

# New dipteromantispids (Insecta: Neuroptera: Dipteromantispidae) from mid-Cretaceous Myanmar amber

Hongyu Li <sup>a</sup>, De Zhuo <sup>b</sup>, Bo Wang <sup>c</sup>, Xingyue Liu <sup>a,\*</sup>

<sup>a</sup> Department of Entomology, China Agricultural University, Beijing, 100193, China

<sup>b</sup> Beijing Xiachong Amber Museum, 9 Shuanghe Middle Road, Beijing, 100023, China

<sup>c</sup> State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China

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## ABSTRACT

A new genus and two new species of Dipteromantispidae, an extinct raptorial family of Mantispoidea, are described from mid-Cretaceous (lowermost Cenomanian) Myanmar amber. The forewing of *Paradipteromantispia polyneura* gen. et sp. nov. possesses trichosors distally, bifurcate humeral veinlet, 1ma-mp connecting RP + MA and MP1, which are distinctive but probably plesiomorphic character states in Dipteromantispidae. The new genus also shares some characters with *Dipteromantispia brevisubcosta* Makarkin, Yang & Ren, 2013, i.e. the large body size, the medially dilated forewing costal space, and the forewing 1ma-mp distad the first branching point of MP. *Kurtodipteromantispia xiai* sp. nov. is separated from *K. zhuodei* Li & Liu, 2020 by the absence of forewing rp-ma and 2ma-mp, and the male genitalia with posterolaterally protruding tergum 9. Based on new materials with well-preserved forelegs, some fine structures on foreleg previously unknown in dipteromantispids are reported. Our finding provides new morphological evidence for understanding the placement of Dipteromantispidae in Mantispoidea.

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## 1. Introduction

Dipteromantispidae is a specialized extinct family of lacewings, placed in the superfamily Mantispoidea, with minute body size (forewing length 2.6–7.9 mm), raptorial forelegs, reduced venation of forewing, and haltere-like hind wing (Makarkin et al., 2013a; Liu et al., 2016, 2017). The earliest described species of this family, i.e., *Mantispidiptera enigmatica* Grimaldi, 2000 and *Jersimantispia henryi* (Grimaldi, 2000) from the Upper Cretaceous (Turonian) of New Jersey, were originally assigned to Mantispidae and allied with the mantidfly subfamily Symphrasinae (Grimaldi, 2000). With the description of *Dipteromantispia brevisubcosta* Makarkin, Yang & Ren, 2013 from the Lower Cretaceous (upper Barremian) of northeastern China, Makarkin et al. (2013a) erected the family, Dipteromantispidae. All remaining fossil records of dipteromantispids are found from the mid-Cretaceous (lowermost Cenomanian) Myanmar amber, including four genera and four species: *Halteriomantispia grimaldii* Liu, Lu & Zhang, 2016, *Burmodipteromantispia jixiaobao* Liu, Lu & Zhang, 2017, *Mantispidipterella longissima* Liu, Lu & Zhang, 2017, and *Kurtodipteromantispia zhuodei* Li & Liu, 2020.

Hitherto, the definite placement of Dipteromantispidae within Mantispoidea still remains controversial. Grimaldi (2000) and Engel & Grimaldi (2008) considered dipteromantispids should be a highly specialized group in Mantispidae, with several modified features probably caused by miniaturization. However, based on *D. brevisubcosta*, Makarkin et al. (2013a) assumed that dipteromantispids may be a specialized subfamily of Berothidae (including Rhachiberothidae), or a specialized stem group of Mantispoidea, while the latter hypothesis was accepted by Makarkin et al. (2013b) with an illustration in a phylogenetic tree of fossil and recent Neuroptera. Besides, mainly in light of genital morphology, Liu et al. (2016, 2017) demonstrated that this family may be placed among the transitional lineages between Berothidae and advanced mantispids.

Here we report one new genus and two new species of Dipteromantispidae from the mid-Cretaceous Myanmar amber. These new dipteromantispids show some distinctive characters that were previously unknown in the family, such as the profusely branched forewing longitudinal veins, the presence of trichosors, etc. More importantly, morphology of various fine integumentary structures on the raptorial foreleg, such as femoral integumentary processes bearing Stitz organs and the specialized setae row along the ventral ridge of tibia, in new dipteromantispid materials are described in

\* Corresponding author.

E-mail address: [xingyue\\_liu@yahoo.com](mailto:xingyue_liu@yahoo.com) (X. Liu).

detail. Thus, new dipteromantispids highlight the species and morphological diversity of this family, and provide further evidence to infer the phylogenetic status of dipteromantispids in Mantispoidea.

## 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), deposited in the Beijing Xiaochong Amber Museum, Beijing (BXAM), the Lingpoge Amber Museum, Shanghai (LPAM), and the Nanjing Institute of Geology and Palaeontology (NIGP), Nanjing. The age of the amber deposit has been investigated and dated to be  $98.8 \pm 0.6$  million years by U–Pb dating of zircons from the volcanoclastic matrix of the amber (Shi et al., 2012).

Photographs were taken by using a Zeiss SteREO Discovery V12 stereo microscope system and a Leica DM 2000 optical microscope with Nikon D90 and Nikon D800 digital camera. Wing drawings were prepared by Zeiss SteREO Discovery V12 stereo microscope system, while genital drawings were made by Nikon SMZ745 stereoscope. The figures were prepared with Adobe Photoshop CC®.

Terminology of wing venation generally follows Aspöck et al. (1980) and Kukalová-Peck & Lawrence (2004). Other morphological terminology except genitalia follows Lambkin (1986). Terminology of genitalia follows Aspöck & Aspöck (2008). Abbreviations used for wing veins are as follows: 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. Measurements (in millimeters) follow Lambkin (1986) and are given in parentheses and ratios outside them. The abbreviation used in measurements as follows: LP, length of pronotum; LPT: length of pterothorax; LFF, length of fore femur; WFF, width of fore femur; LFW, length of forewing; WFW, width of forewing.

## 3. Systematic palaeontology

Class Insecta Linnaeus, 1758

Order Neuroptera Linnaeus, 1758

Family Dipteromantispidae Makarkin, Yang & Ren, 2013

Type genus: *Dipteromantispa* Makarkin, Yang & Ren, 201

**Revised diagnosis.** 1) Small to minute mantispid-like lacewings (forewing length 2.6–7.9 mm long). 2) Prothorax short, not tubular; 3) forelegs inserted at posterior portion of prothorax, raptorial; 4) fore femur swollen, not compressed ventrally, without any long spine, bearing two or three rows of short denticles or at least a row of very short spines distally equipped with a Stitz organ; 5) a row of oblique specialized setae present along ventral ridge of fore tibia in some species. 6) Mesothorax enlarged conspicuously; 7) antero-lateral margins of scutum rounded; 8) anterior portion of scutum enlarged, larger than lateral portion; 9) mesoscutellum subtriangular, large. 10) Metathorax strongly reduced. 11) Forewing venation generally strongly reduced, but complicated in *Paradipteromantispa polyneura* gen et sp. nov.; 12) trichosors present or not; 13) costal crossveins mostly simple; 14) ScA sometimes present; 15) ScP relatively short, distally remote from RA, straight or deflexed distally; 16) unusual fusion among R, RP + MA, MP, Cu and A1 sometimes present; 17) CuA and CuP both simple, but CuA occasionally forked distally in *P. polyneura* gen et sp. nov.. 18) Hind wing strongly reduced, modified into a haltere-like structure. 19) Male gonocoxites, gonapophyses, and gonostyli 10 integrated into an unpaired complex, with a long penisfilum (at least present in two species: *Mantispidipterella longissimi* and *Kurtodipteromantispa*

*xiai* sp. nov.). 20) Female gonocoxites 7 sometimes present and paired; 21) tergum 9 partially fused with ectoprocts; 22) pseudohypocaudae present in some species.

**Remarks.** The revised diagnosis is modified based on Makarkin et al. (2013) and Liu et al. (2017), and the characters 4), 11), 12), 15), 17), 21), 22) are herein updated or newly supplemented.

### *Paradipteromantispa* gen. nov.

(Figs. 1, 2)

urn:lsid:zoobank.org:act:EA97BC75-4EB6-4399-A296-BA991A5C5C7C.

Type species: *Paradipteromantispa polyneura* sp. nov.

**Diagnosis.** Large-sized dipteromantispids, body length 8.0 mm, forewing length 6.3 mm. Forewing: Venation generally enriched; trichosors present along distal margin; costal space strongly dilated at middle; costal crossveins with some forked ones; ScP distinctly deflexed just proximal to scp-ra, distally profusely branched; 2r cell with 13 forked branches; RP abruptly and angularly curved at ra-rp, with four main branches, most of which are forked distally, but lacking crossveins among them; MA with three main branches; rp-ma absent; one or two ma-mp crossveins present, 1ma-mp distad first branching point of MP; MP1 bifurcate, MP2 with four or five branches; gradate series of crossveins absent; cua-cup proximal to and slightly longer than mp-cua; A1 with four branches. Hind wing haltere-like, but with vestigial veins. Female tergum 9 posterodorsally fused with ectoprocts, ventrally completely detached as a subtriangular sclerite (putative pseudohypocauda); gonocoxites 9 paired and ovoid, anteriorly extended to gonocoxites 8.

**Etymology.** The generic name consists of prefix “para-” (Greek, meaning “near”) and “*Dipteromantispa*” (typical generic name of Dipteromantispidae).

**Remarks.** The new genus can be easily distinguished from all other dipteromantispid genera by the presence of trichosors and the enriched venation in the forewing. Notably, the forewing ScP distinctly deflexed proximad scp-ra is shared by the new genus and *Kurtodipteromantispa* (most dipteromantispid species have straight forewing ScP proximad scp-ra). *Paradipteromantispa* gen. nov. also resembles *Dipteromantispa* in having relatively large body size, medially dilated forewing costal space, and forewing 1ma-mp distad first branching point of MP. However, the forewing venation of *Dipteromantispa* is much simpler than that of the new genus (Makarkin et al., 2013a: figs. 1, 3A, B).

*Paradipteromantispa* gen. nov. appears to be the basalmost lineage of Dipteromantispidae. This new genus is the only group known to date in the family possessing trichosors. The presence of trichosors is generally considered as a plesiomorphy in Neuroptera, while trichosors are variously reduced or lost in Dipteromantispidae and Mantispidae (Liu et al., 2015). The forewing venation in the new genus is more complicated and not simplified as in all remaining dipteromantispids, showing some plesiomorphies, e.g. the presence of bifurcate humeral veinlet, the longitudinal veins with more branches, the 1ma-mp distad the first branching point of MP, connecting MP1 and RP + MA [The last character is very common in the Mantispoidea and considered as a plesiomorphy by Makarkin & Ohl (2015)].

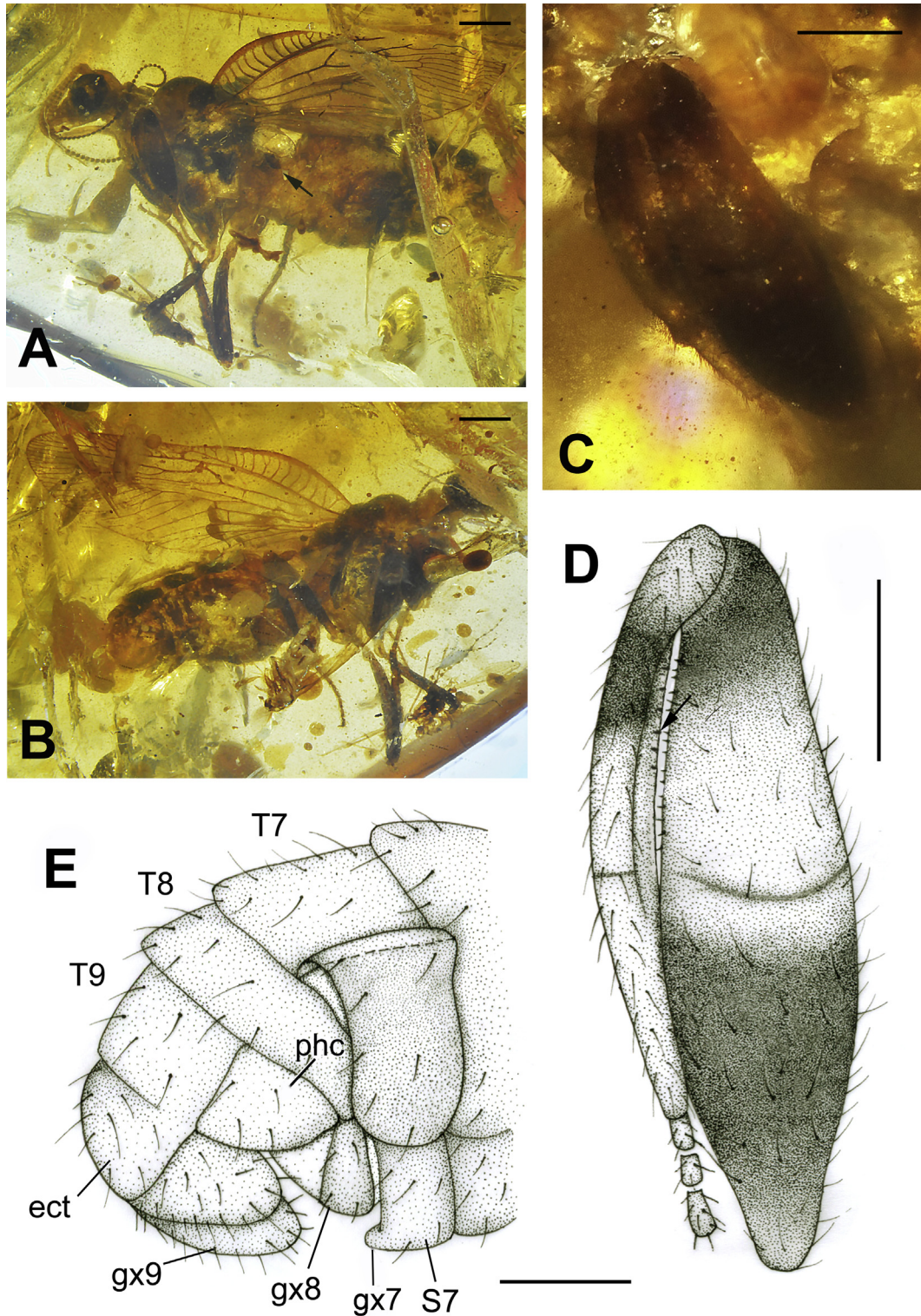
### *Paradipteromantispa polyneura* sp. nov.

(Figs. 1, 2)

urn:lsid:zoobank.org:act:F1CC0CA8-743E-4184-BF9D-B619A45D95FD.

**Diagnosis.** Same as for the genus.

**Type material.** Holotype. NIGP173215, amber piece preserving a complete adult female of *P. polyneura* gen. et sp. nov., and it is polished



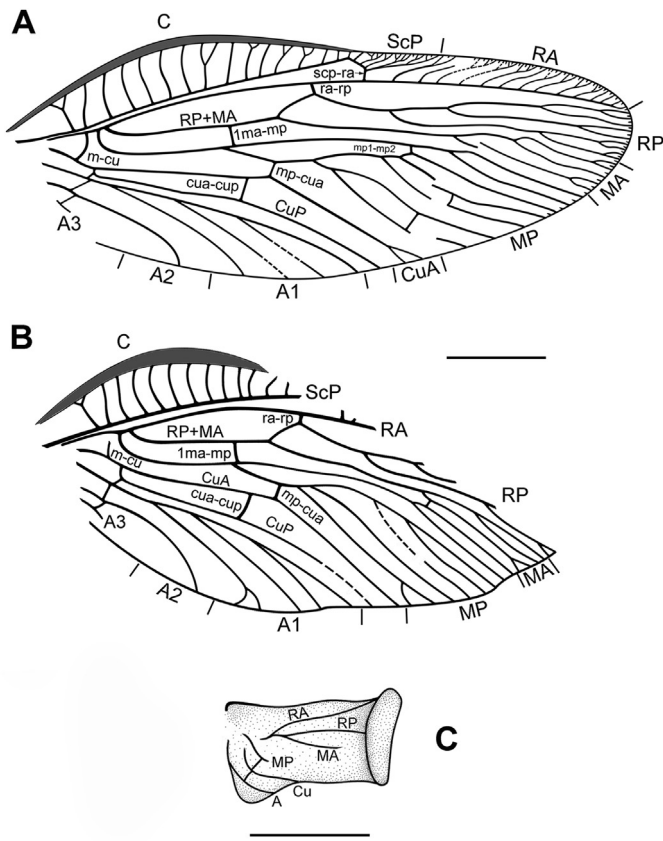
**Fig. 1.** *Paradipteromantispa polyneura* gen. et sp. nov., holotype, NIGP173215, female. A. Habitus photo, left lateral view, arrow indicates the haltere-like hind wing; B. Habitus photo, right lateral view; C. Photo of left foreleg, lateral view; D. Drawing of left foreleg, lateral view, arrow indicates the trace of setae row on ventral ridge of fore tibia; E. Drawing of genitalia, lateral view. T: tergum; S: sternum; ect: ectoproct; gx: gonocoxites; phc: pseudohypocaudae. Scale bar = 1.0 mm (A–B), 0.5 mm (C–E).

in the form of an elliptical transparent cabochon, with length  $\times$  width about  $20.2 \times 15.9$  mm, height about 7.2 mm.

**Etymology.** The specific epithet “polyneura” is a combination of prefix “poly-” (Greek, meaning “many”) and “neura” (Greek, meaning “vein”) in reference to the complex forewing venation of the new species.

**Description.** Holotype, female. Measurements (mm) and proportions: Body length: 8.0; LP (0.7): LPT (2.7) = 0.3; LFF (2.0): WFF (0.5) = 4.0; LFW (6.3): WFW (2.6) = 2.4.

Head hypognathous, subtriangular; vertex slightly domed with fine setae posteriad antennae; postocular region broad in lateral view. Antenna filiform, sparsely setose; scape swollen and stout, slightly



**Fig. 2.** *Paradipteromantispa polyneura* gen. et sp. nov., holotype, NIGP173215, female. A. Right forewing; B. left forewing; C. Left hind wing. Scale bar = 1.0 mm (A–B), 0.5 mm (C).

longer than wide, as long as total length of proximal three flagellomeres; pedicel feebly swollen; flagellum with about 57 flagellomeres, each nearly as long as wide.

Prothorax very short, nearly half length of mesothorax. Mesothorax enlarged conspicuously, dorsally domed; anterolateral margins of scutum rounded; anterior portion of scutum enlarged and subtriangular, larger than lateral portion; mesoscutellum subtriangular, domed, nearly  $\frac{1}{3}$  × as long as mesothorax. Metathorax strongly reduced. Foreleg (Fig. 1C, D): Raptorial, coxa elongated; trochanter invisible; femur black, but outer surface with distal half largely pale except dark tip, distinctly swollen on proximal half, not laterally compressed, ventrally with at least a row of very short, black, spine-like setae visible; tibia slender, brown, sub-basally black, with a lateroventral longitudinal ridge along which specialized setae are invisible but their traces are detectable basally. Mid and hind legs: Slender, bearing long setae; tibia slightly shorter than femur; tarsus 5-segmented, with tarsomere 1 nearly equal to remaining tarsomeres combined; 2–5 tarsomeres subequal in length; pretarsal claws simple, paired, arolium invisible.

Forewing (Fig. 2A, B) ovate, membrane hyaline and immaculate, with complex venation; distal margin with distinct tiny trichosors; pterostigma absent; wing margin and veins setose; costal vein robust; costal space about two third of forewing length, broad, strongly dilated at middle; humeral veinlet slightly recurrent and bifurcate; ~20 costal crossveins present, some of them forked; ScA absent; ScP distinctly deflexed just proximal to scp-ra, terminating on costal margin nearly at distal  $\frac{1}{3}$ , distally branched; subcostal space narrow proximally, gradually broaden to scp-ra; 2r cell with 13 marginally forked branches distal to scp-ra; one short ra-rp present; RP + MA separating from R near wing base, RP and MA

diverging from each other near midpoint of wing; RP abruptly and angularly curved at ra-rp, with four main branches, most of which are secondarily forked but lack crossveins among them; MA with two distally forked and one simple branches; rp-ma absent; MP strongly curved proximally and diverging from R distal to lm-cu, MP1 bifurcated, MP2 with five main branches (posterior two branches fused for a short distance in right forewing, posterior-most branch marginally forked in left forewing); one or two crossveins (ma-mp) present between MA and MP; 1ma-mp distal to first branching point of MP; two crossveins present among MP branches in right forewing; gradate series of crossveins absent; one m-cu present near wing base, approximate and proximal to divergent point of MP and R; one mp-cua present; CuA simple or forked marginally, angularly bending at mp-cua; CuP simple; cua-cup proximal to and slightly longer than mp-cua; mp-cua, cua-cup and longitudinal vein related to them not distinctly thickened; one cu-a present, approximate and distal to branching point of Cu; A1 with four branches; A2 and A3 simple; one a1-a2 and one a2-a3 present. Hind wing (Fig. 2C) haltere-like, nearly rectangular; venation vestigial, with putative remnants of RA, RP, MA, MP, Cu and A (all simple).

Abdomen stout, setose; pregenital segments swollen. Putative gonocoxites 7 short tubercular; gonocoxites 8 sub-trapezoidal, much shorter than sternum 7 in lateral view; tergum 9 posterodorsally fused with ectoprocts, ventrally detached as a subtriangular sclerite (putative pseudohypocauda); gonocoxites 9 paired and ovoid, anteriorly extended to gonocoxites 8; ectoprocts subtriangular in lateral view.

#### Genus *Kurtodipteromantispa* Li & Liu, 2020

*Kurtodipteromantispa* Li & Liu, 2020: 101. Type species: *Kurtodipteromantispa zhuodei* Li & Liu (2020): 101 (original designation)

*Diagnosis.* See Li & Liu (2020).

#### *Kurtodipteromantispa xiai* sp. nov.

(Figs. 3, 4)

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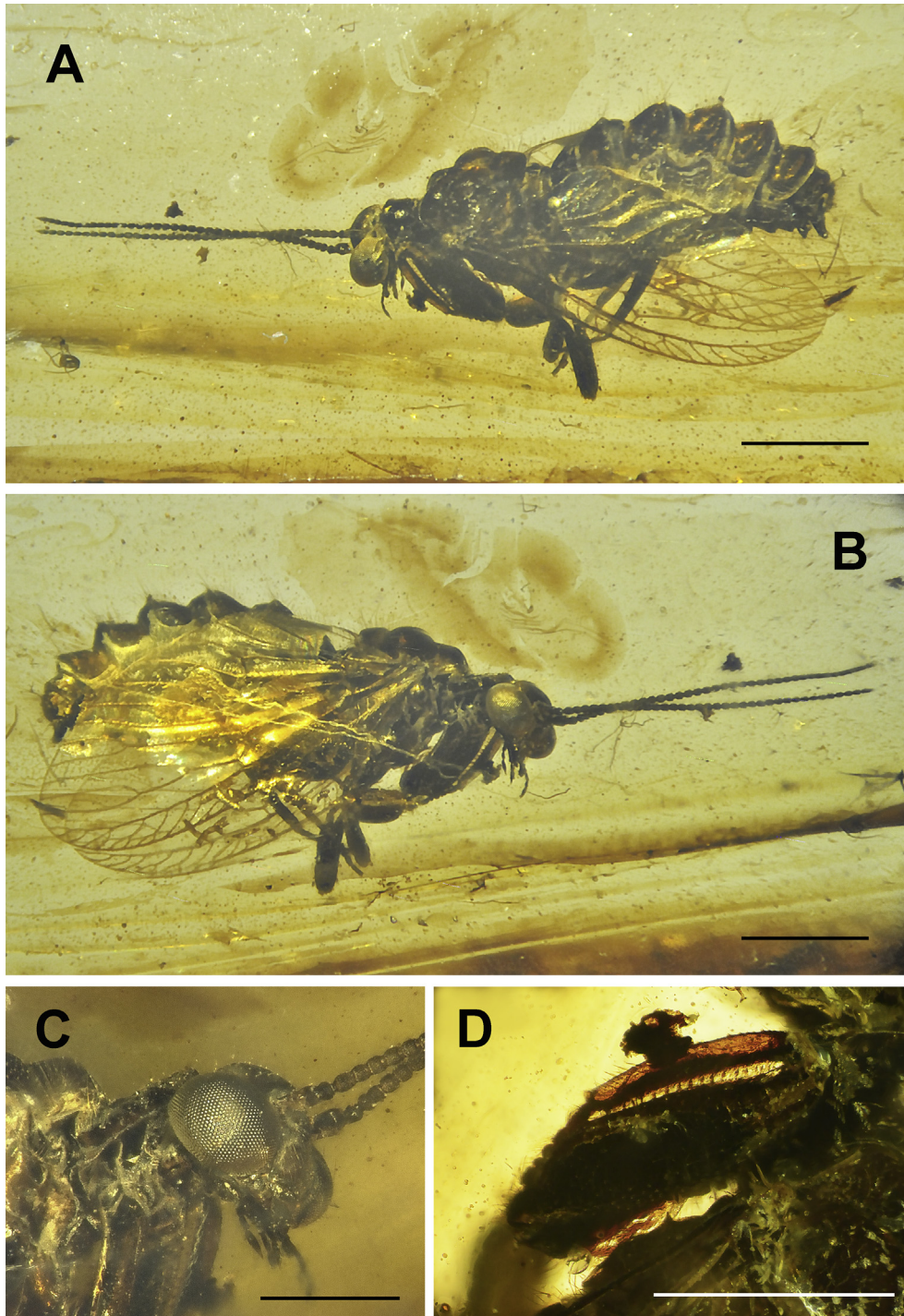
*Diagnosis.* Minute dipteromantispids, body length 3.8 mm, forewing length 3.1 mm. Forewing: costal crossveins c. 13–15, simple; 2r cell with 6–7 forked or simple branches running to costal margin; RP with three branches and no crossveins among them; rp-ma absent; only one crossvein (ma-mp) present between MA and MP, proximal to first branching point of MP, connecting MP stem and RP + MA; gradate series absent; cua-cup proximal to and nearly as long as mp-cua; cu-a, a1-a2, and a2-a3 aligned. Male tergum 8 nearly half length of tergum 7; tergum 9 very short dorsally, ventrally strongly expanded and produced posteriad; sternum 9 present as a plate with posterior margin slightly concave medially; gonostyli 10 (pseudopenis) present as a slender penisfilum with acute tip; ectoprocts rounded and domed, with dense long setae.

*Type material.* Holotype. LPAM BA-NEU-001, amber piece preserving a complete adult male of *K. xiai* sp. nov. and a caddis fly, and it is polished in the form of an elliptical transparent cabochon, with length × width about 20.8 × 14.5 mm, height about 3.3 mm.

*Etymology.* The new species is dedicated to Mr. Fangyuan Xia who kindly provided the specimen of this new species for our study.

*Description.* Holotype, male. Measurements (mm) and proportions: Body length 3.8; LP (0.4): LPT (1.0) = 0.4; LFF (1.0): WFF (0.3) = 3.3; LFW (2.9): WFW (1.2) = 2.4.

Head (Fig. 3C) hypognathous, sparsely setose; vertex distinctly domed; postocular region narrow; eyes very large and globular; antenna filiform, setose, about two third of body length; scape swollen and stout, longer than wide, twice as long as proximal two

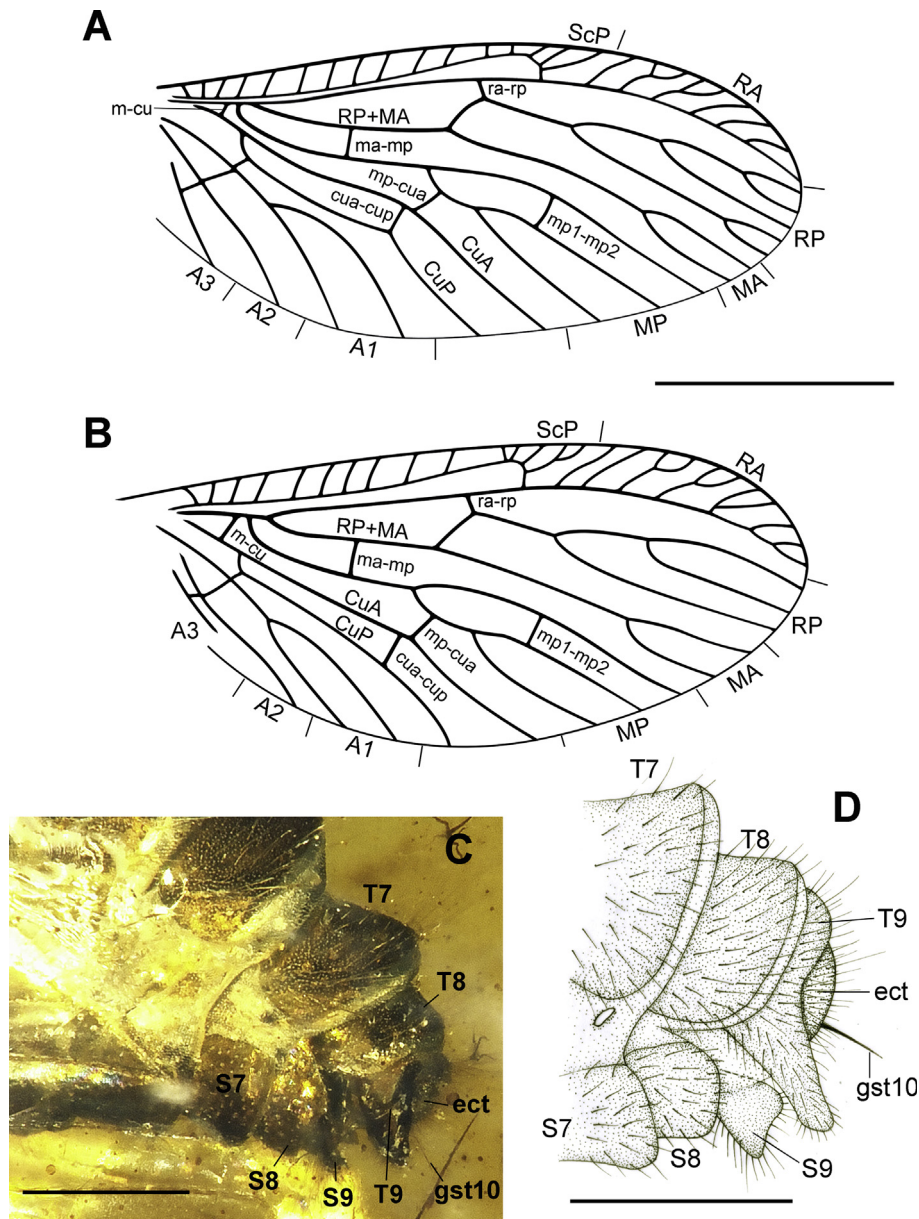


**Fig. 3.** *Kurtodipteromantispa xiai* sp. nov., holotype, LPAM BA-NEU-001, male. A. Habitus photo, left lateral view; B. Habitus photo, right lateral view; C. Head, lateral view; D. Left foreleg, lateral view. Scale bar = 1.0 mm (A–B), 0.5 mm (C–D).

flagellomeres combined; pedicel similar to proximal flagellomere in length and shape; flagellum with about 36 flagellomeres, nearly as long as wide except terminal flagellomere elongated and bullet-like; clypeus nearly rectangular, half length of labrum; maxillary palpus 4-segmented, terminal palpomere acutely tapering, twice as long as palpomere 3.

Thorax covered by long setae. Prothorax half length of mesothorax. Mesothorax enlarged conspicuously, dorsally domed; anterolateral margins of scutum rounded; anterior portion of scutum enlarged

and subtriangular, larger than lateral portion, with median suture; mesoscutellum subtriangular, domed, nearly  $1/3 \times$  as long as mesothorax. Metathorax strongly reduced. Foreleg (Fig. 3D): Setose, femur swollen, not laterally compressed along spine row, ventrally with at least a row of very short spines each apically equipped with a Stitz organ; tibia slender, with a narrow lateroventral longitudinal ridge along which specialized setae are invisible; tarsus 5-segmented, tarsomere 1 nearly as long as tarsomere 5, but much shorter than 2–5 tarsomeres combined,



**Fig. 4.** *Kurtodipteromantispa xiai* sp. nov., holotype, LPAM BA-NEU-001, male. A. Left forewing; B. Right forewing; C. Photo of genitalia, lateral view; D. Drawing of genitalia, lateral view. T: tergum; S: sternum; ect: ectoproct; gst: gonostyli. Scales bar = 1.0 mm (A–B), 0.5 mm (C–D).

tarsomeres 2–4 subequal in length (each shorter than tarsomere 5); pretarsal claws paired and simple, arolium invisible. Fore tibia and fore tarsus together slightly longer than fore femur. Mid and hind legs: Slender, bearing long setae, tarsus, pretarsal claws and arolium invisible.

Forewing (Fig. 4A, B) elliptical, membrane hyaline and immaculate; pterostigma and trichosors absent; wing margin and veins setose; costal space about two third of forewing length, narrow, feebly dilated at middle; humeral veinlet simple; about 13–15 simple costal crossveins present; ScA absent; ScP distinctly deflexed proximad scp-ra, terminating on costal margin nearly at distal 1/3, distally branched or simple; subcostal space narrow proximally, gradually broaden to scp-ra; 2r cell with six or seven marginally forked or simple branches; one short ra-rp present; RP + MA separating from R near wing base, RP and MA diverging from each other near midpoint of wing; RP abruptly and angularly curved at ra-rp, with three branches (two of them with secondary fork in left

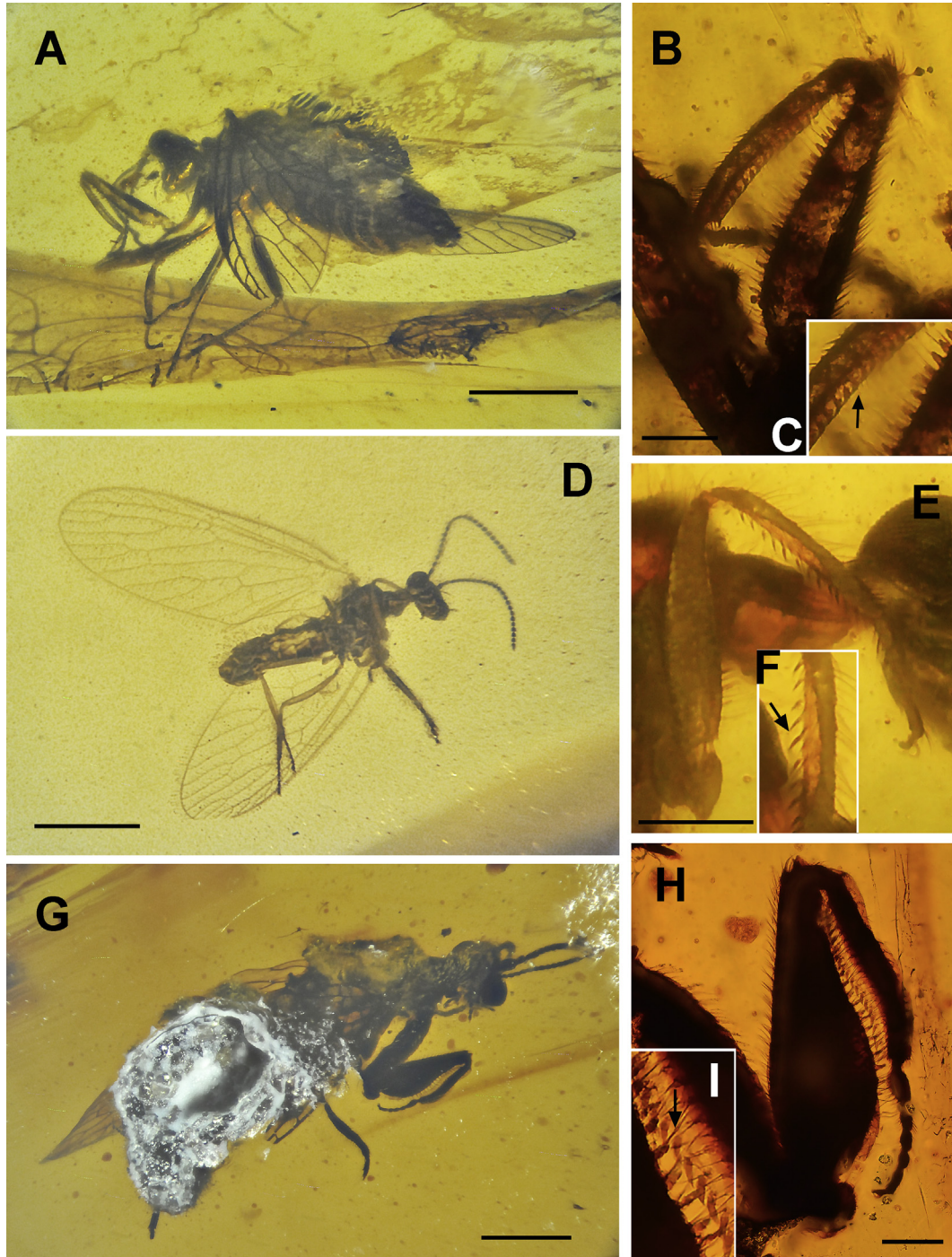
forewing), but without crossveins among them; MA bifurcated; rp-ma absent; MP strongly curved and fused with R proximally, with simple MP1 and bifurcate MP2 diverged nearly at midpoint; one ma-mp present between MA and MP, proximal to first branching point of MP; one mp1-mp2 present; gradate series of crossveins absent; m-cu present near wing base, approximate and proximal to diverging point of MP from R; one mp-cua present; CuA and CuP simple, both nearly parallel toward wing margin; cua-cup proximal to and nearly as long as mp-cua; mp-cua, cua-cup, and longitudinal vein related to them slightly thickened; one cu-a present, approximate and distal to branching point of Cu; A1 with two branches; A2 and A3 simple; one a1-a2 and one a2-a3 present; cu-a, a1-a2, and a2-a3 aligned.

Hind wing haltere-like, veins completely lost. Abdomen bearing long setae; terga 2–7 posteriorly strongly convex; spiracle of segment 7 visible; tergum 8 about half length of tergum 7; sternum short, nearly as long as tergum 8, subquadrate in lateral view;

tergum 9 very narrow dorsally, posteroventrally strongly produced into a long projection, which surpasses ectoprocts laterally; sternum 9 present as a plate with posterior margin slightly concaved medially; putative gonostyli 10 (pseudopenis) present, thread-like, straightly directed posteriad; ectoprocts short, ovoid, partially covered by tergum 9, with dense long setae (Fig. 4C, D).

**Remarks.** The new species is assigned to *Kurtodipteromantispa* mainly based on the minute body size (body length 3.8 mm,

forewing length 2.9 mm), the forewing ScP distinctly deflexed proximad scp-ra, and the simplified forewing venation. It can be distinguished from *K. zhuodei* by the absence of forewing rp-ma and 2ma-mp and by the male genitalia with posterolaterally protruding tergum 9. In the latter species, the forewing rp-ma and 2ma-mp are present, and the male tergum 9 is not protruded posterolaterally.



**Fig. 5.** *Burmodipteromantispa jiaxiaoae* Liu, Lu & Zhang (2017), BXAM BA-NEU-003, female. A. Habitus photo, lateral view; B. Foreleg, showing the spine row. C. The specialized setae along the ventral ridge of fore tibia, indicated by arrow. *Mantispidpterella* sp., NIGP173216, female. D. Habitus photo, ventral view; E. Foreleg; F. The specialized setae on ventral ridge of fore tibia, indicated by arrow. Dipteromantidpidae Incertae sedis, BXAM BA-NEU-004, sex unknown. G. Habitus photo, dorsal view; H. Foreleg, showing the spine row; I. The specialized setae row on ventral ridge of fore tibia, indicated by arrow. Scale bar = 1.0 mm (A, D, G), 0.2 mm (B, E, H).

### Description of foreleg based on additional materials of Dipteromantispidae

#### (Fig. 5)

*Burmodipteromantispa jiaxiaoe* (Fig. 5A-C). Female, body length 3.1 mm, LFF (0.9 mm): WFF (0.2 mm) = 4.5. Fore coxa slenderly elongate; fore femur slender, slightly swollen, not laterally compressed along spine row, ventrally with at least a row of very short spines visible, each apically equipped with a Stitz organ; tibia slender, with a row of specialized setae, which are distinctly curved distad, along ventral longitudinal ridge; tarsus, pretarsal claws and arolium obscure.

*Mantispidipterella* sp. (Fig. 5D-F). Female, body length 2.2 mm, LFF (0.4 mm): WFF (0.1 mm) = 4.0. Fore coxa slenderly elongate; fore femur slender, slightly swollen, not laterally compressed, ventral spine row invisible; tibia slender, with a row of spine-like setae, which are straight but directed distad, along ventral longitudinal ridge; tarsus 5-segmented, tarsomere 1 nearly as long as tarsomere 5, but much shorter than 2–5 tarsomeres combined, tarsomeres 2–4 subequal in length (each shorter than tarsomere 5); pretarsal claws paired and simple, arolium present.

Dipteromantispidae Incertae sedis (Fig. 5G-I). Sex unknown, body length 4.5 mm, LFF (1.1 mm): WFF (0.4 mm) = 2.8. Foreleg deformed, laterally compressed strongly, because of the state of preservation. Fore coxa slenderly elongate; fore femur ventrally with at least a row of spines visible, each apically equipped with a Stitz organ; tibia slender, with a row of spine-like setae, which are slightly curved distad, along ventral longitudinal ridge; tarsus 5-segmented, tarsomere 1 nearly as long as tarsomere 5, but much shorter than 2–5 tarsomeres combined, tarsomeres 2–4 subequal in length (each shorter than tarsomere 5); pretarsal claws paired and simple, arolium present.

**Material examined.** BXAM BA-NEU-003, amber piece preserving a complete adult female of *B. jiaxiaoe* and a dipteran, and it is polished in the form of an elliptical transparent cabochon, with length × width about 19.2 × 12.8 mm, height about 4.3 mm NIGP173216, amber piece preserving a complete adult female of *Mantispidipterella* sp., and it is polished in the form of an elliptical transparent cabochon, with length × width about 13.5 × 7.7 mm, height about 4.5 mm. BXAM BA-NEU-004, amber piece preserving a thrips and an incomplete adult of dipteromantispid, sex unknown because of the apex of abdomen destroyed, and it is polished in the form of an elliptical transparent cabochon, with length × width about 25.7 × 16.2 mm, height about 6.3 mm.

## 4. Discussion

Dipteromantispidae is one of the highly specialized lacewing lineages in morphology yet with uncertain phylogenetic status. With the present new findings, there have been nine species in eight genera described in Dipteromantispidae, while about 70% (five genera and six species) of the known genera and species are from the mid-Cretaceous of Myanmar. The Burmese amber dipteromantispids provide not only the information on the Cretaceous palaeodiversity of this group but also the valuable evidence for understanding its phylogenetic position. In light of the new dipteromantispids herein described, important morphological data on the foreleg and the genitalia with phylogenetic relevance could be acquired.

The forelegs of Dipteromantispidae are located at the posterior portion of prothorax, which is short and not tubular, in all specimens we examined. Unlike that in Mantispidae, this character state, which is shared by Rhachiberothidae and Berothidae, stands as one of the main arguments to separate this family from Mantispidae, although it

is plesiomorphic. By contrast, the elongation of prothorax posteriad the insertion of forelegs and its tubular modification was repeatedly considered as an autapomorphy of Mantispidae (Aspöck & Mansell, 1994; Liu et al., 2015; Lu et al., 2020).

Concerning the morphology, especially the integumentary structures, of the raptorial forelegs in dipteromantispids, there are some characters shared by either Mantispidae or Rhachiberothidae or even both. The fore femur is generally rather thick, robust, but not compressed ventrally in Dipteromantispidae, being different from most species of Rhachiberothidae except the extant genus *Hoelzeliella* (Aspöck & Aspöck, 1997: fig. 35), but shared by the mantidfly subfamilies Mesomantispinae and Symphrasinae. Makarkin et al. (2013a) noted that there are two or three rows of short fore femoral denticles (considered to be short and thick spine-like setae and categorized as the fore femoral integumentary specialization Type A in Pérez-de la Fuente and Peñalver, 2019). This type of specialized setae has been found in five dipteromantispid genera, i.e. *Dipteromantispa*, *Kurtodipteromantispa*, *Mantispidiptera*, *Mantispidipterella*, and *Paradipteromantispa* gen. nov.. Pérez-de la Fuente and Peñalver (2019) classified the Type A setae into Dipteromantispidae only. However, similar fore femoral setae seem to be present also in Mesomantispinae (see Jepson et al., 2013: figs. 6–7). Besides this type of fore femoral setae, it is notable that longer fore femoral integumentary processes (IPs) bearing minute chitinous cones (Stitz organs) are found in our new materials of the Burmese amber dipteromantispids (see Figs. 1D, 5). In detail, they are almost identical to the IPs Type J and K, which were previously known only in Mantispidae (Pérez-de la Fuente and Peñalver, 2019). However, dipteromantispids lack the fore femoral major spine (= IPs Type L in Pérez-de la Fuente and Peñalver, 2019), which is present in Drepanicinae, Calomantispinae, and Mantispinae. Therefore, dipteromantispids share more fore femoral characters with the basal mantidfly subfamilies Mesomantispinae and Symphrasinae than with the other mantispoids.

The fore tibial integumentary specializations, first described here in dipteromantispids, consist of a single row of specialized setae along the ridge on ventral portion of fore tibia (Fig. 5B, C, E, F, H, I). Interestingly, there are two types of specialized fore tibial setae found in the Burmese amber dipteromantispids. In *Burmodipteromantispa* these setae are erect but distinctly curved distad (Fig. 5B, C), which is similar to the fore tibial seta Type iii in Mesomantispinae (Pérez-de la Fuente and Peñalver, 2019). In *Mantispidipterella* these setae are erect and spine-like, which is almost the same to the fore tibial seta Type v previously known only in the rhachiberothid subfamily Paraberotherinae (Pérez-de la Fuente and Peñalver, 2019). Notably, Nakamine et al. (2020) described four genera and seven species of Paraberotherinae from Burmese amber, revealing rich diversity of morphology of fore tibial setae in this subfamily. The setal Types i, iii, iv, v could be observed in different genera of Paraberotherinae, and even two types of setae are present in same species (e.g. *Micromantispa sipcata* Nakamine et al., 2020 and *Astioberothera falcipes* Nakamine et al., 2020, which have the types iii and iv; see Nakamine et al., 2020: figs. 4c, 13b). In some paraberotherine species (e.g. *A. falcipes* and *Stygioberothera siculifera* Nakamine et al., 2020, see Nakamine et al., 2020: figs. 4c, 6b, 15b-c), there are merely 2–4 setae remained on the distal portion or both of proximal and distal portions of fore tibial ridge. Therefore, morphological diversity of specialized fore tibial setae in mantispoids with raptorial foreleg seems very rich in Mesozoic, even in the same taxa, but obviously in extant species, this character has been simplified (Symphrasinae, Drepanicinae and Calomantispinae) or absent (Rhachiberothinae and Mantispinae).

Considering the male genitalia, the long penisfilum, which may be formed by the complex of gonocoxites, gonapophyses and



gonostyli 10 [previously found in *Mantispidipterella longissimi* (Liu et al., 2017: fig. 4)], is herein found in another dipteromantispid species, i.e. *K. xiai* sp. nov.. Possibly, this male genital trait may be present in all dipteromantispid species. Liu et al. (2017) postulated that Dipteromantispidae is closely related to Rhachiberothidae or Symphrasinae because these three groups share the presence of long penisfilum in males although not all rhachiberothid species have this trait. This male genital trait clearly appears to be apomorphic, but whether it might have been independently derived in the above three mantispoid groups is unknown. At any rate, the presence of long penisfilum is the most important male genital character hitherto known for inferring the phylogenetic position of Dipteromantispidae.

Considering the female genitalia, the present and recent findings on the Burmese amber dipteromantispids (Li & Liu, 2020) provide further evidence to depict the groundplan of female genitalia of Dipteromantispidae. In all dipteromantispid female specimens with genitalia well preserved, the characteristic genital features refer to the presence of gonocoxites 7, the presence of pseudohypocaudae, and the fusion between tergum 9 and ectoprocts. Additionally, the hypocaudae (an anterior modification on gonocoxites 9) are present in *D. brevisubcosta* and *Halteriomantispa grimaldii*. As mentioned in Liu et al. (2016), although the female genitalia shows similarity to Berothidae and Rhachiberothidae, whether these similar female genital sclerites are apomorphic has not yet been determined. Actually, some female genital characters similar to those aforementioned can be found also in Mantispidae but appear to be named differently without interpretation of homology. For example, in some species of the drepanicine genus *Theristria* Gerstaecker, 1885 (Lambkin, 1986: figs. 144, 194, 269), the female gonocoxite 9 is produced anteriorly, probably being homologous with hypocauda. The pseudohypocaudae appears to be a ventral modification of the female tergum 9 and was previously interpreted as a synapomorphy of Berothidae + Rhachiberothidae (Aspöck & Mansell, 1994). However, similar sclerites are present in some drepanicine genera, e.g. *Ditaxis* McLachlan, 1867, *Theristria*, and *Gerstaeckerella* Enderlein, 1910, but were described as “tergum 9 with ventral region detached/separated” in Lambkin (1986) and Liu et al. (2015), being actually equivalent to pseudohypocaudae. Therefore, the female genital sclerites of dipteromantispids provide few evidence for assignment of Dipteromantispidae with any other mantispoid families.

In summary, it is still hard to definitely determine the placement of Dipteromantispidae in Mantispoidea as those phylogenetically significant characters are shared by either Mantispidae or Rhachiberothidae, and therefore the interfamilial relationships among the three extant mantispoid families are still elusive. This problem is highlighted by a recent phylogenomic study for the higher phylogeny of Neuropterida based on the anchored hybrid enrichment (AHE) data (Winterton et al., 2018), in which a paraphyletic Mantispidae was recovered, with Symphrasinae as the sister group of Rhachiberothidae, whereas with the other mantidfly subfamilies as a monophylum to be the sister group of Berothidae. In light of some difficulties unsolved in the big-data phylogenetics, such as the proper modelling, the elimination of the random noise etc., this result requires further investigation. However, the backbone tree constructed for Mantispoidea is essential to evaluate the evolutionary pattern of raptorial foreleg, prothorax etc., and to clarify the phylogenetic position of dipteromantispids eventually.

## 5. Conclusions

The new taxa herein described enrich our knowledge on the palaeodiversity of Dipteromantispidae from the mid-Cretaceous of Myanmar. Moreover, combining the new morphological evidence

from these Burmese amber dipteromantispids, the foreleg and forewing characters among all dipteromantispid species appear to reach a relatively high level of disparity. Although some of these characters are phylogenetically informative, their mosaic pattern in Dipteromantispidae brings difficulties for the recovery on the phylogenetic position of this family and obscures the already complex evolutionary history of Mantispoidea solely based on morphological data.

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