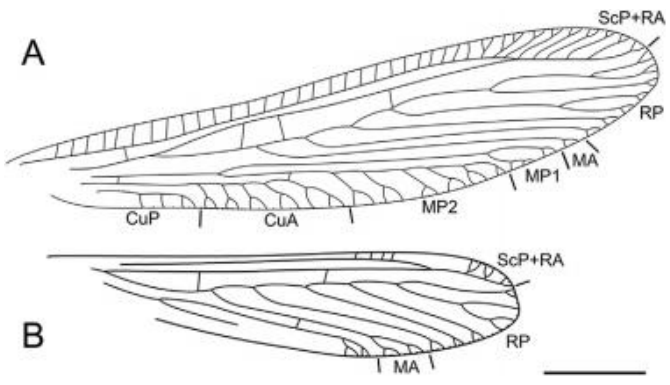

Fig. 22. Ansoberotha jiewenae Yang et al. (2019), NIGP171714, female. A. Drawing of forewing; B. Drawing of hind wing. Scale bar = 1.0 mm.

Dolichoberotha gen. nov. However, in the other genera with hypocaudae, this structure is present as a pair of widely spaced digitiform or tubercular projections.

4.1. Phylogenetic position of Ansoberotha, Cornoberotha gen. nov., and Dolichoberotha gen. nov.

First, it is reasonable to infer the close relationship among these three genera, which should belong to a monophyletic lineage, based on a combination of apomorphic character states, including the strongly elongate antennae, the presence of three or more ra-rp crossveins proximad the fusion of ScP and RA in the forewing, the presence of forewing MA stem between RP+MA and MP1, the modified female sternum 7, and the flattened and closed hypocaudae. The strongly elongate antennae are unique in Berothidae and only present in these three genera, probably representing an

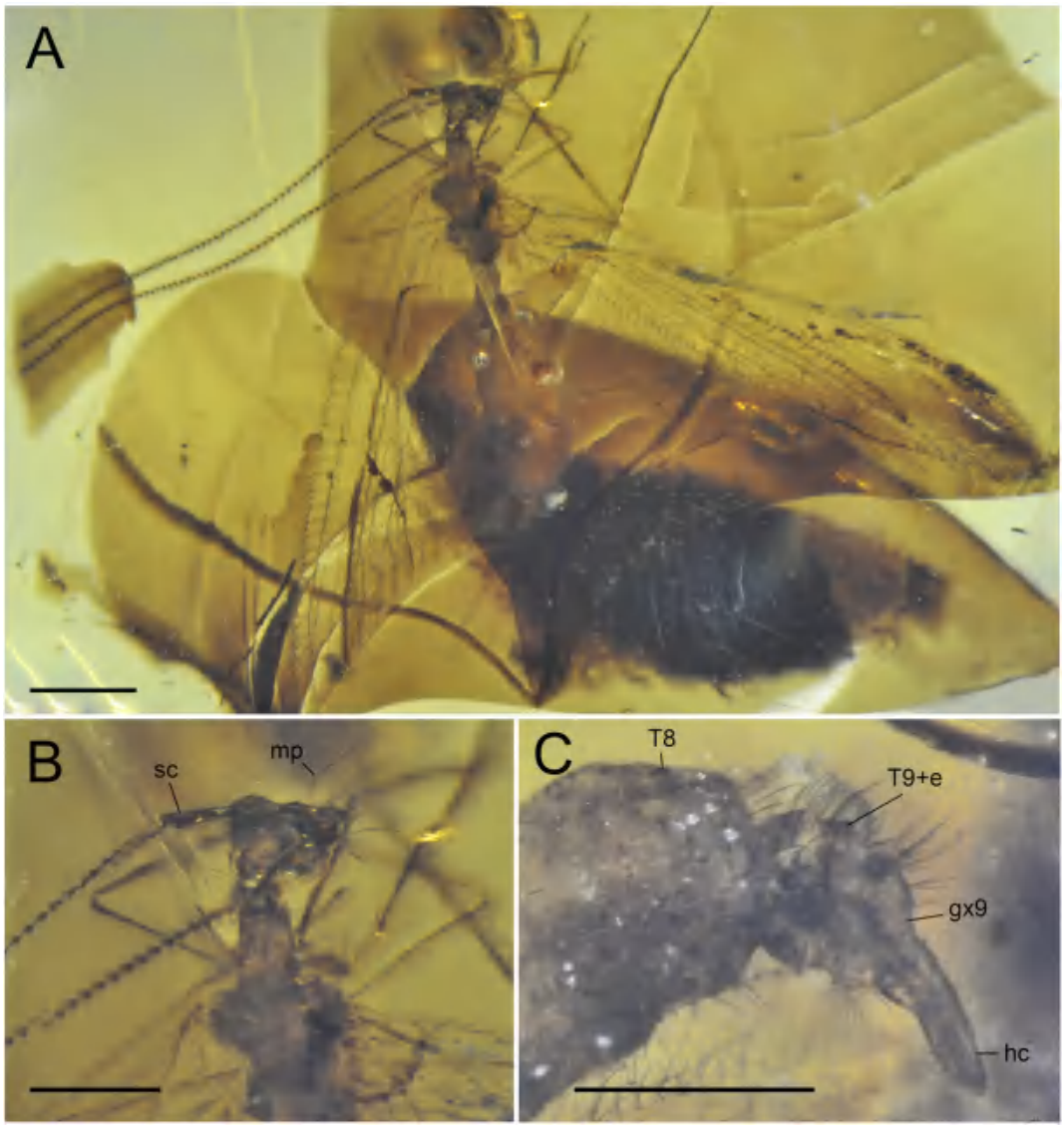

Fig. 23. Ansoberotha jiewenae Yang et al. (2019), NIGP171715, female. A. Habitus photograph, dorsal view; B. Photograph of head, frontal view; C. Photograph of genitalia. e: ectoproct; gx9: gonocoxite 9; hc: hypocauda; mp: maxillary palpus; sc: scape; T: tergum. Scale bar = 1.0 mm (A); 0.5 mm (B, C).

autapomorphy of this lineage. However, the remaining aforementioned apomorphic states are shared by some other berothid genera but are phylogenetically informative for inferring the subfamilial affinity of these "long-antennae" berothids (see below).

The "long-antennae" Burmese amber berothids (at least some species of this lineage) possess a number of apomorphic character states that are present in higher subfamilies of Berothidae, e.g. Nosybinae and Berothinae. These character states comprise the slightly falcate wing apex, the paired female sternum 7, and the well developed hypocaudae of the female gonocoxites 9. However, these "long-antennae" berothids also retain some characters that are present principally in the basal subfamilies Cyrenoberothinae and Nyrminae, including the complete hind wing CuP, the separation of male tergum 9 and ectoprocts, the slender male gonocoxites 9, and the absence of bristles on the male gonocoxites 10 complex, all of which are plesiomorphic in Berothidae.

Therefore, it is hard to definitely place these "long-antennae" berothids into any known subfamily. They might represent a stem-group of higher berothids, at least including Nosybinae and Berothinae. However, a phylogenetic analysis combining fossil and extant berothid genera is needed to further recover the position of these interesting berothids in the tree of life of Berothidae. At present the morphological evidence from the fossils is still insufficient to conduct such analysis.

5. Conclusions

The new taxa herein described enrich the palaeodiversity of beaded lacewings from the Upper Cretaceous of Myanmar. The spectacular characters on head of these berothids are significant for understanding morphological diversity of the Mesozoic lacewings. Based on the possession of some distinct apomorphic genital characters, the three genera might represent a stem-group of higher berothids, at least including Nosybinae and Berothinae.

CRediT authorship contribution statement

Ying Yang: Conceptualization, Methodology, Investigation, Visualization, Writing - original draft. Hongyu Li: Conceptualization, Methodology, Investigation, Visualization, Writing - original

draft. Bo Wang: Conceptualization, Methodology, Investigation, Visualization, Writing - original draft. Weiwei Zhang: Conceptualization, Methodology, Investigation, Visualization, Writing - original draft. Xingyue Liu: Conceptualization, Methodology, Investigation, Visualization, Writing - original draft.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2019.104348.