

ORIGINAL ARTICLE

Halteriomantispa grimaldii gen. et sp. nov.: A new genus and species of the family Dipteromantispidae (Insecta: Neuroptera) from the mid-Cretaceous amber of Myanmar

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Abstract The family Dipteromantispidae, previously with only two genera and three species, is one of the enigmatic groups of the Cretaceous Neuroptera by the mantispid-like appearance combined with strongly reduced hind wings specialized into a haltere-like structure. A new genus and species of Dipteromantispidae, namely *Halteriomantispa grimaldii* **gen. et sp. nov.**, is herein described based on an exquisitely preserved specimen from the mid-Cretaceous amber of northern Myanmar. It represents the first record of Dipteromantispidae from the amber deposit of mid-Cretaceous (Albian-Cenomanian) of Myanmar. A brief discussion on the homology of forewing venations and female genital sclerites of Dipteromantispidae is given.

Key words Neuropterida, Mantispidae, taxonomy, Burmese amber, Mesozoic.

1 Introduction

The family Dipteromantispidae, erected by Makarkin *et al.* (2013a), is one of the bizarre groups among the Mesozoic Neuroptera. The adults of Dipteromantispidae are characterized by the mantispid-like appearance (mainly referring to the presence of raptorial forelegs) combined with strongly reduced hind wings specialized into a haltere-like structure. Hitherto, this family is only recorded in two deposits of Cretaceous, including the Early Cretaceous of northeastern China and the Late Cretaceous amber of New Jersey, U.S.A. (Grimaldi, 2000; Makarkin *et al.*, 2013a). Currently, only three species sorted in two genera are known for this family. The phylogenetic status of Dipteromantispidae is still debatable. Engel & Grimaldi (2008) advocated the placement of dipteromantispids (only including the two *Mantispidiptera* species from the New Jersey amber at that time) as a highly specialized lineage of Mantispidae. However, Makarkin *et al.* (2013a, b) gave a full family status of Dipteromantispidae and considered it to be the sister group of Mantispidae + Berothidae.

Here we report a new genus and species of Dipteromantispidae from the mid-Cretaceous amber of Myanmar, based on a finely preserved female specimen. A revised homology interpretation of the forewing venations of Dipteromantispidae is proposed based on morphological comparisons among the species of this family. In addition, the phylogenetic status of Dipteromantispidae is also discussed, particularly based on the characters of female genitalia.

2 Materials and methods

The amber sample under present study is from the Hukawng Valley in Tanaing Township, Myitkyina District of

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Kachin State, Myanmar. The age of this deposit has been investigated and dated to be 98.8 ± 0.6 million years by U-Pb dating of zircons from the volcanoclastic matrix of the amber (Shi *et al.*, 2012).

The type specimen is currently housed in the Entomological Museum, China Agricultural University (CAU), Beijing, and they will eventually be deposited in the Three Gorges Entomological Museum (EMTG), Chongqing (specimen available for study by contacting XL or WZ). Photographs and drawings were taken and made using a Zeiss SteREO Discovery V12 stereo microscope system. The figures were prepared with Adobe Photoshop CS4®. Terminology of wing venation generally follows Aspöck *et al.* (1980) and Kukalová-Peck & Lawrence (2004). Terminology of genitalia follows Aspöck & Aspöck (2008).

Abbreviations used for wing veins and spaces 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;
ScA—subcosta anterior;
ScP—subcosta posterior.

3 Systematic palaeontology

Class Insecta Linnaeus, 1758

Order Neuroptera Linnaeus, 1758

Family Dipteromantispidae Makarkin, Yang & Ren, 2013

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

Genera checklist.

Dipteromantispa Makarkin, Yang & Ren, 2013 from the Early Cretaceous of China;

Halteriomantispa **gen. nov.** from the mid-Cretaceous amber of Myanmar;

Mantispodiptera Grimaldi, 2000 from the Late Cretaceous amber of New Jersey.

Diagnosis. See Makarkin *et al.* (2013a).

Halteriomantispa **gen. nov.** (Figs 1–5, 9–10)

Type species: *Halteriomantispa grimaldii* **sp. nov.**

Diagnosis. Body small-sized (forewing length about 5 mm). Head suboval, with vertex slightly domed. Antennae filiform, with large scape and pedicel, and with flagellum slightly flattened. Pronotum slightly longer and narrower than head. Mesonotum with a prominent scutellum. Forelegs raptorial; profemur without spines or denticles, but with only rows of upright setae along ventral margin. Forewing subtriangular, with a small dark dot on distal portion of subcostal space and an ovoid, much larger, dark marking medially; hind wing strongly reduced into a haltere-like structure. Forewing venation: Pterostigma, nygma, and trichosores absent. Costal space about $3/4 \times$ wing length, slightly dilated at subproximal portion, and strongly narrowed distad. Costal crossveins simple. ScA present as a short, straight veinlet. 1scP-ra crossvein absent, 2scP-ra crossvein present. Veinlets of RA with small marginal forks. RP+MA separating from RA near wing base. RP separating from RP+MA approximately at midpoint of wing, with five simple, closely spaced branches. MA with two simple branches. MP proximally strongly curved and fused with R, with three simple branches. Four crossveins among branches of RP and M allied into a short gradate series. 1m-cu crossvein present, nearly upright, slightly proximad forking of Cu. Cu deeply forked into long and simple CuA and CuP. A1 with free stem, forked nearly at its midpoint into two simple branches. Female gonocoxites 7 paired, digitiform; tergum 9 posterolaterally with a pair of ovoid valvate lobes

(putative pseudohypocaudae); gonocoxite 9 subtrapezoid, anteriorly with a small subtriangular lobe (putative hypocauda), and posteriorly with a membranous crescent lobe.

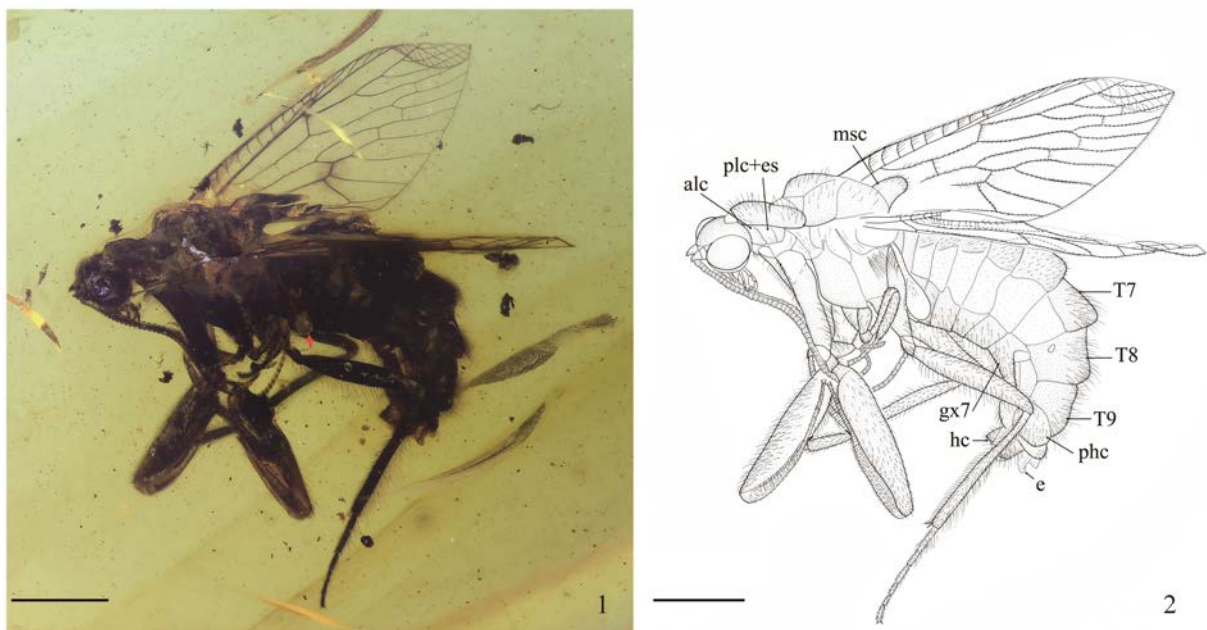
Etymology. The generic epithet is a combination of ‘*Halteria*’ (in reference to the haltere-like hindwing of the new genus) and ‘*Mantispa*’ (typical genus name of the family Mantispididae). The name is feminine.

Remarks. The new species greatly differs from *Dipteromantispa* from the Early Cretaceous of China by a number of forewing features, such as long costal space (*Dipteromantispa*: costal space short, about half of forewing length), RA richly branched distad (*Dipteromantispa*: RA simple), narrowly spaced branches of RP (*Dipteromantispa*: RP branches widely spaced), and MA bifurcated distad (*Dipteromantispa*: MA simple). In general, the new species appears to be closely related to *Mantispidiptera* from the Late Cretaceous amber of New Jersey by sharing the aforementioned forewing features. However, it can be distinguished from *Mantispidiptera* by the larger body size (*Mantispidiptera*: minute-sized, forewing length 2.6–3.1 mm), the slightly prolonged pronotum (*Mantispidiptera*: pronotum shorter than head), the forewing with two dark markings (*Mantispidiptera*: forewing immaculate), and the presence of free Cu stem (*Mantispidiptera*: Cu fused with R or A1). Judging from the distinctly differed forewing venations (especially the basal parts of R, M and Cu) between the two species of *Mantispidiptera*, they might eventually be verified to represent two different genera. *Halteriomantispa* **gen. nov.** differs from *M. enigmatica* by the following forewing features: presence of a straight ScA, the distally forked RA veinlets, the basal fusion of R and MP; while it is distinguished from *M. henryi* by the pectinately branched RP and the free stem of Cu.

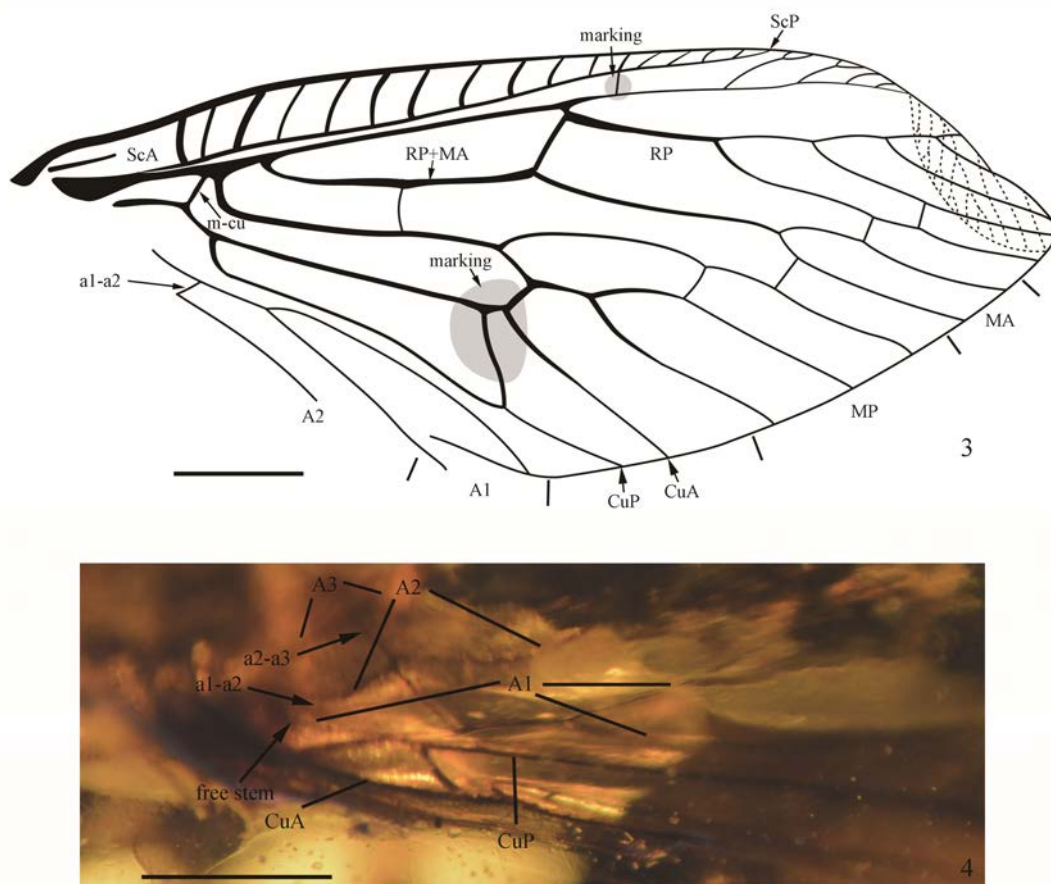
***Halteriomantispa grimaldii* sp. nov.** (Figs 1–5, 9–10)

Diagnosis. As for the genus.

Description. Female. Measurements (mm) and ratios. Total body length 7.4. Head length 0.6. Pronotal length, measured along lateral margin 1.0. Mesothorax length 1.8. Metathorax length 0.15. Procoxa length 1.6; protrochanter length 0.1; profemoral length 2.4, width 0.3; fore femoral ratio (length: width)=8; protibial length 1.1, width 0.1; profemoral length: protibial length=2.2; protarsus length 0.7. Mesocoxa length 0.3; mesotrochanter length 0.1; mesofemoral length 0.6; mesotibial length 0.6; mesotarsus length 0.4. Metacoxa length 0.3; metatrochanter length 0.1; metafemoral length 1.8; metatibial length 1.8; metatarsus length 1.3. Forewing length 5.2, width 2.3 at broadest portion. Hind wing (haltere-like structure) length 1.3; head of haltere-like structure width 0.4. Abdomen length 3.8.



Figures 1–2. *Halteriomantispa grimaldii* **gen. et sp. nov.**, holotype female, habitus, left lateral view. 1. Photo. 2. Drawing. Abbreviation: alc—anterior lateral cervical sclerite; plc—posterior lateral cervical sclerite; e—ectoproct; es—episternum; hc—hypercauda; msc—mesoscutellum; gx—gonocoxite; T—tergum; phc—pseudohypercauda; Arrow indicates haltere-like hind wing. Scale bars = 1.0 mm.



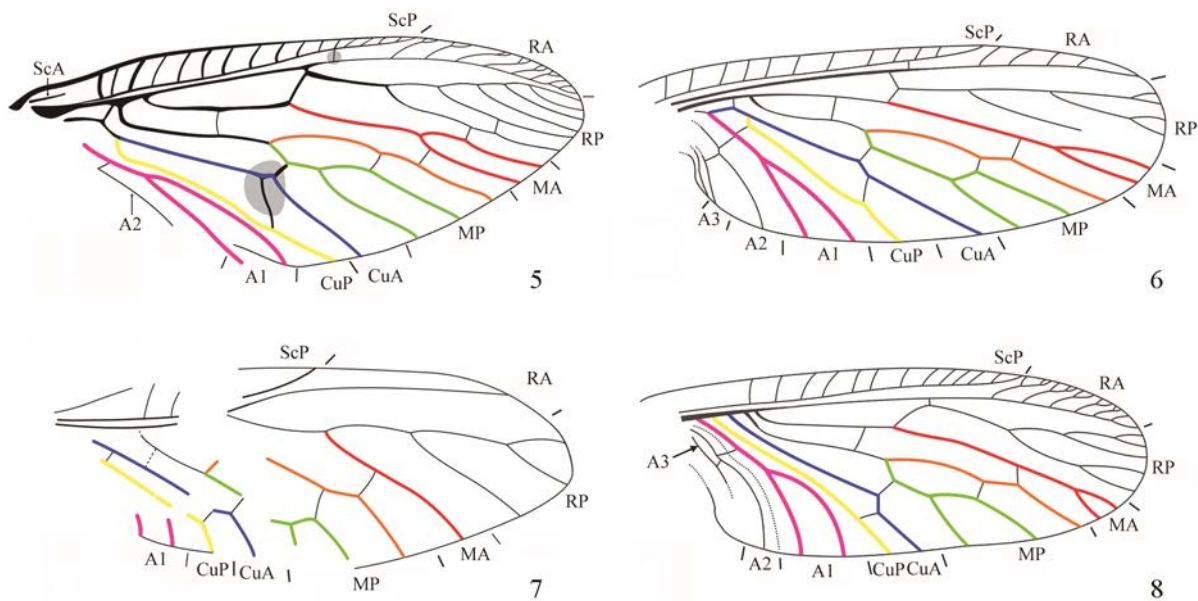
Figures 3–4. *Halteriomantispa grimaldii* **gen. et sp. nov.**, holotype female. 3. Right forewing, drawing. 4. Posteroproximal part of left forewing, microphotograph. Scale bars = 1.0 mm.

Head orthognathous, suboval; vertex slightly domed; postocular region feebly expanded. Compound eyes large and globular. Antennae long, bearing dense short setae; scape short, length much shorter width, distinctly larger than flagellomeres; pedicel nearly conical, much larger than flagellomeres; flagellum slightly flattened, with about 62 flagellomeres, each flagellomere nearly as long as wide except for terminal flagellomere slightly prolonged and tapering distad. Mouthparts discernible in only lateral view, with short labrum, mandible, 4-segmented maxillary palp, and 3-segmented labial palp.

Prothorax short, slightly longer than head; pronotum moderately setose, rounded anteriorly, not extended ventrally, with lateral margin nearly straight. Anterior lateral cervical sclerite (alc) large, pear-shaped, with broad anterior part, and short, narrow posterior part. Posterior lateral cervical sclerite (plc) and episternum (es) about double length of alc, with an oblique suture line dividing these two parts. Mesothorax rather large, moderately hairy dorsad, with subtriangular prescutum, broad scutum, and small prominent scutellum; episternum and epimeron broad, epimeron anterodorsally with a long and slender lateral wing process, and posterodorsally with a setose region bearing a few long hairs. Metathorax strongly reduced.

Forelegs raptorial; procoxa elongate, stout, covered with dense hairs; protrochanter rather small; profemur broad, rather narrowly elliptical, covered with dense hairs, ventral margin lacking spines or denticles, but with dense, vertical setae; protibia much narrower than profemur, densely hairy, with spinous apex, rather thin ridge present along ventral margin; protarsus 5-segmented, tarsomere 1 much longer than remaining tarsomeres, tarsomere 2–4 subequal in length (each shorter than tarsomere 5); a pair of short pretarsal claws present; arolium present. Middle legs short, densely hairy, feature of mesotarsus similar to protarsus, a few spinous setae present on ventral surface of mesotarsus. Hind legs much longer than middle legs, densely hairy; two tibial spurs present; feature of metatarsus similar to protarsus, a few spinous setae present on ventral surface of metatarsus.

Forewing subtriangular in shape, with a small dark dot on subdistal portion of subcostal space and an ovoid, much



Figures 5–8. Revised interpretation on homology of forewing venations in Dipteromantispidae. 5. *Halteriomantispa grimaldii* gen. et sp. nov. (wing apex slightly reconstructed). 6. *Dipteromantsipa brevisubcosta* Makarkin, Yang & Ren. 7. *Mantispidiptera enigmatica* Grimaldi. 8. *Mantispidiptera henryi* Grimaldi (5–8 redrawn from Makarkin *et al.*, 2013a). Colored veins: MA (red), MP1 (orange), MP2 (green), CuA (blue), CuP (yellow) and A1 (pink).

larger, dark marking medially. Pterostigma, nygma, and trichosores absent. Wing margins and all veins setose. Costal space about $3/4 \times$ wing length, slightly dilated at subproximal portion, and strongly narrowed distad. Sixteen simple costal crossveins present. ScA present as a short, straight veinlet. ScP long, entering costal margin apparently distad wing midpoint. Subcostal space narrow proximally, broadened towards termination of ScP; one scp-ra crossvein present subdistally. RA entering margin before wing apex, with seven veinlets, each of which bears a small marginal fork. Single short ra-rp crossvein present. RP+MA separating from RA near wing base. RP separating from RP+MA approximately at midpoint of wing, with five simples, closely spaced branches. Single crossvein respectively present between posterior two branches of RP, and between RP and MA. MA with two simple branches. Two crossveins present between MA and MP. MP proximally strongly curved and fused with R, with three simple branches. One crossvein present between branches of MP, and allied with preceding crossveins into a gradate series. 1m-cu crossvein present, nearly upright, slightly proximad forking of Cu. A distal mp-cua crossvein present. Cu deeply forked into long and simple CuA and CuP. A long and oblique cua-cup crossvein present. A1 with free stem, and forked nearly at its midpoint into two simple branches. An oblique a1-a2 crossvein present proximally. A2 simple, proximally strongly curved posteriad. A short a2-a3 crossvein present proximally. A3 present, but distal part not preserved.

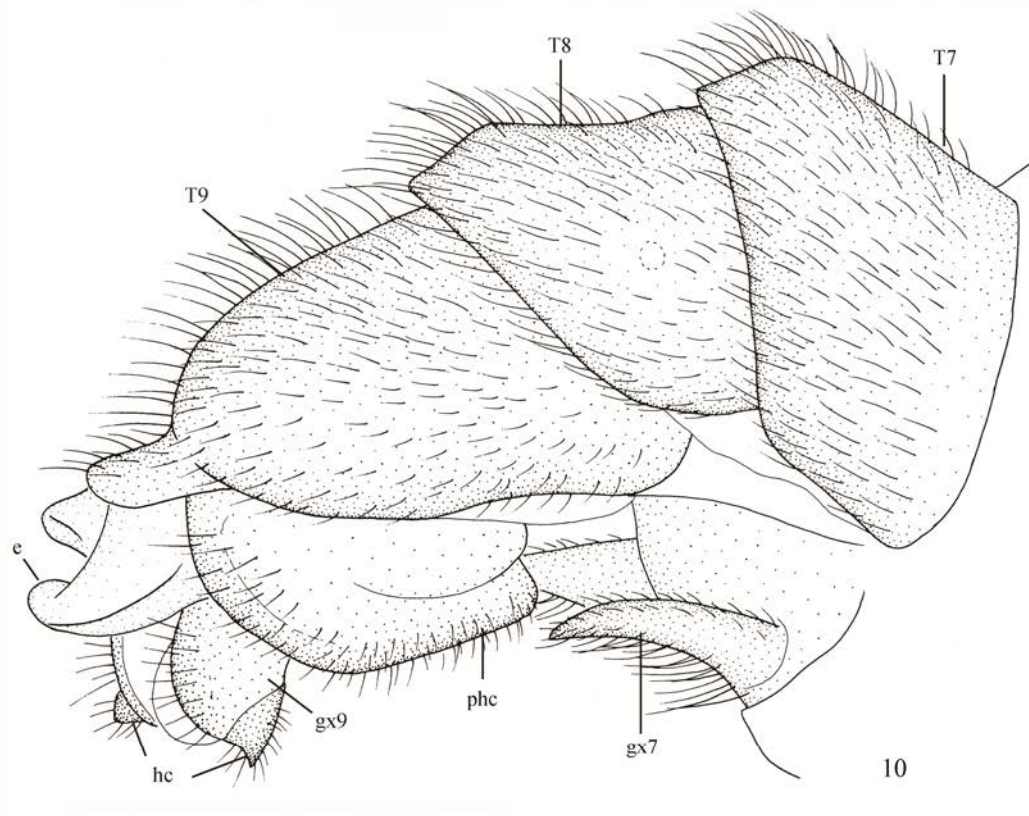
Hind wing haltere-like. Base of haltere-like structure bearing dense long hairs; head of it with slightly fewer and shorter setae on anterior margin and middle portion. Veins completely lost.

Abdomen stout and robust, densely hairy; each pregenital segment of segments 2–7 slightly larger than its anteriorly neighboring one; spiracles invisible due to poor preservation. Gonocoxites of segment 7 paired, digitiform. Segment 8 with tergum laterally enclosing spiracles, and ventrally broadly hollowed. Segment 9 with tergum slightly shorter than tergum 8 and laterally short; tergum 9 posterolaterally with a pair of ovoid valvate lobes (putative pseudohypocaudae); gonocoxite subtrapezoid, anteriorly with a small subtriangular lobe (putative hypocauda), and posteriorly with a membranous crescent lobe. Ectoprocts paired, subtriangular, feebly sclerotized, and glabrous; callus cercus absent.

Male. Unknown.

Type material. Holotype. EMTG BU-001924, amber piece preserving an almost complete adult female of *H. grimaldii* (left forewings mostly not preserved); it is polished in the form of a subquadrate cabochon, clear and transparent, with length $\times$ width about 22.1×14.5 mm, height about 7.6 mm.

Etymology. The new species is dedicated to Dr. David Grimaldi who first described the species of Dipteromantispidae and made tremendous contributions on the study of fossil insects.



Figures 9–10. *Halteriomantispa grimaldii* **gen. et sp. nov.**, holotype female, genitalia in right lateral view. 9. Microphotograph. 10. Drawing. Abbreviation: e—ectoproct; hc—hypercauda; gx—gonocoxite; T—tergum; phc—pseudohypercauda. Scale bars = 1.0 mm

4 Discussion

4.1 Revised interpretation of forewing venation

As discussed in Makarkin *et al.* (2013a), the strong reduction of hind wings in Dipteromantispidae is a remarkable example of parallel evolution with Diptera, probably suggesting strengthened flight ability of dipteromantispids as active fliers. Being associated with the haltere-like hindwing, the forewings of dipteromantispids probably also underwent significant specialization, such as the reduction of forking of longitudinal veins and number of crossveins, and the strong fusion of some veins near wing base. For example, in *M. henryi* the forewing RP+MA, MP, and CuA are all fused proximally with R, which is a rare character in Neuroptera. Probably, this modification functions to form a stronger basal part of forewing for better flight. Due to such highly specialization, previous homology interpretation of some veins in Dipteromantispidae (Grimaldi, 2000; Makarkin *et al.*, 2013a) is problematic. First, the “MA” of *D. brevisubcosta* in Makarkin *et al.* (2013a) should be the anterior branch of MP, while the “posterior simple branch of Rs” should be MA (Fig. 6). Our interpretation is based on the presence of two crossveins, similarly spaced between MA and MP in all dipteromantispid species, as the landmark to distinguish these two parts of M. Second, the “CuP” of the two *Mantispidiptera* species in Grimaldi (2000) should be A1 (Figs 7–8). The “CuP” is deeply forked in *Mantispidiptera*, either fused with CuA or R near forewing base. In *Halteriomantispa* **gen. nov.**, a deeply forked vein similar to that “CuP” is also present, but it has a free stem. Moreover, a more deeply forked vein anterior “CuP” has its posterior branch arcuately curved proximally, which represents a typical condition of CuP in Neuroptera. As such, the A1 vein at least in *Halteriomantispa* **gen. nov.** and *Mantispidiptera* is deeply forked, with free stem (plesiomorphic condition) or with stem fused with R or Cu (apomorphic condition), and both CuA and CuP are simple.

4.2 Phylogenetic status of Dipteromantispidae

There is no doubt that Dipteromantispidae belongs to the Berothid clade which is characterized by its hypometamorphosis and also include Berothidae, Rhachiberothidae and Mantispidae. However, the original placement of dipteromantispids under Mantispidae considered by Grimaldi (2000) and Engel & Grimaldi (2008) was challenged by Makarkin *et al.* (2013a) due to lacking of principal apomorphy of Mantispidae, i.e. the pronotum prolonged posteriorly and formed into a tube by ventral extension. Makarkin *et al.* (2013a) proposed two possible positions of Dipteromantispidae: 1) a specialized subfamily of Berothidae; 2) a specialized stem group of Mantispidae + Berothidae (including Rhachiberothidae as a subfamily under their consideration). Nevertheless, they apparently favor the latter hypothesis and illustrated this relationship in a phylogenetic tree of fossil and recent Neuroptera (Makarkin *et al.*, 2013b).

In the presently described new genus, the female genitalia shows remarkable similarity to Berothidae and Rhachiberothidae by the presence of paired gonocoxites 7, pseudohypocaudae of tergum 9, and hypocaudae of gonocoxites 9 (Figs 9–10). Putative female gonocoxites 7 and hypocaudae are also present in *Dipteromantispa* (Makarkin *et al.*, 2013a). These features might provide evidence to support close relationships among Dipteromantispidae, Berothidae and Rhachiberothidae, although dipteromantispids lack long scape of antennae and trichosores, which are present in most Berothidae and Rhachiberothidae. The combination of paired gonocoxites 7, pseudohypocaudae of tergum 9, and hypocaudae of gonocoxites 9 is unique in recent Neuroptera and only shared by Berothidae and Rhachiberothidae (Aspöck & Aspöck, 2008), but whether it stands as an apomorphy to support the sister-group relationship between these two families has not been determined. Conversely, recent phylogenetic studies based on multi-locus DNA sequence data (Winterton *et al.*, 2010), complete mitochondrial genomic data (unpublished data of first author), and total-evidence data (Liu *et al.*, 2015) suggest Berothidae is the sister group of Rhachiberothidae + Mantispidae. Notably, the raptorial foreleg is assigned to be an autapomorphic character of Rhachiberothidae + Mantispidae (Liu *et al.*, 2015) although Paraberothinae currently recognized as a subfamily of Berothidae with raptorial forelegs was not included in the aforementioned studies. In this respect, the presence of paired gonocoxites 7, pseudohypocaudae of tergum 9, and hypocaudae of gonocoxites 9 might be interpreted as the groundplan of the Berothid clade, while they might be lost in the crown group (e.g., extant Mantispidae). Thus, all lineages of the Berothid clade with raptorial forelegs, including Dipteromantispidae, could form a monophyletic group, being the sister group of some or all remaining berothids without raptorial forelegs. However, the raptorial foreleg was mentioned to be a possible synapomorphic character of the entire Berothid clade (Makarkin, 2015) or was considered as independently originated character, at least in Mantispidae and Rhachiberothinae (e.g., Aspöck & Mansell, 1994). At present, the conclusive assignment of Dipteromantispidae within the Berothid clade cannot be obtained, and re-consideration on the systematic position of this enigmatic family has to be made under further phylogenetic study based on total-evidence data. Nonetheless, the discovery of Dipteromantispidae from the

Burmese amber expands our knowledge of palaeodiversity of the Berothid clade and provides unique information on the phylogeny of this lacewing lineage.

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