

A new genus of mantidflies discovered in the Oriental region, with a higher-level phylogeny of Mantispidae (Neuroptera) using DNA sequences and morphology

XINGYUE LIU¹, SHAUN L. WINTERTON², CHAO WU³,
ROSS PIPER⁴ and MICHAEL OHL⁵

¹Department of Entomology, China Agricultural University, Beijing, China, ²California State Arthropod Collection, California Department of Food and Agriculture, Sacramento, CA, U.S.A., ³Institute of Zoology, Chinese Academy of Sciences, Beijing, China, ⁴The Faculty of Biological Sciences, University of Leeds, Leeds, U.K. and ⁵Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany

Abstract. A remarkable new genus and two new species of Mantispidae (Neuroptera) are described from the Oriental region. *Allomantispia* Liu, Wu, Winterton & Ohl **gen.n.**, currently including *A. tibetana* Liu, Wu & Winterton **sp.n.** and *A. mirimaculata* Liu & Ohl **sp.n.** The new genus is placed in the subfamily Drepanicinae based on a series of morphological characteristics and on the results of total evidence phylogenetic analyses. Bayesian and Parsimony analyses were undertaken using three gene loci (*CAD*, *16S* rDNA and *COI*) combined with 74 morphological characters from living and fossil exemplars of Mantispidae (17 genera), Rhachiberothidae (two genera) and Berothidae (five genera), with outgroup taxa from Dilaridae and Osmylidae. The resultant phylogeny presented here recovered a monophyletic Mantispidae with †Mesomantispinae sister to the rest of the family. Relationships among Mantispidae, Rhachiberothidae and Berothidae support Rhachiberothidae as a separate family sister to Mantispidae. Within Mantispidae, Drepanicinae are a monophyletic clade sister to Calomantispinae and Mantispinae. In a combined analysis, *Allomantispia* **gen.n.** was recovered in a clade comprising *Ditaxis* McLachlan from Australia, and two fossil genera from the Palaeartic, †*Promantispia* Panfilov (Kazakhstan; late Jurassic) and †*Liassochrysa* Ansoerge & Schlüter (Germany; Jurassic), suggesting a highly disjunct and relictual distribution for the family.

This published work has been registered in ZooBank, <http://zoobank.org/urn:lsid:zoobank.org:pub:464B06E8-47E6-482E-8136-83FE3B2E9D6B>.

Introduction

Mantispids, or mantidflies, are a remarkable family of the holometabolous order Neuroptera, notable for their specialized morphological (adults with elongate prothorax and raptorial forelegs) and biological traits (hypermetamorphic larvae present as parasites in the egg sacs of spiders or the nests of aculeate Hymenoptera). Currently, there are over 400 extant described

species (Ohl, 2004, 2005), divided among four subfamilies: Symphrasinae, Drepanicinae, Mantispinae and Calomantispinae (Lambkin, 1986a). Mantispid fossils are relatively uncommon with only 19 named species (Engel & Grimaldi, 2007; Wedmann & Makarkin, 2007; Poinar & Buckley, 2011; Jepson *et al.*, 2013; Khramov, 2013; Shi *et al.*, 2014). However, the diversity of Mantispidae in the Mesozoic and Palaeocene was likely very high. Besides Symphrasinae, Drepanicinae and Mantispinae, which have been recorded from the Mesozoic and Palaeocene, there are other fossil mantispids representing taxa very different from extant subfamilies, such as †*Mesomantipa* together with its related genera from the middle Jurassic to Early Cretaceous of Eurasia (representing the subfamily †Mesomantispinae) and

Correspondence: Xingyue Liu, Department of Entomology, China Agricultural University, Beijing 100193, China. E-mail: xingyue_liu@yahoo.com

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†*Doratomantispa* from the Cretaceous Burmese amber (considered to possibly represent a new subfamily) (Wedmann & Makarkin, 2007; Poinar & Buckley, 2011). Very recently, Shi *et al.* (2014) described a genus (†*Micromantispa* Shi, Ohl, Wunderlich & Ren) from Cretaceous-age deposits in Myanmar. This genus is very similar to †*Doratomantispa* and these two genera possibly represent ancestral drepanicines, or even a separate stem group subfamily. Unfortunately, we were not able to include †*Micromantispa* in this study in time, but it is clearly an important component of any future studies on the group. †*Liassochrysa stigmatica* Ansoerge & Schlüter, from the early Jurassic of Germany, represents the oldest definitive mantispid fossil currently known, demonstrating that Mantispidae originated no later than the early Jurassic. The divergence time estimation based on molecular phylogeny of Neuropterida (Winterton *et al.*, 2010) shows that the splitting between Mantispidae and its putative sister group Berothidae happened at the beginning of the Jurassic (~200 Ma), which generally conforms to the age of mantispids inferred from the fossil record. A hypothesis of the evolutionary history of mantispids proposed by Wedmann & Makarkin (2007) suggests that Symphrasinae and Drepanicinae were once widespread, but that now their current distribution is a relict and restricted to the southern continents; Calomantispinae at present show a disjunct relict distribution, whereas the clearly more derived and species-rich Mantispinae seem to have 'ousted' the other groups as they are presently distributed worldwide.

Hitherto, all extant mantispid species from Asia belong to the Mantispinae, with other subfamilies represented in the region only by fossils (Wedmann & Makarkin, 2007; Poinar & Buckley, 2011; Jepson *et al.*, 2013; Khramov, 2013). Recently, we obtained two remarkable adult mantispids collected from Xizang Autonomous Region (Tibet) of China and northern Myanmar, representing a new genus of Mantispidae. The morphological characteristics of these mantispids largely conform to those of the subfamily Drepanicinae, a relict group with extant species previously recorded only in Australia and South America. In this paper, we describe this new genus – *Allomantispa* **gen. n.** – including two new species, and reconstruct a higher-level phylogeny of the families Mantispidae, Berothidae and Rhachiberothidae based on morphological and molecular data to determine the phylogenetic position of this new genus.

Material and methods

Taxon sampling

For the phylogenetic analyses, we selected 17 genera of Mantispidae as ingroup taxa, including all genera of Drepanicinae (*Allomantispa* **gen. n.**, *Ditaxis* McLachlan, †*Doratomantispa* Poinar & Buckley, *Drepanicus* Blanchard in Gay, *Gerstaekerella* Enderlein and *Theristria* Gerstaecker), Symphrasinae (*Anchieta* Navás, *Plega* Navás, †*Symphrasites* Wedmann & Makarkin and *Trichoscelia* Westwood), Calomantispinae (*Calomantispa* Banks and *Nolima* Navás), as well as one genus of Mantispinae (*Campion* Navás), †*Mesomantispinae*

(†*Archaeodrepanicus* Jepson, Heads, Makarkin & Ren and †*Mesomantispa* Makarkin) and two fossil genera with uncertain subfamilial placement (†*Liassochrysa* Ansoerge & Schlüter and †*Promantispa* Panfilov). Both species of *Allomantispa* **gen. n.** were included in order to confirm the monophyly of this genus. The bulk of genera of Mantispidae are placed in Mantispinae, but were not sampled here as our focus was on higher-level relationships within Mantispidae and related families, and placement of *Allomantispa* **gen. n.** Relationships among genera of Mantispidae are almost completely unknown except for the classical analysis by Lambkin (1986a) and are in urgent need of comprehensive systematic revision. Recent monographic revisions by Ohl (2009) and Snyman *et al.* (2012) are examples of recent systematic approaches, but larger phylogenetic studies are still lacking. In our analysis, additional ingroup taxa included five genera of Berothidae (*Berotha* Walker, *Lomamyia* Banks, *Podallea* Navás, *Quasispermophorella* Aspöck & Aspöck and *Stenobiella* Tillyard) and two genera of Rhachiberothidae (*Mucroberotha* Tjeder and *Rhachiberotha* Tjeder). Outgroup taxa included one genus of Osmylidae (*Kempynus* Navás) and two genera of Dilaridae (*Dilar* Rambur and *Nallachus* Navás).

The type specimens of the two new species described herein are deposited in the Entomological Museum of China Agricultural University, Beijing (CAU), the personal collection of Chao Wu (PCW), and the Natural History Museum, London (BMNH). Other specimens examined for the phylogenetic analyses, including voucher specimens, are deposited in CAU, BMNH, the California State Arthropod Collection, California Department of Food and Agriculture, Sacramento (CSCA) and the Museum für Naturkunde, Berlin (ZMB).

Genitalia preparations were made by clearing the apex of the abdomen in a cold, saturated potassium hydroxide (KOH) solution for 8–10 h. After rinsing the KOH with acetic acid and water, the apex of the abdomen was transferred to glycerine for further dissection and examination. After examination it was moved to fresh glycerine and stored in a microvial pinned below the specimen. Interpretation of the wing venation follows Aspöck *et al.* (1980) and Lambkin (1986a). Terminology of the genitalia follows Lambkin (1986a) and Aspöck & Aspöck (2008).

Morphological characters

Seventy-four adult and larval characters were numerically coded for three outgroup and 25 ingroup taxa. Morphological characters used in the phylogenetic analysis are listed in Appendix. Sixty-two characters were coded as binary and 12 as multistate. Inapplicable and unknown characters were coded as '-' and '?', respectively. The data matrix is given in Supporting Information (Table S1).

DNA sequencing and alignment

Specimen voucher and Genbank accession numbers for taxa sequenced are presented in Table 1. Individuals were stored in 95–100% EtOH at –80°C. Genomic DNA was

Table 1. Exemplars used for sequencing. Accession numbers are provided with gene sequences deposited in Genbank (<http://www.ncbi.nih.gov/>).

Family/subfamily	Exemplar	<i>16S</i>	<i>COI</i>	<i>CAD</i>	Collection origin; depository; reference
Berothidae	<i>Lomamyia banksi</i> Carpenter	EU734869	EU839737	EU860122	U.S.A.; Winterton <i>et al.</i> (2010)
	Berothinae				
	<i>Podallea madegassica</i> Aspöck & Aspöck	EU734892	EU839759	EU860145	Madagascar; Winterton <i>et al.</i> (2010)
	<i>Quasispermophorella ingwa</i> Aspöck & Aspöck	EU734898	EU839765	EU860150	Australia; Winterton <i>et al.</i> (2010)
	<i>Stenobiella muellerorum</i> Aspöck & Aspöck	EU734900	EU839766	EU860152	Australia; Winterton <i>et al.</i> (2010)
	<i>Berotha</i> sp.	AY620165.1	–	–	Thailand; Haring <i>et al.</i> (2004)
Rhachiberothidae	<i>Mucroberotha vesicaria</i> Tjeder	EU734872	EU839740	EU860125	South Africa; Winterton <i>et al.</i> (2010)
Dilaridae	<i>Nallachius americanus</i> (MacLachlan)	EU734874	EU839742	EU860127	U.S.A.; Winterton <i>et al.</i> (2010)
	<i>Dilar duelli</i> Aspöck & Aspöck	AY620164	–	–	Italy; Haring & Aspöck (2004)
Mantispidae					
Drepanacinae	<i>Ditaxis biseriata</i> (Westwood)	EU734862	EU839732	EU860114	Australia; Winterton <i>et al.</i> (2010)
	<i>Theristria imperfecta</i> Lambkin	EU734909	EU839774	EU860160	Australia; Winterton <i>et al.</i> (2010)
	<i>Gerstaekerella chilensis</i> (Hagen)	KM051513	KM051519	–	Chile; ZMB
	<i>Allomantispia mirimaculata</i> gen. et sp.n.	KM009123	KM009124	–	Myanmar; BMNH
	<i>Drepanicus</i> sp.	KM051512	KM051518	KM051524	Chile; ZMB
Mantispinae	<i>Campion rubellus</i> Navás	KM051511	KM051517	KM051523	Australia; CSCA
Symphrasinae	<i>Plega dactylota</i> Rehn	EU734891	EU839758	EU860144	Australia; Winterton <i>et al.</i> (2010)
	<i>Anchieta eurydella</i> (Westwood)	KM051510	KM051516	KM051522	Colombia; ZMB
	<i>Trichoscelia iridella</i> Westwood	KM051515	KM051521	KM051526	French Guiana; ZMB
Calomantispinae	<i>Nolima pinal</i> Rehn	KM051514	KM051520	KM051525	Mexico; CSCA
Osmyliidae					
Kempyninae	<i>Kempynus kimminsi</i> New	EU734867	DQ515501	EU860120	Australia; Winterton <i>et al.</i> (2010)

extracted from thoracic muscle tissue using the DNeasy® kit (Qiagen, Maryland USA) with specimens incubated in the extraction buffer/proteinase-K mixture for 24–48 h. Extractions were air-dried and re-suspended in 50–150 µL of TE buffer before storage at –80°C. Three partial gene regions were sequenced and analysed in comparative analyses, specifically *16S* ribosomal DNA and two protein-encoding genes [CPSase region of carbamoyl-phosphate synthetase-aspartate transcarbamoylase-dihydroorotase (*CAD*) and cytochrome oxidase I (*COI*)]. Genbank accession numbers are presented in Table 1. Primer sequences are presented in Supporting Information (Table S2). Amplifications of DNA using standard polymerase chain reaction (PCR) were performed using the following cycling conditions. A 540-bp fragment of *16S* rDNA (3'-end) was amplified using a single primer pair originally from Simon *et al.* (1994) with the following PCR protocol: initial denaturation at 95°C (3 min); five cycles of 92°C (15 s), 48°C (45 s), 62°C (2 min 30 s); 29 cycles of 92°C (15 s), 52°C (45 s), 62°C (2 min 30 s); final extension at 62°C for 7 min. The complete c. 1500-bp sequence of *COI* mtDNA was amplified using primers modified after Simon *et al.* (1994): initial denaturation at 94°C (2 min); 35 cycles of 94°C (40 s), 55°C (50 s), 72°C (1 min); final extension at 72°C for 10 min. An approximately 2100-bp sequence of *CAD* was generated with the following two-stage protocol. Stage 1: initial denaturation at 94°C (4 min); five cycles of 94°C (30 s), 52°C (30 s) and 72°C (2 min); seven cycles of 94°C (30 s), 49°C (1 min) and 72°C (2 min); 37 cycles of 94°C (30 s), 45°C (20 s) and 72°C (2 min 30 s); 72°C (3 min) for final extension. The reamplification PCR cycling protocol involved an initial denaturation at 94°C (4 min); five cycles of 94°C (30 s), 51°C (30 s) and 72°C (1 min 30 s); 37 cycles of

94°C (30 s), 45°C (30 s) and 72°C (1 min 20 s); 72°C (3 min) for final extension. Sequencing electropherograms were edited and proofed using Sequencher™ 5.0 series (GeneCodes Corp., Michigan, USA).

Protein-encoding genes were aligned manually with reference to translated amino acid sequences using Mesquite v2.75 (Maddison & Maddison, 2011). Examination of unedited sequences showed complete fidelity with the reading frame and single peaks at all nucleotide positions, indicating that the sequences recovered were all functional homologues and not nuclear pseudogenes. The *16S* ribosomal gene was aligned in Mesquite using a secondary structure model-based mask delineated for *Rapisma zayuanum* Yang by Wang *et al.* (2013). Ambiguously aligned regions of *16S*, where positional homology could not be inferred with a reasonable level of confidence, were excluded prior to analysis.

Phylogenetic analysis

The analysis was performed using WinClada v1.00.08 (Nixon, 2002) and NONA v2.0 (Goloboff, 1993). The heuristic search was used with maximum trees to keep setting to 10 000 and number of replication setting to 100. The branch support values were calculated with the function implemented in TNT (TBR from existing trees, retain trees suboptimal by ten steps) (Goloboff *et al.*, 2008). All characters were treated as unordered and with equal weight. Character states were mapped on a most-parsimonious tree (MPT) using WinClada v1.0 (Nixon, 2002), showing only unambiguous changes.

The total evidence analysis, combining morphological and molecular data was undertaken using both parsimony

and Bayesian Likelihood methods. Bayesian analyses were performed using MrBayes 3.2 (Ronquist *et al.*, 2011) and parsimony analyses performed using TNT and PAUP*4.0b10 (Swofford, 1999). The third codon positions in *CAD* and *COI* were excluded for all analyses as inclusion of these characters resulted in tree topologies that compromised the monophyly of clades which were well established previously, based on extraneous evidence. The data were partitioned by data type (DNA sequence, morphology), locus and by codon position. The most appropriate models were determined for each partition using jModelTest 1.1 (Guindon & Gascuel, 2003; Felsenstein, 2005; Posada, 2008) with the Bayesian Information Criterion (BIC) invoked. Separate nucleotide substitution models were applied to each DNA locus as follows (*I6S*: TVM+G; *CAD* & *COI*: GTR+I+G). Analysis consisted of four MCMC chains run simultaneously for 10G generations during which convergence was obtained. Trees were sampled every 1000th generation with the first 25% of trees discarded as burn-in. A majority-rule consensus tree was computed with posterior probabilities for each node. Nonparametric bootstrap support values (Felsenstein, 1985) were calculated using PAUP*4.0b10 from 1000 heuristic search (TBR) pseudoreplicates of re-sampled datasets (constant characters excluded), each with 20 random additions.

Results

Taxonomy

Subfamily Drepanicinae Enderlein

Drepanicini Enderlein, 1910: 343. Type genus: *Drepanicus* Blanchard in Gay, 1851.

Diagnosis. (1) Fore femur not laterally compressed along the spine row and as long as tibia plus tarsus, with a long basal spine; (2) fore tarsi 5-segmented with a pair of tarsal claws; (3) anterolateral margins of mesoscutum rounded; (4) forewing Sc approximating or fused with R or connecting to R by a short crossvein; (5) forewing MP with branching point from R near wing base (close to 1m-cu); (6) forewing 2A and 3A not fused proximally; (7) at least three forewing r-rs present; (8) one or two and occasionally three forewing gradate crossvein series present; (8) male sternite 9 not surpassing apices of ectoproct; (9) male pseudopenis short, not elongated and coiled; (10) callus cerci present in both male and females; (11) female sternite 7 mostly with crumena; (12) female gonocoxite 8 reduced and usually paired.

Included genera. *Allomantispa* **gen.n.**, *Ditaxis* McLachlan, *Drepanicus* Blanchard in Gay, *Gerstaeckerella* Enderlein, †*Liassochrysa* Ansoerge & Schlüter, †*Promantispa* Panfilov and *Theristria* Gerstaecker. †*Doratomantispa* Poinar & Buckley has been included previously, but is considered as *incertae sedis* here.

Distribution (Figs 1–6). *Allomantispa* **gen.n.** represents the first record of a living Drepanicinae in the Oriental region,

with all other extant genera distributed in the Southern Hemisphere (i.e. South America and Australia). However, fossils of Drepanicinae are known from deposits in the Western Palaearctic (†*Liassochrysa*), and the Eastern Palaearctic (†*Promantispa*, *Gerstaeckerella*) regions.

Remarks. The two Mesozoic genera (†*Liassochrysa* and †*Promantispa*) were considered to represent a ‘suprageneric taxa’ in Mantispidae by Wedmann & Makarkin (2007), but in our phylogenetic analysis they always form a monophyletic group with extant genera of Drepanicinae. Therefore, here we place †*Liassochrysa* and †*Promantispa* into Drepanicinae. The monophyly of Drepanicinae was corroborated in our phylogenetic analysis (Fig. 5). We retain the subfamilial taxonomic classification proposed by Lambkin (1986a), although it is clear that a more comprehensive re-evaluation is needed of the higher-level relationships of Drepanicinae relative to Mantispinae and Calomantispinae. In particular, the position of †*Doratomantispa* requires further study and at this stage should be considered as *incertae sedis* in the family.

Key to genera of Drepanicinae

1. Pterostigma quite remote from R, connected by one crossvein (Fig. 3D); two gradate crossvein series (inner series sometimes absent in *Drepanicus chrysopinus* Brauer) (Fig. 2); forewing with Sc only slightly approximating costal margin just proximal to pterostigma (Fig. 2) 2.
 - Pterostigma very close to R, separated only by a very narrow hyaline strip, which is crossed by at least two very short veins (Poivre, 1978: fig. 5E); one gradate crossvein series (Poivre, 1978: fig. 5C); forewing with Sc very closely approximating costal margin just proximal to pterostigma (Lambkin, 1986a: fig. 28) 6.
2. Forewing MP proximally sinuate (Ansoerge & Schlüter, 1990: fig. 3) 3.
 - Forewing MP proximally straight (Fig. 2) 4.
3. Forewing (Ansoerge & Schlüter, 1990: fig. 3) inner gradate series of crossveins complete; marginal crossveins mp-cua, cua-cup, and 1a–2a present; marginal forks of 1A and 2A present (Germany) †*Liassochrysa* Ansoerge & Schlüter.
 - Forewing (Willmann, 1994: fig. 17) inner gradate series of crossveins incomplete; marginal crossveins mp-cu, cua-cup, and 1a–2a absent; marginal forks of 1A and 2A absent (Kazakhstan) †*Promantispa* Panfilov.
4. Forewing (Fig. 12B) CuA with *c.* ten branches near distal margin; hind wing with remnant CuP (South America) *Drepanicus* Blanchard in Gay.
 - Forewing (Fig. 2) CuA with 2–4 branches near distal margin; hind wing without CuP 5.
5. Both fore tarsal claws not bifid; male ectoproct widely separated, male sternite 9 posteriorly without large median projection (Lambkin, 1986a: figs. 42–43); female ectoproct (Lambkin, 1986a: fig. 35) subquadrate, posterodorsally prominent (Australia) *Ditaxis* McLachlan.



Fig. 1. Living adult of *Allomantispa tibetana* sp.n. and its habitat. (A) Living male adult, lateral view; (B) type locality of *A. tibetana* sp.n.

– Both fore tarsal claws bifid (Fig. 3G); male ectoproct proximally fused with each other, male sternite 9 posteriorly with a large median projection (Fig. 4B–C); female ectoproct (Fig. 6A) subtriangular (Asia) *Allomantispa* gen.n. 6. Forewing MP with posterior main branch proximally approximating CuA; hind wing with remnant CuP (Poivre, 1978: fig. 5C, D); male ectoproct (Fig. 9F) largely fused medially, gonarcus (Fig. 9H) medially enlarged into a shield-like plate [South America (extant); Kazakhstan (fossil)] *Gerstaeckerella* Enderlein.

– Forewing MP with posterior main branch not approximating CuA; hind wing without CuP (Lambkin, 1986a: fig. 126); male ectoproct (Lambkin, 1986a: fig. 69) not fused medially, gonarcus (Lambkin, 1986a: fig. 73) rather small medially (Australia) *Theristria* Gerstaecker.

***Allomantispa* Liu, Wu, Winterton & Ohl gen.n.**

<http://zoobank.org/urn:lsid:zoobank.org:act:7EFE4C59-690D-42BD-A464-13E416AB5C4E>
(Figs 1–6)

Type species. Allomantispa tibetana Liu, Wu & Winterton sp.n.

Included species. Allomantispa tibetana Liu, Wu & Winterton sp.n. and *Allomantispa mirimaculata* Liu & Ohl sp.n.

Diagnosis. This genus is characterized by the presence of a pair of bifid fore tarsal claws, the forewing with two gradate crossvein series, the pterostigma with one short crossvein connecting to R, the male sternite 9 posteriorly with a large median projection, the female sternite 7 fused with gonocoxite 8, and the absence of crumena.

Description. Head: Facial region just dorsal to antennae rugose, sculptured, without a median hump; vertex slightly or distinctly domed, without a median ridge; postocular margin broad. Antennae reaching to nearly total length along pronotum; scape without a whorl of thick setae; flagellar segments not longitudinally compressed, each flagellum nearly 2.0× as long as wide.

Thorax: Pronotum strongly swollen in anterior 1/2 and tubular in posterior 1/2, slightly rugose dorsally, but strongly rugose ventrally on posterior 1/2, without a raised area anteromedial to maculae; dorsal surface with dense short setae; one or two pairs of maculae. Pterothorax with mesoscutal furrows strongly impressed, distinct; mesoscutellum slightly more than 1/2 length of exposed mesonotum; scutoscutellar sutures sinuous (Fig. 3C). Foreleg with coxa slightly shorter than femur, with lateral face distinctly longitudinally impressed on distal 1/2; femur narrow, sometimes slightly elliptical, not flattened along ventral margin, with major spine at c. 1/4 length (Fig. 3F), and with a row of cuticular spines along closed tibia, 4–7 spines much larger than remaining short spines; tibia not acutely produced on medial apical margin, with short, thick, black, prostrate setae; tarsus with segment 1 nearly as long as segment 5, segments 2–4 subequal in length (each shorter than segment 5), ventral surfaces of segments 1–4 each with a transverse pair of short, thick, black, prostrate (apices pointing distally) setae, each tarsal claw bifid distad (Fig. 3G), arolium present. Mid and hind tarsi each with segment 1 longer than segment 5 but shorter than segments 2–5 combined, each tarsal claw bifid distad (Fig. 3H, I), arolium present. Wings (Fig. 2) finely pubescent on veins and entire wing margins; costal space continuous with pterostigma distally; radial cells elongate, sometimes disrupted by additional crossveins; Rs branches nearly straight or zigzagged. Forewing with costal space broad; Sc slightly deflexed toward costal margin just proximal to pterostigma, terminating on costal margin at level of distal most r-rs; subcostal space proximal to pterostigma with one distinct crossvein (1sc-r) at proximal 1/4 and rather distal to level of 1m-cu; pterostigma with one short crossvein (2sc-r) to R (Fig. 3D), distal margin nearly straight and slightly oblique; MP diverging from R at or slightly proximal to 1m-cu; MP₁₊₂ and Rs stem joined by a short crossvein; ventral surface of Cu cell smooth; 1m-cu upright, at or distal to forking of Cu; CuA and CuP distinctly divergent proximally; CuA with 2–3 simple branches; CuP distinctly curved proximally, right or obtuse angled, and closely approximating or distant to 1A at cu-a (Fig. 3E), with 2–3 simple branches; 1A simple or with two branches, 2A with two branches, 3A simple, normally developed; jugal lobe small, jugal strut distinct, curved toward



Fig. 2. Habitus photo of *Allomantispa tibetana* sp.n., holotype male. Scale bar: 5.0 mm.

axillaries. Hind wing with humeral plate bearing thick setae; middle section of Sc slightly curved towards costal margin; pterostigma similar to that of forewing; MA separate from Rs stem, with stem nearly straight and upright; M diverging from R considerably proximal to lm-cu; CuA deflexed towards 1A, with 2–4 branches; cu-a short, straight, emerging from stem of CuA; 1A with 2–3 branches.

Abdomen (Figs 1A, 5A): Relatively short, not extending beyond apices of folded wings. Male genitalia (Fig. 4): Tergite 8 with posteroventral margins not extended to incorporate eight spiracles. Tergite 9 deeply arched anteroventrally, in dorsal view anterior margin with continuous transverse apodeme. Sternite 9 broadly scoop-like, reaching just distal to entire length along ectoprocts, posteromedially with a laterally flattened digitiform process produced nearly perpendicular to longitudinal axis of sternite 9. Ectoproct thickly digitiform, proximally fused with each other; callus cerci present, ovoid. Gonarcus in lateral view distinctly curved, apex of gonarcus arm broadened, anterodorsal portion bifurcated into a pair of claw-like lobes. Gonocoxite 9 strongly sclerotized, and distally with several claw-like spines. Hypomeres present as a pair of short and narrow sclerites. Mediuncus rather narrow. Pseudopenis slender elongate and distinctly sclerotized. Hypandrium internum deep, not curved, strongly pigmented. Female genitalia (Fig. 6): Sternite 7 posteriorly fused with gonocoxite 8; crumena absent. Gonapophysis 8 present as a robust, subcylindrical sclerite, laterally with a pair of smaller sclerites. Tergite 9 fused with ectoprocts ventrally. Gonocoxite 9 largely separated with tergite 9, only with posterodorsal portion fused with ectoproct. Bursa copulatrix strongly sclerotized, anteriorly produced into

a digitiform lobe; spermatheca proximally with a pair of laterally produced, ball-like lobes, and with a short additional lobe nearly at proximal 1/3.

Etymology. The generic epithet is a combination of Greek 'allo-' (unusual, in reference to the quite peculiar appearance of the new genus) and 'Mantispa' (type genus of the family Mantispidae). The name is feminine.

Distribution. China; Myanmar.

Remarks. *Allomantispa* gen.n. is the only extant member of the Drepanicinae known from the Northern Hemisphere and from the Oriental region as all other extant mantispids in the region belong to the subfamily Mantispidinae. *Allomantispa* gen.n. is placed in the subfamily Drepanicinae based on the following diagnostic morphological characters: pronotum with maculae, anterolateral margins of mesoscutum rounded, fore coxa without a transverse sulcus, fore femur not laterally compressed along the spine row and as long as tibia plus tarsus, fore tarsus with two claws and an arolium, no eversible gland between male tergites 5–6, male sternite 9 not surpassing apices of ectoproct, paired female gonapophysis 8, and presence of callus cerci. This genus differs from *Theristria* and *Gerstaeckerella* by having two gradate crossvein series in the forewing and the configuration of pterostigma, but appears to be somewhat similar to *Ditaxis* and *Drepanicus*. *Allomantispa* gen.n. can be easily distinguished from all other genera of the Drepanicinae by the bifid fore tarsal claws, the male sternite 9 posteriorly having a large median projection, the female sternite 7 posteriorly

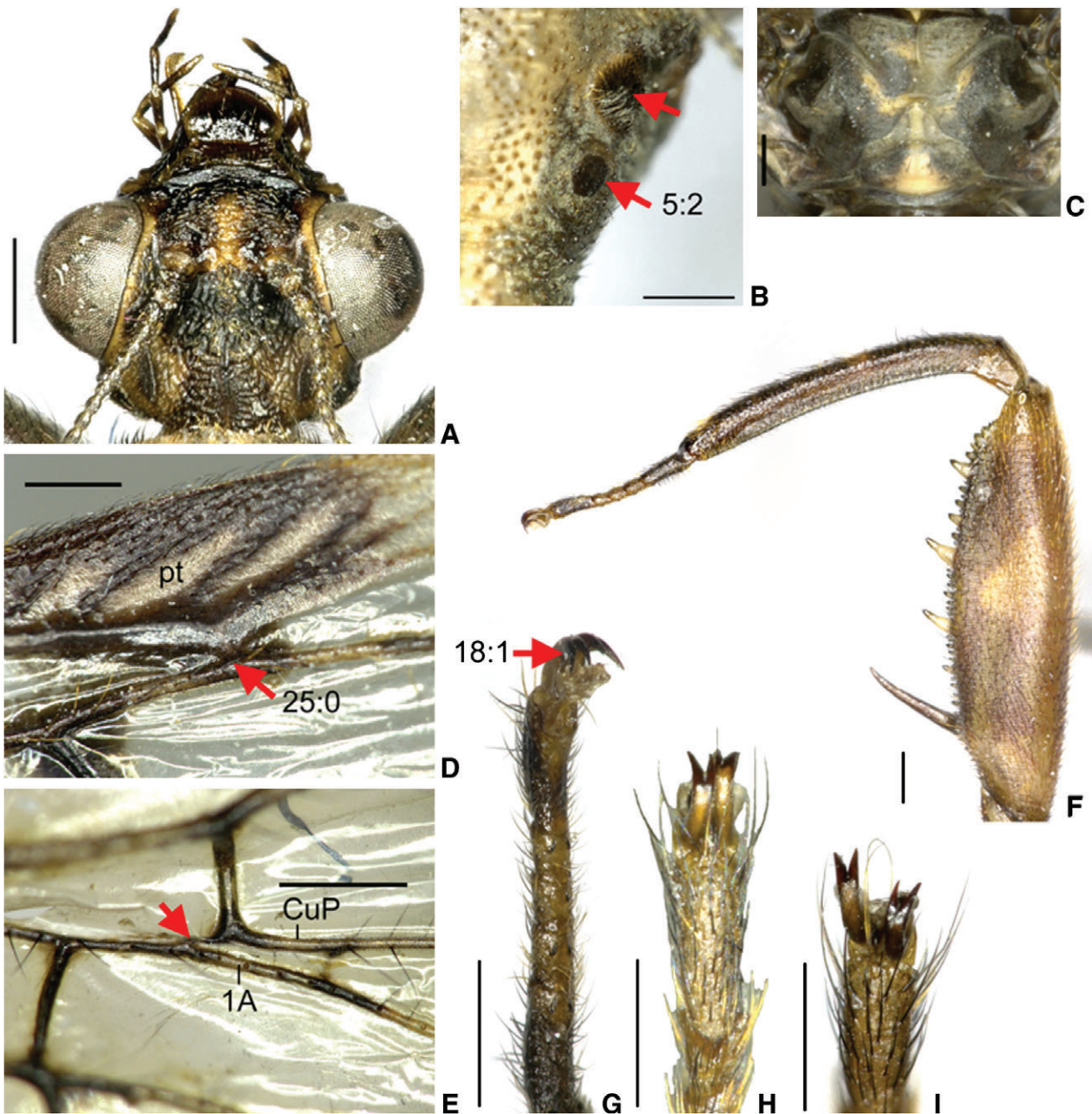


Fig. 3. *Allomantispa tibetana* sp.n., holotype male. (A) Head, frontal dorsal view; (B) anterolateral portion of pronotum, dorsal view; (C) mesonotum, dorsal view; (D) forewing pterostigma; (E) base of forewing CuP; (F) fore femora, tibia and tarsus, lateral view; (G) fore tarsus, ventral view; (H) apex of mid tarsus, dorsal view; (I) apex of hind tarsus, dorsal view. Scale bars: 0.5 mm.

fused with unpaired gonocoxite 8, and the absence of female crumena.

Key to species of *Allomantispa* gen.n.

1. Head (Fig. 3A) largely blackish-brown, frons with a yellowish-brown longitudinal stripe; pronotum with two pairs of maculae; forewing (Fig. 2) with a series of faintly brownish

markings along wing margin, but without brown edging on posterior margin; forewing CuP approximating 1A; 1A simple *A. tibetana* Liu, Wu & Winterton **sp.n.**
 – Head (Fig. 5B) pale yellowish-brown, with three transverse dark markings respectively on frons and vertex; pronotum with one pair of maculae; forewing (Fig. 5B) without faintly brownish markings, but with a distinct brown edging on posterior margin; forewing CuP not approximating 1A; 1A with two branches *A. mirimaculata* Liu & Ohl **sp.n.**

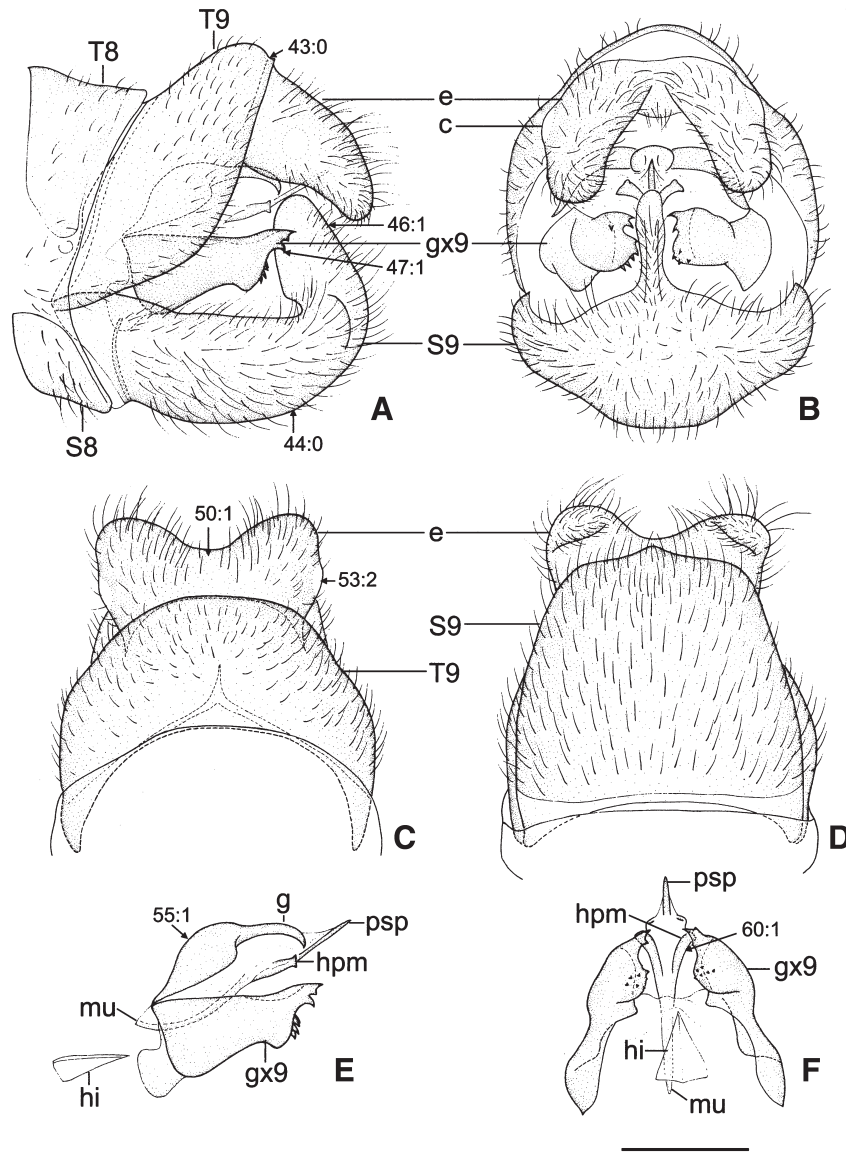


Fig. 4. *Allomantispa tibetana* sp.n., holotype male. (A) Genitalia, lateral view; (B) genitalia, caudal view; (C) genitalia, dorsal view; (D) genitalia, ventral view; (E) internal genitalia, lateral view; (F) internal genitalia, ventral view. Abbreviations: T8–9, tergite 8–9; S8–9, sternite 8–9; c, callus cercus; e, ectoproct; gx9, gonocoxite 9; g, gonarcus; hi, hypandrium internum; hpm, hypomere; mu, mediuncus; psp, pseudopenis. Scale bars: 1.0 mm.

***Allomantispa tibetana* Liu, Wu & Winterton sp.n.**

<http://zoobank.org/urn:lsid:zoobank.org:act:3A66777A-4BB2-4F65-8393-3C0E4ACD33A8>

(Figs 1–4)

Description of holotype male. Measurements (mm) and ratios: Minimum frontal eye distance (WBE) 1.25; maximum frontal head width including eyes (WAE) 2.65. Pronotal length, measured along dorsal midline (LP) 3.65; pronotal width at maculae (WAM) 2.50. Maximum fore femoral length (LFF) 4.50; maximum fore femoral width (WFF) 1.15; fore femoral ratio (length: width) (LFF: WFF) 3.91. Maximum fore tibial length (LFT) 3.50. Fore femoral length: fore tibial length (LFF:

LFT) 1.29. Maximum mid femoral length (LMF) 2.50; mid femoral ratio (midfemoral length: head width including eyes) (LMF: WAE) 0.94. Maximum forewing length (LFW) 24.0; maximum forewing width (WFW) 7.50; forewing ratio (length: width) (LFW: WFW) 3.20. Maximum forewing pterostigma length (LFPt) 5.0; maximum forewing pterostigma width (WFPT) 0.75. Maximum hind wing length 21.0; maximum hind wing width 6.7; hind wing ratio (length: width) 3.13. Total body length 20.6.

Colouration (Figs 1B, 2): Head largely blackish-brown, frons with a yellowish-brown longitudinal stripe, ocular margins entirely yellow, vertex laterally with a pair of annular yellowish markings. Compound eyes glossy grey, but dark brown

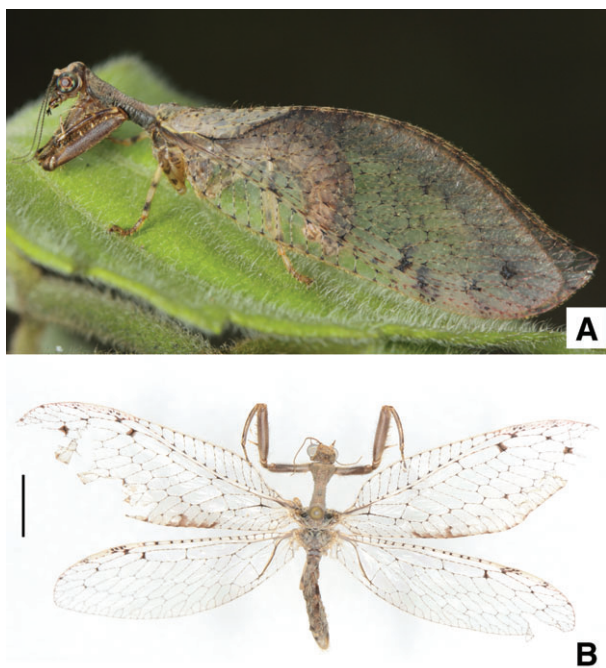


Fig. 5. *Allomantispa mirimaculata* sp.n. (A) Living female adult, lateral view; (B) habitus of holotype female. Scale bar: 5.0 mm.

in living specimen. Antennae blackish-brown throughout. Mouthparts blackish-brown; maxillae and labium yellow, except for maxillary and labial palpi blackish-brown but yellowish on joints between segments as well as on tips of terminal segments; labrum with outer margin also faintly yellow. Pronotum dark reddish-brown, with dorsal surface largely yellow; maculae black. Pterothorax blackish-brown; mesonotum with yellow stripes along scutal furrows and with a sub-triangular yellow marking on scutellum; metanotum medially with a yellow longitudinal stripe, pleural region yellow. Foreleg: coxa blackish-brown, with a pale marking medially on inner surface; trochanter blackish-brown; femur reddish-brown, outer surface with three broad yellow markings spread along length, inner surface largely faintly yellow, major spine yellowish-brown, 6–7 larger minor spines pale yellow with blackish-brown tips, other minor spines blackish-brown; tibia blackish-brown with mottled yellowish spots, more distinctive at middle and apex; tarsus blackish-brown, with tarsomeres 2–4 yellow, tarsal claws yellow with apices reddish-brown. Mid leg: coxa blackish-brown; trochanter largely yellow; femur yellow, but blackish-brown on proximal 1/3 and sub apical portion; tibia yellow, slightly darker at proximal 1/3 and sub apical portion; tarsus yellow, tarsal claws yellow with apices reddish-brown. Hind leg: coxa blackish-brown; trochanter largely yellow; femur blackish-brown, with extreme apex yellow; tibia yellowish-brown; tarsus yellow, tarsal claws yellow with apices reddish-brown. Forewing: transparent with faintly brownish markings near posterior margin and on gradate crossveins, and with blackish stripes on r-rs crossveins; pterostigma cream-yellow, but brownish medially;

longitudinal veins alternately blackish-brown and yellow, crossveins blackish-brown except for costal crossveins on proximal 1/2 of costal region yellow at middle. Hind wing: similarly patterned with forewing, but with markings near posterior margin much more indistinct; veins blackish-brown, except for C, Sc, R and stem of Rs alternately blackish-brown and yellow. Abdomen mostly blackish-brown, tergites 1–8 with a longitudinal median stripe, pleural region on 2–3 segments and 7–8 segments yellow, sternites 1–8 with posterior margins yellow.

Morphology: Head (Fig. 3A) sub-trapezoidal in frontal view, sparsely setose, rugose on dorsal surface, vertex slightly domed with complete epicranial suture. Antenna with 33 segments. Pronotum (Figs 2, 3B) densely setose, dorsally with a number of Stitz organs; anterior pair of maculae densely setose, slightly larger than posterior pair of maculae, which are glabrous. Pterothorax robust, mesonotum sparsely setose, but metanotum glabrous. Legs densely setose. Wings finely setose on veins and margins. Forewing (Fig. 2) not widened at middle; 21–22 crossveins present on costal region; R distally with three forked branches, radial region subdivided by 3–4 r-rs crossveins; Rs with 5–6 main branches, each distally with two simple or forked sub-branches; MA distally with two forked branches; MP with two main branches, each of them distally with two simple or forked sub-branches; CuA distally with two simple branches, CuP proximate 1A, distally with three simple branches; 1A simple, 2A with two branches, 3A simple; gradate crossveins in two series. Hind wing (Fig. 2) with 20–22 crossveins on costal region; R distally with three forked branches, radial region subdivided by 4–6 r-rs crossveins; Rs with eight main branches, each distally with two simple or forked sub-branches; MA distally with two forked branches; MP with two main branches, each of them distally with two simple or forked sub-branches; CuA distally with two simple branches, CuP absent; 1A with three branches, 2A and 3A simple; gradate crossveins in two series. Abdomen moderately setose, strongly swollen on segments 7–9.

Male genitalia (Fig. 4): Tergite 9 deeply arched anteroventrally and closely associated with base of sternite 9 ventrally, in dorsal view anterior margin with continuous transverse apodeme, which is distinctly extended posteriorly, posterior margin strongly convex. Sternite 9 broadly scoop-like, reaching just distal to entire length along ectoprocts, clothed with short fine setae, in ventral view elongate sub trapezoid, apex medially with a laterally flattened digitiform process produced nearly upright to longitudinal axis of sternite 9. Bases of ectoprocts fused. Ectoproct thickly digitiform, gradually narrowed distad, and directed lateroventrad; finely pubescent throughout with much denser but shorter setae at tip; callosus cerci present, ovoid. Gonarcus in lateral view distinctly curved, apex of gonarcus arm broadened, anterodorsal portion bifurcated into a pair of claw-like lobes. Gonocoxite 9 strongly sclerotized, not reaching to level of apex of mediuncus, anterior 1/2 flattened, posterior 1/2 inflated, distally claw-like, with *c.* five additional short spines. Dorsal region between gonocoxites membranous. Hypomeres present as a pair of short and narrow sclerites that are directed laterally with slightly

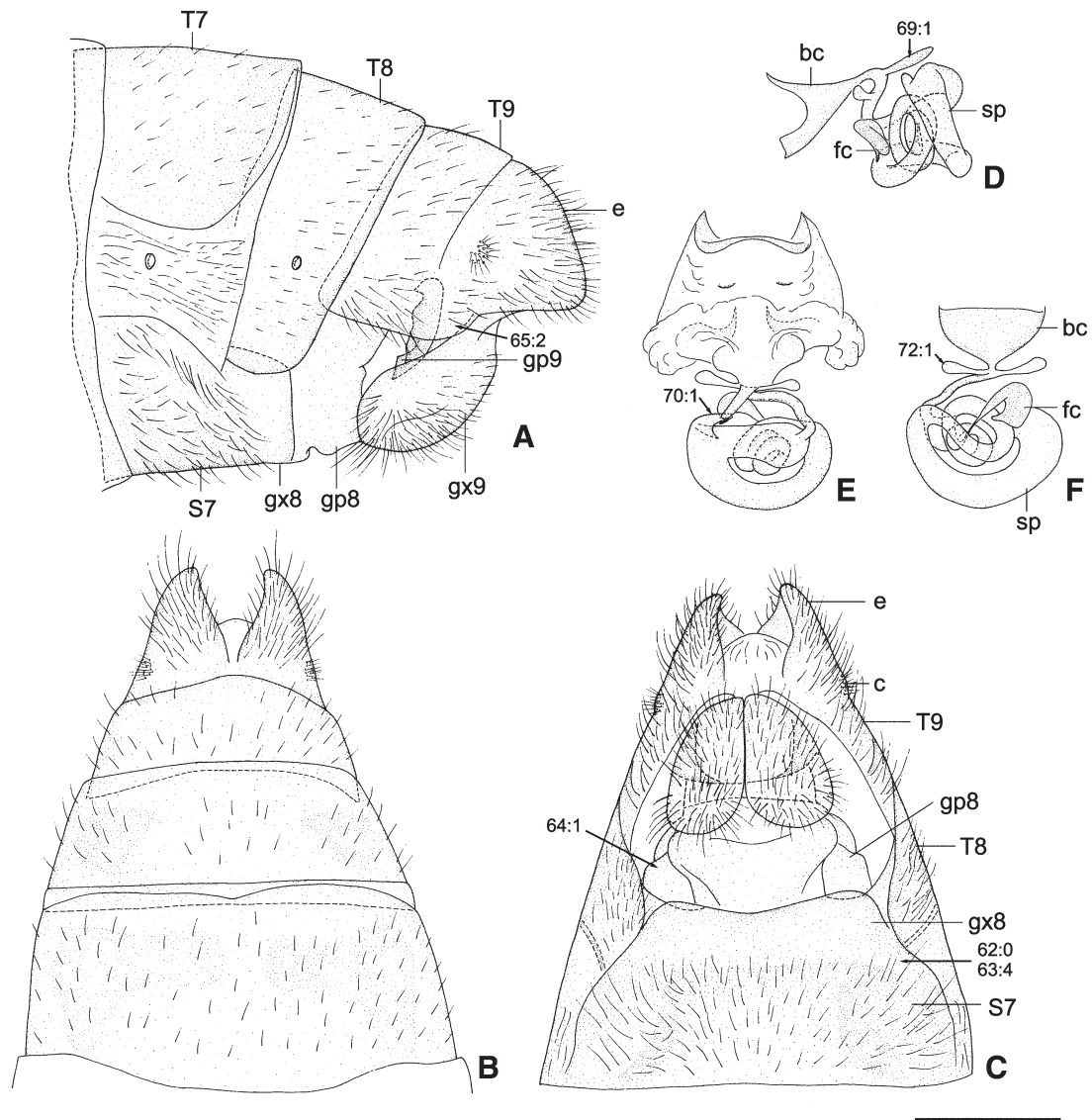


Fig. 6. *Allomantispa mirimaculata* sp.n., holotype female. (A) Genitalia, lateral view; (B) genitalia, dorsal view; (C) genitalia, ventral view; (D) bursa copulatrix and spermatheca, lateral view; (E) bursa copulatrix and spermatheca, dorsal view; (F) bursa copulatrix and spermatheca, ventral view. Abbreviations: T7–9, tergite 7–9; S7, sternite 7; c, callus cercus; e, ectoproct; gx8–9, gonocoxite 8–9; gp8–9, gonapophysis 8–9; bc, bursa copulatrix; fc, fertilization canal; sp, spermatheca. Scale bars: 1.0 mm.

broadened tips. Mediuncus rather narrow, extended anterior to gonocoxites, slightly up curved basally, in ventral view of about uniform width, posteriorly weakly sclerotized. Pseudopenis slender-elongate, distinctly sclerotized, and directed posterodorsad with acutely apex. Hypandrium internum deep, not curved, strongly pigmented.

Type material. Holotype ♂, CHINA: Xizang Autonomous Region (=Tibet), Motuo County, 80 K (=80 km point of road from Bomi County to Motuo County, 29°39'59.7"N, 95°29'45.4"E, 1000 m a.s.l.), 8.viii.2012, Xiaodong Yang (CAU) Paratype 1 ♂, CHINA: Xizang Autonomous Region, Motuo County, 1900 m, 28.vii.2014, Xiaodong Yang (PCW).

Etymology. The specific epithet '*tibetana*' refers to the type locality, Tibet, of the new species. An adjective in the feminine gender.

Distribution. This species is currently known only from Motuo of the Xizang Autonomous Region in southwestern China.

Remarks. *Allomantispa tibetana* sp.n. is probably restricted to the region with subtropical rainforest in a relatively low-altitude area of Motuo. The holotype of the new species was found when it dropped serendipitously onto the collector. The collector tried to find more specimens in the collecting

site of the holotype using sweeping net and light trap, but no additional specimens could be found. One month later after the acceptance of this manuscript, another male of this species was collected, and therefore, added as a paratype of this species.

***Allomantispa mirimaculata* Liu & Ohl sp.n.**

<http://zoobank.org/urn:lsid:zoobank.org:act:35D3E27B-C023-404D-B2B9-FEF9212A23AD>

(Figs 5, 6)

Description of holotype female. Measurements (mm) and ratios: Minimum frontal eye distance (WBE) 1.20; maximum frontal head width including eyes (WAE) 2.70. Pronotal length, measured along dorsal midline (LP) 3.40; pronotal width at maculae (WAM) 1.50. Maximum fore femoral length (LFF) 4.50; maximum fore femoral width (WFF) 1.00; fore femoral ratio (length: width) (LFF: WFF) 4.50. Maximum fore tibial length (LFT) 3.50. Fore femoral length: fore tibial length (LFF: LFT) 1.29. Maximum mid femoral length (LMF) 2.70; mid femoral ratio (midfemoral length: head width including eyes) (LMF: WAE) 1.00. Maximum forewing length (LFW) 23.2; maximum forewing width (WFW) 8.20; forewing ratio (length: width) (LFW: WFW) 2.83. Maximum forewing pterostigma length (LFPt) 5.0; maximum forewing pterostigma width (WFPt) 0.70. Maximum hind wing length 20.3; maximum hind wing width 6.7; hind wing ratio (length: width) 3.03. Total body length 17.9.

Coloration (Fig. 5): Head pale yellowish-brown, frons with a black transverse stripe, vertex with a broad blackish-brown transverse marking on posterior 1/2 and with a narrow, sinuate, transverse stripe near antennal bases. Compound eyes glossy grey, but blackish-brown in living specimen. Antennae blackish-brown except for scape pale yellowish-brown. Mouthparts yellow; mandible with distal 1/2 blackish brown, maxillary and labial palpi blackish-brown but yellowish on joints between segments as well as tips of terminal segments. Pronotum pale reddish-brown, with a pair of black vittae along lateral margins, and dorsally with a pair of faintly blackish markings on anterior 1/2 and a faintly blackish marking at middle of posterior 1/2; maculae black. Pterothorax blackish-brown with some irregular-shaped yellowish spots. Foreleg: coxa brown, with a longitudinal pale stripe on proximal 1/2; trochanter pale brown; femur brown, major spine yellow with proximal 1/2 and tip blackish brown, all other minor spines, four of which much larger than others, yellow with blackish-brown tips; tibia blackish-brown, with inner side largely yellow, and with yellow markings at base, middle and apex of outer side; tarsi yellow, with proximal 2/3 of tarsomere 1 and entire tarsomere 5 blackish-brown, tarsal claws yellow with distal 1/2 reddish-brown. Mid leg: yellow with coxa largely blackish-brown; femur with a blackish-brown marking respectively on proximal 1/3 and subapical portion; tibia with a blackish-brown marking respectively at proximal 1/3 and subapical portion; tarsal claws reddish-brown on distal 1/3. Hind leg: with same coloration and marking patterns as mid leg. Forewing: transparent, posterior margin with a brown edging, which is slightly broadened between MP and CuP; four dark brown markings present on 2sc-r, 2r-rs, 3r-rs, and a crossvein

between distal branches of Rs; pterostigma purplish-yellow; all veins alternately blackish-brown and yellow. Hind wing: transparent, three dark brown markings present on 2sc-r, 2r-rs and 3r-rs; veins alternately blackish-brown and yellow except for costal crossveins and stem of CuA blackish-brown. Abdomen greyish-brown, pleural region yellow-brown, sternites 1–7 laterally with blackish stripes.

Morphology: Head (Fig. 5A) sub-trapezoidal in frontal view, moderately setose, vertex distinctly domed, with complete epicranial suture. Antenna with 43 segments. Pronotum (Fig. 5) densely setose, dorsally with a number of Stitz organs; a pair of small glabrous maculae present. Pterothorax robust, mesonotum sparsely setose, but metanotum glabrous. Legs densely setose. Wings finely setose on veins and margins. Forewing (Fig. 5B) distinctly widened at middle; 20–21 crossveins present on costal region; R distally with two forked branches, radial region subdivided by three r-rs crossveins; Rs with eight main branches, each distally with two simple or forked sub-branches; MA distally with one simple and one forked branches; MP with two main branches, each of them distally with two simple or forked sub-branches; CuA distally with three simple branches, CuP distant to 1A, distally with two simple branches; 1A with two branches, 2A with two branches, 3A simple; gradate crossveins in two series. Hind wing (Fig. 5B) with 21 crossveins on costal region; R distally with two forked branches, radial region subdivided by three r-rs crossveins; Rs with eight main branches, each distally with two simple or forked sub-branches; MA distally with one simple and one forked branches; MP with two main branches, each of them distally with two simple or forked sub-branches; CuA distally with four simple branches, CuP absent; 1A with two branches, 2A and 3A simple; gradate crossveins in two series. Abdomen sparsely setose on segment 1–6 but densely setose on segments 7–10.

Female genitalia (Fig. 6): Sternite 7 densely setose, posteriorly fused with completely bald gonocoxite 8 into a subtrapezoidal sclerite, which is slightly concave on posterior margin; crumena absent. Gonapophysis 8 present a robust, subcylindrical sclerite with a pair of lateral sclerites, having an opening connecting to bursa copulatrix. Tergite 9 fused with ectoprocts ventrally. Gonocoxite 9 ovoid in lateral view, largely separated with tergite 9, only with posterodorsal portion fused with ectoproct; gonapophysis 9 strongly sclerotized, connecting to inner side of gonocoxite 9 at its anterodorsal portion. Ectoproct subtriangular. Bursa copulatrix strongly sclerotized, funnel-shaped, anteriorly produced into a digitiform lobe, posterodorsally connected with a sclerotized and strongly rugose structure; spermatheca proximally with a pair of laterally produced, ball-like lobes, and with a short additional lobe nearly at proximal 1/3; fertilization canal broad, distally with an additional projection.

Type material. Holotype ♀, MYANMAR: Sagaing State, Htamanthi Wildlife Reserve Basecamp, 25°17'40.3"N, 95°27'43.3"E, 10–21.iii.2013, Ross Piper, BBC Expedition, BMNH(E) 2013-132 (BMNH).

Etymology. The specific epithet '*mirimaculata*' is derived from the Latin *miri*-, bizarre, and *maculatus*, marking, in

reference to the spectacular cephalic and wing marking patterns of the new species. An adjective in the feminine gender.

Distribution. This species is currently known only from Htamanthi Wildlife Reserve of the Sagaing State in northern Myanmar.

Remarks. Although only the female is known, *A. mirimaculata* **sp.n.** can be easily distinguished from *A. tibetana* **sp.n.** by the marking pattern on the body and wings, wing shape and by the presence of only one pair of maculae.

The holotype of *A. mirimaculata* **sp.n.** was serendipitously collected by Ross Piper in the Htamanthi Wildlife Reserve during the dry season. It was flying during the day under the canopy of a tropical evergreen and semi-evergreen forest.

Phylogenetic analyses

The aligned matrix comprised 4279 characters, including 4205 DNA sequence characters and 74 morphological characters. Of the 28 taxa included in the matrix, all were scored for most morphological characters where possible, whereas 19 were represented by DNA sequence data for at least one locus. Taxa for which only morphological scoring was available included *Calomantispa*, *Rhachiberothera*, †*Archaeodrepanicus*, †*Mesomantispa*, †*Promantispa*, †*Symphrasites*, †*Doratomantispa* and †*Liassochrysa*. After exclusion of the third positions of protein encoding genes, the remaining 3057 characters comprised 2131 constant characters, 302 single apomorphies and 625 phylogenetically informative characters. Parsimony analysis of the combined dataset yielded six most-parsimonious trees (length = 2440 steps; consistency index C.I. = 0.51; retention index R.I. = 0.43). A tree with a very similar topology was recovered from the Bayesian analysis and a consensus of the trees recovered from the Bayesian and parsimony analyses is presented as Fig. 7. An heuristic parsimony analysis of the 74 morphological characters alone yielded nine most-parsimonious trees of length 183 steps (C.I. = 0.49; R.I. = 0.76). A consensus of these most-parsimonious trees (Fig. 8) recovered the monophyly of Mantispidae, Berothidae and Rhachiberotheridae. Relationships among the families in this part of the tree were moderately supported, and Rhachiberotheridae was recovered to be the sister group of Mantispidae in all analyses. Although under parsimony Berothidae were sometimes not recovered as monophyletic, in the Bayesian analysis Berothidae were recovered as monophyletic with strong statistical support. Berothidae were recovered as sister to Rhachiberotheridae + Mantispidae in the Bayesian analysis, but equivocally supported in the parsimony analysis. Based on the molecular data only (Figure S1), the internal phylogeny was poorly resolved concerning the relationships among Berothidae, Rhachiberotheridae and Mantispidae and not used for further discussion.

Mantispidae was always recovered as a weakly supported monophylum and supported by four synapomorphic character states [i.e. pronotum elongate (2:1) and ventrally fused (4:1); prostrate setae present on ventral margin of fore tibia (12:1)

(reversed in Mantispiniae); mid and hind tarsi sub equal in length (20:1)] (Fig. 8). The enigmatic †*Mesomantispa*, comprising †*Mesomantispa* and †*Archaeodrepanicus*, were always recovered as a clade either sister to the remaining Mantispidae (morphology only) or in a larger polytomy with the other subfamilies (combined data) and is recognised as a subfamily of Mantispidae rather than a separate family. Symphrasinae, including the extant New World genera *Anchieta*, *Plega* and *Trichoscelia* and the extinct †*Symphrasites*, was usually placed as an intermediate clade, although †*Symphrasites* was placed as part of a larger polytomy and only rarely recovered in some parsimony trees in a monophylum with the remaining Symphrasinae. Although *Plega* and *Anchieta* were recovered with *Trichoscelia* as a monophyletic group supported by numerous homoplasious and nonhomoplasious character states, statistical support for the internal relationship among the three genera was contradictory between Bayesian and parsimony analyses. In all analyses, Drepanicinae were monophyletic except for †*Doratomantispa*. †*Doratomantispa* was always recovered in an isolated position in a polytomy with the other clades of Mantispidae and †*Symphrasites*. Statistical support for the clade comprising Drepanicinae, Calomantispinae and Mantispiniae was moderate to weak in all analyses. Nonhomoplasious changes supporting this clade include a short basal spine on the fore femur (11:1) and the stem of hind wing MA separate from the stem of MP (40:1). Calomantispinae, comprising only two genera (*Calomantispa* and *Nolima*) was always recovered as monophyletic, supported by synapomorphies such as a large bulb proximally on the spermatheca (71:1) and an enlarged male sternite 9 (46:1), this subfamily was always recovered in a sister group relationship with Mantispiniae. In Drepanicinae (exclusive of †*Doratomantispa*) the Australian genus *Theristria* was typically recovered as sister to the remaining genera. The South American genera *Gerstaeckerella* and *Drepanicus* were always recovered as a strongly supported sister group, and as an intermediate grouping or in a polytomy with all drepanicine genera exclusive of *Theristria*. The sister grouping of these two South American genera is supported by multiple homoplasious as well as nonhomoplasious character states, including enlarged gonocoxite (50:1), globose lateral lobes of hypomere (60:1) and female spermatheca with spherical lobes proximally (72:1). In the combined analysis, *Allomantispa* **gen.n.** was recovered in a clade of Old World drepanicine genera, comprising the extant Australian genus *Ditaxis*, and the extinct Palaeartic genera †*Liassochrysa* and †*Promantispa*. *Allomantispa* **gen.n.** was frequently placed as either sister to *Ditaxis* or as an intermediate between *Ditaxis* and the fossil genera. †*Liassochrysa* and †*Promantispa* were always recovered as sister genera with strong statistical support.

Discussion

Family-level relationships

Previous morphological studies have considered Dilaridae, Berothidae, Rhachiberotheridae and Mantispidae combined as a monophyletic group (referred to as the Dilaridae clade) based on morphology alone (e.g. Withycombe, 1925; MacLeod, 1964;

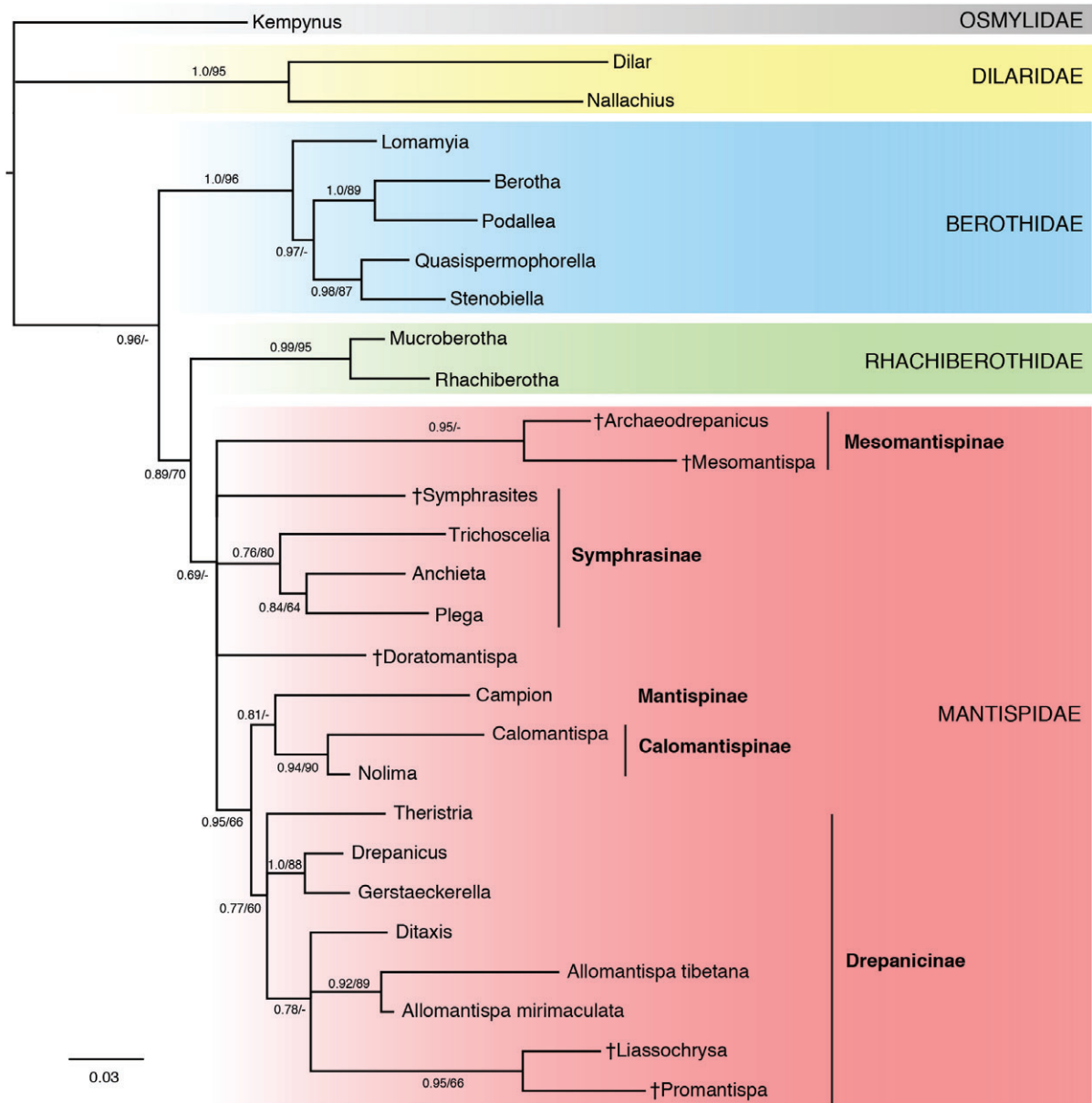


Fig. 7. Phylogeny of higher-level relationships among Rhachiberothidae, Berothidae and subfamilies of Mantispidae based on a consensus of topologies resulting from Bayesian and parsimony analyses of DNA sequence data and 74 morphological characters. Fossil taxa are indicated with a dagger symbol (†). Bayesian posterior probabilities (PP) and parsimony bootstrap (BS) values are indicated on unambiguous branches.

Aspöck *et al.*, 2001; Aspöck & Aspöck, 2008), but studies using DNA sequences alone or in combination with morphological data have repeatedly recovered Dilaridae as a more distantly related group (Winterton, 2003; Haring & Aspöck, 2004; Winterton *et al.*, 2010; Yang *et al.*, 2012). Our analysis could not test this hypothesis, as Dilaridae were included here as an outgroup, but it was clear that the clade comprising Mantispidae, Berothidae and Rhachiberothidae represent a well-supported monophylum. Inclusion of Dilaridae is still debatable, requiring analysis with more extensive taxon sampling and characters.

Rhachiberothidae comprise three extant genera restricted to the Afrotropical region, but with a more extensive distribution evident in the geological record. Multiple genera are described from various amber deposits including Palaeogene-aged Baltic (Makarkin & Kupryjanowicz, 2010) and Cretaceous-aged deposits in North America (Grimaldi, 2000; McKellar & Engel, 2009), Europe (Nel *et al.*, 2005) and South-east Asia (Engel, 2004). The phylogenetic placement of Rhachiberothidae has been contentious, proposed as a subfamily of Berothidae (Tjeder, 1959; MacLeod & Adams, 1967; Makarkin & Kupryjanowicz, 2010; Winterton *et al.*, 2010), a subfamily of

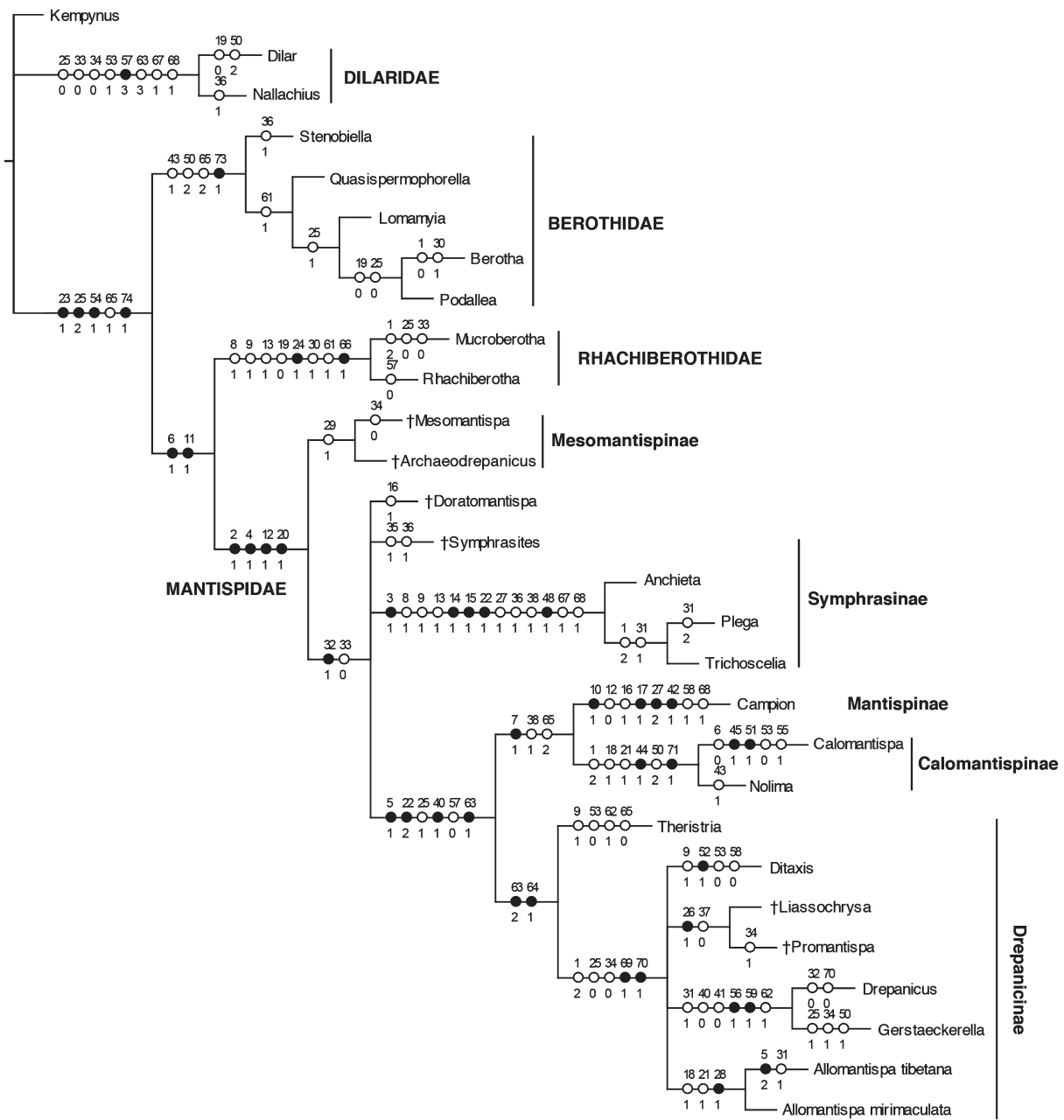


Fig. 8. Phylogeny of higher-level relationships among Rhachiberothidae, Berothidae and subfamilies of Mantispidae with morphological character state changes mapped onto the tree. Topology represents the strict consensus tree of the nine most-parsimonious trees recovered from the parsimony analysis of 74 morphological characters.

Mantispidae (Willmann, 1990) or as a separate family (Aspöck & Mansell, 1994; Grimaldi & Engel, 2005). In no analysis herein was Berothidae or Mantispidae rendered paraphyletic by Rhachiberothidae. Instead it was recovered as sister to Mantispidae, although with only weak to moderate statistical support, or in a polytomy with both Berothidae and Mantispidae, suggesting that this group could minimally be regarded as a separate family, or possibly as a subfamily sister to the remaining Mantispidae as proposed by Willmann (1990). Further complicating

this issue, Makarkin *et al.* (2013) recently described the family †Dipteromantispidae from Cretaceous-aged deposits, comprising two genera of distinctive lacewings with raptorial forelegs, reduced wing venation and highly reduced hind wings (putative ‘halters’). Clearly this new family is very closely related to Rhachiberothidae and Mantispidae. Considering the only moderate statistical support for the various family relationships recovered here, as well as the rampant, but unlikely convergent, occurrence of raptorial forelegs in families in this part of the

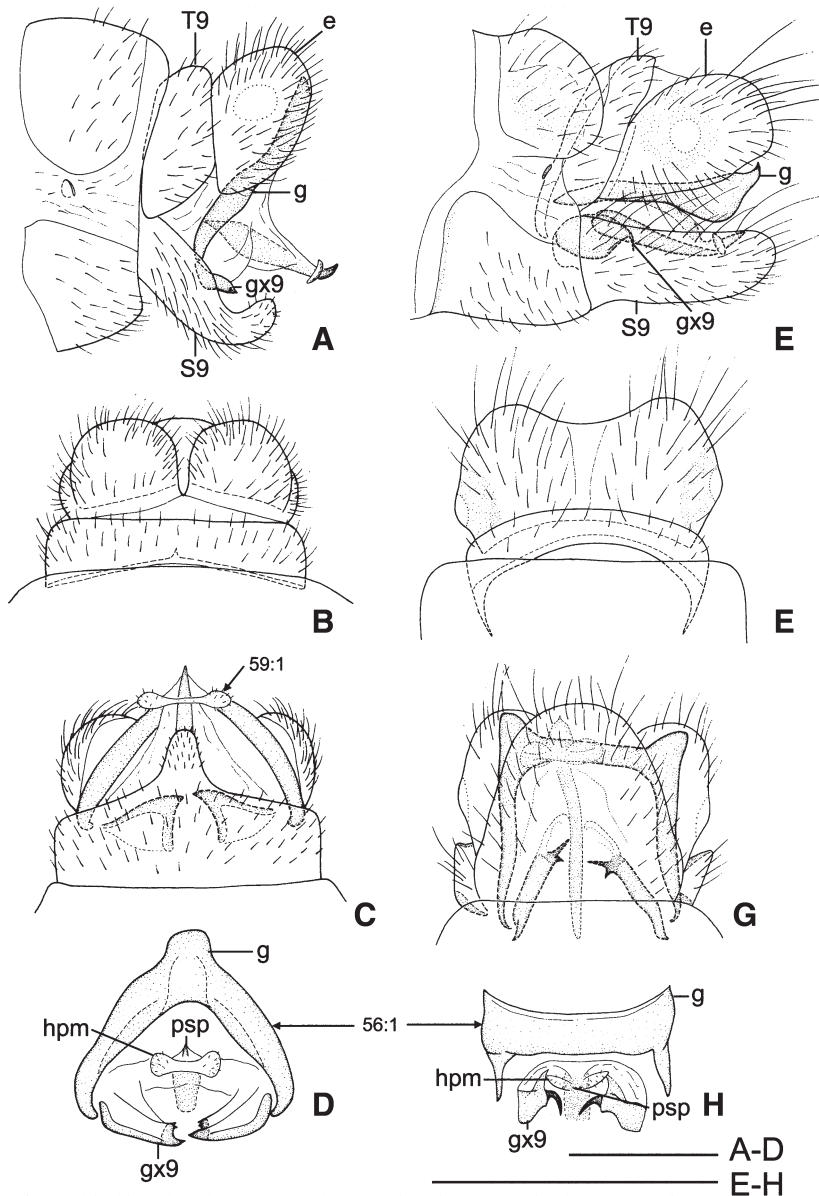


Fig. 9. Male genitalia of *Drepanicus* and *Gerstaeckerella*. (A–D) *Drepanicus chrysopinus* Brauer; (E–H) *Gerstaeckerella chilensis* (Hagen). (A, E) Genitalia, lateral view; (B, F) genitalia, dorsal view; (C, G) genitalia, ventral view; (D, H) internal genitalia, caudal view. Abbreviations: T9, tergite 9; S9, sternite 9; e, ectoproct; gx9, gonocoxite 9; g, gonarcus; hpm, hypomere; psp, pseudopenis. Scale bars: 1.0 mm.

lacewing evolutionary tree, the issue of rank for Rhachiberothidae and evolution of raptorial forelegs in Neuroptera will clearly require further study in a broader context of neuropteran phylogeny.

Mantispidae subfamilial relationships

The monophyly of Mantispidae is well established based on a series of morphological and life history synapomorphies, with an origin for the family estimated to be around the Late Triassic to early Jurassic based on evidence from both fossil (Wedmann & Makarkin, 2007; Jepson *et al.*, 2013) and molecular data (Winterton *et al.*, 2010). Internal relationships among Mantispidae subfamilies have been difficult to elucidate,

but there is broad consensus among previous authors that †Mesomantispinae are sister to the remaining Mantispidae, with Symphrasinae and Drepanicinae forming intermediate clades, and Calomantispinae and Mantispinae being highly derived (Penny & da Costa, 1983; Lambkin, 1986a; Wedmann & Makarkin, 2007). Our results similarly recover †Mesomantispinae as a monophyletic subfamily sister to the remaining Mantispidae. Jepson *et al.* (2013) recently revised the subfamily, recognising four genera (†*Calvifemora* Jepson, Heads, Makarkin & Ren, †*Sinomesomantispina* Jepson, Heads, Makarkin & Ren, †*Archaeodrepanicus* and †*Mesomantispina*). Jepson *et al.* (2013) could not identify any synapomorphies for the subfamily, and there was only one diagnostic character state identified in this analysis; the forewing CuA is pectinate (29:1) in †Mesomantispinae and is synapomorphic relative to other

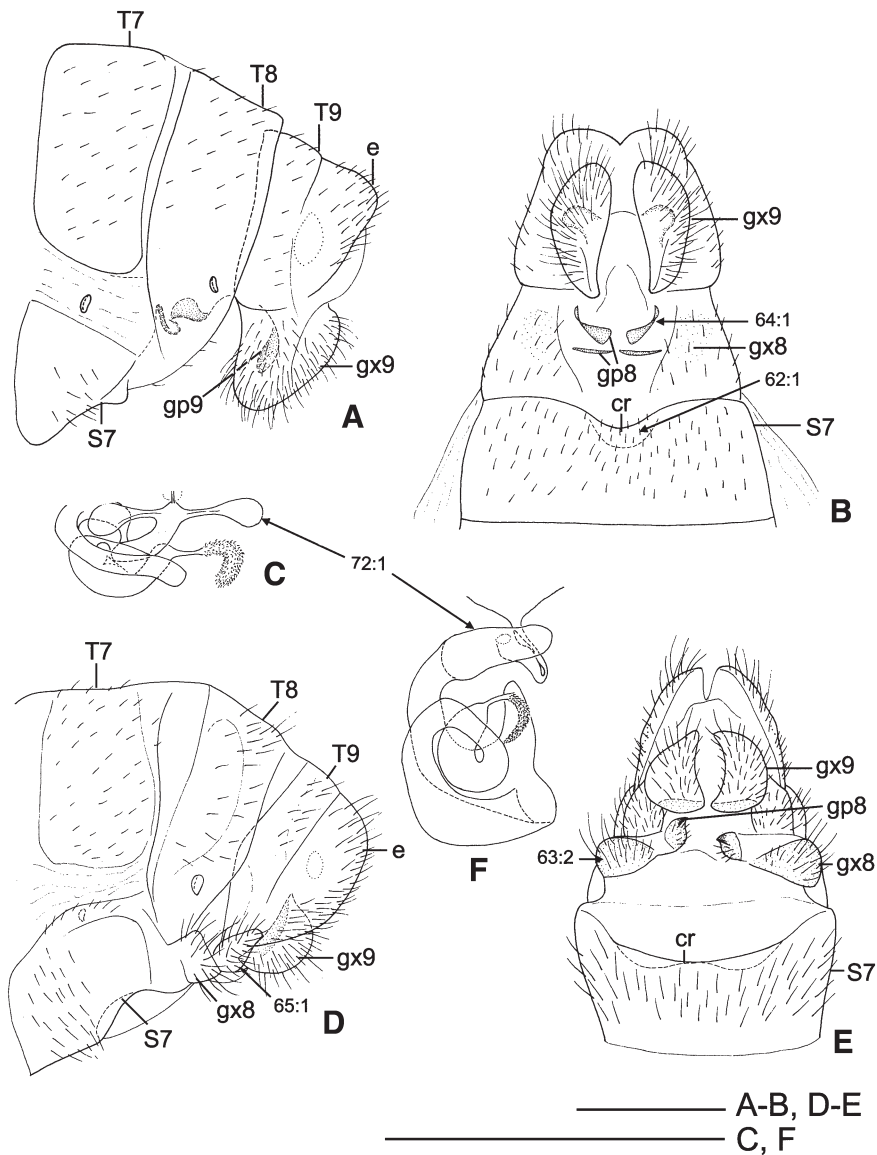


Fig. 10. Female genitalia of *Drepanicus* and *Gerstaeckerella*. (A–C) *Drepanicus chrysopinus* Brauer; (D–F) *Gerstaeckerella chilensis* (Hagen). (A, D) Genitalia, lateral view; (B, E) genitalia, ventral view; (C, F) bursa copulatrix and spermatheca, ventral view. Abbreviations: T7–9, tergite 7–9; S7, sternite 7; cr, crumena; e, ectoproct; gx8–9, gonocoxite 8–9; gp8–9, gonapophysis 8–9. Scale bars: 1.0 mm.

Mantispidae, although a similar condition is also found in other families (e.g. Osmylidae). Khramov (2013) recently described two new species in the genus †*Mesithone* Panfilov from late Jurassic-aged deposits (Karatau), and placed †*Mesithone* with †*Mesomantispa* in the subfamily †Mesithoninae (= †Mesomantispinae) within Mantispidae. †*Mesithone* has previously been postulated as a stem group of Rhachiberothidae or Berothidae, or both, based solely on wing venation (Grimaldi & Engel, 2005). The new species are more complete specimens with raptorial forelegs and short prothorax clearly evident, lending support for placement as a stem-group of Rhachiberothidae, although several wing venation characters provide evidence in favour of the present placement within †Mesomantispinae as

a subfamily of Mantispidae. The wealth of new fossil species of Mantispidae, Berothidae and Rhachiberothidae described recently, as well as new families (e.g. †Dipteromantispidae), indicates that the issues of intra- and interfamilial relationship among these families will remain in flux for some time as this historical diversity is documented.

Symphrasinae comprise three extant genera in the New World (*Plega*, *Anchieta* and *Trichoscelia*) and a single fossil genus from the Mid-Eocene deposits in Germany (Wedmann & Makarkin, 2007). As previously proposed by other authors (e.g. Penny & da Costa, 1983; Lambkin, 1986a), our results confirm that the subfamily is an intermediate clade between †Mesomantispinae and more derived mantispids. Only the three

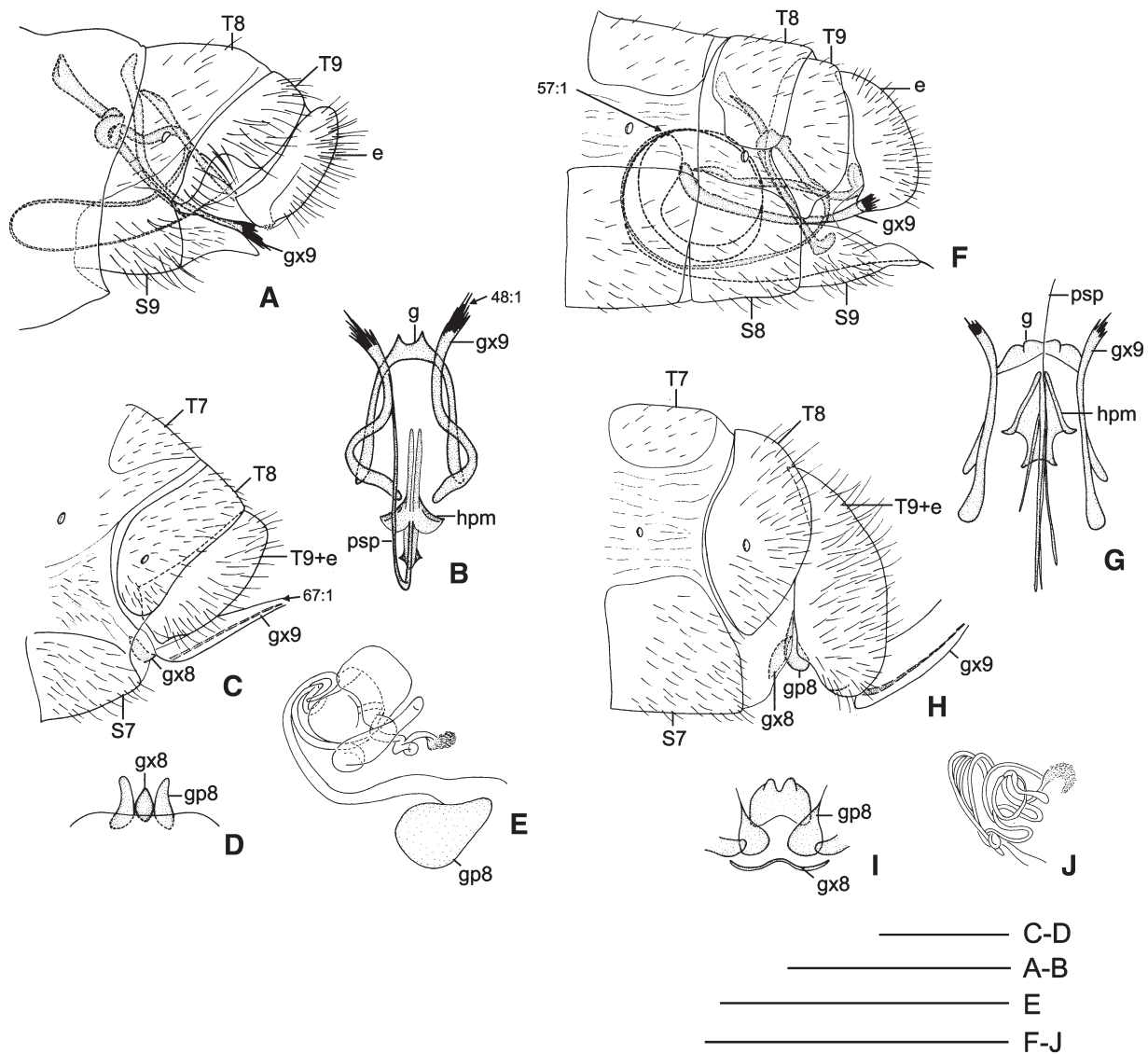


Fig. 11. Genitalia of *Plega* and *Trichoscelia*. (A–E) *Plega fasciatella* (Westwood); (F–J) *Trichoscelia anae* Penny. (A, F) Male genitalia, lateral view; (B, G) internal genitalia, ventral view; (C, H) female genitalia, lateral view; (D, I) female gonapophysis 8 and base of bursa copulatrix, ventral view; (E, J) bursa copulatrix and spermatheca, lateral view. Abbreviations: T7–9, tergite 7–9; S7, sternite 7; e, ectoproct; gx8–9, gonocoxite 8–9; gp8–9, gonapophysis 8–9; g, gonarcus; hpm, hypomere; psp, pseudopenis. Scale bars: 1.0 mm.

extant genera of Symphrasinae form a well-supported monophylum, whereas †*Symphrasites* is recovered in a larger polytomy. This is probably due to the limited number of characters scored for the taxon, including the numerous synapomorphic genital characters of Symphrasinae not preserved in the fossil specimen. The clade representing the extant genera has relatively strong support and numerous unique character state changes to support it. Internal relationships among these extant genera are contradictory based on the analytical method used, and with relatively weak statistical support in general. The limited number of mutually exclusive synapomorphies identified to delineate *Trichoscelia* and especially *Anchieta* and *Plega*, suggest that the generic limits of these genera should be re-evaluated.

The clade comprising Drepanicinae, Mantispinae and Calomantispinae was previously defined by Lambkin (1986a) based on several synapomorphies in the thorax, fore femur (e.g. 11:2) and wing (e.g. 40:1), and is supported by the combined data presented here. Drepanicinae are an archaic and heterogeneous subfamily with extant representatives in Australia, South America and now Asia, with extinct representatives throughout the rest of the Palaearctic and Oriental regions (Fig. 13). It is clear from both the molecular and morphological data here, that the subfamily is monophyletic and sister to Calomantispinae + Mantispinae. †*Doratomantispa* is an extinct genus described from the Cretaceous Burmese amber. Poinar & Buckley (2011) tentatively placed the genus in Drepanicinae as

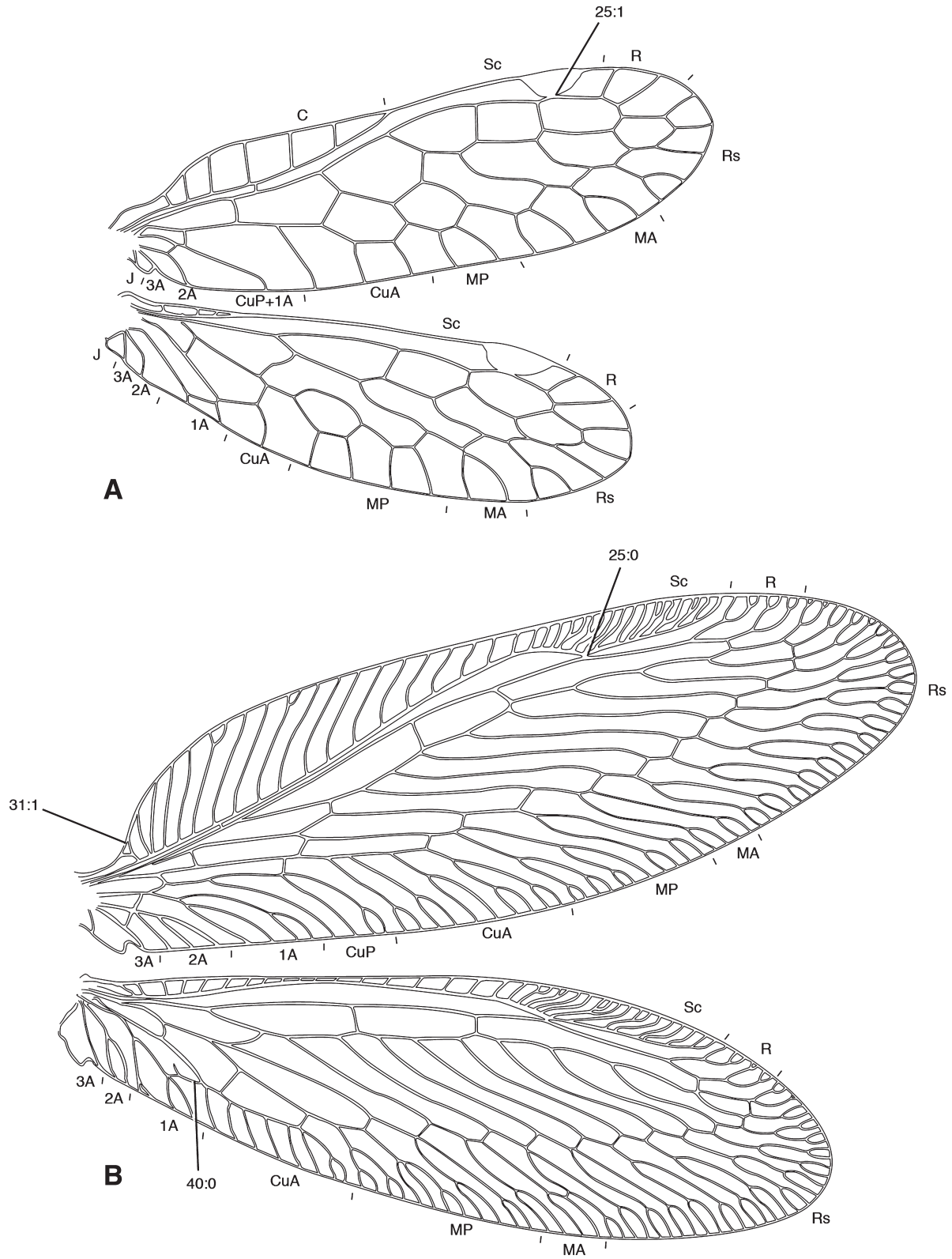


Fig. 12. (A, B) Wing venation of *Nolimina pinal* Rehn and *Drepanicus chrysopinus* Brauer (female). Scale bar: 2.5 mm.

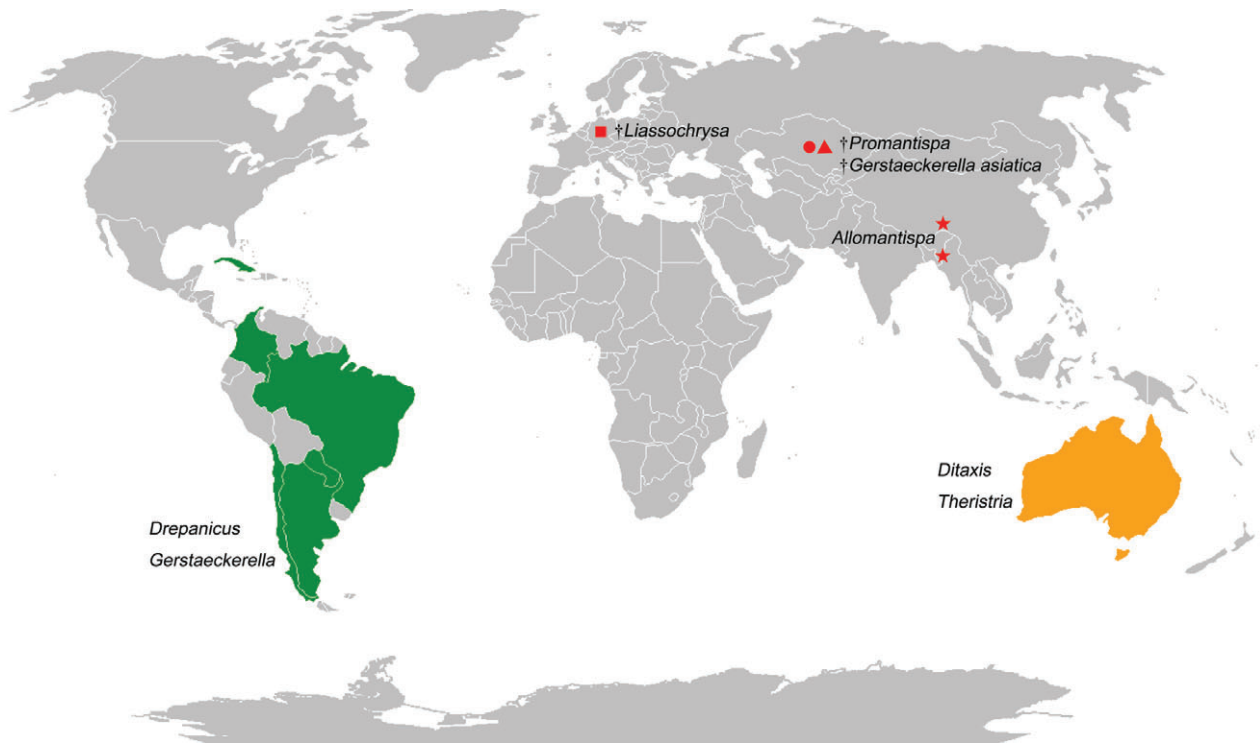


Fig. 13. Distribution map of extinct and living Drepanicinae genera (Mantispidae).

it displays a mixed combination of wing and leg characteristics that suggest that it is an intermediate form between Symphrasinae and Drepanicinae. For example, †*Doratomantispa* has marginal wing trichosors found extensively in both wings, a character state absent in all other Drepanicinae, Mantispinae and Calomantispinae (22:2), and lacks pronotal maculae, the presence of which is synapomorphic for these derived subfamilies (5:1). It is recovered in our analyses outside of Drepanicinae, in a polytomy with †*Symphrasites* and the remaining Mantispidae, and is thus considered *incertae sedis* in the family.

Among the remaining Drepanicinae, South America genera (*Gerstaeckerella* and *Drepanicus*) form a strongly supported sister-group relationship based on multiple synapomorphies, many found in the male and female genitalia. Among the Old World genera, the species-rich Australian genus *Theristria* (24 species) occupies an isolated position, not grouping with any other genus. Based on the total evidence analysis, the other Australian genus *Ditaxis* forms a clade with *Allomantispia*, as well as two Jurassic-aged fossil taxa, †*Liassochrysa* and †*Promantispia*. Relationships among drepanicine genera have been difficult to resolve. Lambkin (1986a) was unable to determine the relationship among these genera, although he did present a list of potentially informative characters that may be of use in future studies. †*Liassochrysa* was transferred to Mantispidae from Chrysopidae by Wedmann & Makarkin (2007). They suggested that it was a stem mantispid closely related to †*Promantispia*. †*Promantispia* was considered previously as an indeterminate taxon by Lambkin (1986a) and Willmann

(1994), either a stem group of higher Mantispidae or closely related to Drepanicinae. A well-supported sister-group relationship between †*Liassochrysa* and †*Promantispia* is indeed recovered here, but the sister pair instead occupy a highly derived position in Drepanicinae. Wedmann & Makarkin (2007) describe the similarity in wing venation between †*Liassochrysa* and *Ditaxis*, which is also a characteristic of this analysis, with the two genera closely related based on characters like regular gradate series; this feature is also found in *Allomantispia* **gen.n.** †*Liassochrysa* and †*Promantispia* are known from the Jurassic to Cretaceous-aged deposits and are clearly placed in Drepanicinae based on our results, supporting the hypothesis of Wedmann & Makarkin (2007) that Drepanicinae (along with †*Mesomantispinae* and *Symphrasinae*) were already well established during the early Jurassic. Current distributions of Drepanicinae in Australia, South America and Asia likely represent relicts of a much broader distribution of the subfamily with fossil taxa found in the Palaearctic and Oriental regions. This is particularly evident with *Gerstaeckerella*, with six extant species occurring in South America and a seventh, extinct species from the Eastern Palaearctic (Wedmann & Makarkin, 2007).

Calomantispinae and Mantispinae form a monophylum in our analysis, which is consistent with the previous hypothesis accepted by various authors (Lambkin, 1986a; Wedmann & Makarkin, 2007). Calomantispinae comprise two disparately distributed genera in Central and South America (*Nolima*) and Australia (*Calomantispia*). Their sister-group relationship is strongly supported by multiple apomorphies, including the bifid tarsal claws (18:1, 21:1), enlarged male sternite 9 (44:1)

and female spermatheca with a proximal bulb (71:1) (see also Lambkin, 1986a).

Mantispinae are clearly a highly derived and species-rich clade of Mantispidae, but their position relative to the remaining subfamilies is problematic. The likely sister-group relationship between Mantispinae and Calomantispinae is supported by our analysis, although weakly (cf. Figs 7, 8). Mantispinae are represented here only by a single genus (*Campion*) and the relationship among the numerous genera of this diverse subfamily was not the focus of this study. Further research focussing on this subfamily using a combination of DNA and morphological data is necessary before we can fully understand the evolution of this clade.

Conclusions

The discovery of *Allomantispa* gen.n. shows that Drepanicinae are still living in Asia and represent a relict lineage that originated at least in the early Jurassic. Our results present the first comprehensive phylogenetic analysis of Mantispidae and related families based on a total evidence approach combining morphological scoring with DNA sequences in a simultaneous analysis. We also provide quantitative evidence for the systematic placement of previously enigmatic fossil taxa such as †*Mesomantispa*, †*Liassochrysa* and †*Promantispa*, and document another important empirical example of the utility of combined molecular and morphological analyses in placing fossil taxa within the context of closely related extant forms (e.g. Winterton & Makarkin, 2010; Yang *et al.*, 2012). The monophyly of Mantispidae is confirmed here along with the placement of †*Mesomantispinae* as the sister subfamily to a clade comprising Symphrasinae + remaining Mantispidae. Drepanicinae are confirmed as a monophyletic assemblage sister to Mantispinae and Calomantispinae. The phylogenetic placement of †*Symphrasites* and especially †*Doratomantispa* remains enigmatic, and the latter at least is considered *incertae sedis* at this stage. This study is hoped to build on previous foundational studies on Mantispidae evolution (e.g. Lambkin, 1986a) and provide additional data for future studies into relationships of the diverse and species rich subfamily Mantispinae, where the bulk of Mantispidae diversity currently resides.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12096

Figure S1. Strict consensus tree from the four MPTs (C.I. = 0.54, R.I. = 0.39; length = 1881) inferred from the parsimonious analysis based on molecular data only. Bootstrap values over 50 are indicated at nodes.

Table S1. Morphological matrix.

Table S2. Primer sequences used to amplify and sequence genes.

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Appendix

Morphological character state descriptions.

1. Head: (0) with vertex flat (Lambkin, 1986a: fig. 16); (1) with cephalic tubercles (Aspöck *et al.*, 1980: fig. 421); (2) with vertex domed (Lambkin, 1986a: fig. 11). Generally, the adult head in Neuroptera is flat on the vertex although there are ocellar tubercles in Osmyliidae. However, Dilariidae and some genera of Berothidae and Rhachiberthidae have cephalic tubercles. In some genera of Rhachiberthidae and Mantispidae, the vertex is distinctly domed as a single tubercle.
2. Pronotum: (0) not elongate posterior to fore coxae (Willmann, 1990: fig. 7); (1) elongate posterior to fore coxae (Willmann, 1990: fig. 10). The fore coxae are generally located at the base of prothorax in Neuroptera, whereas in Mantispidae, they are located distant from the base of prothorax, forming pronotum elongate posterior to fore coxae.
3. Pronotum: (0) lacking transverse suture (Willmann, 1990: fig. 7); (1) having transverse suture posteriorly on pronotum, giving appearance of weakly separated pair of sclerites (Ferris, 1940: fig. 8). Lambkin (1986a) referred to image in Ferris (1940) of the prothorax of *Plega* (p. 44, figure 8) and interpreted this as two sclerites, following the speculation by Ferris (1940) that the origin of this structure was derived from secondary sclerotization of the intersegmental membrane. This feature is shared by the genera of Symphrasinae.
4. Pronotum: (0) not fused ventrally (Willmann, 1990: fig. 7); (1) ventrally fused into a tubular pronotum (Willmann, 1990: fig. 10).
5. Maculae: (0) absent (Ferris, 1940: fig. 8); (1) one pair (Lambkin, 1986a: fig. 32); (2) two pairs (Fig. 3B).
6. Forelegs: (0) not raptorial; (1) raptorial.
7. Fore femur: (0) not flattened (Lambkin, 1986a: figs. 33, 62); (1) laterally flattened (Lambkin, 1986b: figs. 434, 485). Derived state was used by Lambkin (1986a) as a synapomorphy for Calomantispinae + Mantispidae. This state is constant and well developed among all examined Mantispidae and *Calomantispa*, but poorly developed in at least *Nolima pinal*.
8. Fore femur macrosetae: (0) absent along lateral surface (Lambkin, 1986a: fig. 24); (1) present along lateral surface (Penny, 1982: figs. 10–12; Aspöck & Mansell, 1994: fig. 11). The macrosetae along lateral surface of fore femur spine ridge is present, often as just a few setae distally, in Rhachiberthidae and Symphrasinae.
9. Fore femur: (0) without macrosetae medially; (1) with a row of macrosetae medially. Besides the macrosetae on distal portion of fore femur, there is an additional row of macrosetae, which are much smaller than distal macrosetae, in Rhachiberthidae, Symphrasinae, and two genera (i.e. *Ditaxis* and *Theristria*) of Drepanicinae.
10. Fore femur: (0) as long as fore tibia plus tarsi (Fig. 3F); (1) longer than fore tibia plus tarsi (Lambkin, 1986a: fig. 24). The state 1 was used by Lambkin (1986a) as a synapomorphy for Calomantispinae + Mantispidae. However, in *Calomantispa* and *Nolima* the combined length of the fore tibia and fore tarsus is clearly sub-equal to the fore femur length. Therefore, although somewhat variable in Mantispidae, state 1 appears to represent a synapomorphy for this subfamily only.
11. Fore femur, length of basal spine: (0) absent; (1), short, sub-equal to more distal spines if present (Willmann, 1990: figs. 5, 8); (2) relatively long (Lambkin, 1986a: fig. 33).
12. Fore tibia with prostrate setae: (0) absent; (1) present (Lambkin, 1986a: fig. 23; Poivre, 1978: fig. 4A, B; Poinar & Buckley, 2011: fig. 5). There is a row of thick but very short setae on the ventral margin of fore tibiae in Calomantispinae, Drepanicinae, and Symphrasinae. The prostrate setae are enlarged in †*Doratomantispa*.
13. Male fore tarsus: (0) with five segments; (1) with four segments (Willmann, 1990: fig. 19; Aspöck & Mansell, 1994: fig. 21).
14. Female fore tarsus: (0) with five segments; (1) with four segments.
15. Fore tarsus arrangement: (0) second segment sub-equal in length to remaining segments, terminal on first segment; (1) second segment much longer than remaining segments, arising midway along first segment (Willmann, 1990: fig. 19). State 1 is a synapomorphy for Symphrasinae.
16. Arolium of foreleg: (0) present (Lambkin, 1986a: fig. 23); (1) absent (Lambkin, 1986a: fig. 24). State 1 is a synapomorphy for Mantispidae.
17. Fore tarsal claw: (0) with two claws (Willmann, 1990: fig. 19); (1) with single claw (Lambkin, 1986a: fig. 24). State 1 is a synapomorphy for Mantispidae.
18. Fore tarsal claw: (0) simple, not bifurcated distally (Willmann, 1990: fig. 19); (1) distally bifurcated (Fig. 3G). Lambkin (1986a) considered that the distinctly bifid fore tarsal claws strongly support the monophyly of Calomantispinae. However, the presence of bifid fore tarsal claws in *Allomantispa* indicates that this character is also variable among different mantispid subfamilies or genera.
19. Mid and hind tarsi with second segment: (0) longer than 1/2 of first segment (Willmann, 1990: fig. 6); (1) shorter than 1/2 of first segment (Willmann, 1990: fig. 13).

20. Mid and hind tarsi with third segment: (0) longer than fourth segment (Willmann, 1990: fig. 6); (1) as long as fourth segment (Willmann, 1990: fig. 13). The above two characters come from Willmann (1990): character 21, [i.e. 'The second to fourth tarsal segments of the middle and hind legs are subequal in length; the second segment is always less than half as long as the first and the third segment is almost as short as the fourth. The plesiomorphic state, as in *Mucroberotha* and *Rhachiberotha* (Tjeder, 1959), is that the second segment is much longer than broad and more than half as long as the first and the third segment is longer (and narrower) than the fourth']. Willmann (1990) incorporated these two characters into a single character, which was not considered by Aspöck & Mansell (1994). We chose to separate these two characters here due to the slight variability in the states and that we cannot assume that the two characters are dependent.
21. Mid and hind tarsal claws: (0) simple, not bifurcated distally; (1) distally bifurcated (Fig. 3H, I). The distally bifid mid and hind tarsal claws are shared by Calomantispinae and *Allomantispa* **gen.n.**
22. Wing trichosors: (0) present, only one between two veins (Aspöck & Mansell, 1994: fig. 43); (1) present, two to four between two veins (Ferris, 1940: fig. 15); (2) absent. Trichosors are present as a plesiomorphic condition in Neuroptera, but is variously reduced in Mantispidae. Almost the entire wing margin in the three extant genera of Symphrasinae has 2–4 trichosors, whereas in Drepanicinae the trichosors, if present, are restricted to the wing apex and are few in number. In the four fossil genera – †*Archaeodrepanicus*, †*Mesomantispa*, †*Symphrasites* and †*Doratomantispa* – there is only one trichosor between each veinlet. In Calomantispinae and Mantispinae trichosors are absent.
23. Nygmata: (0) present; (1) absent.
24. Vesicae: (0) absent; (1) present (Aspöck & Mansell, 1994: fig. 6).
25. Pterostigma with posterior margin: (0) reaching to Sc (Fig. 2); (1) reaching to R + Sc (Lambkin, 1986a: fig. 27); (2) reaching to R (Ferris, 1940: fig. 15).
26. Forewing MP: (0) straight; (1) sinuate (Ansorge, 1990: fig. 3; Willmann, 1994: fig. 17). The sinuate forewing M vein is present in two fossil genera, †*Liassochrysa* and †*Promantispa*, and it was considered to be a synapomorphy of these two genera (Wedmann & Makarkin, 2007).
27. Forewing MP with branching point from R: (0) near wing base, close to 1m-cu (Lambkin, 1986a: fig. 34); (1) distal to 1m-cu (Ferris, 1940: fig. 15); (2) distal to 1m-cu but proximally deflexed into a small triangular cell (Lambkin, 1986b: fig. 451).
28. Forewing MP with anterior branch approximating Rs + MA: (0) absent; (1) present (Figs 2, 5B). State 1 is present in *Allomantispa* **gen.n.**
29. Forewing CuA: (0) distally with two main branches; (1) multiply pectinate.
30. Forewing 2A and 3A: (0) parallel with each other; (1) tending to form a loop (Aspöck & Mansell, 1994: figs. 6, 17, 29).
31. Forewing humeral crossvein: (0) not recurrent, simple (Lambkin, 1986a: fig. 34); (1) recurrent, bifurcate (Fig. 2); (2) recurrent with multiple branches (Ferris, 1940: fig. 15).
32. Forewing costal crossveins: (0) dense (Aspöck & Mansell, 1994: fig. 43); (1) sparse (Fig. 2). State 0 refers to the forewing costal area having more than 20 crossveins proximal to pterostigma, whereas state 1 refers to the forewing costal area having less than 15 crossveins proximal to pterostigma.
33. Forewing costal crossveins: (0) mostly simple; (1) mostly forked.
34. Forewing gradate crossveins: (0) two series (Fig. 2); (1) one series (Lambkin, 1986a: fig. 78).
35. Forewing sc-r crossveins: (0) 1–2 (Fig. 2; Ferris, 1940: fig. 15); (1) ≥ 3 (Aspöck & Mansell, 1994: fig. 43).
36. Forewing r-rs crossveins: (0) ≥ 3 (Fig. 2); (1) 2 (Ferris, 1940: fig. 15).
37. Forewing distal cup-1a: (0) present (Ansorge & Schluter, 1990: fig. 3; Willmann, 1994: fig. 17); (1) absent (Fig. 2).
38. Hind wing costal area: (0) long, extending to sub distal portion of hind wing (Fig. 2); (1) short, as long as 1/2 of hind wing (Ferris, 1940: fig. 15; Lambkin, 1986b: figs. 404, 452).
39. Hind wing MA: (0) basally connecting to stem of MP (Ferris, 1940: fig. 15); (1) separate (Fig. 2).
40. Hind wing with remnant CuP: (0) present (Ferris, 1940: fig. 15; Aspöck & Mansell, 1994: fig. 43); (1) absent (Fig. 2).
41. Hind wing 2A: (0) bifurcated (Aspöck & Mansell, 1994: fig. 43); (1) simple (Fig. 2).
42. Male abdominal segment 5–6 with protruding gland: (0) absent; (1) present.
43. Male tergite 9: (0) not fused with ectoproct (Fig. 2); (1) fused with ectoproct (Aspöck & Aspöck, 1984: fig. 2).
44. Male sternite 9: (0) not enlarged (Fig. 4A); (1) strongly enlarged and scoop-like (Lambkin, 1986b: fig. 410). State 1 is a synapomorphy of Calomantispinae.
45. Male sternite 9 distally with bristle: (0) absent; (1) present (Lambkin, 1986b: fig. 410). State 1 is an autapomorphy for *Calomantispa*.
46. Male sternite 9 with a large median projection: (0) absent; (1) present (Fig. 4B). State 1 is an autapomorphy for *Allomantispa* **gen.n.**
47. Male gonocoxite 9 distally with cla: (0) absent (Lambkin, 1986b: fig. 463); (1) present (Fig. 4B). The male gonocoxite 9 has at least one distal claw in Drepanicinae and Calomantispinae.
48. Male gonocoxite 9: (0) not slender with branched tip; (1) slender with branched tip (Fig. 9B, G; Ferris, 1940: fig. 16). The male gonocoxite 9 is very elongate and slender, having multiple tiny branches, in extant Symphrasinae.
49. Male gonocoxite 9: (0) separated from gonarcus (Fig. 4E); (1) fused with gonarcus (Aspöck & Mansell, 1994: figs. 24, 25).

50. Male ectoproct: (0) paired (Lambkin, 1986a: fig. 42); (1) basally fused (Fig. 4C); (2) entirely fused (Lambkin, 1986b: fig. 412).
51. Male ectoproct with comb of short bristle-like setae: (0) absent; (1) present (Lambkin, 1986b: fig. 411). State 1 is an autapomorphy of *Calomantispa*.
52. Male ectoproct: (0) close to each other (Lambkin, 1986a: fig. 69); (1) widely separated (Lambkin, 1986a: fig. 42). The widely separated male ectoproct may be an autapomorphy of *Ditaxis*.
53. Male callus cercus: (0) present (Lambkin, 1986a: fig. 42); (1) absent; (2) present, but raised and prominent (Fig. 4C; Poivre, 1978: fig. 6B).
54. Male gonocoxite 10: (0) not fused into a single sclerite; (1) fused into single sclerite. State 1 was considered by Aspöck & Aspöck (2008) as a synapomorphy of Mantispidae, Berothidae and Rhachiberothidae.
55. Male gonarcus basally with lateral arm: (0) not widened (Lambkin, 1986a: fig. 71); (1) widened (Fig. 4E; Lambkin, 1986a: fig. 44).
56. Male gonarcus: (0) with median part narrow and small (Fig. 4E); (1) with median part enlarged (Fig. 9D, H). The median part of gonarcus is usually narrow and small, whereas in *Drepanicus* and *Gerstaeckerella* it is distinctly enlarged.
57. Male pseudopenis: (0) short (Fig. 4F); (1) long, coiled (Fig. 11A, F; Ferris, 1940: fig. 16); (2) long, with banded bristles (Aspöck & Aspöck, 1984: fig. 4); (3) absent.
58. Male hypomere: (0) absent; (1) present, feebly developed (Lambkin, 1986a: fig. 45; Lambkin, 1986b: fig. 463); (2) well developed (Fig. 4F).
59. Male hypomere: (0) not globose or vertically directed (Fig. 4F); (1) globose and vertically directed (Fig. 9C, G).
60. Male hypomere: (0) membranous; (1) sclerotized (Fig. 4F; Lambkin, 1986b: fig. 415).
61. Female sternite 7: (0) unpaired (Lambkin, 1986a: fig. 36); (1) paired (Aspöck & Mansell, 1994: fig. 14).
62. Female sternite 7 with crumena: (0) absent; (1) present (Lambkin, 1986a: fig. 64). The presence of crumena on the female sternite 7 was considered to be a possible synapomorphy of Drepanicinae by Lambkin (1986a). However, it is apparently absent in *Allomantispa* **gen.n.** and *Ditaxis*.
63. Female gonocoxite 8: (0) not plate-like, unpaired (Ferris, 1940: fig. 17; Aspöck & Mansell, 1994: fig. 14); (1) plate-like, unpaired (Lambkin, 1986b: fig. 421); (2) paired (Lambkin, 1986a: fig. 36); (3) degenerated or absent; (4) fused with sternite 7 (Fig. 6C). The female sternite 8, which was frequently used as the term for the subgenital plate on the abdominal segment 8 in Neuropterida by many authors (e.g. Lambkin, 1986a), was considered to be the gonocoxite 8 according to Aspöck & Aspöck (2008). The paired female gonocoxite 8 is present in most genera of Drepanicinae except for *Allomantispa* **gen.n.**, in which it is fused with sternite 7.
64. Female gonapophysis 8: (0) not paired; (1) paired and sometimes with a bilobed median lobe (Lambkin, 1986a: fig. 64). The female gonapophysis, interpreted as gonocoxite 8 by Lambkin (1986a), is present as a pair of lateral lobes. A bilobed median lobe is sometimes present in *Drepanicus* and *Theristria*. Furthermore, in *Drepanicus* the median lobe is completely separated into a pair of lobes.
65. Female tergite 9: (0) with trace of separation by apodeme (Lambkin, 1986a: fig. 63); (1) distinctly separated ventrally (Lambkin, 1986a: figs. 35, 48); (2) not separated (Lambkin, 1986b: fig. 420). The female tergite 9 sometimes has a pair of additional sclerites ventrally, which is distinctly separated from the main part of tergite 9, e.g. in *Ditaxis*, *Drepanicus*, and *Gerstaeckerella* (see Lambkin, 1986a: figs. 35, 48; Fig. 10). The female pseudohypocaudae belong to such separated sclerites in Rhachiberothidae. In Osmyliidae, Dilaridae and some mantidflies (e.g. *Theristria*), there is a darkened line of apodeme, as trace for such separation on female sternite 9 (see Lambkin, 1986a: fig. 63), which may be plesiomorphic in Neuropterida because it is also found in Megaloptera and Raphidioptera. However, in Calomantispinae and Mantispinae as well as *A. mirimaculata* **sp.n.**, the female sternite 9 does not have such separated sclerites even the trace for separation.
66. Female tergite 9 with pseudohypocaudae: (0) absent; (1) present (Aspöck & Mansell, 1994: fig. 14). State 1 is present in Rhachiberothidae.
67. Female gonocoxite 9: (0) short; (1) elongate (Fig. 11C, H; Ferris, 1940: fig. 17).
68. Female callus cercus: (0) present; (1) absent.
69. Female bursa copulatrix anteriorly with a digitiform lobe: (0) absent; (1) present (Fig. 6D). State 1 is present in *Allomantispa* **gen.n.**, *Ditaxis*, *Drepanicus*, and *Gerstaeckerella*.
70. Female spermatheca with an additional lobe: (0) absent; (1) present (Fig. 6E). State 1 is present in *Allomantispa* **gen.n.**, *Ditaxis*, and *Gerstaeckerella*.
71. Female spermatheca with a large proximal bulb: (0) absent; (1) present (Lambkin, 1986b: fig. 423a). State 1 is a synapomorphy of Calomantispinae.
72. Female spermatheca with a pair of very strongly laterally produced, ball-like lobes on proximal portion: (0) absent; (1) present (Figs 6F, 10C, F). State 1 is present in *Allomantispa* **gen.n.**, *Drepanicus* and *Gerstaeckerella*.
73. Female pudiculum: (0) absent; (1) present (Aspöck & Aspöck, 1986: fig. 33). State 1 is a synapomorphy of Berothidae.
74. Hypermetamorphosis: (0) absent; (1) present. Aspöck *et al.* (2001) considered that hypermetamorphosis is an apomorphic development characterized by additional metamorphoses in the life cycle, supporting the monophyly of Mantispidae, Rhachiberothidae and Berothidae. Only the first instar of Rhachiberothidae is known (Minter, 1990) but the developmental morphology of Rhachiberothidae is assumed to exhibit some degree of hypermetamorphosis.