



NEW FOSSIL MANTIDFLIES (INSECTA: NEUROPTERA: MANTISPIDAE) FROM THE MESOZOIC OF NORTH-EASTERN CHINA

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Abstract: Three new genera and four new species of the extinct mantidfly subfamily Mesomantispinae (Insecta: Neuroptera: Mantispidae) are described from the Lower Cretaceous Yixian Formation of Liaoning and the Middle Jurassic Jiulongshan Formation of Inner Mongolia: *Archaeodrepanicus nudsi* gen. et sp. nov., *A. acutus* gen. et sp. nov., *Sinomesomantispa microdentata* gen. et sp. nov., (Yixian Formation) and *Clavifemora rotundata* gen. et sp. nov. (Jiulongshan Formation). The specimens described herein represent the first Mesozoic mantidfly compression fossils to have body parts

preserved, including the specialized raptorial forelegs articulated to the prothorax anteriorly, an autapomorphy of the family. These new taxa further confirm the placement of the subfamily Mesomantispinae within the family Mantispidae; however, the monophyly of Mesomantispinae has not been confirmed, and it is likely that it will prove to be paraphyletic.

Key words: Neuropterida, Hemerobiiformia, Jiulongshan Formation, mantisflies, Mesomantispinae, Yixian Formation.

MANTISPIDAE, or ‘mantidflies’ (also known as mantisflies), are a highly specialized group of hemerobiiform Neuroptera characterized by their raptorial forelegs, large eyes and elongation of the pronotum behind the forelegs (Lambkin 1986; New 1989; Grimaldi and Engel 2005). Their specialization extends beyond morphology to their behaviour and life history, with some species being parasites of Araneae or aculeate Hymenoptera; the larvae developing within the egg cases of spiders or inside the nests of wasps (Redborg 1998; Wedmann and Makarkin 2007). Indeed, some tropical species are remarkable mimics of their hymenopteran hosts, a feature that affords them some protection from predators (Grimaldi and Engel 2005). The family is most diverse and abundant in tropical regions and comprises approximately 400 extant species divided into four extant subfamilies: Symphrasinae, Drepanicinae, Calomantispinae and Mantispinae (Lambkin 1986; Ohl 2004; Grimaldi and Engel 2005; Wedmann and Makarkin 2007); and the extinct subfamily Mesomantispinae (Makarkin 1997; Wedmann and Makarkin 2007). Mantispinae constitutes the most diverse subfamily in terms of numbers of species and are highly specialized, obligate predators of

spider egg cases (Lambkin 1986; Redborg 1998). Little is known of the life histories of the subfamilies Symphrasinae and Calomantispinae, and the biology of Drepanicinae remains almost entirely unknown (Grimaldi and Engel 2005).

Mantidflies are rare in the fossil record (Wedmann and Makarkin 2007), but, nevertheless, have a geological range dating back to the Lower Jurassic (Table 1). All four extant subfamilies are known from fossil representatives, along with the extinct Mesomantispinae (Wedmann and Makarkin 2007). The oldest mantidflies are *Liassochrysa stigmatica* Ansorge and Schlüter, 1990 from the Lower Jurassic of Dobbertin, Germany, and *Promantispa similis* Panfilov, 1980 from the Upper Jurassic of Karatau. In the Cretaceous, the family is represented by *Mesomantispa sibirica* Makarkin, 1997 from Baissa, East Siberia, *Gers-taeckerella asiatica* Makarkin, 1990 from Kzyl-Zhar, Kazakhstan, and *Doratomantispa burmanica* Poinar and Buckley, 2011 from Burmese amber. Cenozoic Mantispidae are known from the Eocene oil shales of Grube Messel, Germany, with *Symphrasites eocenicus* Wedmann and Makarkin, 2007, an unnamed larva from the Eocene

TABLE 1. The fossil record of Mantispidae.

Taxon	Deposit	Age	Reference
<i>Feroseta prisca</i>	Dominican amber	Miocene	Poinar 2006
<i>Dicromantispa moronei</i>	Dominican amber	Miocene	Engel and Grimaldi 2007
<i>Dicromantispa electromexicana</i>	Mexican amber	Miocene	Engel and Grimaldi 2007
<i>Climaciella(?) henrotayi</i>	Dauphin, France	Oligocene	Nel 1989
<i>Prosagittalata oligocenica</i>	Céreste, France	Oligocene	Nel 1989
<i>Vectispa relictata</i>	Bembridge Marls, Isle of White	Eocene	Cockerell 1921; Jarzembowski 1980
Unnamed larva	Baltic amber	Eocene	Ohl 2011
<i>Symphrasites eocenicus</i>	Messel, Germany	Eocene	Wedmann and Makarkin 2007
<i>Doratantispa burmanica</i>	Burmese amber	Upper Cretaceous	Poinar and Buckley 2011
<i>Gerstaeckerella asiatica</i>	Kzyl-Zhar, Kazakhstan	Upper Cretaceous	Makarkin 1990
<i>Sinomesomantispa microdentata</i> gen. et sp. nov.	Yixian Formation, China	Lower Cretaceous	Herein
<i>Archaeodrepanicus</i> sp.	Yixian Formation, China	Lower Cretaceous	Herein
<i>Archaeodrepanicus acutus</i> gen. et sp. nov.	Yixian Formation, China	Lower Cretaceous	Herein
<i>Archaeodrepanicus nudsi</i> gen. et sp. nov.	Yixian Formation, China	Lower Cretaceous	Herein
<i>Mesomantispa sibirica</i>	Baissa, Russia	Lower Cretaceous	Makarkin 1997; Wedmann and Makarkin 2007
<i>Promantispa similis</i>	Karatau, Kazakhstan	Upper Jurassic	Panfilov 1980
<i>Clavifemora rotundata</i> gen. et sp. nov.	Jiulongshan Formation, China	Middle Jurassic	Herein
<i>Liassochrysa stigmatica</i>	Dobbertin, Germany	Lower Jurassic	Ansorge and Schlüter 1990

Baltic amber (Ohl 2011), the Eocene–Oligocene Bembridge Marls of the Isle of Wight, England, with *Vectispa relictata* Cockerell, 1921 (Jarzembowski 1980), *Prosagittalata oligocenica* Nel, 1989 from the Late Oligocene of Céreste and *Climaciella? henrotayi* Nel, 1989 from Dauphin, France, and the youngest from Dominican and Mexican ambers (*Feroseta prisca* Poinar, 2006, *Dicromantispa moronei* Engel and Grimaldi, 2007 and *D. electromexicana* Engel and Grimaldi, 2007). Here we describe the first Mesomantispidae mantidflies from the Mesozoic of China. The new specimens are remarkably well preserved and include some specimens with almost complete bodies, confirming their placement in Mantispidae and providing additional morphological characters to further characterize the subfamily Mesomantispidinae.

GEOLOGICAL SETTINGS

The Jiulongshan Formation is a lacustrine sequence that crops out in north-eastern China (Ren *et al.* 1995; Tan and Ren 2002). The section at Daohugou Village is composed of grey tuffaceous sandstone and sandy mudstone. The palaeoenvironment has been reconstructed as a volcanic region with mountain streams and lakes (Ren *et al.* 2002). General reviews of the Middle Jurassic Yanliao insect fauna of north China have been given by Hong (1983), Ren *et al.* (1995) and Ren and Lu (1996).

It contains an exceptionally preserved diverse insect fauna, composed of complete specimens of Ephemeroptera, Odonata, Plecoptera, Blattodea, Orthoptera, Hemiptera, Neuroptera, Coleoptera, Hymenoptera and Diptera described by Hong (1983), Ren *et al.* (1995), Ren and Krzemiński (2002). In addition to the insects, there are freshwater conchostracans (Zhang and Shen 1987), salamanders (Gao and Shubin 2003) and dinosaurs (Ji and Yuan 2002). The surrounding gymnosperm forests were dominated by Ginkgopsida, Coniferopsida, Lycoposida, Sphenopsida, Filicopsida and Cycadopsida (Mi *et al.* 1996). The wealth of palaeontological data has led to the interpretation of a humid and warm-temperate climate (Tan and Ren 2002). Geochemical dating (using Ar–Ar and SHRIMP U–Pb techniques) has given the age of intermediate-acid volcanic rocks, which overlie the Daohugou fossil-bearing beds as 164–165 Ma, therefore the age of the fossil-bearing beds is older or equal to 165 Ma (Chen *et al.* 2004). This gives a Middle Jurassic (Bathonian) age of the Daohugou biota (Zhang and Shen 1987; Ren *et al.* 1995, 2002; Wang 2000; Shen *et al.* 2003; Gao and Ren 2006; Shih *et al.* 2009; Ren *et al.* 2010).

The Yixian Formation of north-eastern China, together with the overlying Jiufotang Formation, has yielded a remarkable array of exceptionally preserved fossils that comprise the ‘Jehol Biota’ (Barrett 2000; Chang *et al.* 2003; Zhou *et al.* 2003). These two conformable and

lithologically similar formations comprise a sequence of low-energy freshwater lacustrine deposits intercalated with extrusive basalts and tuffaceous sediments deposited in a geologically complex region close to the Pacific Rim. Both formations are Lower Cretaceous in age, with the Barremian Yixian Formation and the Aptian Jiufotang Formation (Zhou *et al.* 2003; Sha 2007).

The Jehol Lagerstätte achieved international celebrity following the discovery of its diverse vertebrate assemblage which includes feathered theropod dinosaurs (Chen *et al.* 1998; Ji *et al.* 1998; Xu *et al.* 2001), birds (Chiappe *et al.* 1999; Zhang and Zhou 2000; Zhou and Zhang 2001, 2002a, b) and some of the earliest mammals (Hu *et al.* 1997; Ji *et al.* 1999; Hu and Wang 2002). In addition, the Jehol deposits also yield an abundant and diverse flora including some of the earliest putative angiosperms (Sun *et al.* 1998; Sun *et al.* 2001; Zhou *et al.* 2003). Although less well popularized, the insect fauna probably constitutes the most diverse and abundant component of the entire assemblage comprising approximately 500 species representing over 100 families within 17 orders (Zhang and Zhang 2003). Makarkin *et al.* (2012) recently analysed the neuropteran assemblage of the Yixian Formation.

MATERIAL AND METHODS

The specimens described herein were collected by one of us (DR) from the Yixian Formation in Huangbanjigou Village, Beipiao City, Liaoning Province, China and the Jiulongshan Formation in Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China. They were studied using an Olympus SZH stereomicroscope with a camera lucida for producing drawings. Photographs were taken using a Canon EOS 450D digital SLR mounted on a rostrum stand. The terminology adopted here follows Lambkin (1986) for morphology and Wedmann and Makarkin (2007) for wing venation.

Wing vein abbreviations. C, costa; Sc, subcosta; R, radius; R1, first branch of R; Rs, radial sector; Rs1, most proximal branch of Rs; M, media; MA, media anterior; MP, media posterior; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; 1A–3A, first to third anal veins. The principal crossveins are designated by the longitudinal veins which they connect and numbered by the gradate series to which they belong in sequence from the wing base, for example, 2m-cu, the crossvein connecting M and Cu in the second gradate series; 2r-m, the crossvein connecting R and M systems (i.e. between R (R1, Rs) and M (MA)) in the second gradate series; 1sc-r, the (basal) crossvein between Sc and R in the first series.

Repository. All specimens are deposited in the fossil insect collection of the Key Laboratory of Insect Evolution & Environmental

Changes, College of Life Sciences, Capital Normal University, Beijing (CNUB).

SYSTEMATIC PALAEOLOGY

Order NEUROPTERA Linnaeus, 1758

Suborder HEMEROBIFORMIA *sensu* Aspöck *et al.*, 2001

Family MANTISPIDAE Leach, 1815

Subfamily MESOMANTISPINAE Makarkin, 1997

Emended diagnosis. Prothorax short, broad. Femur of foreleg without major spines. Tibia slightly arched, with prostrate setae. Tarsus with five approximately equally sized simply constructed tarsal segments and two tarsal claws. Forewings with trichosors present around entire wing margin, subcostal space not narrowed distally; humeral vein recurrent; Sc veinlets closely spaced, mainly forked; Sc distally bends sharply towards R1 but apparently not fused with it; pterostigma inconspicuous; M forked distal to origin of Rs; MA and MP parallel not branched before distal gradate series; CuA and CuP multibranching, in general pectinate (emended from Makarkin 1997).

Composition. Four genera from the Mesozoic of East Asia: *Clavifemora* gen. nov. (China; Middle Jurassic, Bathonian; Jiulongshan Formation), *Mesomantispa* Makarkin, 1997 (Russia; Transbaikalia: Baissa locality; Lower Cretaceous, pre-Barremian; Zaza Formation) and *Archaeodrepanicus* gen. nov., *Simomesomantispa* gen. nov. (China; Lower Cretaceous, Barremian; Yixian Formation).

Remarks. The principal autapomorphy of Mantispidae (the pronotum posterior to the forelegs is prolonged forming a tube in the vast majority of species) is detected in all examined specimens. However, many of the character states included in the diagnosis are plesiomorphic and shared by other mantidfly subfamilies, in particular Drepanacinae (comparatively short prothorax, Sc distally curved towards R1 and the inconspicuous pterostigma) and to a lesser extent Symphrasinae. Some of these character conditions are also plesiomorphic for other neuropteran families, for example, Rhachiberothidae (trichosors around entire wing margin). Therefore, it is possible that Mesomantispinae is paraphyletic and representative of the mantispid stem-group. However, until more specimens are discovered or a cladistic study is completed, the subfamily is retained here.

Genus *ARCHAODREPANICUS* gen. nov.

Derivation of name. Genus-group name formed from a combination of the Greek words *archaios* (meaning 'ancient') and

Drepanicus, the type genus of Drepanicinae, in reference to the similarities in wing venation. Gender masculine.

Type species. *Archaeodrepanicus nuddsi* sp. nov.

Diagnosis. Proximal segments of antennae elongate, forewing elongate, 12–15.6 mm long; Rs with only six branches; between branches of Rs one gradate series of crossveins; CuP pectinately branched; small and narrow anal area; colour pattern, consisting of two–three dark bands.

Comparison. In *Sinomesomantispa* gen. nov., the proximal segments of the antennae are transverse, the forewing length is 16 mm and Rs has nine preserved branches. *Mesomantispa* forewing length is estimated as 20–22 mm, three gradate series of crossveins between the branches of Rs, Rs has 11 branches and the wing colour pattern consists of five to six black spots. *Clavifemora* gen. nov. has a forewing length of 17 mm, nine branches of Rs preserved wing colour pattern consisting of two to three black spots and a swollen (broad and short) femora.

Remarks. The genus has been placed within the subfamily Mesomantispinae on the basis of trichosors being present around almost the entire wing margin (absent basally), majority of subcostal veinlets being forked and closely spaced, Sc is sharply bent to R1 apically, pterostigma inconspicuous, subcostal space broadened distally, M forked far distally to origin of Rs, CuA and CuP

multibranched, most distal branch of CuA terminating past the mid-point of the wing (Wedmann and Makarkin 2007).

Archaeodrepanicus nuddsi sp. nov.

Figures 1–3

Derivation of name. Named in honour of Dr. John R. Nudds, palaeontologist at the University of Manchester.

Material. Holotype CNU-NEU-LB2011001P/C (Fig. 1); almost complete insect preserved in lateral view. Paratype CNU-NEU-LB2011002 (Fig. 2); almost complete insect preserved in lateral view. Paratype CNU-NEU-LB2011003 (Fig. 3); almost complete insect preserved in lateral view.

Type horizon and locality. Yixian Formation (Lower Cretaceous, Barremian); Huangbanjigou locality, Liaoning Province, north-eastern China.

Diagnosis. Small forewing 12–15 mm, head to wing apex length 16–18.5 mm; basal 1sc-r, after origin of M; CuA with 4–5 pectinate branches.

Description of holotype. Head elongate, 2 mm long, 1.2 mm wide (including eyes); postocular lobe strongly expanded; coronal suture distinct. Eyes preserved as dark ‘halos’ 1 mm long, 0.75 mm wide. Mouthparts preserved; unable to determine individual parts. Antennae incomplete; 13 flagellomeres preserved of fairly uniform size: 0.15 mm long, 0.1 mm wide. Possible basal

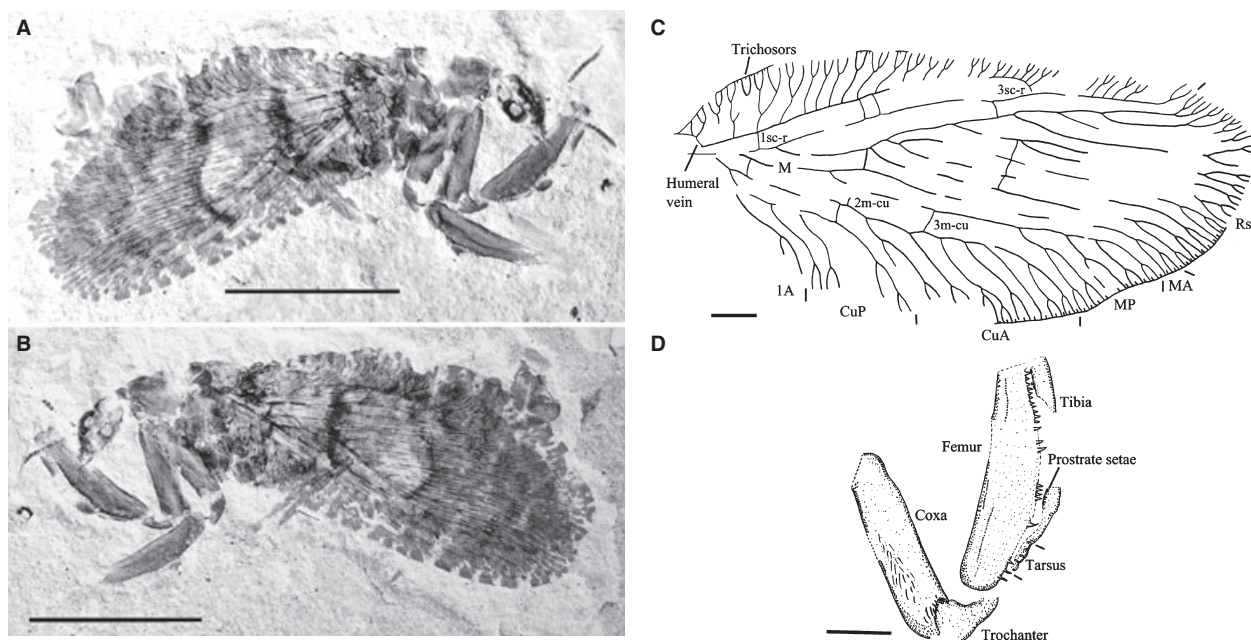


FIG. 1. *Archaeodrepanicus nuddsi* gen. et sp. nov. Photograph of holotype CNU-NEU-LB2011001P/C. A, B, part and counterpart. C, wing venation drawing. D, foreleg drawing. Scale bars represent 5 mm (A, B) and 1 mm (C, D).

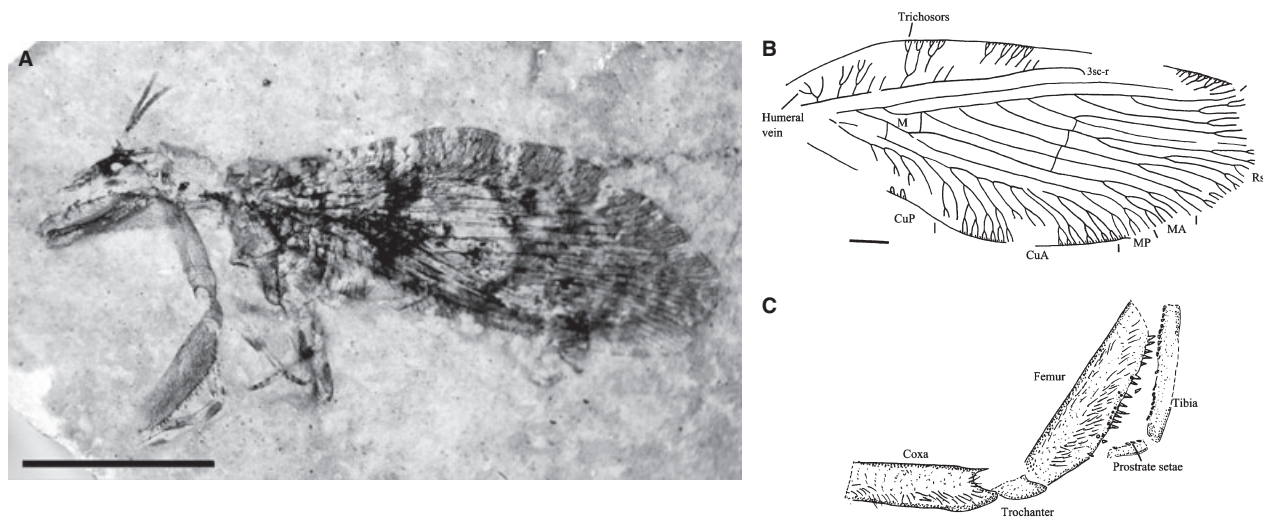


FIG. 2. *Archaeodrepanicus nuddsi* gen. et sp. nov. A, photograph of paratype CNU-NEU-LB2011002. B, wing venation drawing; C, foreleg drawing. Scale bars represent 5 mm (A) and 1 mm (B, C).

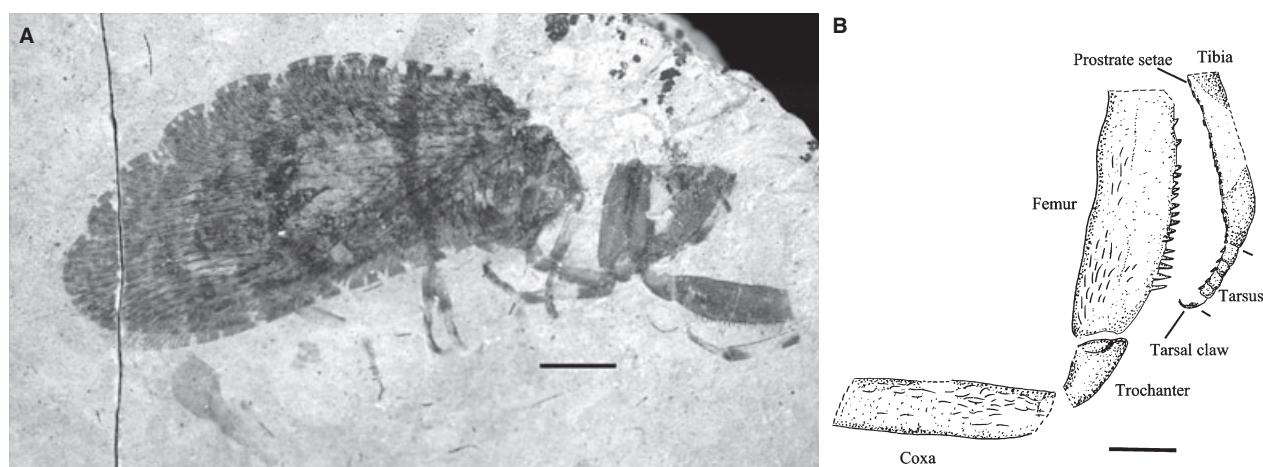


FIG. 3. *Archaeodrepanicus nuddsi* gen. et sp. nov. Paratype CNU-NEU-LB2011003. A, photograph. B, foreleg drawing. Scale bars represent 2 mm (A) and 1 mm (B).

segments of antennae preserved. Prothorax wide, comparatively short, about 2.5 mm long, 1.3 mm wide.

Forelegs are incomplete, raptorial, hairs preserved. Coxa elongate, stout, 2.9 mm long, 0.7 mm wide. Trochanter incomplete, approximately 0.7 mm long, 0.5 mm wide. Femur 3.8 mm long, 0.9 mm wide, with two rows of ventral spines: approximately 22 minor spines (0.1–0.15 mm long), many disarticulated. Tibia incomplete; with prostrate setae. Tarsus incomplete; four segments preserved.

All four midlegs preserved, however very incomplete, all covered with hairs. In the hindlegs, femur is incomplete. Tibia about 3 mm long. Tarsus incomplete.

Forewing is 12.1 mm long, 5.0 mm wide. Trichosors present on anterior and posterior wing margins. Costal space narrows towards wing apex. Subcostal veinlets closely spaced; all forked, some dichotomously. Humeral vein recurrent, few branched. Sc

sharply bends towards R1 distally, however, probably terminates on anterior wing margin. Between Sc and R four crossveins. Sc and R parallel for most of length. R1 long, entering wing margin before wing apex. Rs originates near wing base. Rs with six primary branches; some forking before mid-point of vein. Between branches of Rs, one (3rd, 'inner') gradate series of crossveins visible; 4th ('outer') series not detected (although one crossvein visible). Crossvein 2r-m preserved. M originates near wing base; M deeply forked. MA and MP simple for most of their length; forked distally; MP dichotomously forked, proximal to fork of MA. Crossveins 1m-cu, 2m-cu and 3m-cu preserved. Cu primary fork close to origin. CuA pectinately branched with six primary branches, proximal-most branch deeply forked; distal-most branches of CuA terminate on posterior wing margin after mid-point of wing. CuP pectinately branched, with three primary branches preserved (probably five when complete); some deeply

forked. All branches of Rs, M, Cu with end twigging. 1A incomplete, at least once forked. 2A, 3A not preserved. Abdomen is incomplete, four segments partially preserved.

Description of CNU-NEU-LB2011002. Head incomplete, preserved in lateral aspect; postocular lobe strongly expanded. Eyes preserved as dark 'halos' 0.9 mm long, 0.4 mm wide. Mouthparts and palps preserved. Antennae incomplete; scape incomplete, probably not enlarged; 15 flagellomeres preserved of fairly uniform size: 0.2 mm long, 0.1 mm wide. Thorax is incomplete. Prothorax short, about 2.0 mm long, 1.4 mm wide (possible postmortal compression).

Forelegs are incomplete, raptorial, hairs preserved. Coxa elongate, about 2.5 mm long, 0.6 mm wide. Trochanter approximately 0.7 mm long, 0.5 mm wide. Femur approximately 3.5 mm long (incompletely preserved), 0.9 mm wide, with two rows of ventral spines; approximately 16 minor spines (0.1–0.25 mm long) preserved, many disarticulated. Tibia incomplete, with prostrate setae. Tarsus incomplete.

Forewing 12.1 mm preserved length, approximately 5.0 mm wide. Trichosors present on anterior and posterior wing margins. Costal space narrows towards wing apex. Subcostal veinlets closely spaced; some forked dichotomously. Humeral vein recurrent. Sc distally bends towards R1 (termination poorly preserved). Two sc-r crossveins preserved. Sc and R1 parallel most of length. R1 long, entering wing margin before wing apex. Rs originates near wing base. Rs with six primary branches, some forking before mid-point of vein. Between branches of Rs, one (3rd, 'inner') gradate series of crossveins detected. Crossveins 2r-m and 3r-m preserved. M originates near wing base; M deeply forked. MA and MP simple for most of their length; dichotomously forked distally. Crossvein 1m-cu preserved. CuA pectinately branched with seven primary branches; some dichotomously forked. Distal-most branches of CuA terminate on posterior wing margin after mid-point of the wing. CuP incomplete, pectinately branched, with three primary branches preserved, some of them forked.

Description of CNU-NEU-LB2011003. Head and thorax not preserved. Forelegs are incomplete, raptorial, hairs preserved. Coxa elongated and incomplete. Trochanter incomplete; femur incom-

plete, 1 mm wide, with two rows of ventral spines; approximately 40 minor spines (0.1–0.21 mm long), many disarticulated. Tibia incomplete, curved with prostrate setae. Tarsus incomplete, five segments fully preserved, one tarsal claw preserved.

Midlegs are poorly preserved, hairs present. Femur 2.3 mm long, 0.4 mm wide. Tibia 2.6 mm long, 0.35 mm wide. Tarsus quite poorly preserved, basitarsus longer than other segments.

Hindlegs are poorly preserved, only tarsus complete; basitarsus longer than other segments. Wings are poorly preserved, unable to determine venation. Forewing about 14.5 mm long. Colour pattern in general similar to that of holotype.

Archaeodrepanicus acutus sp. nov.

Figure 4

Derivation of name. From the Latin *acutus*, meaning acute, in reference to the acute apex of the forewing.

Holotype. CNU-NEU-LB2011004 (Fig. 4); almost complete insect preserved in lateral view.

Type horizon and locality. Yixian Formation (Lower Cretaceous, Barremian); Huangbanjigou locality, Liaoning Province, north-eastern China.

Diagnosis. Larger wing (15.6 mm) and head to wing apex length (21 mm); 1sc-r more proximal, before origin M; CuA with seven pectinate branches.

Comparison. *Archaeodrepanicus nuddsi* gen et sp. nov. is smaller with a forewing length of 12–15 mm and a head to wing apex length of 16–18.5 mm. Also in *A. nuddsi* sp. nov., the 1sc-r crossvein is more distal, being after the origin of M, and its CuA has fewer branches, that is, four to five.

Description. Head poorly preserved in dorsal/ventral aspect, 2.6 mm long (including mandibles), 1.6 mm wide (including eyes); maxillary palps rather short, with somewhat enlarged

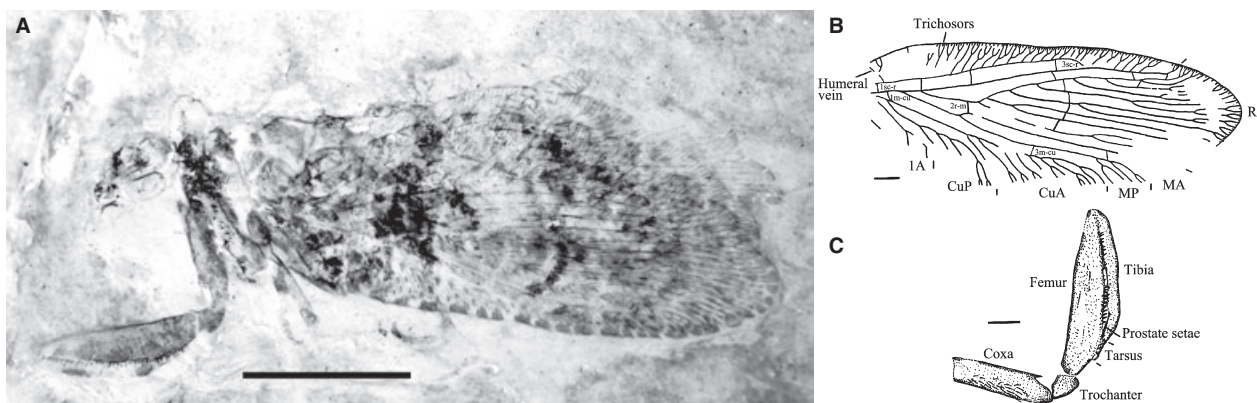


FIG. 4. *Archaeodrepanicus acutus* gen. et sp. nov. A, photograph of holotype CNU-NEU-LB2011004. B, wing venation drawing, C, foreleg drawing. Scale bars represent 5 mm (A) and 1 mm (B, C).

acute terminal segment; coronal suture distinct; postocular lobe expanded; antennae not preserved.

Thorax is poorly preserved; prothorax is about 2.0 mm long. Mesonotum preserved in dorsal aspect; prescutum transverse; scutellum relatively large, triangular. Abdomen not preserved.

Forelegs are incomplete, raptorial, hairs preserved. Coxa elongate, incomplete, 0.8 mm wide covered with dense, quite long hairs. Trochanter about 1.0 mm long, 0.7 mm wide. Femur nearly complete, about 5.2 mm long, 1.0 mm wide, with two rows of ventral spines; approximately 24 minor spines (0.1–0.2 mm long), many disarticulated. Tibia long, curved; with prostrate setae. Tarsus incomplete, four segments preserved. Midlegs and hindlegs fragmentary preserved. Segments of hindleg tarsus short, pretarsus longer than others; two claws.

Forewing is 15.6 mm long, 6.3 mm wide (preserved). Trichosors present on anterior and posterior wing margins. Costal space narrows towards wing apex. Subcostal veinlets closely spaced; forked, some dichotomously. Humeral vein recurrent. Sc bends towards R1, probably terminates on anterior wing margin. Three sc-r crossveins. Sc and R1 parallel for most length. R1 long, entering margin well before wing apex. Rs originates near wing base. Rs with seven primary branches; some forking before mid-point of vein. Between branches of Rs, one (third, 'inner') gradate series of crossveins detected. Crossvein 2r-m preserved. M originates near wing base (appear fused basally with R), deeply forked. MA and MP simple for most of their length; forked distally. 1m-cu and 3m-cu preserved. CuA pectinately branched with eight primary oblique branches; many forked. Distal-most branches of CuA terminate on posterior wing margin after mid-point of wing. CuP incomplete, pectinately branched, with four branches. 1A incomplete with two pectinate branches.

Archaeodrepanicus sp.

Figure 5

Material. CNU-NEU-LB2011005. Almost complete insect very poorly preserved in lateral view. Wing venation not preserved. Possibly having undergone deformation.

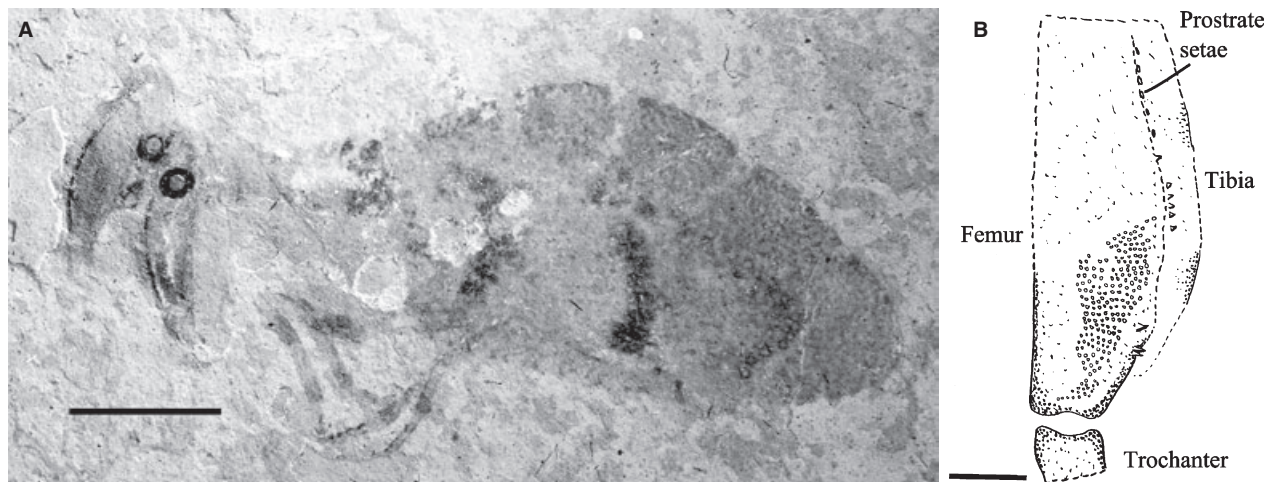


FIG. 5. *Archaeodrepanicus* sp. Specimen CNU-NEU-LB2011005. A, photograph. B, drawing of foreleg. Scale bars represent 5 mm (A) and 1 mm (B).

Description. Head is incomplete. Two eyes present, preserved as dark halos; approximately 1.1 mm long, 1.3 mm wide. Antenna filiform, incomplete; approximately seven preserved flagellomeres of fairly uniform size 0.2 mm long, 0.1 mm wide.

Thorax is poorly preserved and without discernible features. All legs are preserved. Forelegs incomplete, raptorial. Coxa not preserved. Trochanter incomplete. Femur poorly preserved, about 5.0 mm long, 1.7 mm wide, with small (<0.1–0.2 mm) ventral spines, mainly disarticulated. Circular pits present on femur. Tibia incomplete, arched; prostrate setae. Tarsus not preserved. Midlegs and hindlegs rather poorly preserved, covered with dense hairs; four proximal tarsomeres of hind tarsus with ventral bunch of dark bristles each. Wing venation not preserved. Colour pattern (of forewing?) consists of three dark bands.

Remarks. The wing venation has not been preserved in this specimen making it difficult to assign to a species. The body parts (such as the raptorial forelegs and antennal segments elongate) and size allow it to be assigned to *Archaeodrepanicus* gen. nov.

Occurrence. Yixian Formation (Lower Cretaceous, Barremian); Huangbanjigou locality, Liaoning Province, north-eastern China.

Genus *SINOMESOMANTISPA* gen. nov.

Derivation of name. Genus-group name formed from a combination of *Sina*, Latin for China, and *Mesomantispa*, the type genus of the subfamily. Gender feminine.

Type species. *Sinomesomantispa microdentata* sp. nov.

Diagnosis. Wide profemur with small spines with regard to femur (<0.10–0.16 mm long); proximal segments of antennae transverse, costal margin of the forewing concave before wing mid-point (not concave in other

genera); distinct colour patterning of forewing (distinct thick dark band in distal part of wing).

Remarks. *Sinomesomantispa microdentata* gen. et sp. nov. is placed within Mesomantispa on the basis of having trichosors present at least on anterior margin, subcostal veinlets forked, pterostigma indistinct as is general configuration of the venation. The shape of the foreleg is also similar, however, wider and with smaller spines. This difference and the characteristic shape of the costal space justify the erection of a new genus.

Sinomesomantispa microdentata sp. nov.

Figure 6

Derivation of name. Specific epithet from the Greek *micros*, small, and the Latin *dentatus*, dentate, serrate, in reference to minute spines on the fore femur of the holotype.

Holotype. CNU-NEU-2011006P/C (Fig. 6) a complete but poorly preserved specimen exposed in lateral aspect.

Type horizon and locality. Yixian Formation (Lower Cretaceous); Huangbanjigou locality, Liaoning Province, northeastern China.

Diagnosis. As for the genus.

Description. Head poorly preserved; postocular lobe not strongly expanded. Eyes preserved as dark 'halos', 1.2 mm long, 0.9 mm wide. Antennae filiform; both complete; scape and pedicel indistinct, 27 flagellomeres, basal flagellomeres transverse (0.1 mm long, 0.2 mm wide), apical nearly as wide as long.

Thorax incomplete, poorly preserved. Forelegs covered with dense, rather short hairs. Coxa elongate, very stout, about 4 mm long, 1.2 mm wide. Trochanter 0.7 mm long, 0.7 mm wide.

Femur, 5.0 mm long, 1.6–1.7 mm wide with small ventral spines (<0.1–0.16 mm long), mainly disarticulated. Tibia long, with prostrate setae. Tarsus incomplete; poorly preserved.

Midlegs all covered with hairs. Coxa poorly preserved. Femur 2.2 mm long, 0.5 mm wide, covered with dense rather long hairs. Tibia and tarsus overlapped, with hairs rather short.

Hindlegs all covered with hairs. Coxa partly hidden by wings. Femur 2.9 mm long, 0.5 mm wide. Tibia long, about 4.8 mm long, 0.4 mm wide. Basitarsus nearly as long as three next tarsomeres together.

Forewing poorly preserved, all four wings overlapping, about 16 mm long. No character states of venation clearly recognizable beyond general agreement with that of Mesomantispa (i.e. subcostal veinlets forked; trichosors present; pterostigma indistinct; general configuration of venation). Costal space of forewing sharply narrowed towards apex, with some concavity of costal margin before mid-point of the wing. Colour pattern mainly consists of distinct thick dark band in distal part of wing. Abdomen not preserved.

Genus CLAVIFEMORA gen. nov.

Derivation of name. From the Latin *clava* meaning club and femora. In reference to the swollen club-like forelegs. Gender feminine.

Type and only species. *Clavifemora rotundata* sp. nov.

Diagnosis. May be easily distinguished from other genera of Mesomantispa by swollen (broad and short) femora.

Remarks. This genus has been erected on the basis of the stout club-like forelegs, which separate it from *Archaeodrepanicus* gen. nov. and *Sinomesomantispa* gen. nov. The wing venation completely agrees with that of Mesomantispa, even though fragmentary due to strong overlapping.

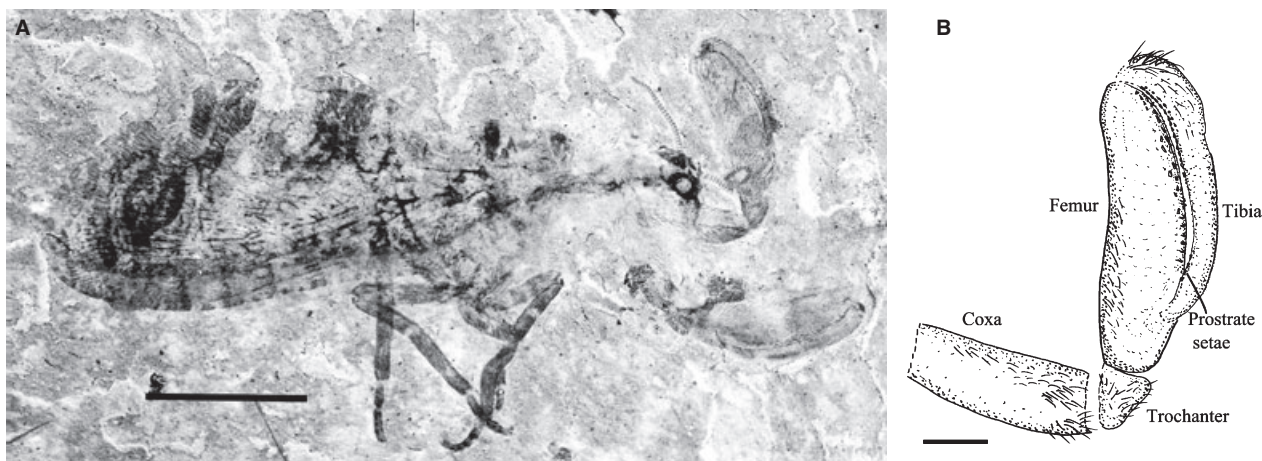


FIG. 6. *Sinomesomantispa microdentata* gen. et sp. nov. Holotype CNU-NEU-LB2011006. A, photograph of holotype. B, foreleg drawing. Scale bars represent 5 mm (A) and 1 mm (B).



FIG. 7. *Clavifemora rotundata* gen. et sp. nov. Holotype CNU-NEU-NN2011001. A, photograph of holotype. B, drawing of forelegs. Scale bars represent 5 mm (A) and 1 mm (B).

Clavifemora rotundata sp. nov.

Figure 7

Derivation of name. Specific epithet from the Latin *rotundatus*, round, in reference to the shape of the swollen profemora.

Holotype. CNU-NEU-NN2011001 (Fig. 7). Almost complete insect.

Type horizon and locality. Jiulongshan Formation (Middle Jurassic, Bathonian); Daohugou, Inner Mongolia, China.

Diagnosis. As for the genus.

Description. Head is poorly preserved, incomplete, preserved in frontal aspect; postocular lobe not expanded (or not preserved). Eye poorly preserved. Antennae incomplete, filiform (maximum number of flagellomeres preserved is 13); flagellomeres of fairly uniform size 0.15 mm long and 0.1 mm wide, with hairs preserved. Thorax is poorly preserved, difficult to obtain measurements and satisfactorily identify parts except that prothorax short and broad.

Fore-, mid- and hindlegs are preserved. Forelegs stout, raptorial. Coxa elongate, approximately 3 mm long, 1 mm wide. Many thick dark hairs preserved. Trochanter, 1 mm long, 0.8 mm wide (at widest point), with hairs preserved. Femur swollen (very stout, rounded), 3.3 mm long, 1.6 mm wide, with ventral spines, over 50, 0.07–1.14 mm long, partly forming two distinct rows, many disarticulated. Circular pits present on femur. Tibia incomplete, thick, arched, prostrate setae preserved on inside surface. Tarsus not preserved. Midlegs and hindlegs poorly preserved, femur and tibia covered with long dense hairs. Tarsus five segmented, basitarsus longest of tarsomeres; four proximal segments ventrally with dark bristles; one claw preserved.

Forewing elongated, about 17.5 mm long, 6.1 mm wide. Venation poorly preserved due to overlaying of all four wings. Trichosors present on both wing margins. Costal space narrowing distally. Subcostal veinlets closely spaced, mainly forked. CuA and CuP pectinately branched. Colour pattern quite similar to that of *Mesomantispa*, probably with three black spots.

Hindwing venation partly visible; 'outer' gradate series of crossvein apparently complete, margined with black forming black stripe parallel to outer margin. Possibly abdomen is very partially preserved, but parts are indistinguishable.

DISCUSSION

The placement of Mesomantispinae in Mantispidae is strongly supported by the Chinese mantidflies described herein, from the evidence of the forelegs being articulated to the prothorax anteriorly, which is an autapomorphy of the family. However, the monophyly of the subfamily has not been confirmed, and it is likely that it represents a paraphyletic assemblage of stem-group mantidflies. The subfamily is composed of four genera *Mesomantispa*, *Archaeodrepanicus* gen. nov., *Sinomesomantispa* gen. nov., and *Clavifemora* gen. nov. The raptorial forelegs of these Mesozoic mantidflies are lacking in major spines, which are observed in all extant species and also the other Cretaceous mantidfly *Doramantispa burmanica* Poinar and Buckley, 2011. The Mesozoic Chinese mantidflies have rows of many small spines along the anterior edge of the femora and thick, prostrate setae on the tibiae. The prostrate setae create a 'scissor-like' effect when the femur and tibia closes; they are observed in many extant species, but are much smaller (Poivre 1978; Lambkin 1986). With respect to the wing venation, they, like *Mesomantispa* (see Wedmann and Makarkin 2007), are most similar to the subfamily Drepanicinae (especially *Drepanicus* Blanchard, 1851), in having Sc bending towards R1 (at point of 3sc-r) and an inconspicuous pterostigma. The body structures of the subfamily Mesomantispinae are also most similar to those of Drepanicinae, that is, the head with strongly expanded postocular lobe; short stout prothorax; similar structure of tarsi. However, they also resemble Symphrasinae, in that the terminal portion of Sc, distal to 3sc-r, and pterostigma is not evident. They differ from extant

taxa in possessing plesiomorphic characters, such as a dense and complex venation (e.g. trichosors present; majority of subcostal veins forked; branches of Rs not uniformly forked; pectinate branching of veins (e.g. CuA)). Due to the plesiomorphic characters and the drepanicine and symphrasine similarities, it is most likely that Mesomantispinae represents a paraphyletic assemblage of stem-group mantidflies that gave rise to the modern subfamilies sometime in the Late Cretaceous/Early Cenozoic.

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