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A New Mesopsychid (Mecoptera) from the Middle Jurassic of Northeastern China

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Abstract: The family Mesopsychidae Tillyard, 1917 presently consists of ten described genera from the Early Permian to the Early Cretaceous of Australia, China, Kyrgyzstan, Russia, South Africa, Tajikistan, and Ukraine. Herein, a new genus and a new species of fossil mesopsychid, *Epicharmesopsyche pentavenulosa* gen. et sp. nov., is described from the Middle Jurassic Jiulongshan Formation of Inner Mongolia, China, supplementing the family-level diversity. The well-preserved, new material reveals many characters, including antennae, wing venation, shape and genitalia that increase our morphological understanding of the family, although unfortunately the mouthparts and most of the legs are not preserved. Diagnosis of the Mesopsychidae is emended to include a four- or five-branched MP in both the fore- and hind wings. This is the first documentation of a wing coupling structure in the Mesopsychidae, consisting of three to four frenula bristles on the humeral lobe at the base of the costal margin of both hind wings. Asymmetrical shape and size of the left and right wings on a specimen of *E. pentavenulosa* gen. et sp. nov., seems to be a common condition for mesopsychid taxa from northeastern China.

Key words: new genus and species, wing coupling, asymmetric wings, taxonomic diversity, Inner Mongolia

1 Introduction

The Mesopsychidae Tillyard, 1917 is an extinct and small family of Mecoptera formerly ranging from the Late Permian to the mid Early Cretaceous, and distributed variously from deposits in Australia, Kyrgyzstan, South Africa, Ukraine, Tajikistan and China. Novokshonov and Sukacheva (2001) revised the generic composition of the Mesopsychidae to include seven described genera. Bashkuev (2011) described the earliest Mesopsychidae, *Permopsyche issadensis* Bashkuev, 2011 and *P. rasnitsyni* Bashkuev, 2011, from the Late Permian (Changhsingian Stage) of Isady locality, Vologda Province, Russia, and the first pre-Triassic *Mesopsyche*, *M. incompleta* Bashkuev, 2011 from the uppermost Permian of the town of Vyazniki, Vladimir Province, Russia. Furthermore, Bashkuev (2011) considered that the type species of the type genus *Mesopanorpodes* Tillyard, 1918, *Mesopanorpodes wianamattensis* Tillyard, 1918, as closely related to *Mesopsyche* Tillyard, 1917, and transferred it to the Mesopsychidae *Mesopanorpodes* Tillyard, 1917 (=Mesopanorpodidae Tillyard, 1918). Two species described under *Mesopanorpodes* from the Upper Permian of Australia are also included within *Permopsyche*: *P. belmontensis* (Riek, 1953), and *P. robustus* (Riek, 1953). In addition, Bashkuev (2011) also identified *Bittacopanorpa javorskii* Zalessky, 1935 from the uppermost Permian or basal Triassic of the Kuznetsk Basin in southwestern Siberia, Russia, as a hind wing of *Mesopsyche*, renaming it as *M. javorskii* (Zalessky, 1935). These species were identified solely on isolated fore- or hind wings.

The body structure of mesopsychids was unknown until *Lichnomesopsyche gloriae* Ren, Labandeira & Shih, 2010 and *L. daohugouensis* Ren, Labandeira & Shih, 2010 from the late Middle Jurassic of Inner Mongolia, China, and

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Vitimopsyche kozlovi Ren, Labandeira & Shih, 2010 from the mid-Early Cretaceous of Liaoning Province, China, were described (Ren et al., 2009, 2010c). These three species document the first known fossils of Mesopsychidae with intact body features, including head, antennae, mouthparts, legs, abdomen, and genitalia. These scorpionflies, constituting the first record of Mesopsychidae in China, are important because of their unique mouthparts with significantly elongated proboscides, which indicate that this taxon, as well as pseudopolycentropodids and aneuretopsychids, fed on pollination drops while pollinating contemporaneous gymnosperm plants (Ren et al., 2009, 2010a, 2010c, 2011; Labandeira, 2010).

Recently, a rare specimen was collected from the Jiulongshan Formation the late Middle Jurassic at Daohugou Village, Wuhua Township, Ningcheng County, in Inner Mongolia, China. Based on the presence of leg setae not arranged in rings, fore- and hind wings bearing a posterior margin distinctly emarginated at CuP veinal apex, a Sc vein with one inclined anterior branch, bifurcating Rs and MA veins, and single CuA, 1A and 2A veins, it is assigned to the Mesopsychidae. Nevertheless, as this specimen has a five-branched MP vein, in contrast to all previously described mesopsychids with a four-branched MP vein, the diagnosis of the Mesopsychidae is also emended herein.

The age of the Jiulongshan Formation is late Middle Jurassic, about 165 Ma (Ren et al., 1995, 2002; Liu et al., 2004; Chen et al., 2004; Gao and Ren, 2006), corresponding to the Callovian–Bathonian boundary from the most recent geochronologic time scale (Ogg et al., 2008). The deposits of the Jiulongshan Formation at Daohugou have produced diverse insects, often preserving fine microstructural ornamentation, color patterns, and delicate morphological details (Ren, 1994; Ren et al., 2010b; Wu and Huang, 2012), along with abundant conchostracans (Shen et al., 2003), plants (Dong and Sun, 2012; Zhou et al., 2003; Wang et al., 2007), salamanders (Gao and Shubin, 2003), and a swimming mammaliaformes vertebrate (Ji et al., 2006).

2 Material and Methods

This study is based on one fossil specimen (CNU-MEC-NN2011095p/c), with part and counterpart, that is housed in the fossil insect collection of the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (CNUB; Dong Ren, Curator). The specimen was examined using a Leica MZ12.5 dissecting microscope, and illustrated with the aid of a drawing tube attached to the microscope. Camera lucida drawings were made with CoreDRAW X4 graphic software. The wing venation nomenclature is based on Novokshonov (1997, 2002).

3 Systematic Paleontology

3.1 Family Mesopsychidae Tillyard, 1917

Type genus: *Mesopsyche* Tillyard, 1917

Emended diagnosis: The MP is four- or five-branched in the fore- and hind wings.

Included genera: Previously, ten genera were known, the taxonomic placement of which was discussed by Novokshonov & Sukacheva (2001), Ren et al. (2010c) and Bashkuev (2011), in addition, the new genus described herein.

3.1.1 Cretaceous

Vitimopsyche Novokshonov & Sukacheva, 2001: Zaza Formation; Lower Cretaceous of Buryatia, Eravnenskii District, Baissa, Transbaikalia, Russia; forewing only. Yixian Formation, Lower Cretaceous of Hebei, China; complete body with wings.

Baissopsyche Novokshonov & Sukacheva, 2001: Zaza Formation; Lower Cretaceous of Buryatia, Eravnenskii District, Baissa, Transbaikalia, Russia; fore- and hind wings.

3.1.2 Jurassic

Ferghanopsyche Martynov, 1937: Shurab II, series H deposit; Liassic of Shurab, Tajikistan; forewing only.

Ptychopteropsis Martynov, 1937: Shurab II, series H deposit; Liassic of Shurab, Tajikistan; forewing only.

Turanopsyche Martynov, 1937: Shurab II, series H deposit; Liassic of Shurab, Tajikistan; hind wing only.

Lichnomesopsyche Ren, Labandeira & Shih, 2010: Jiulongshan Formation; Middle Jurassic (Bathonian–Callovian boundary) of Inner Mongolia, China; complete body with wings.

3.1.3 Triassic

Mesopsyche Tillyard, 1917: Blackstone Formation; Upper Triassic of Mount Crosby, western Brisbane, Queensland, Australia; fore- and hind wings. Protopivskaya Formation, Upper Triassic; Khar'kov Region, Ukraine; fore- and hind wings. Madygen Formation; Middle–Upper Triassic of Osh Region, Kyrgyzstan; fore- and hind wings.

Mesoses Riek, 1976: Molteno Formation; Upper Triassic of Bird's River, South Africa; incomplete forewing only.

Mesopanorpodes Tillyard, 1918: Ashfield Shale, Wianamatta Group; Middle Triassic, New South Wales,

Australia; incomplete forewing only.

3.1.4 Permian

Mesopsyche Tillyard, 1917: Maltseva Formation; Uppermost Permian or basal Triassic of the Kuznetsk Basin, near the town of Vyazniki, Vladimir Province, southwestern Siberia, Russia; fore- and hind wings.

Permopsyche Bashkuev, 2011: Poldarsa Formation; Upper Permian (Changsinghian Stage) of Isady, Vologda Province, Russia; fore- and hind wings. Croudace Bay Formation, Newcastle Group; Upper Permian of Belmont, Queensland, Australia; fore- and hind wings (Riek, 1953).

3.2 *Epicharmesopsyche* gen. nov.

Type species: *Epicharmesopsyche pentavenulosa* sp. nov.

Etymology: The genus name is a combination of the Greek prefix, "*epichar–*," meaning beautiful, and "*Mesopsyche*," the type genus for the family. The gender is feminine.

Diagnosis: Antennae long and filiform. Fore- and hind wings with Sc long, lacking distal bifurcation and reaching anterior margin at about the same level of the Rs forking; the first bifurcation of MP basad of the forking of Rs+MA; MP with five branches.

Comparison. *Epicharmesopsyche* gen. nov. is differentiated from all other genera in Mesopsychidae by a long Sc that extends to the wing margin at about the same level of the Rs forking. The MP has five branches in the fore- and hind wings.

3.3 *Epicharmesopsyche pentavenulosa* sp. nov. (Figs. 1, 2)

Holotype: Incomplete specimen with well-preserved body and wings, but missing mouthparts and most of the legs; male, No. CNU-MEC-NN-2011095p/c, part and counterpart. This specimen is housed at the fossil insect collection of the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China.

Etymology: The specific name is referred to five-branched nature of the MP veins.

Diagnosis: As for the genus, by monotype.

Description: The specimen with extended and overlapping fore- and hind wings; right and left wings asymmetrical. Body length (excluding antennae) 20.8 mm.

Head: Small, almost triangular in dorsal view. Antennae almost completely preserved, filiform, long (16.6 mm), and tapering apically. Compound eyes large, oval and three ocelli visible. Mouthparts not preserved. (Figs. 1b, 1c, 1f)

Thorax and legs: Meso- and metanotum about the same size; larger than pronotum. Partial femora of fore legs visible.

Wings: Left forewing (Fig. 2a) broad, length 25.0 mm, width 9.0 mm (length/width ratio 2.8) as preserved; Membrane delicate. Sc long, with only one inclined anterior branch, extending beyond MA, forking and reaching wing margin at about the same level of the Rs forking. Pterostigma distinct; R1 slightly bent near its ending. Both Rs and MA with two branches, Rs forking much later than MA forking; MA stem and MA_1 branch forming a distinct S-shape; MP originating from stem of MP+CuA more basally than Rs+MA from R1; MP forking slightly basad of the Rs+MA forking, MP with five branches, and MP_{1+2} forking distal to MP_{3+4+5} forking. Thyridium not evident. CuA single, bending toward the base at its terminus; CuP, 1A, 2A single and well developed; one crossvein between CuP and 1A. Right forewing (Fig. 2b) similar to the left forewing (Fig. 2a), but longer and narrower, length 28.8 mm, width 8.4 mm (length/width ratio 3.4), as preserved. Symmetrical dark spots present on both forewings. Hind wings similar to forewings, but smaller. Left hind wing (Fig. 2c) length 22.9 mm, width 8.2 mm; length/width ratio 2.8. MP forking basad of the Rs+MA forking, with five branches; one crossvein between MA_1 and MA_2; four long frenula bristles at the base of costal margin of the left hind wing. Right hind wing (Fig. 2d) similar to left hind wing, but longer and narrower, length 24.9 mm, width 7.3 mm; length/width ratio 3.4, as preserved; bearing three long frenula bristles.

Abdomen: Elongate, broadening apically, with eight segments visible. Basitergum fused to metathorax, shortened but not constricted at attachment to thorax. Cerci absent but lower/posterior surface bearing a small genital bulb and other features indicating male characters.

Locality and stratigraphic horizon: Jiulongshan Formation, Middle Jurassic (Bathonian–Callovian boundary), Daohugou Village, Ningcheng County, Inner Mongolia, China.

4 Discussions

New mesopsychid described here adds to the broad diversity of the family in China during the Middle Jurassic. At present, Paleozoic and Mesozoic Mesopsychidae consist of eleven reported genera from the Late Permian to the mid-Early Cretaceous of Australia, China, Kyrgyzstan, Russia, South Africa, Tajikistan, and Ukraine. The widespread but disjunct distributional pattern of mesopsychids supports a Permian origin in the Gondwana parts of Pangea, perhaps in the southeast (Australia), and a subsequent evolutionary history in Laurasia, after the supercontinent of Pangaea split apart into the proto-Eurasia and southern land masses (Ren et al., 2010c).

There are more than 250,000 insect fossils from the Middle Jurassic of the Daohugou locality in the extensive

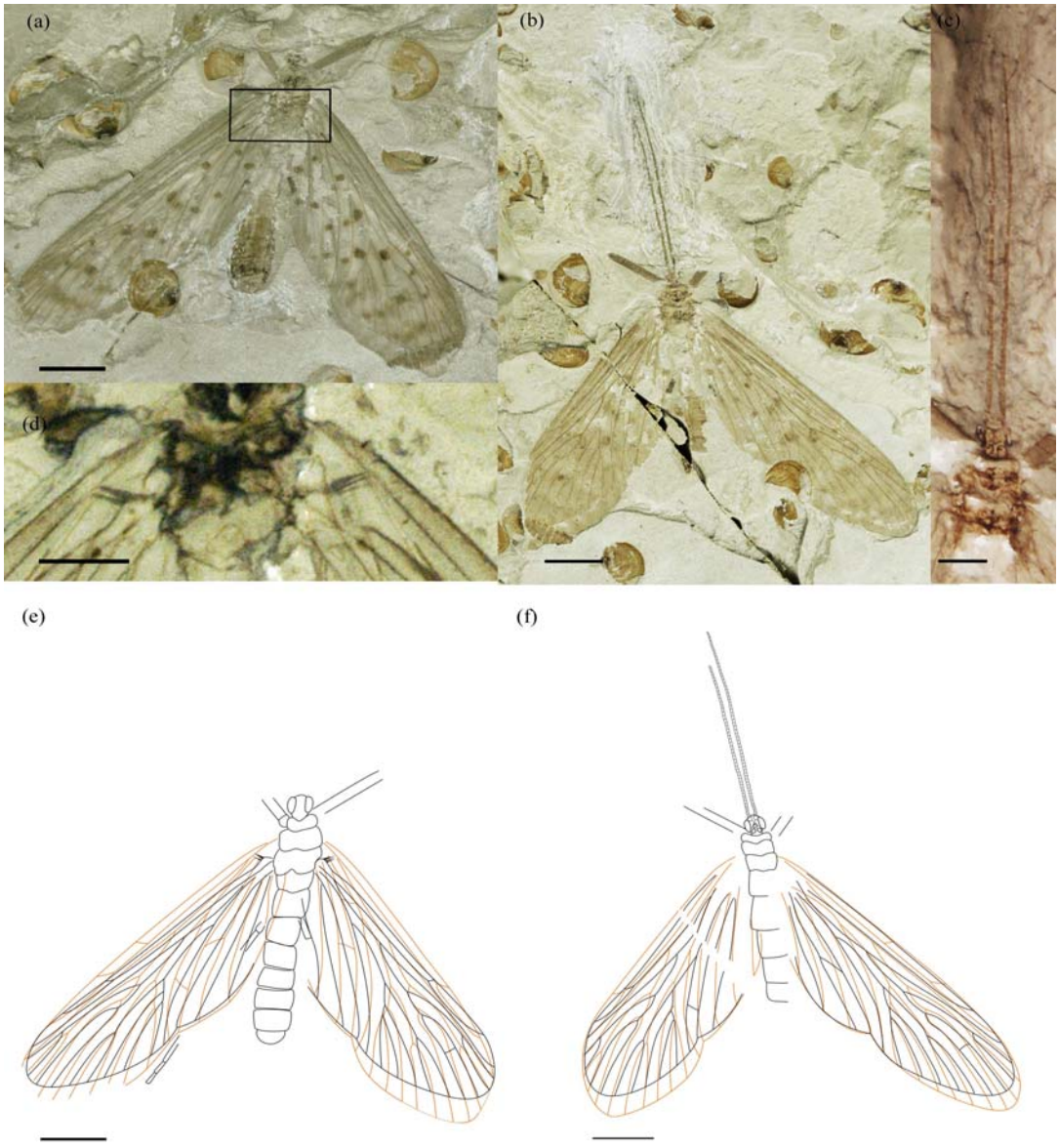

Fig.1. A to D, Photographs of the holotype of specimen CNU-MEC-NN2011095p/c.
(a), Part (CNU-MEC-NN2011095p). (b), Counterpart (CNU-MEC-NN2011095c). (c), Antennae of the counterpart photographed under alcohol. (d), Enlargement of the rectangular outline in (a) photographed under alcohol, showing long frenular bristles at the costal-margin base of both hind wings. (e), Camera lucida drawing of the part. (f), Camera lucida drawing of the counterpart. Scale bars = 5 mm for a, b, e and f; Scale bars = 2 mm for c and d.

CNU collection. However, only one specimen of *Epicharmesopsyche pentavenulosa* gen. et sp. nov. has been found. In comparison, 16 specimens of *Lichnomesopsyche gloriae* have been collected, and one specimen of *Lichnomesopsyche daohugouensis* was recovered from the same collection. The new species exhibits an unique combination of characters: both fore- and hind wings with a long Sc vein that reaches the wing margin at about the same level as the forking of the Rs vein. The new species also possesses five MP vein branches, the posterior margin of the wings emarginate at the CuP vein apex, the presence of symmetrically positioned dark spots on the wing membrane, and very long filiform antennae. Unfortunately, the mouthparts are not preserved.

Previously, all described mesopsychids bore a MP vein with four branches. Despite having a habitus and most venational characters consistent with the diagnosis of the Mesopsychidae, *E. pentavenulosa* gen. et sp. nov. exhibits a significant difference in that the MP vein has five branches. Within the Order Mecoptera, the Belmontiidae Tillyard, 1919 (= Parabelmontiidae Tillyard, 1922) and Holcorpidae Willmann 1989 have a five-branched MP vein in both fore- and hind wings; species of

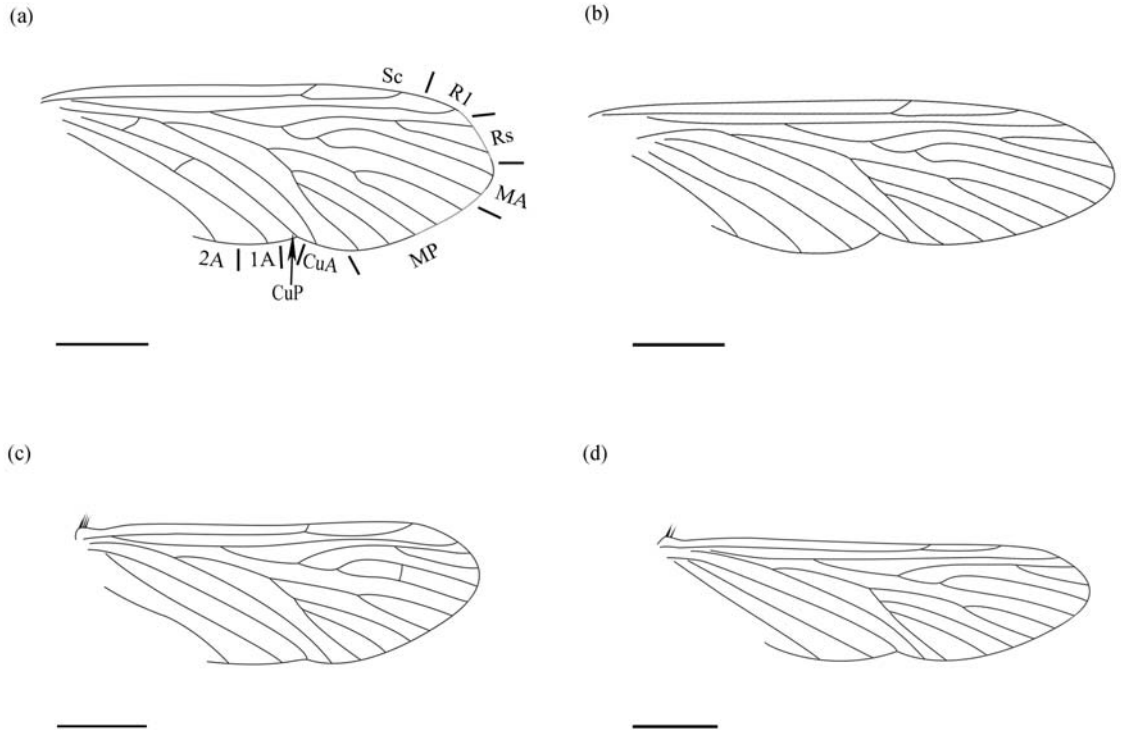

Fig. 2. Wing structure of specimen CNU-MEC-NN-2011095p/c.
(a), Camera lucida drawing of the left forewing of the part. (b), Camera lucida drawing of the right forewing of the counterpart. (c), Overlay drawing of the left hind wing of the part. (d) Camera lucida drawing of the right hind wing of the part. Scale bars = 5 mm for a–d.

Choristopsychidae Martynov, 1937 also have a five-branched MP vein, but only in the forewing (based on a forewing only). A comparison of our new species with these three families reveals significant differences for excluding this new genus from these taxa. The Belmontiidae (Late Permian) has a forewing with the thyridium shifted apicad on the MP_{1+2} vein stalk, versus the thyridium not evident for *E. pentavenulosa* gen. et sp. nov. Also, the forewing Sc vein has a distal bifurcation of the Sc_1 and Sc_2 veins (vs. no distal bifurcation); a costal space with a humeral crossvein present (vs. absence); both radial and median cells closed (vs. open); and a CuA vein with two branches (vs. one branch). *Choristopsyche tenuinervis* Martynov, 1937, from the Jurassic of Tajikistan, has a smaller and broader forewing with a wider costal area (vs. larger and slender wing with narrower costal area); a MP_{1+2+3} vein forking from the MP_{4+5} vein (vs. MP_{1+2} forming a fork with MP_{3+4+5}); and a posterior margin of the wing that is not emarginate (vs. posterior margin of the wings emarginate at the CuP vein apex). Holcorpids, from the early to late Eocene (Ypresian to Priabonian) of western North America (Archibald 2010) have a Rs vein with four branches (vs. 2 branches); posterior margin of the wing not emarginate (vs. posterior margin of the wings emarginate at the CuP vein apex); and abdominal segments 6–8 elongate for both males and females, with the 8^{th} segment distinctly the longest (vs. not elongate). Collectively, these features justifiably allow classification of *E. pentavenulosa* gen. et sp. nov. within the Mesopsychidae.

It is interesting to note that *L. gloriae* and *L. daohugouensis* have short and filiform-like antennae in which the flagellomere is gracile and extends to mid-proboscis, which is much shorter than those of fossil and modern scorpionflies. It is reasonable to assume that these mesopsychids were a highly modified and specialized lineage that evolved distinctive antennae and proboscis for feeding specializations (Labandeira, 2010; Ren et al., 2010c). However, *E. pentavenulosa* gen. et sp. nov. has much longer antennae, about eight-tenths as long as the body length, similar to those of typical, modern scorpionflies. Based on the shape and length of the antennae, we suggest that *E. pentavenulosa* gen. et sp. nov. might have borne mandibulate mouthparts similar to more typical and solid-food feeding mecopterans, rather than elongate proboscides.

In most four-winged insects, the fore- and hind wings are coupled anatomically such that they move together to gain aerodynamic efficiency in flight. There are various wing-coupling mechanisms in insects. Examples include coupling by jugal for some trichopterans and hepialids (Lepidoptera), jugo-frenate coupling in micropterygids (Lepidoptera), coupling by frenula for many lepidopterans, and coupling with hamule for many hymenopterans

Table 1 Size and wing shape asymmetry for left and right forewings of Mesopsychids

Species	Specimen number	Right Wing Length (mm)	Right Wing width (mm)	Right Wing L/W Ratio	Left Wing Length (mm)	Left Wing width (mm)	Left Wing L/W Ratio
Lichnomesopsyche gloriae	CNU-M-NN2005020-1&2 Holotype	25.0	7.0	3.6	21.3	7.1	3.0
	CNU-M-NN2005021-1&2	24.0	8.0	3.0	23.9	8.7	2.7
	CNU-M-NN2005023	23.2	6.4	3.6	20.3	6.6	3.1
	CNU-M-NN2005025-1&2	23.3	8.0	2.9	22.3	8.3	2.7
	CNU-M-NN2005027-1&2	27.8	8.4	3.3	26.4	8.9	3.0
	CNU-MEC-NN2011104	25.3	7.7	3.3	24.4	7.8	3.1
	CNU-MEC-NN2011110	20.3	5.7	3.6	20.0	6.2	3.2
	CNU-MEC-NN2011111	26.0	6.8	3.8	25.5	7.1	3.6
	CNU-MEC-NN2011112	27.8	7.6	3.6	26.6	8.5	3.1
	CNU-MEC-NN2011114	25.2	7.8	3.2	23.9	8.2	2.9
Lichnomesopsyche daohugouensis	CNU-M-NN2005022-1&2 Holotype	21.7	6.6	3.3	20.2	6.8	3.0
Vitimopsyche kozlovi	CNU-M-HP2005001-1&2 Holotype	25	8	3.1	24	8.4	2.9
Epicharmesopsyche pentavenulosa gen. et sp. nov.	CNU-MEC-NN2011095p/c Holotype	28.8	8.4	3.4	25.0	9.0	2.8

[1]Six specimens of *L. gloriae* are not included due to lack of clear preservation of left and right forewings.
[2]Left and right wing nomenclature are based on the dorsal specimen aspect.

(Chapman, 1998). For the mecopteran family Choristidae (Riek, 1973), a primitive coupling structure is present in which short jugal bristles on the jugal lobe of forewing and two long frenula bristles on the humeral lobe, at the base of costal margin of the hind wing, are used to link the fore- and hind wings (Riek, 1973; Chapman, 1998). We found three to four frenula bristles on the humeral lobe at the base of the costal margin of both hind wings of *E. pentavenulosa* gen. et sp. nov. (Fig. 1d). This is the first time that a wing coupling structure has been documented on a mesopsychid.

Epicharmesopsyche pentavenulosa gen. et sp. nov. exhibits an asymmetric wing shape and size between the left and right wings, a phenomenon occurring in other fossil insect lineages, particularly cockroaches (Vršanský, 2008). The left forewing is 25.0 mm long and 9.0 mm wide, vs. the right forewing with a length of 28.8 mm and a width of 8.4 mm. Notably, the asymmetric wing shape and size of the left wings are broader than the right wings, which seems to be common for mesopsychids as reported by Ren et al. (2009, 2010c) and in other specimens collected after the publication of those two papers. The data on wing length, wing width and length/width ratio for left and right wings are summarized in Table 1 to highlight the asymmetry. Asymmetrically unequal wings also occur in the dipteran family Ptychopteridae, as reported for *Eoptychopterina elenae* Ren & Krzemiński, 2002, and for *E. postica* Liu, Shih & Ren, 2012. For *Eoptychopterina,* only a few of the more than 100 specimens have asymmetric wings. Although it is possible that these dipteran specimens had inherently asymmetrical wings, we cannot rule out other possibilities, such as rock deformation during the fossilization process. But, for mesopsychids, because of the high frequency of asymmetry in several deposits of varying styles of preservation, we can infer that this group most likely bore inherently asymmetrical wings.

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References

Archibald, S.B., 2010. A revision of the scorpionfly family Holcorpidae (Mecoptera), with description of a new species from Early Eocene McAbee, British Columbia, Canada. *Annals of the Entomological Society of France*, 46(1–2): 173–182.

Bashkuev, A.S., 2011. The earliest Mesopsychidae and revision of the family Mesopanorpodidae (Mecoptera). In: Shcherbakov, D.E., Engel, M.S., and Sharkey, M.J. (Eds) Advances in the Systematics of Fossil and Modern Insects: Honouring Alexandr Rasnitsyn. *ZooKeys*, 130: 263–279. doi: 10.3897/zookeys.130.1611

Chapman, R.F., 1998. *The insects – structure and function.* New York: Cambridge University Press, pp. 192–194.

Chen Wen, Ji Qiang, Liu Dunyi, Zhang Yan, Song Biao and Liu Xinyu, 2004. Isotope geochronology of the fossil-bearing beds in the Daohugou area, Ningcheng, Inner Mongolia. *Geological Bulletin of China*, 23(12): 1165–1169.

Dong Man and Sun Ge, 2012. Ginkgo *houlinhensis* sp. nov. from the Lower Cretaceous of Houlinhe Coal Field, Inner Mongolia, China. *Acta Geologica Sinica* (English edition), 86(1): 11–19.

Gao Keqin and Shubin, N., 2003. Earliest known crown-group salamanders. *Nature*, 422: 424–428.

Gao Keqin and Ren Dong, 2006. Radiometric dating of ignimbrite from Inner Mongolia provides no indication of a post-Middle Jurassic age for the Daohugou Beds. *Acta Geologica Sinica* (English edition), 80(1): 42–45.

Ji Qiang, Luo Zhexi, Yuan Chongxi, Tabrum and Alan, R., 2006. A swimming mammaliaform from the Middle Jurassic and ecomorphological diversification of early mammals. *Science*, 311(5764): 1123–1127.

Labandeira, C.C., 2010. The pollination of mid-Mesozoic seed plants and the early history of long-proboscid insects. *Annals of the Missouri Botanical Garden*, 97(4): 469–513.

Liu Luxi, Shih Chungkun and Ren Dong, 2012. Two new species of Ptychopteridae and Trichoceridae from the Middle Jurassic of northeastern China (Insecta: Diptera: Nematocera). *Zootaxa*, 3501: 55–62.

Liu Yongqin, Liu Yanxue, Li Peixian, Zhang Hong, Zhang Lijun, Li Yin and Xia Haodong, 2004. Daohugou biota-bearing lithostratigraphic succession on the southeastern margin of the Ningcheng Basin, Inner Mongolia, and its geochronology. *Geological Bulletin of China*, 23(12): 1180–1187.

Martynov, A.V., 1937. Liassic Insects from Shurab and Kyzyl-Kiya. *Trudy Paleontologischekogo Instituta Akademii Nauk, SSSR*, 7: 1–231. (in Russian)

Novokshonov, V.G., 1997. Some Mesozoic scorpionflies (Insecta: Panorpida = Mecoptera) of the Families Mesopsychidae, Pseudopolycentropodidae, Bittacidae, and Permochoristidae. *Paleontological Journal*, 31(1): 65–71.

Novokshonov, V.G., and Sukacheva, I.D., 2001. Fossil Scorpionflies of the "Suborder" Paratrichoptera (Insecta: Mecoptera). *Paleontological Journal*, 35(2): 173–182.

Novokshonov, V.G., 2002. Order Panorpida Latreille, 1802. The scorpionflies, pp. 194–199. In: Rasnitsyn, A.P., and Quicke, D.L.J. (Eds.), *History of Insects*. Kluwer Academic Publisher, Dordrecht.

Ogg, J.G., Ogg, G., and Gradstein, F.M., 2008. *The Concise Geologic Time Scale*. New York: Cambridge University Press, 177 pp.

Ren Dong, 1994. Discovery of fossil Bittacids in China. *Acta Geologica Sinica* (English edition), 7(2): 219–224.

Ren Dong, Lu Liwu, Guo Ziguang and Ji Shu'an, 1995. *Faunae and Stratigraphy of Jurassic–Cretaceous in Beijing and the Adjacent Areas.* Beijing: Seismic Publishing House, pp. 64–73.

Ren Dong and Krzemiński, M., 2002. Eoptychopteridae (Diptera) from the Middle Jurassic of China. *Annales Zoologici*, 52(2): 207–210.

Ren Dong, Gao Keqin, Guo Ziguang, Ji Shu'an, Tan Jingjing and Song Zuo, 2002. Stratigraphic division of the Jurassic in the Daohugou area Ningcheng, Inner Mongolia. *Geological Bulletin of China*, 21(8–9): 584–591.

Ren Dong, Labandeira C.C., Santiago-Blay, J.A., Rasnitsyn, A.P., Shih Chungkun, Bashkuev, A., Logan, M.A.V., Hotton, C.L., and Dilcher, D., 2009. A probable pollination mode before angiosperms: Eurasian, long-proboscid scorpionflies. *Science*, 326(5954): 840–847.

Ren Dong, Shih Chungkun and Labandeira C.C., 2010a. New Jurassic Pseudopolycentropodids from China (Insecta: Mecoptera). *Acta Geologica Sinica* (English edition), 84(1): 22–30.

Ren Dong, Shih Chungkun, Gao Taiping, Yao Yunzhi and Zhao Yunyun, 2010b. *Silent stories – insect fossil treasures from dinosaur era of the northeastern China.* Beijing: Science Press, 324 pp.

Ren Dong, Labandeira C.C., and Shih Chungkun, 2010c. New Mesozoic Mesopsychidae (Mecoptera) from northeastern China. *Acta Geologica Sinica* (English edition), 84(4): 720–731.

Ren Dong, Shih Chungkun and Labandeira, C.C., 2011. A well-preserved aneuretopsychid from the Jehol Biota in China (Insecta: Mecopteroidea: Aneuretopsychidae). *Zookeys*, 129: 17–28. doi: 10.3897/zookeys.129.1282

Riek, E.F., 1953. Fossil mecopteroid insects from the Upper Permian of New South Wales. *Records of the Australian Museum*, 23(2): 55–87.

Riek, E.F., 1973. A revision of Australian scorpionflies of the family Choristidae (Mecoptera). *Journal of the Australian Entomological Society*, 12(2): 103–112.

Riek, E.F., 1976. A new collection of insects from the Upper Triassic of South Africa. *Annals of the Natal Museum*, 22: 791–820.

Shen Yanbin, Chen Penji and Huang Diying, 2003. Age of the fossil conchostracans from Daohugou of Ningcheng, Inner Mongolia. *Journal of Stratigraphy*, 27(4): 311–313.

Tillyard, R.J., 1917. Mesozoic insects of Queensland. *Proceedings of the Linnean Society of New South Wales*, 42: 175–200.

Tillyard, R.J., 1918. Permian and Triassic insects from New South Wales, in the collection of Mr. John Mitchell. *Proceedings of the Linnean Society of New South Wales*, 42: 720–756.

Tillyard, R.J., 1919. A fossil insect wing belonging to the new order Paramecoptera, ancestral to the Trichoptera and Lepidoptera from the Upper Coal-Measures of Newcastle, N.S.W. *Proceedings of the Linnean Society of New South Wales*, 44: 231–256.

Tillyard, R.J., 1922. Mesozoic insects of Queensland. 9. Orthoptera, and additions to the Protorthoptera, Odonata, Hemiptera and Planipennia. *Proceedings of the Linnean Society of New South Wales*, 47: 447–470.

Vršanský, P., 2008. New blattarians and a review of dictyopteran assemblages from the Lower Cretaceous of Mongolia. *Acta Palaeontologica Polonica*, 53(1): 129–136.

Wang Xin, Duan Shuying, Geng Baoyin, Cui Jinzhong and Yang Yong, 2007. *Schmeissneria*: A missing link to angiosperms? *BMC Evolutionary Biology*, 7(14): 1–13.

Willmann, R., 1989. Evolution und phylogenetisches system der Mecoptera (Insecta: Holometabola). *Abhandlungen der senckenbergischen naturforschenden Gesellschaft*, 544: 1–153.

Wu Hao and Huang Diying, 2012. A new species of *Liadotaulius* (Insecta: Trichoptera) from the Middle Jurassic of Daohugou, Inner Mongolia. *Acta Geologica Sinica* (English edition), 86 (2): 320–324.

Zalessky, G., 1935. Sur deux restes d'insectes fossiles provenant du bassin de Kousnetzk et sur l'age geologique des depots qui les renferment. *Bulletin de la Société Géologique de France*, 5 (5): 687–695.

Zhou Zhonghe, Barrett, P.M., and Hilton, J., 2003. An exceptionally preserved Lower Cretaceous ecosystem. *Nature*, 421(6925): 807–814.