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A new dipteromantispid from the mid-Cretaceous Burmese amber (Neuroptera: Dipteromantispidae)

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Abstract

Enigmadipteromantispa dimyi **gen. et sp. nov.**, a new dipteromantispid from the mid-Cretaceous amber of Myanmar is described, illustrated, characterized, and its taxonomic position is discussed. *Enigmadipteromantispa dimyi* **gen. et sp. nov.** is the seventh dipteromantispid to be discovered from the Burmese amber and provides new insight for understanding the palaeobiodiversity of this Cretaceous family.

Keywords: Mesozoic, *Enigmadipteromantispa dimyi* **gen. et sp. nov.**, fossil insect, Myanmar

Introduction

Mid-Cretaceous Burmese amber is considered to be the richest in species among the Cretaceous ambers (Grimaldi *et al*., 2002; Ross, 2019, 2020). To date more than 1380 species were described from this material (and the number is growing very fast recently) among which about 98 neuropterans (Li & Liu, 2020; Li *et al.* (in press) Ross, 2019, 2020).

Dipteromantispidae Makarkin *et al*., 2013, represents a bizarre small Cretaceous neuropteran family characterized by its general resemblance with the mantispids family with the relatively elongate pronotum and the raptorial forelegs, but differing from it by strongly reduced haltere-like hind wings. Eight fossil genera are described to date with nine species: *Dipteromantispa brevisubcosta* Makarkin, Yang & Ren, 2013 (from the upper Barremian of Liaoning, northeastern China); *Burmodipteromantispa jiaxiaoae* Liu, Lu & Zhang, 2017; *Halteriomantispa grimaldii* Liu, Lu & Zhang, 2016; *Kurtodipteromantispa zhuodei* Li & Liu, 2020; *Kurtodipteromantispa xiai* Li, Zhuo, Wang & Liu, online 29 July 2020 (in press); *Mantispidipterella longissima* Liu, Lu & Zhang, 2017; *Paradipteromantispa polyneura* Li, Zhuo, Wang & Liu, online July 2020 (in press) (from the mid-Cretaceous amber of Myanmar); *Mantispidiptera enigmatica* Grimaldi, 2000; *Jersimantispa henryi* (Grimaldi, 2000) (from the New Jersey Turonian amber). Originally dipteromantispids were considered as belonging to Mantispidae by Grimaldi (2000) and by Engel and Grimaldi (2008); then Makarkin *et al*. (2013) erected a new family (Dipteromantispidae) to accommodate them. Liu *et al*. (2016, 2017) and Li & Liu (2020) followed the classification of Makarkin *et al*. (2013) and described four species within four genera from the mid-Cretaceous Burmese amber, doubling the number of representatives of this curious extinct family. Liu *et al*. (2016, 2017) proposed that Dipteromantispidae belongs to a monophyletic clade which also includes Berothidae, Rhachiberothidae and Mantispidae. This opinion is shared by Makarkin *et al*. (2013) who considered nevertheless the Rhachiberothidae as a subfamily of the Berothidae. However, the concrete placement of Dipteromantispidae within this clade (berothid clade) is still unknown and debatable as dipteromantispids present a complex mosaic set of characters shared with the different groups of the clade. Only the discovery of more complete specimens could help in resolving the phylogeny relationship within the 'berothid clade'.

Herein we describe *Enigmadipteromantispa dimyi* **gen. et sp. nov.**, an additional representative of the Dipteromantispidae from mid-Cretaceous Burmese amber.

Material and methods

Studied material originated from Hukawng Valley in Tanai

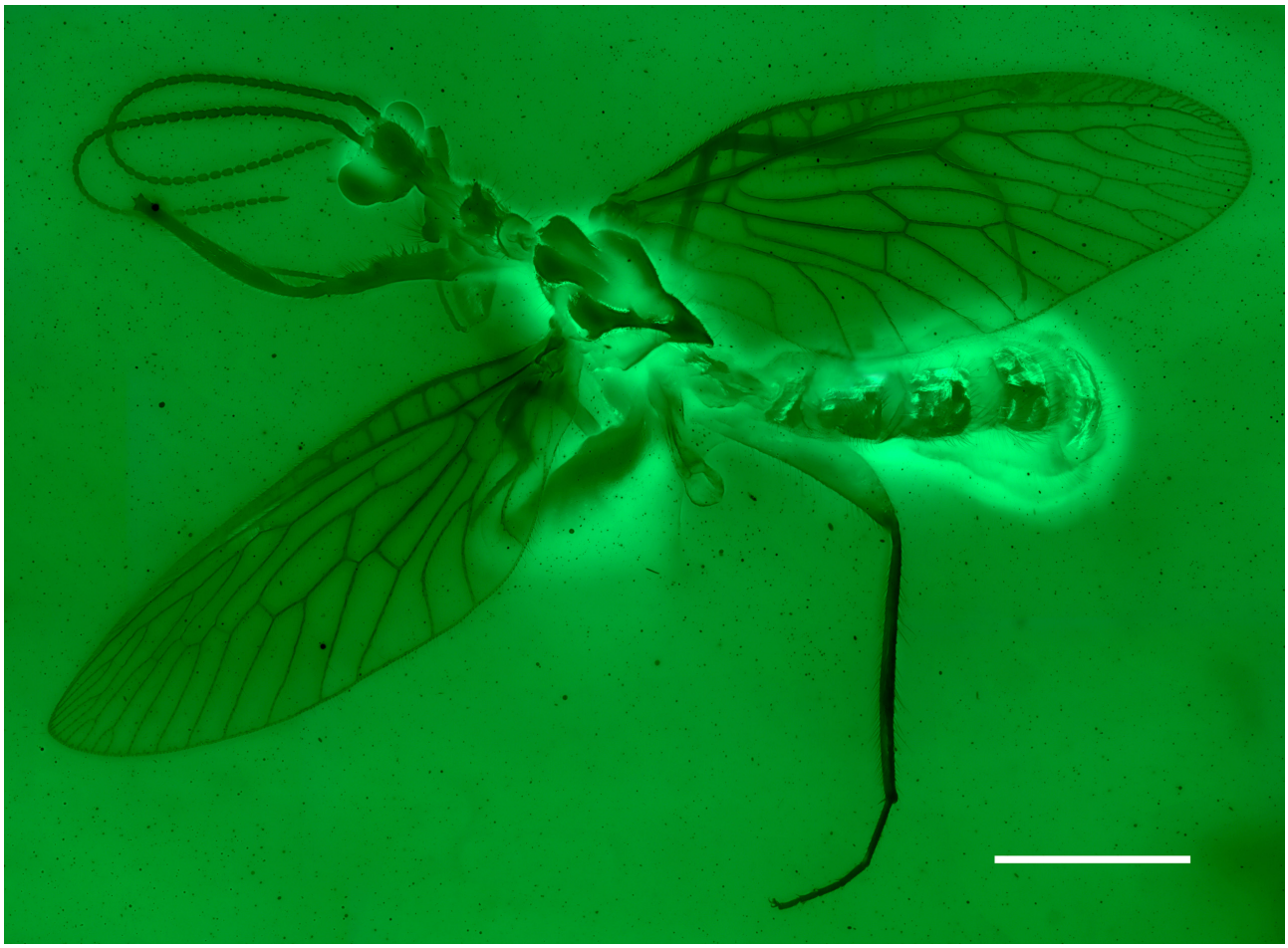

FIGURE 1. *Enigmadipteromantispa dimyi* **gen. et sp. nov.**, holotype, female, NIGP173377. Habitus, dorsal view under fluorescence; scale bar = 1 mm.

Township, Myitkyina District of Kachin State, Northern Myanmar (for details refer to Kania *et al*., 2015). The age of this amber is believed to be earliest Cenomanian (~99 Ma) after U-Pb dating of zircons (Shi *et al*., 2012), but could be older (Mao *et al*., 2018).

The type material, holotype number NIGP173377, female, is deposited in the collections of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Specimen examination and photographs were made using a Zeiss AXIO Zoom V16, a Zeiss SteREO Discovery V20 stereo microscopes and a Zeiss AXIO Imager Z2 compound microscope equipped with fluorescence laser. The figures were prepared with Adobe Photoshop. Terminology of wing venation generally follows Aspöck *et al*. (1980), Kukalová-Peck & Lawrence (2004) and Liu *et al*. (2016, 2017). Terminology of genitalia follows Aspöck & Aspöck (2008).

Abbreviations used for wing veins and spaces are: 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; ScA, subcosta anterior; ScP, subcosta posterior.

Systematic palaeontology

Class Insecta Linnaeus, 1758
Order Neuroptera Linnaeus, 1758
Family Dipteromantispidae Makarkin, Yang & Ren, 2013

Type genus. *Dipteromantispa* Makarkin, Yang & Ren, 2013.

Revised diagnosis (after Liu *et al*., 2017)**.** Small to minute mantispid-like lacewings (forewing 2.6–7.9 mm long). Prothorax short, not tubular, not distinctly prolonged posteriad procoxae; fore legs raptorial; profemur without any long spine, only bearing two or three rows of short denticles in some species. Mesothorax large, mesonotum usually distinct midsagittal and V-shaped sutures. Metathorax strongly reduced. Forewing venation strongly reduced, with small number of crossveins; trichosors, dark

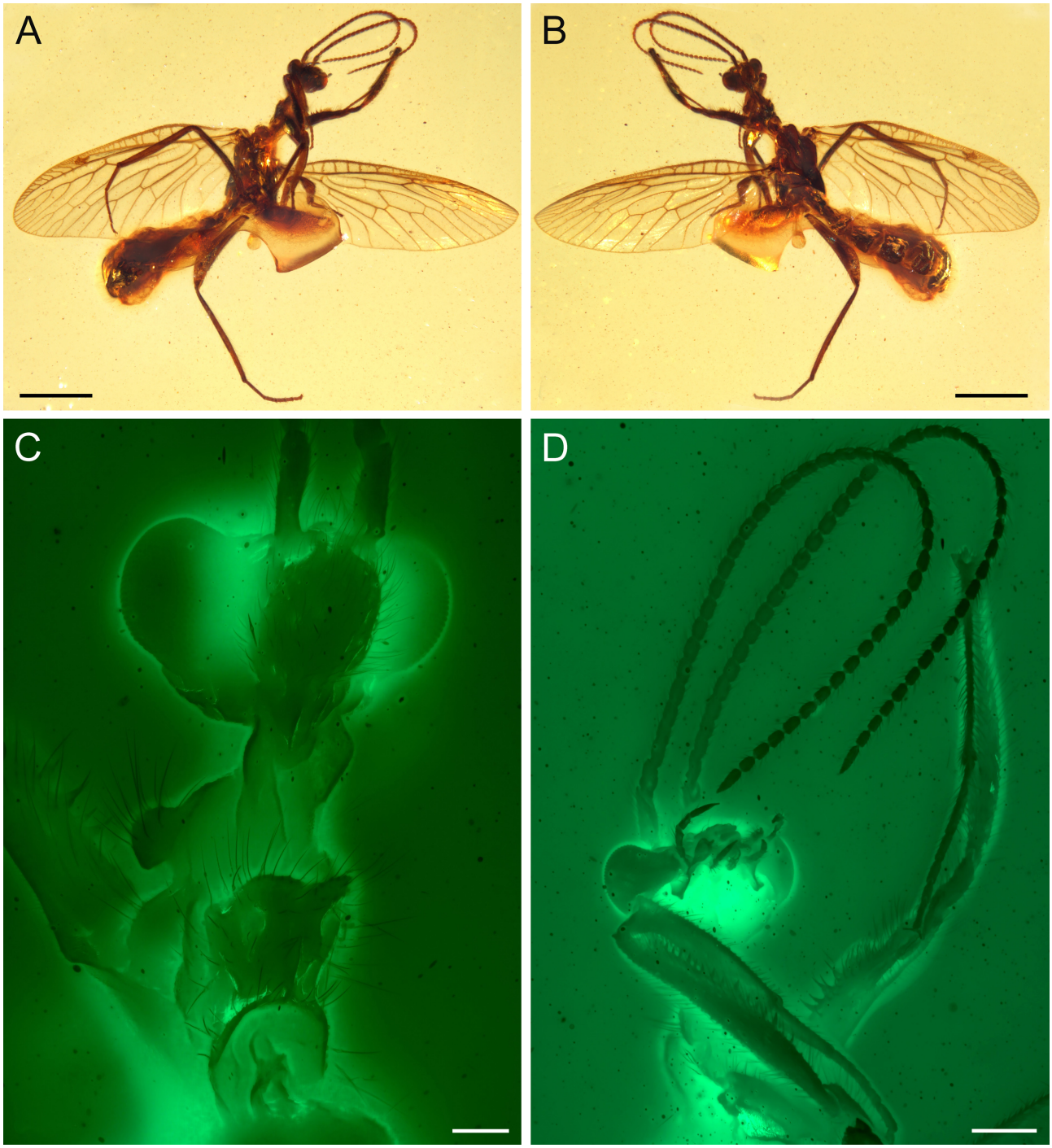

FIGURE 2. *Enigmadipteromantispa dimyi* **gen. et sp. nov.**, holotype, female, NIGP173377. **A**, Habitus, ventral view. **B**, Habitus, dorsal view. **C**, Head, under fluorescence, dorsal view. **D**, Head and antennae, under fluorescence, ventral view. Scale bars = 1 mm in **A** and **B**, 0.2 mm in **D**, 0.1 mm in **C**.

marking patches, pterostigma present or absent; costal crossveins simple; ScA sometimes present; ScP relatively short, widely separated distally from RA; unusual fusion among R, RP + MA, MP, Cu and A1 sometimes present; CuA and CuP both simple. Hind wing strongly reduced, modified to haltere-like structure. Male and female genitalia in general similarly constructed to Berothidae, Rhachiberothidae and Mantispidae; male gonocoxites, gonapophyses, and gonostyli 10 organized to an unpaired complex, an extremely long thread-like penisfilum present (at least in one species); female gonocoxites 7 sometimes present and paired.

***Enigmadipteromantispa* gen. nov.**

Type species. *Enigmadipteromantispa dimyi* **sp. nov.**

Etymology. The generic epithet is a combination of 'enigma' from Greek αίνιγμα =

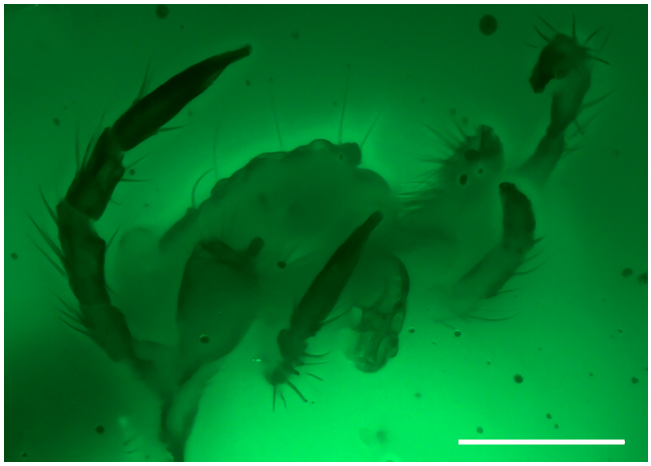

FIGURE 3. *Enigmadipteromantispa dimyi* **gen. et sp. nov.**, holotype, female, NIGP173377, detail of mouth parts, under fluorescence, ventral view. Scale bar = 0.1 mm.

mystery + 'Dipteromantispa' (typical genus name of Dipteromantispidae). The name is feminine.

Diagnosis. Body small-sized, less than 4.5 mm, with forewing length ~3.5 mm. Head sub-lozenge in shape, with vertex strongly domed, eyes ovoid. Antennae filiform, with 40 flagellomeres; last flagellomere pointed, two times longer than remaining flagellomeres; scape nearly two times the length of flagellomeres; scape and pedicel slightly larger than flagellomeres. Pronotum shorter and much narrower than head. Mesothorax large, mesonotum with midsagittal and V-shaped sutures. Forelegs raptorial with femoral integumentary processes bearing Stitz organs and specialized setae. Forewing elliptical, with slightly darken pterostigma and presence of trichosors along costal and distal margin. Forewing venation: Costal space nearly 3/4 of wing length, dilated at 1/4 of wing length basally. Some costal crossveins bifurcate, others simple. ScA absent. ScP joining R apically in a point (or with a very small crossvein) then directing convexly toward costal margin, forming as such a pterostigma. Veinlets of RA mostly branched. RP + MA separating from RA at basal 1/4 of wing. RP and MA diverging approximately at midpoint of wing; RP with four branches distally forked; MA bifurcate distally. MP diverging approximately at basal third of wing, strongly curved basally and fused with R, with one simple and one bifurcated branches apically. Three or four crossveins among branches of RP and M allied into a short gradate series. A crossvein m-cu present, arched, slightly basad forking of Cu. Cu deeply forked into long and simple CuA and CuP, slightly

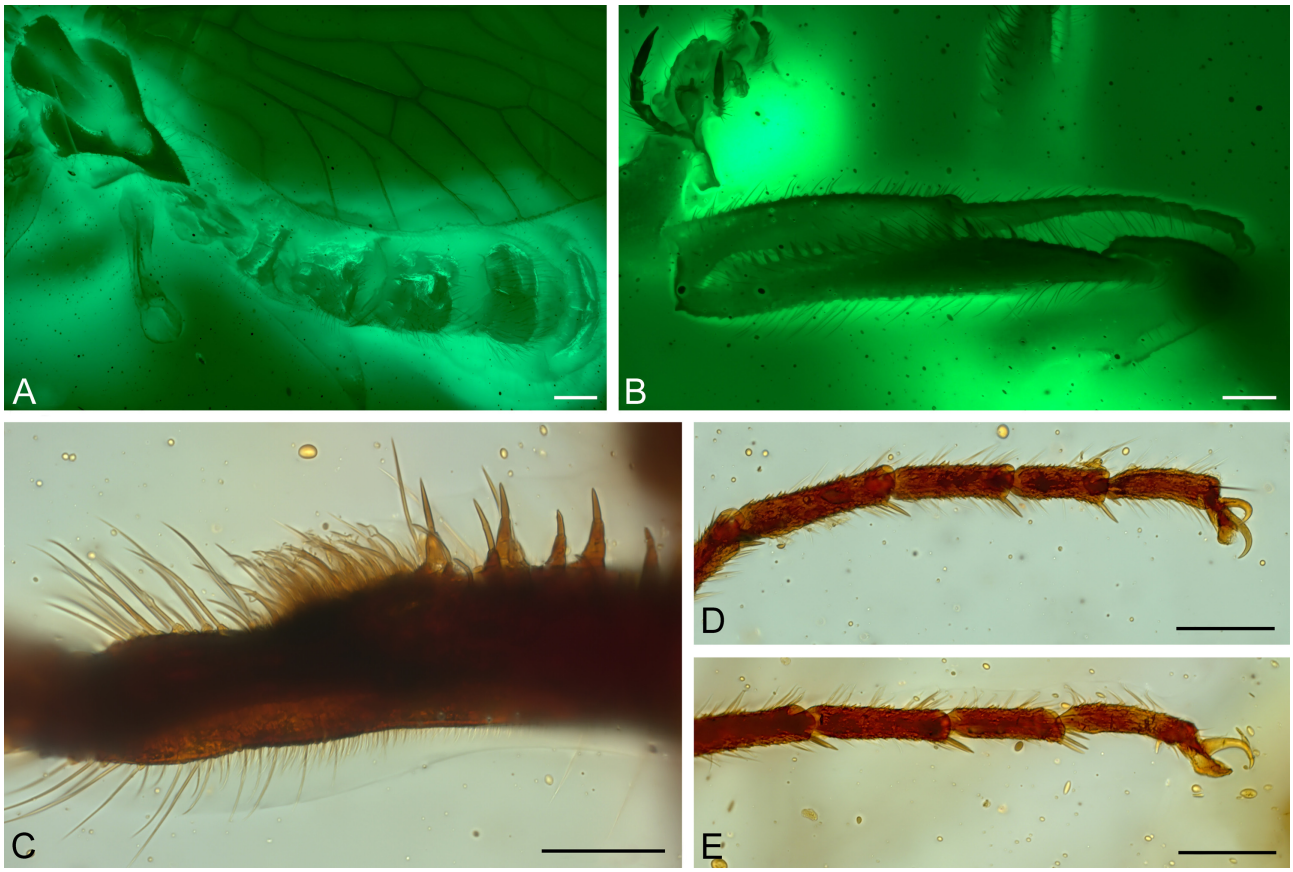

FIGURE 4. *Enigmadipteromantispa dimyi* **gen. et sp. nov.**, holotype, female, NIGP173377. **A**, Mesothorax and abdomen, under fluorescence, ventral view. **B**, Foreleg, under fluorescence. **C**, Procoxa with stemmed spines. **D** and **E**, Tarsus of hind leg. Scale bars = 0.2 mm in **A**, 0.1 mm in **B**–**E**.

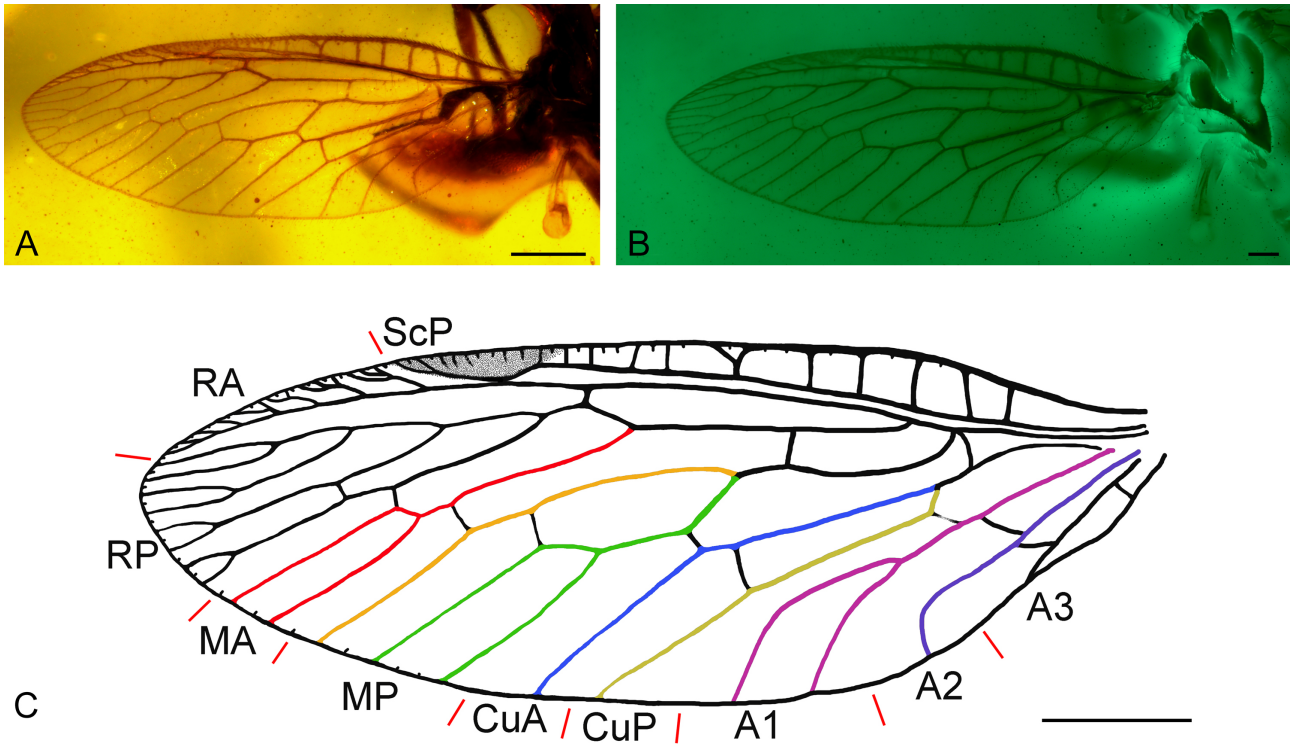

FIGURE 5. *Enigmadipteromantispa dimyi* **gen. et sp. nov.**, holotype, female, NIGP173377, left hindwing. **A**, Under normal transmitted and lateral light. **B**, Under fluorescence. **C**, Line drawing. Scale bars = 0.5 mm in **A** and **C**, 0.2 mm in **B**.

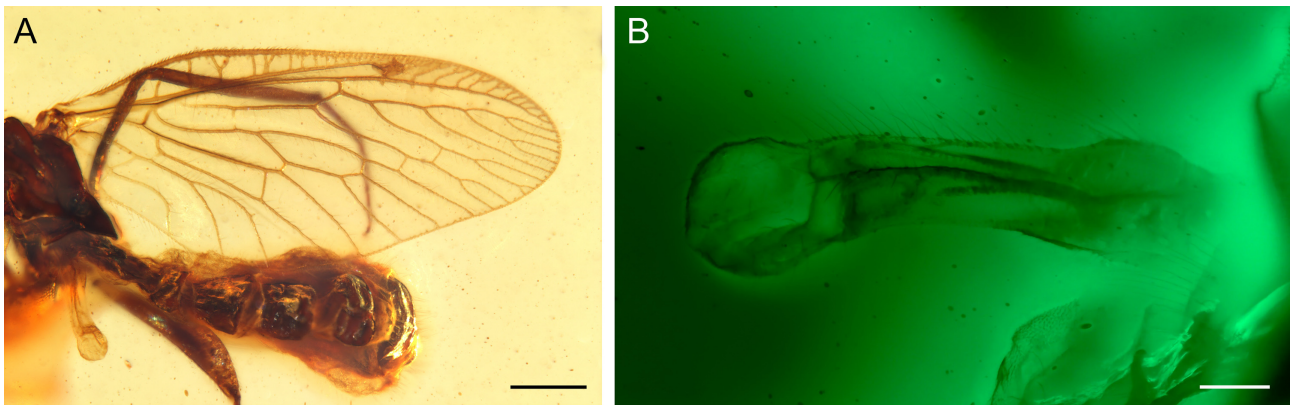

FIGURE 6. *Enigmadipteromantispa dimyi* **gen. et sp. nov.**, holotype, female, NIGP173377. **A**, Right forewing and left hind wing. **B**, Hind wing under fluorescence. Scale bars = 0.5 mm in **A**, 0.1 mm in **B**.

converging toward wing margin; cua-cup crossvein short, forming an acute angle with CuA. A1 forked apically into two simple branches. A2 and A3 simple. Female tergum 9 posterolaterally with a pointed extension directed inward (putative pseudohypocaudae); gonocoxite 9 ovoid.

***Enigmadipteromantispa dimyi* sp. nov.**
(Figs 1–7)

Type material. Holotype: specimen number NIGP173377, female, deposited in the collections of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (Figs 1, 2A, B).

Etymology. The new species is dedicated to Dimy Azar, son of DA and SM.

Diagnosis. As for the genus (*vide supra*).

Locality and horizon. Mid-Cretaceous, Tanai Village, Hukawng Valley, northern Myanmar.

Description. Female. All measurements are in mm. Total body length *circa* 4.26.

Head sub-lozenge in shape, 0.59 long, 0.58 wide, with vertex strongly domed (Fig. 2C), compound eyes elliptical, large diameter 0.3, small diameter 0.14. Antennae filiform (Fig. 2D), length 2.87, with 40 flagellomeres; last flagellomere pointed, two time longer than remaining flagellomeres; scape nearly two times the

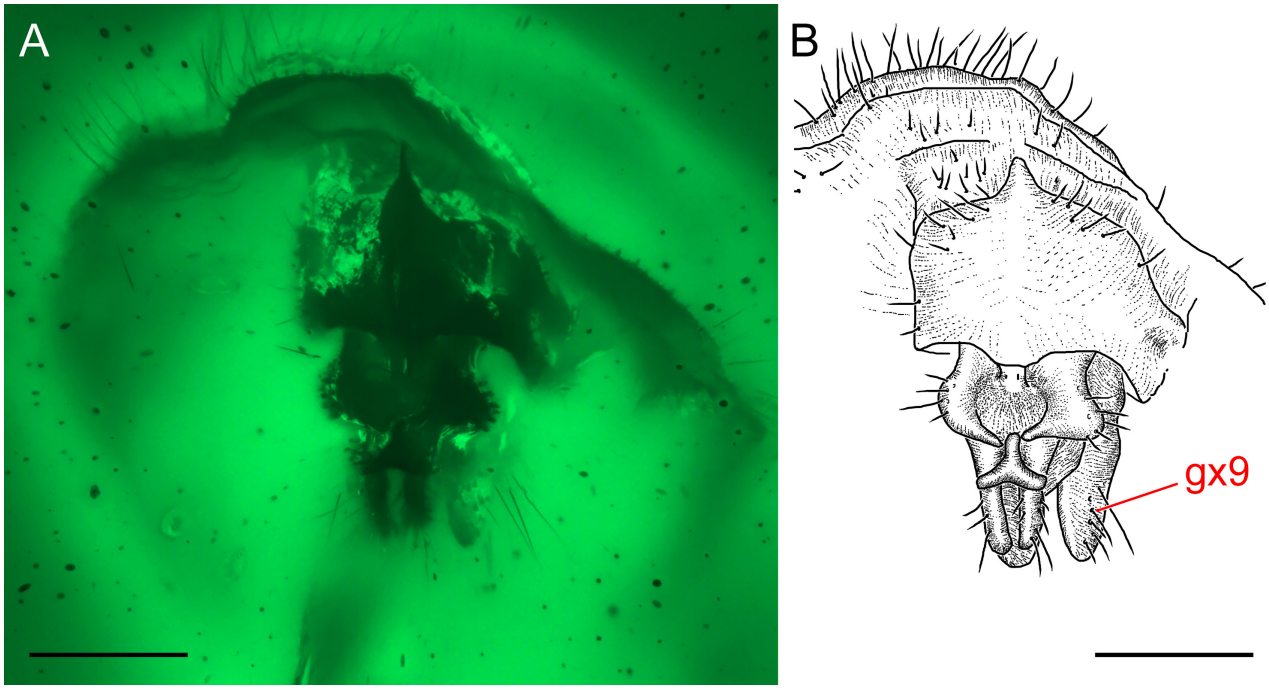

FIGURE 7. *Enigmadipteromantispa dimyi* **gen. et sp. nov.**, holotype, female, NIGP173377, female genitalia. **A**, Photography under fluorescence, dorso-caudal view. **B**, Line drawing, dorso-caudal view, gx9 = gonocoxite 9. Scale bars = 0.2 mm.

length of flagellomeres, 0.17 long, 0.05 wide; pedicel slightly larger than flagellomeres, 0.09 long, 0.05 wide. Mouthparts chewing mandibulate (Fig. 3); maxillary palp 5-segmented, 0.25 long; last maxillary palpomere longest and tapering distally; maxillary palpomeres respectively: I – 0.02, II – 0.03, III – 0.06, IV – 0.05, V – 0.09; labial palp 3-segmented, 0.15 long, last labial palpomere longest and tapering distally; labial palpomeres respectively: I – 0.02, II – 0.04, III – 0.09.

Pronotum (Fig. 2C), 0.23 long, 0.24 wide, densely setose, larger proximally with two frontal and marginal bulges transforming distally to two carinae reaching distad margins of pronotum; a lateral depression medially occurring from each side of pronotum. Mesothorax large, mesonotum with midsagittal and V-shaped sutures (Fig. 4A).

Fore legs raptorial; procoxa elongate (Fig. 4C), densely setose apically, with two rows of stemmed spines basally (Stitz organ). Protrochanter short without spines (Fig. 2B). Profemur (Fig. 4B) densely setose with a row of 17 stemmed spines. Protibia densely setose with a row of spines directed distally. Protarsus 5-segmented (Fig. 4B), tarsomere 1 much longer than remaining tarsomeres; a pair of short pretarsal claws present; arolium present. Middle leg shortest, densely hairy, tibial spur present, feature of mesotarsus similar to protarsus. Hind leg much longer than middle leg, densely hairy, tibial spur present, feature of metatarsus similar to protarsus (Fig. 4D, E).

Forewing elliptical (Figs 5A–C, 6A), 3.44 long, 1.36 large, with slightly darken pterostigma and presence of trichosors along the forewing costal and distal margins. Forewing venation: Costal space reaching nearly 3/4 of wing length, dilated at 1/4 of wing length basally. Some costal crossveins bifurcate, while others simple. ScA absent. ScP joining R apically from wing base at 2.19 in a point then directing convexly toward costal margin, forming as such a darkened pterostigma. Veinlets of RA mostly branched. RP + MA separating from RA at basal 1/4 of wing. RP and MA diverging approximately at midpoint of wing; RP with four branches distally forked; MA bifurcate distally at 2.54 from wing base. MP diverging approximately at basal third of wing, strongly curved basally and fused with R, with one simple and one bifurcated branches apically. Three or four crossveins among branches of RP and M organised into a short gradate series. A crossvein m-cu present, arched, slightly basad forking of Cu. Cu deeply forked into long and simple CuA and CuP at 0.74 from wing base, slightly converging toward wing margin and reaching it respectively at 2.13 and 1.92 apically; cua-cup crossvein short, forming an acute angle with CuA. A1 forked apically into two simple branches at 0.90 apically. A2 and A3 simple reaching wing margin respectively at 1.47 and 1.21 from wing base. Hind wing strongly reduced (Fig. 6A, B), haltere-like, 0.78 long, with globular apex; veins strongly reduced.

Abdomen *circa* 2.12 long (Fig. 3A). Female terminalia (Fig. 6A, B) with tergum 9 posterolaterally with a pointed extension directed inward (putative pseudohypocaudae); gonocoxite 9 ovoid.

Male. Unknown.

Discussion

Being a typical neuropteran with raptorial foreleg, vein reduction for forewing and hind wing strongly reduced and haltere-like, *Enigmadipteromantispa dimyi* **gen. et sp. nov.** belongs undeniably to the extinct family Dipteromantispidae. The new genus differs from all the seven known genera of Dipteromantispidae by the presence of a darkened pterostigma, from most of them by the presence of some costal crossveins bifurcate (in both wings at same place), by the presence of trichosors on costal and distal margins and by the presence of Stitz organs, which justify the creation of a new genus. Using the keys to genera of Dipteromantispidae of Liu *et al*. (2017), the new fossil runs to *Mantispidipterella* Liu, Lu & Zhang, 2017, but *Enigmadipteromantispa* differs from it (in addition to the features cited above) by having veinlets of RA mostly bifurcate, presence of A3, RP with four branches distally forked, and the distal position of the crossvein mp-cua comparatively to the position of the crossvein cua-cup.

Conclusion

Representatives of the extinct Cretaceous family Dipteromantispidae are generally rare. The discovery of a fifth genus of this family from the amber of Myanmar demonstrates that this family was well diversified in the Burmese amber forest during early Cenomanian, and may indicate that the origin of this family is older than its oldest occurrence in the Barremian (Liaoning, northeastern China). Despite it being clear that the Dipteromantispidae belongs to the berothid clade, the phylogenetic relationships of this family with the other families of this clade are still unclear because dipteromantispids present a complex mosaic set of characters shared with the different groups of the clade. Only the discovery of more complete specimens can help in resolving the phylogenetic relationships and increase our knowledge on the dipteromantispid. It is obvious that the discovery of this extinct family from different outcrops of Laurasian (Liaoning and New Jersey) and Gondwanan (Myanmar) origins, demonstrates that this family had a global distribution during the Cretaceous.

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