


Revision of the long-proboscid scorpionflies, *Lichnomesopsyche* Ren, Labandeira, and Shih, 2010

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Abstract.—The Mesozoic mecopteran family Mesopsychidae has attracted extensive attention by their long proboscis that is presumably associated with pollination of early gymnosperms. Three previously reported species of *Lichnomesopsyche* Ren, Labandeira, and Shih, 2010 from the Middle–Upper Jurassic Haifanggou Formation at Daohugou (Inner Mongolia, northeastern China) display distinct resemblances in wing venation, so that their classification, based on currently described characters, remains elusive. Herein, we describe and figure exquisitely preserved male genital structures of *L. glorieae* Ren, Labandeira, and Shih, 2010, *L. daohugouensis* Ren, Labandeira, and Shih, 2010, and *L. prochorista* Lin et al., 2016, which can be used for defining and recognizing the three species. Our discovery indicates that the male genitalia are the major critical structures for species-level classification of the peculiar genus *Lichnomesopsyche*. Details of the maxillary palps and legs of *L. glorieae* and *L. daohugouensis* are also described.

Introduction

Mecoptera, also known as scorpionflies, are named from the modern Panorpididae in which upward-tilted male genitalia possess enlarged claspers resembling the stingers of scorpions. The extant Mecoptera is a small relic order that consists of ~600–650 species placed in nine families (Cai et al., 2008; Bicha, 2010), although the number of families is much smaller than during geological history (Zhang et al., 2011; Lin et al., 2019b). The earliest fossil record of Mecoptera dates back to the early Permian (Rasnitsyn et al., 2004). Mecoptera flourished during the Jurassic (Grimaldi and Engel, 2005; Soszyńska-Maj et al., 2018), but significantly declined since the Cretaceous (e.g., Bittacididae; Kopeć et al., 2016).

The suborder Aneuretopsychina Rasnitsyn and Kozlov, 1990 consists of five extinct families—Mesopsychidae Tillyard, 1917, Pseudopolycentropodidae Handlirsch, 1925, Aneuretopsychidae Rasnitsyn and Kozlov, 1990, Nedubroviidae Bashkuev, 2011, and Dualulidae Lin et al., 2019 (Lin et al., 2019b)—which played a dominant role in Mecoptera from the late Permian to the Middle Jurassic (Rasnitsyn and Kozlov, 1990; Ren et al., 2009; Bashkuev, 2011; Lin et al., 2019a; Zhao et al., 2020). Aneuretopsychina taxa possess a long proboscis probably associated with gymnosperm pollination (Labandeira et al., 2007; Ren et al., 2009; Labandeira, 2010). Ren et al. (2009) reported that Aneuretopsychina fed on liquid pollination drops on gymnosperms and co-evolved with early gymnosperm seed plants. Anatomical features of some Aneuretopsychina have been discussed in detail (Grimaldi et al., 2005; Ren et al., 2009; Grimaldi and Johnston, 2014; Lin et al.,

2019a; Zhao et al., 2020). As for Mesopsychidae, however, very little about body structures has been revealed to date.

Lichnomesopsyche Ren, Labandeira, and Shih, 2010, erected based on fossils from the Daohugou Beds, comprise a total of three described species: *L. glorieae* Ren, Labandeira, and Shih, 2010, *L. daohugouensis* Ren, Labandeira, and Shih, 2010, and *L. prochorista* Lin et al., 2016 (Ren et al., 2010; Lin et al., 2016). *Lichnomesopsyche* spp. bear a distinct long proboscis considered to be adapted for the long pollen catchment funnels of early gymnosperms (Ren et al., 2009).

The phylogenetic relationship between Mecoptera and Siphonaptera has long been debated (e.g., Whiting et al., 1997; Whiting, 2002; Grimaldi and Engel, 2005; Beutel et al., 2008; Friedrich and Beutel, 2010; Zhao et al., 2020), and studies have recently supported that Siphonaptera originated from the long-proboscid-bearing Aneuretopsychina (Huang et al., 2012; Gao et al., 2013, 2014) and even that Siphonaptera should be degraded as a suborder of Mecoptera (Tihelka et al., 2020). Herein, we do not intend to settle the phylogenetic problem, but focus on the species-level classification of *Lichnomesopsyche*.

Material and methods

Five specimens of two species of *Lichnomesopsyche* were examined: four of *L. glorieae* and one of *L. daohugouensis*. All fossils were collected from the Middle–Upper Jurassic Daohugou Beds, near Daohugou Village, Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia, northeastern China (for a detailed locality map, see Huang, et al., 2018a, fig. 1c). These specimens were preserved as brownish organic films in the gray-white tuffaceous shale. NIGP 171885 is a male *L. glorieae* collected from White Hill, eastern Beigou

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Village that co-occurred with abundant ‘conchostracans’; NIGP 171884 (male), 171886 (female), and 171887 (female), all identified as *L. gloriae*, were collected from a hill behind Beigou Village. All of these specimens were collected from upper layers of the Daohugou Beds. NIGP 173118, a male *L. daohugouensis*, was collected from the Chentaizi locality co-occurring with cladocerans, indicating a top-layer production (Huang, 2016; Huang et al., 2018b). The above information reveals that *Lichnomesopsyche* seems to more frequently appear in upper layers of the Daohugou Beds, which likely suggests a relatively high-altitude environment (Huang, 2019).

All specimens were carefully prepared using a sharp knife. Photographs of the general habitus were taken using a Canon EOS 5D Mark II camera with a Canon 100 mm macro lens attached. Photomicrographs of detailed structures were taken using a digital camera attached to a Zeiss Discovery V20 microscope; some were moistened with 70% ethanol to more clearly display fine structures, e.g., setae.

Abbreviations used in diagnosis: CuA = anterior cubitus; M = media; Rs = radial sector; Sc = subcosta. Venational terminologies are based on the nomenclature of Grimaldi et al. (2005).

Repositories and institutional abbreviations.—The fossil materials studied here are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGP). Other repository cited in the text is CNU-M-NN = Capital Normal University (Mecoptera), Ningcheng County, Inner Mongolia.

Systematic paleontology

Order Mecoptera Packard, 1886

Family Mesopsychidae Tillyard, 1917

Genus *Lichnomesopsyche* Ren, Labandeira, and Shih, 2010

Type species.—*Lichnomesopsyche gloriae* Ren, Labandeira, and Shih, 2010.

Other species.—*Lichnomesopsyche daohugouensis*, Ren, Labandeira, and Shih, 2010; *L. prochorista* Lin et al., 2016.

Diagnosis.—Forewings and hindwings resembling each other in shape and venation. Sc in forewings with two branches, but with one shorter branch in hindwings; both Rs_{1+2} and Rs_{3+4} armed with two branches; M originating from stem of M + CuA; Rs and M forking roughly simultaneously or slightly different. Male terminalia exposed and enlarged, with dististylus approximately as long as basistylus; dististylus varying in shape.

Remarks.—Emended from Ren et al. (2010) and Lin et al. (2016).

Lichnomesopsyche gloriae Ren, Labandeira, and Shih, 2010
Figures 1, 2

Holotype.—CNU-M-NN 2005020 (1, 2), part and counterpart, a nearly complete specimen with well-preserved body and wings from Daohugou (Ren et al., 2010, pl. 722, pl. 1, fig. 1).

Emended diagnosis.—Male genitalia trapezoid in dorsal view, covered with small setae; basistylus cylindrical, tapering backward gradually; dististylus enlarged apically, forming a large hook.

Description.—Head: proboscis long, sword-shaped; one pair of galeae closed up; hypopharynx visible. Antennae relatively short, filiform, with ~35 flagellomeres; maxillary palps short, with four palpomeres, with two basal palpomeres relatively short, third palpomere elongate, apical palpomere drop-like, pointed distally, shorter than third palpomere (Fig. 1.3).

Wings: with characters resembling description by Ren et al. (2010).

Legs: slender and long, with length increasing from fore- to hindlegs. Femur moderately thick, longer than tibia; tibia somewhat curving, slightly swelling at apex; two long apical spurs visible in apical tibia (Fig. 2.2); tarsus pentamerous; basitarsus longer than other four tarsomeres together; last three tarsomeres relatively short; fourth tarsomere shortest, with one pair of bifid claws visible (Figs. 1.6, 2.3). Fore tarsus approximately as long as femur and tibia together; hind tarsus slightly longer than femur. Legs covered with dense short setae and some long bristles, with rows of bristles staggered on tibia and tarsus.

Abdomen: 10 segments visible, tapering backward; tergites nearly completely sclerotized; sclerotized section rectangular, with length shorter than width; width gradually decreasing backward; tergite VII small, transverse.

Male terminalia: terminalia large, covered with setae (Fig. 1.4, 1.5, 1.10); hypandrium (sternite IX) near semicircle, slightly hollow posteriorly; epandrium (tergite IX) transverse, bow-tie-shaped, with both anterior and posterior margins concave; two oblique grooves armed laterally with row of comb-like denticles on posterior margin (Fig. 1.8); tergite X small, bearing two oblique lines and one pair of paraprocts visible (Fig. 1.5); cerci clavate (Fig. 1.5). Basistyles and dististyles folding into trapezoid, forming clasping organ; basistylus cylindrical, narrowing gradually to apex; dististylus triangular, distinctly enlarged apically, forming rounded outer angle and large hook apically.

Female terminalia comparatively small with one pair of two-segmented cerci (Fig. 2.4).

Remarks.—The wing length/width ratio of *Lichnomesopsyche* mentioned by Ren et al. (2010) could reach 3.8. Such a slender wing ratio could be caused by taphonomic deformation (lateral compression).

Lichnomesopsyche daohugouensis Ren, Labandeira, and Shih, 2010
Figure 3

Holotype.—CNU-M-NN 2005022 (1, 2), part and counterpart, a nearly complete specimen with well-preserved body and wings from Daohugou (Ren et al., 2010, p. 724, pl. 4).

Emended diagnosis.—Basistylus cylindrical; dististylus dividing a prominent projection on outer margin; apical dististylus rounded, armed with many tiny spines.

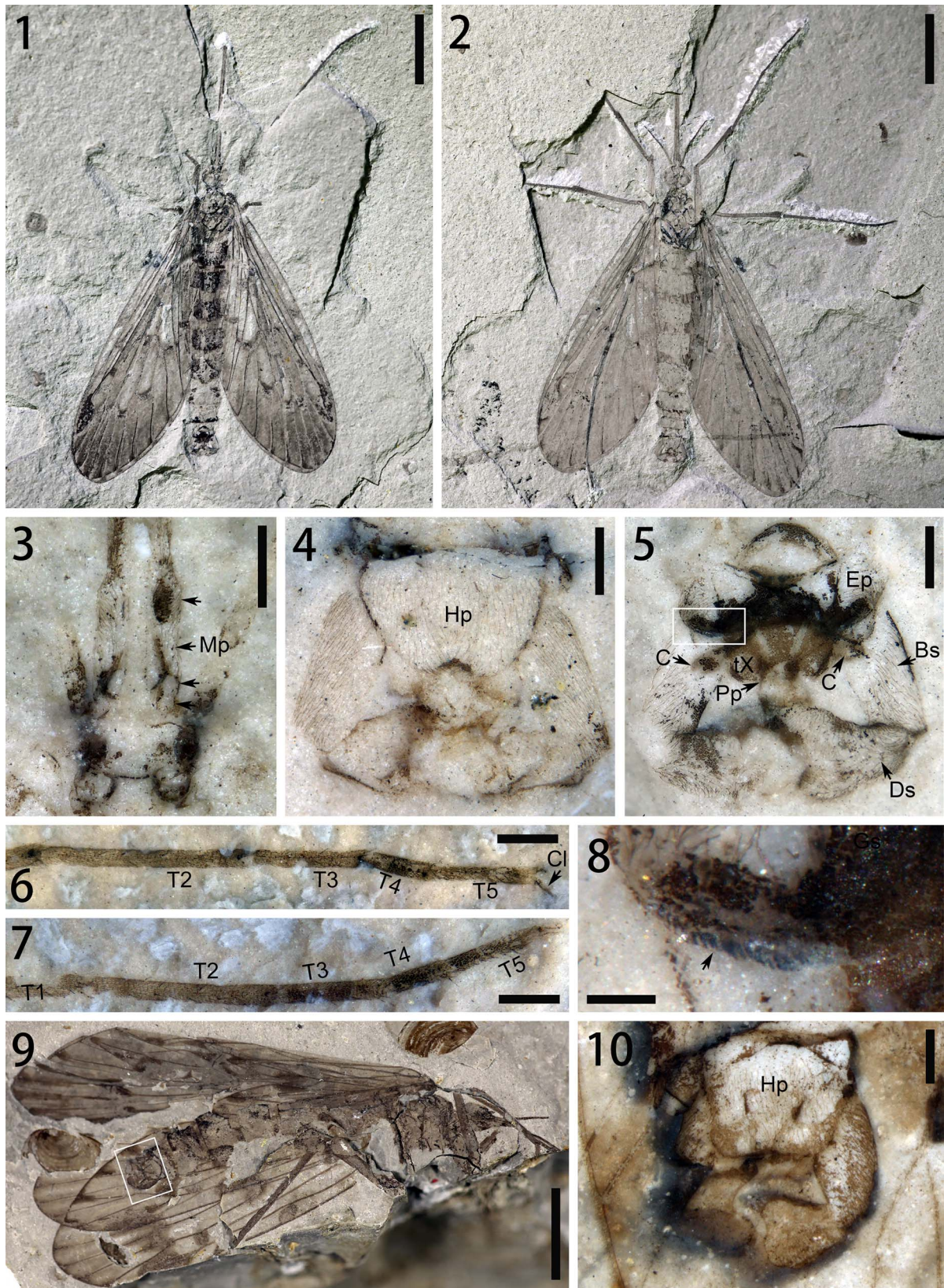


Figure 1. Male *Lichnomesopsyche gloriae* from Middle–Upper Jurassic Daohugou Beds at Beigou: (1–8) NIGP 171884: (1) part (171884a), general habitus; (2) counterpart (171884b), general habitus; (3) enlargement from (1), indicating details of maxillary palps; (4) enlargement from (2), details of terminalia; (5) enlargement from (1), details of terminalia; (6) tarsus of left foreleg, with T2–T5; (7) tarsus of left midleg, with T1–T5; (8) enlargement from (5), showing comb-like denticles of epandrium (arrow); (9, 10) NIGP 171885: (9) general habitus in lateral view; (10) enlargement from (9), details of terminalia. Bs = basistylus; C = cerci; Cl = claws; Ds = dististylus; Ep = epandrium; Hp = hypandrium; Mp (arrows) = maxillary palps; Pp = paraproct; Tn = nth tarsomere; tX = tenth tergite. Scale bars = 5 mm (1, 2, 9); 0.5 mm (3–7, 10); 0.1 mm (8).

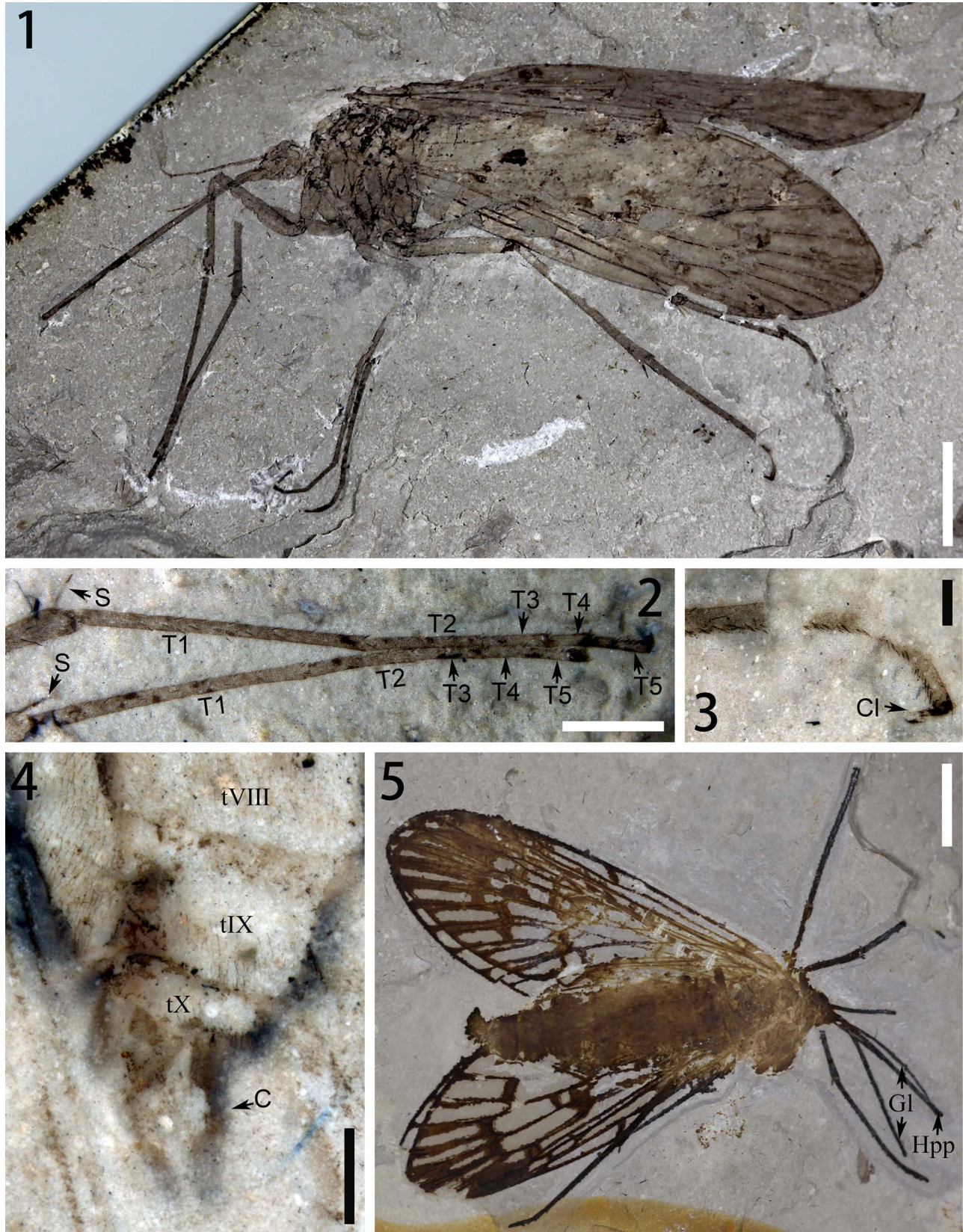


Figure 2. Female *Lichnomesopsyche glorioae* from Middle–Upper Jurassic Daohugou Beds at Beigou: (1–4) NIGP 171886: (1) general habitus in lateral view; (2) tarsus of forelegs, with T1–T5; (3) claws of left hind leg; (4) terminalia; (5) NIGP 171887, general habitus in dorsal view. C = cerci; Cl = claws; Gl = galeae; Hpp = hypopharynx; S = apical spurs; Tn = nth tarsomere; tN = Nth tergite. Scale bars = 5 mm (1, 5); 2 mm (2); 0.5 mm (3, 4).

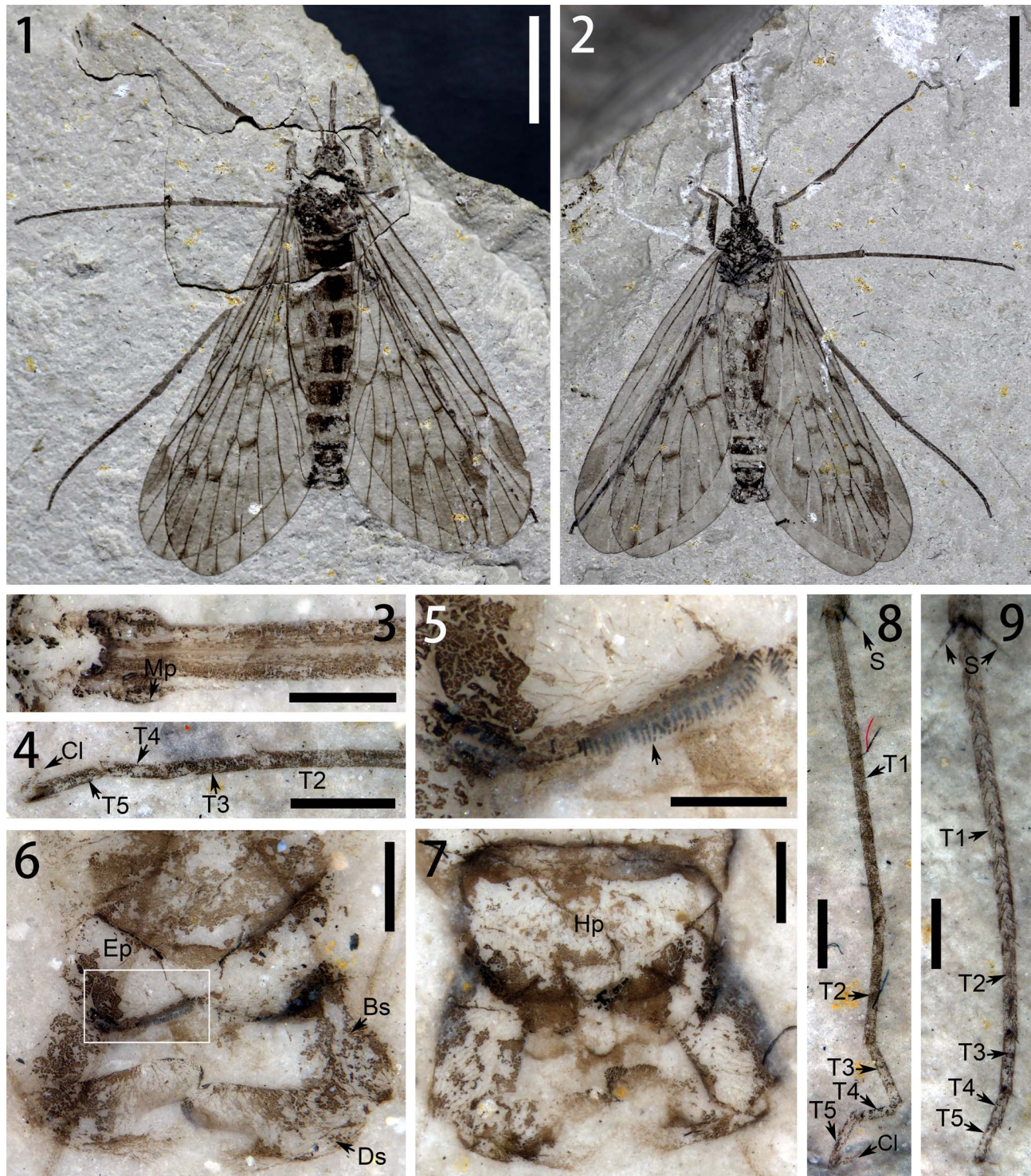


Figure 3. Male *Lichnomesopsyche daohugouensis* from Middle-Upper Jurassic Daohugou Beds at Chentaizi, NIGP 173118: (1) part (173118a), general habitus; (2) counterpart (173118b), general habitus; (3) enlargement from (2), maxillary palps and long proboscis; (4) tarsus with claws in left midleg; (5) enlargement from (6), showing comb-like denticles (arrow); (6) enlargement from (1), details of terminalia; (7) enlargement from (2), details of terminalia; (8) tarsus of left foreleg, with T1–T5; (9) tarsus of left hindleg, with T1–T5. Bs = basistylus; Cl = claws; Ds = dististylus; Ep = epandrium; Hp = hypandrium; Mp = maxillary palps; S = apical spurs; Tn = nth tarsomere. Scale bars = 5 mm (1, 2); 1 mm (4, 8, 9); 0.5 mm (3, 6, 7); 0.2 mm (5).

Description.—General characters of head, legs, and abdomen as in original description of *Lichnomesopsyche gloriae* described above.

Head: Antennae filiform with > 25 flagellomeres. Maxillary palps short, pointed, with four palpomeres; 1–3 palpomeres

relatively short; distal palpomeres drop-like, aristiform apically (Fig. 3.3).

Wings: with characters resembling description by Ren et al. (2010).

Abdomen: tergite VIII triangular; apex with protrusion.

Table 1. Parameters for left and right forewings of *Lichnomesopsyche*. L = length (mm); L/W = length/width ratio; W = width (mm); – = not available.

Species	Gender	NIGP no.	Right L	Right W	Right L/W	Left L	Left W	Left L/W
<i>L. glorieae</i>	male	171884	20.5	7.2	2.8	21.5	6.5	3.3
	male	171885	23.8	8.0	3.0	24.2	–	–
	female	171886	27.9	–	–	26.6	–	–
	female	171887	23.0	8.2	2.8	25.0	8.0	3.1
<i>L. daohugouensis</i>	male	173118	18.0	6.9	2.6	18.0	6.9	2.6

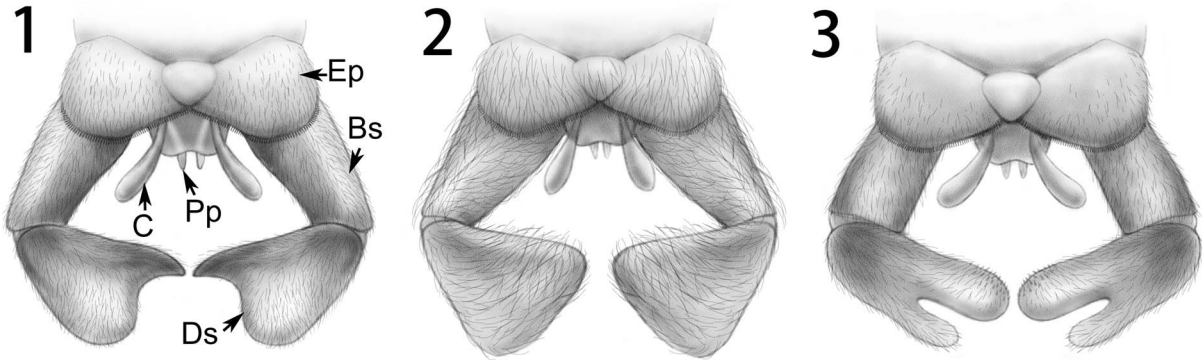


Figure 4. *Lichnomesopsyche*, reconstructed male terminalia in dorsal view: (1) *L. glorieae*; (2) *L. prochorista* (based on Lin et al., 2016, fig. 6c); (3) *L. daohugouensis*. Bs = basistylus; C = cerci; Ds = dististylus; Ep = epandrium; Pp = paraproct.

Terminalia: well-exposed, covered with setae (Fig. 3.6, 3.7); hypandrium oval; epandrium (tergite IX) bow-tie-shaped, with both anterior and posterior margins concave, armed with one row of comb-like denticles on posterior margin (Fig. 3.5); basistyles and dististyles folding into trapezoid, forming clasping organ; basistylus cylindrical; dististylus dividing a prominent projection in outer part, discriminated by tuft of hairs; apical dististylus rounded, with inner portion armed with many tiny spines.

Remarks.—The circular, pale spots on the holotype of *Lichnomesopsyche daohugouensis* could have been produced by pathological factors.

Discussion

Shih et al. (2013) summarized the wing parameters of 13 specimens of Mesopsychidae; based on the high frequency of broader left wings, they concluded that mesopsychids possess asymmetrical wings. However, such characters could be attributed to taphonomic factors that would clearly deform some specimens. The wing ratios of the newly illustrated specimens display variation in wing appearances under different postures, or the left and right wings are simply symmetrical (Table 1). Thus, mesopsychids would have symmetrical wings.

Species of *Lichnomesopsyche* are very similar to one another in wing characters, and previous classifications focused

on very minor differences, e.g., the relative bifurcation between Rs_{1+2} and Rs_{3+4} , and circular and pale spots on the wings, which are not necessarily preserved in all specimens. The present study indicates that the male genitalia of the three species of *Lichnomesopsyche* are clearly different from each other (Fig. 4). The male genitalia of *L. daohugouensis* distinctly differs from those of both *L. glorieae* and *L. prochorista* by a series of characters, including the basistylus not tapering backward and the dististylus not enlarged apically, but with a remarkable projection presented at the outer margin. The male genitalia of *L. glorieae* and *L. prochorista* closely resemble each other, but they differ based on the following characters: the dististylus of both species are somewhat triangular, but the apical dististylus of *L. glorieae* has a large hook instead of rounded angles as in *L. prochorista* (see Lin et al., 2016, fig. 6c). In addition, comparatively long hairs are developed on the surface of the genitalia of *L. prochorista*, whereas the genitalia of *L. daohugouensis* and *L. glorieae* are covered with shorter setae. A key to the species of *Lichnomesopsyche* is presented below. There are no alternative characters that can be clearly used for separating the female species of *Lichnomesopsyche*, although the body sizes of *L. prochorista* and *L. glorieae* are generally larger than that of *L. daohugouensis*. According to all known specimens, the forewing length of *L. daohugouensis* varies from 18.0–22.0 mm, of *L. glorieae* from 20.5–27.9 mm, and of *L. prochorista* from 22.0–25.9 mm.

Key to the species of Lichnomesopsyche based on characters of the male terminalia.—

- 1 Basistylus not tapering; dististylus not enlarged apically; apical dististylus with outer projection *L. daohugouensis*
Basistylus tapering; dististylus enlarged apically..... 2
- 2 Apical dististylus with a large hook..... *L. glorieae*
Apical dististylus with rounded angles *L. prochorista*

The male terminalia of *Lichnomesopsyche* are extraordinary in Mecoptera. The posterior margin of the epandrium is armed with comb-like denticles (Figs. 1.8, 3.5) resembling those of *Parapolycentropus paraburmiticus* Grimaldi and Rasnitsyn in Grimaldi et al., 2005 from mid-Cretaceous Burmese amber (see Grimaldi and Johnston, 2014, fig. 8B). This character represents a synapomorphy of Aneuretropsychina.

The species of *Lichnomesopsyche* from Daohugou biota are rare cases of preserved male genitalia structure that are enabled as diagnostic characters. Meanwhile, little differentiation is found in venation, so it is indisputable to regard genital structures as diagnostic characters within this genus. Our study provides a new perspective on the classification of *Lichnomesopsyche*.

Acknowledgments

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References

- Bashkuev, A.S., 2011, Nedubroviidae, a new family of Mecoptera: The first Paleozoic long-proboscid scorpionflies: *Zootaxa*, v. 2895, p. 47–57, <https://doi.org/10.11646/zootaxa.2895.1.3>.
- Beutel, R.G., Friedrich, F., and Whiting, M.F., 2008, Head morphology of *Caurinus* (Boreidae, Mecoptera) and its phylogenetic implications: *Arthropod Structure & Development*, v. 37, p. 418–433, <https://doi.org/10.1016/j.asd.2008.02.002>.
- Bicha, W.J., 2010, A review of the scorpionflies (Mecoptera) of Indochina with the description of a new species of *Neopanorpa* from northern Thailand: *Zootaxa*, v. 2480, p. 61–67, <https://doi.org/10.11646/zootaxa.2480.1.6>.
- Cai, L.J., Huang, P.Y., and Hua, B.Z., 2008, *Sinopanorpa*, a new genus of Panorpidae (Mecoptera) from the oriental China with descriptions of two new species: *Zootaxa*, v. 1941, p. 43–54, <https://doi.org/10.11646/zootaxa.1941.1>.
- Friedrich, F., and Beutel, R.G., 2010, The thoracic morphology of *Nannochorista* (Nannochoristidae) and its implications for the phylogeny of Mecoptera and Antliophora: *Journal of Zoological Systematics and Evolutionary Research*, v. 48, p. 50–74, <https://doi.org/10.1111/j.1439-0469.2009.00535.x>.
- Gao, T.P., Shih, C.K., Rasnitsyn, A.P., Xu, X., Wang, S., and Ren, D., 2013, New transitional fleas from China highlighting diversity of Early Cretaceous ectoparasitic insects: *Current Biology*, v. 23, p. 1261–1266, <https://doi.org/10.1016/j.cub.2013.05.040>.
- Gao, T.P., Shih, C.K., Rasnitsyn, A.P., Xu, X., Wang, S., and Ren, D., 2014, The first flea with fully distended abdomen from the Early Cretaceous of China: *BMC Evolutionary Biology*, v. 14, p. 168, <https://doi.org/10.1186/s12862-014-0168-1>.
- Grimaldi, D., and Engel, M.S., 2005, *Evolution of the Insects*: Cambridge, UK, Cambridge University Press, 755 p.
- Grimaldi, D., and Johnston, M.A., 2014, The long-tongued Cretaceous scorpionfly *Parapolycentropus* Grimaldi and Rasnitsyn (Mecoptera: Pseudopolycentropodidae): New data and interpretations: *American Museum Novitates*, v. 2014, p. 1–24, <https://doi.org/10.1206/3793.1>.
- Grimaldi, D., Rasnitsyn, A., Zhang, J.F., and Fraser, N., 2005, Revision of the bizarre Mesozoic scorpionflies in the Pseudopolycentropodidae (Mecopteroidea): *Insect Systematics & Evolution*, v. 36, p. 443–458, <https://doi.org/10.1163/187631205794761021>.
- Handlirsch, A., 1925, *Palaeontologie*, in Schröder, C.H., ed., *Handbuch der Entomologie*, Volume 3: Jena, Germany, Verlag Gustav Fischer, p. 117–306.
- Huang, D.Y., ed., 2016, [The Daohugou Biota]: Shanghai, Shanghai Science and Technology Press, 330 p. [in Chinese]
- Huang, D.Y., 2019, [Jurassic integrative stratigraphy and timescale of China]: *Science China Earth Sciences*, v. 62, p. 223–255, <https://doi.org/10.1007/s11430-017-9268-7>. [in Chinese]
- Huang, D.Y., Engel, M.S., Cai, C.Y., and Nel, A., 2012, Diverse transitional giant fleas from the Mesozoic era of China: *Nature*, v. 438, p. 201–204, <https://doi.org/10.1038/nature10839>.
- Huang, D.Y., Cai, C.Y., and Nel, A., 2018a, New damselfly-like wing shape from the Middle Jurassic of China (Odonata: Isophlebiidae: Camptophlebiidae): *Geobios*, v. 51, p. 181–186, <https://doi.org/10.1016/j.geobios.2018.04.003>.
- Huang, D.Y., Cai, C.Y., Fu, Y.Z., and Su, Y.T., 2018b, The Middle–Late Jurassic Yanliao entomofauna: *Palaeontological Research*, v. 1, p. 3–31, <https://doi.org/10.11646/palaeontological.1.1.2>.
- Kopeć, K., Soszyńska-Maj, A., Krzemiński, W., and Coram, R.A., 2016, A new hangingfly (Insecta, Mecoptera, Bittacidae) from the Purbeck Limestone Group (Lower Cretaceous) of southern England and a review of Cretaceous Bittacidae: *Cretaceous Research*, v. 57, p. 122–130, <https://doi.org/10.1016/j.cretres.2015.08.007>.
- Labandeira, C.C., 2010, The pollination of mid Mesozoic seed plants and the early history of long-proboscid insects 1,2,3: *Annals of the Missouri Botanical Garden*, v. 97, p. 469–513, <https://doi.org/10.3417/2010037>.
- Labandeira, C.C., Kvaček, J., and Mostovski, M.B., 2007, Pollination drops, pollen, and insect pollination of Mesozoic gymnosperms: *Taxon*, v. 56, p. 663–695, <https://doi.org/10.2307/25065852>.
- Lin, X.D., Shih, M.J., Labandeira, C.C., and Ren, D., 2016, New data from the Middle Jurassic of China shed light on the phylogeny and origin of the proboscis in the Mesopsychidae (Insecta: Mecoptera): *BMC Evolutionary Biology*, v. 16, p. 840–847, <https://bmcecolvol.biomedcentral.com/articles/10.1186/s12862-015-0575-y>.
- Lin, X.D., Labandeira, C.C., Shih, C.K., Hotton, C.L., and Ren, D., 2019a, Life habits and evolutionary biology of new two-winged long-proboscid scorpionflies from mid-Cretaceous Myanmar amber: *Nature Communications*, v. 10, p. 1–14, <https://doi.org/10.1038/s41467-019-09236-4>.
- Lin, X.D., Shih, C.K., Li, S., and Ren, D., 2019b, Mecoptera-scorpionflies and hangingflies, in Ren, D., Shih, C.K., Gao, T.P., Wang, Y.J., and Yao, Y.Z., eds., *Rhythms of Insect Evolution: Evidence from the Jurassic and Cretaceous in Northern China*: New York, Wiley-Blackwell, 728 p.
- Packard, A.S., 1886, A new arrangement of the orders of insects: *The American Naturalist*, v. 20, p. 808.
- Rasnitsyn, A.P., and Kozlov, M.V., 1990, New group of fossil insects: Scorpions with cicad and butterfly adaptations: *Doklady Akademii Nauk SSSR*, v. 310, p. 233–236.
- Rasnitsyn, A.P., Aristov, D.S., Gorochov, A.V., Rowland, J.M., and Sinitshenkova, N.D., 2004, Important new insect fossils from Carrizo Arroyo and the Permian–Carboniferous faunal boundary: *New Mexico Museum of Natural History and Science Bulletin*, v. 25, p. 215–246.
- Ren, D., Labandeira, C.C., Santiago-Blay, J.A., Rasnitsyn, A., Shih, C.K., Bashkuev, A., Logan, M.A.V., Hotton, C.L., and Dilcher, D., 2009, A probable pollination mode before angiosperms: Eurasian, long-proboscid scorpionflies: *Science*, v. 326, p. 840–847, <https://doi.org/10.1126/science.1178338>.
- Ren, D., Labandeira, C.C., and Shih, C.K., 2010, New Mesozoic Mesopsychidae (Mecoptera) from northeastern China: *Acta Geologica Sinica*, v. 84, p. 720–731, <https://doi.org/10.1111/j.1755-6724.2010.00244.x>.
- Shih, C.K., Qiao, X., Labandeira, C.C., and Ren, D., 2013, A new mesopsychid Orthophlebiidae from the Middle Jurassic of northeastern China: *Acta Geologica Sinica*, v. 87, p. 1235–1241, <https://doi.org/10.1111/1755-6724.12124>.
- Soszyńska-Maj, A., Krzemiński, W., Kopeć, K., Cao, Y.Z., and Ren, D., 2018, Large Jurassic scorpionflies belonging to a new subfamily of the family Orthophlebiidae (Mecoptera): *Annales Zoologici*, v. 68, p. 85–93, <https://doi.org/10.3161/00034541ANZ2018.68.1.004>.
- Tihelka, E., Giacomelli, M., Huang, D.Y., Pisani, D., Donoghue, P.J., and Cai, C.Y., 2020, Fleas are parasitic scorpionflies: *Palaeontological Research*, v. 3, p. 641–653, <https://doi.org/10.11646/palaeontological.3.6.16>.
- Tillyard, R., 1917, Mesozoic insects of Queensland. 1, Planipennia, Trichoptera, and the new order Protomecoptera: *Proceedings of the Linnean Society of New South Wales*, v. 42, p. 175–200.
- Whiting, M.F., 2002, Mecoptera is paraphyletic: Multiple genes and phylogeny of Mecoptera and Siphonaptera: *Zoologica Scripta*, v. 31, p. 93–104, <https://doi.org/10.1046/j.0300-3256.2001.00095.x>.
- Whiting, M.F., Carpenter, J.C., Wheeler, Q.D., and Wheeler, W.C., 1997, The Strepsiptera problem: Phylogeny of the holometabolous insect orders inferred from 18S and 28S ribosomal DNA sequences and morphology: *Systematic Biology*, v. 46, p. 1–68.
- Zhang, J.X., Shih, C.K., Petrulevičius, J.F., and Ren, D., 2011, A new fossil eomeropid (Insecta, Mecoptera) from the Jiulongshan Formation, Inner Mongolia, China: *Zoosystema*, v. 33, p. 443–450, <https://doi.org/10.5252/z2011n4a2>.
- Zhao, X.D., Wang, B., Bashkuev, A.S., Aria, C., Zhang, Q.Q., Zhang, H.C., Tang, W.T., and Engel, M.S., 2020, Mouthpart homologies and life habits of Mesozoic long-proboscid scorpionflies: *Science Advances*, v. 6, p. eaay1259, <https://doi.org/10.1126/sciadv.aay1259>.

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