

A New Fossil Scorpionfly (Insecta: Mecoptera: Holcorpidae) with Extremely Elongate Male Genitalia from Northeastern China

LI Lei¹, Chungkun SHIH^{1,2}, WANG Chen¹ and REN Dong^{1,*}

¹ Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing 100048, China

² Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, USA

Abstract: Since *Holcorpa maculosa* was first described in 1878, it has attracted lots of attention due to its extremely elongate abdominal segments from the sixth to the eighth. Fossil records of family Holcorpidae are very rare, comprising two species in one genus represented by three fossil specimens, resulting in limited knowledge on the structure and function of holcorpids' unique male organ, as well as its evolutionary relationship with other scorpionflies. Herein we describe a new genus with a new species, *Conicholcorpa stigmosa* gen. et sp. nov., of the Holcorpidae from the Middle Jurassic Jiulongshan Formation near Daohugou Village, Inner Mongolia, China. This is the first holcorpids documented from the Daohugou locality, albeit two previously reported species with extremely elongate male organs but deemed as Family Incertae sedis. *C. stigmosa* gen. et sp. nov. is the earliest holcorpids hitherto, extending its existence from the Early Eocene to the Middle Jurassic by 114 million years and providing one more early case of presenting exaggerated male body parts for sexual display and/or selection. Our analysis supports the sister relationship between Holcorpidae and Orthophlebiidae. Our results not only enhance our knowledge of the morphology of Holcorpidae but also elucidate the relationship of known species of this family.

Key words: *Conicholcorpa*, Daohugou, Holcorpidae, Jiulongshan Formation, Middle Jurassic

1 Introduction

The distinctive scorpionfly family of Holcorpidae is known by its extremely elongate male abdominal segments from the sixth through the eighth (A6 to A8) and unique characters of its wing venation (Scudder, 1878). The first two fossils of this family, *Holcorpa maculosa* Scudder 1878, were collected by Mrs. Fisher in 1877 and reported by Scudder in 1878 from the Late Eocene (34.07 ± 0.10 Ma, Priabonian) of Florissant, Colorado, USA. Since then, it has caused a lot of discussions and debates. Scudder placed *Holcorpa* in the family Panorpidae, but Carpenter considered it as a basal member due to the character that both the fore- and hind wings in *Holcorpa* having five media vein (M) branches (vs. both wings with four M branches in all Panorpidae) (Carpenter, 1931). Then, Martynova (1962) and Penny (1975) speculated that it should belong to a separate family. In 1989, Willmann (1989) set up a family of Holcorpidae with *Holcorpa* and its only species as the type species. In the next two

decades, with the in-depth study of Holcorpidae and other scorpionflies, more details of Holcorpidae have been documented (Novokshonov, 2002; Grimaldi and Engel, 2005). In 2010, Archibald described *Holcorpa dillhoffi* from the Early Eocene (~51 Ma, Ypresian) of McAbee, near Cache Creek, British Columbia, Canada (Archibald 2010). He also provided the diagnostic characters of Holcorpidae: (1) fore-, and hind wing media veins (M) with five branches; (2) abdominal segments 6 to 8 (A6 to A8) elongate (both male, female), with A8 distinctly longest; and (3) male: extended, slender dististyli, lacking basal tooth (Archibald 2010).

The other contention of Holcorpidae is the sex of the holotype. The body of the holotype specimen of *H. maculosa* is poorly preserved, the eighth abdominal segment and the genitalia beyond it were incomplete, while all eight abdominal segments of the allotype are well preserved and the male genitalia clearly visible, with distinctive enlarged genital bulb and extended pincer-like gonostyli (Scudder, 1878). The allotype was larger than the holotype which Carpenter (1931) explained as sexual

* Corresponding author. E-mail: rendong@mail.cnu.edu.cn

dimorphism, concluding that the holotype is a female, contrary to Scudder's opinion. But in 2013, Wang, Shih et Ren believed that the holotype should be considered as sex indeterminate due to lack of preserved terminalia. Their justification was the sudden narrowing of A8, comparing with A7, is consistent with the male allotype (Scudder, 1878) and the male specimens in both Archibald's and their studies (Archibald, 2010; Wang et al., 2013).

The fossil records of Holcorpidae and other scorpionflies with extremely elongate male genitalia are very rare. Besides the three specimens of *Holcorpa*, Wang et al. (2013) described *Miriholcorpa forcipata* Wang, Shih et Ren, 2013, which has many diagnostic characters of Holcorpidae such as forewing R1 curving around pterostigma, meeting C on anterior wing margin well before apex, forewing M veins with five branches, abdominal segments 6 to 8 (A6 to A8) elongate with A8 distinctly longest, and male genitalia with gonostyli extended and slender. However, *M. forcipata* is different from the type genus *Holcorpa* of Holcorpidae in branching pattern of forewing M veins and spurs absent at the end of A6. In addition, it is not discernible whether the hind wing has 5-branched M veins, or whether dististyli basal tooth is lacking (Willmann, 1989; Archibald, 2010). Due to uncertainty whether hind wing of *Miriholcorpa* Wang, Shih et Ren, 2013 has 5 branched M veins, Wang et al. deemed this genus as Family Incertae sedis, pending future discovery of new fossil specimens with clear hind wing venation (Wang et al., 2013). Furthermore, *Fortiholcorpa paradoxa* Wang, Shih et Ren, 2013 has affinities with Holcorpidae: (1) both fore- and hind wings have 5-branched M veins; (2) terminal abdominal segments (A6 to A8) elongate exaggeratedly; and (3) genital bulb enlarged and gonostyli extended. But, the genus is different from the type genus *Holcorpa* in branching pattern of hind wing M veins, length of A8 slightly longer than that of A7 (vs. A8 distinctively longest), and lacking spurs at the terminal part of A6 (vs. two spurs present). In addition, it is not discernible whether dististyli basal tooth is lacking (Willmann, 1989; Archibald, 2010). Therefore, Wang et al. also deemed *F. paradoxa* as Family Incertae sedis (Wang et al., 2013).

2 Geological Settings

The type specimen in this study, CNU-NN-MEC-2015023, was collected from Daohugou (N41°18'38", E119°13'20"), Shantou Township, Ningcheng County, Inner Mongolia, northeastern China. The geology age of this deposit is considered as latest Middle Jurassic (late Callovian) (Walker et al., 2013; Xu et al., 2015; Yang et al., 2015; Yi et al., 2017), approximately 165–164 million

years ago (Mya). The lacustrine strata at Daohugou contain abundant exquisite Mecoptera and other insect fossils. Such as Bittacidae (Ren Dong, 1997), Pseudopolycentropodidae (Shih et al., 2013), Aneuretopsychidae (Ren et al. 2009), Mesopsychidae (Ren et al. 2009), Hymenoptera (Gao et al., 2009), Hemiptera (Li et al., 2013; Yao et al., 2014) (Fig. 1).

3 Material and Methods

The holotype 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 photographs of the specimen was taken with a Canon EOS 550D digital camera with a Canon EFS 60 mm macro lens. The line drawings were done using Photoshop CS 6.0 software.

We use the venational nomenclature of Willmann (1989). For Mecoptera systematics, we follow Willmann's (1987, 1989) and Willmann and Novokshonov's (1998), except for Orthophlebiidae and the genus *Orthophlebia*, which were subsequently revised by Hong and Zhang (2004, 2007).

4 Systematic Paleontology

Order MECOPTERA Packard, 1886

Suborder EUMECOPTERA Tillyard, 1919

Family Holcorpidae Willmann, 1989

Genus *Conicholcorpa* Li, Shih, Wang and Ren gen. nov.

Type species. *Conicholcorpa stigmosa* sp. nov.

Etymology. The generic name is a compound word derived from a Latin word, conic- meaning conical, referring to the long and cone-shaped abdomen segments, and *Holcorpa*, the name of type genus of Holcorpidae. Gender feminine.

Diagnosis. Forewing, Rs_1 with 3 branches; the stem of Rs_{1+2} 1.3 times as long as that of Rs_{3+4} ; Rs_{3+4} forking more proximal than Rs_{1+2} forking; M forking almost at the same level with Rs forking; The stem of M bifurcating into M_{1+2} and M_{3+4+5} , then M_{3+4+5} forking into M_3 and M_{4+5} . Hind wing, Sc short, reaching the anterior margin at the middle of C; the stem of Rs_{1+2} 2 times as long as that of Rs_{3+4} ; Rs_{3+4} forking more proximal than Rs_{1+2} forking.

Remarks. This new genus is similar to the type genus, *Holcorpa*, of Holcorpidae. The following characters are shared by these two genera: in both forewing and hindwing, the R unforking, curved just before pterostigma; the Rs_1 with 3 branches, the M with 5 branches. The sixth

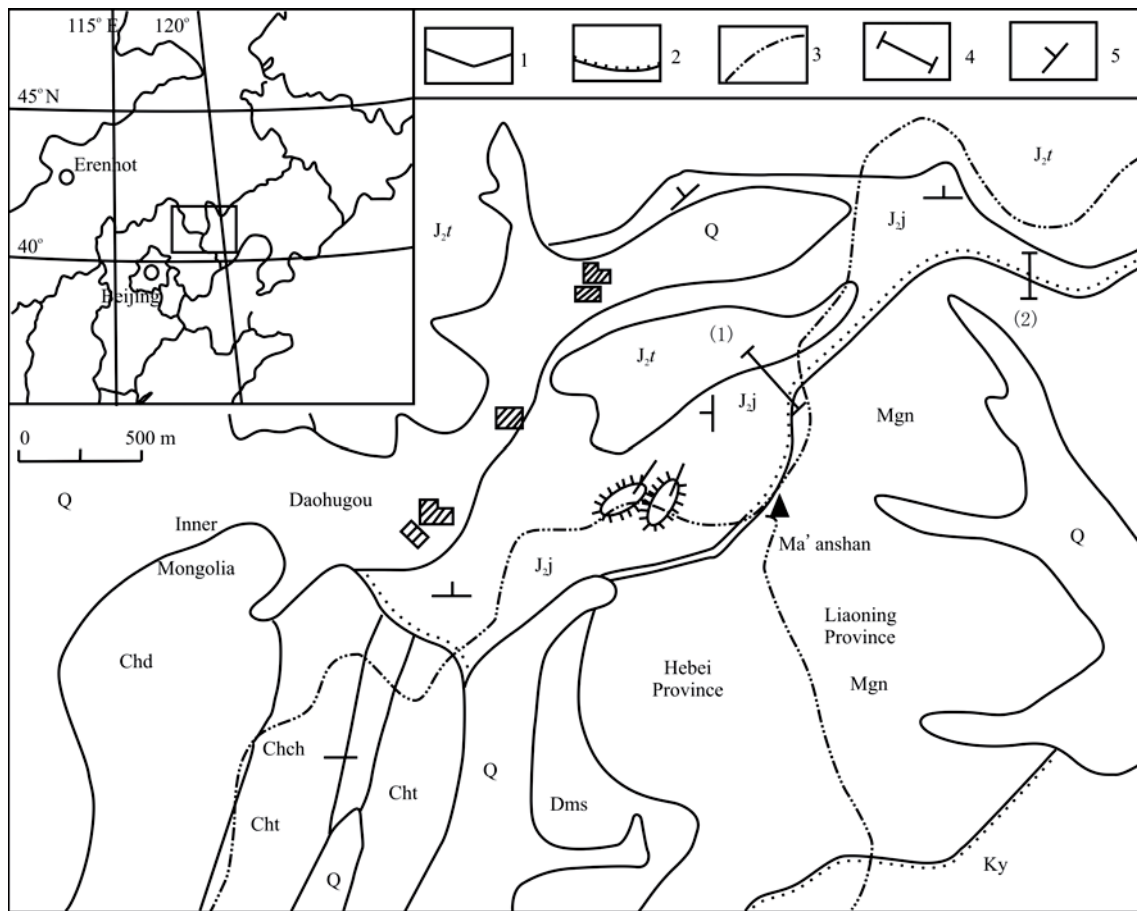


Fig. 1. Simplified geological map of Daohugou area at juncture of three Provinces or Autonomous Region of Liaoning, Hebei, and Inner Mongolia (after Gao and Ren, 2006).

(1), Stratigraphic boundary; (2), unconformity; (3), provincial boundary; (4), location of geological section; (5), strike and dip; Chc, Changchougou Fm.; Chch, Chuanlinggou Fm.; Chd, Dahongyu Fm.; Cht, Tuanshanzi Fm.; Dms, Dalaiyingzi erosion surface; Jj, Jiulongsan Fm.; Ky, Yixian Fm.; Q, Quaternary; Mgn, Maanshan gneiss.

to eighth abdominal segments elongate, the length of A8 1.5 times as long as that of A7.

However, *Conicholcorpa* gen. nov. is distinguished from *Holcorpa* by: (1) the forking of Rs_{3+4} occurs more proximal than Rs_{1+2} forking (vs. more distal for *Holcorpa*); (2) the M_{1+2} forking almost at the same level with Rs_{1+2} forking (vs. M_{1+2} forking distal to the Rs_{1+2} forking); (3) spurs absent at the end of A6 (vs. present); and (4) gonostyli much longer than genital bulb (vs. as long as or slightly longer).

Conicholcorpa gen. nov. is similar to *Miriholcorpa* by: (1) Sc reaching anterior margin; (2) Rs furcation at same level as M forking; (3) Stem of Rs_{3+4} is shorter than stem of Rs_{1+2} . But the new genus is differentiated from *Miriholcorpa* by the stem of M bifurcating into M_{1+2} and M_{3+4+5} , then M_{3+4+5} forking into M_3 and M_{4+5} (vs. M_1 simple. M_{2+3} forking into M_2 and M_3 , and M_{4+5} forking into M_4 and M_5).

Conicholcorpa gen. nov. is similar to *Fortiholcorpa* by: (1) Sc reaching anterior margin and (2) the structure of M. But the new genus is separated from *Fortiholcorpa* by Rs

furcation at the same level with M forking (vs. Rs furcation much proximal of the forking of M in the hind wing [indiscernible in the forewing]).

Furthermore, this new genus is quite different from the genera in Orthophlebiidae, due to the 5 branches in hind wing (vs. 4 branches) and the extremely elongate terminal abdominal segments A6 to A8 (Fig 2).

Conicholcorpa stigmosa Li, Shih, Wang and Ren gen. et sp. nov.

Etymology. The species name is derived from the Latin word *stigmosus*, indicating many dark spots on the wings.

Description Lateral view. Body length 47.4 mm (from head to genital end), male. Left forewing and left hind wing with clear venation, abdominal segments and genitalia well preserved. Right forewing and right hind wing overlapped and obscured.

Head. Subcircular with short chewing mouthparts, antenna filiform; compound eyes large and oval

Thorax. Prothorax short, 0.3 times as long as mesothorax, while metathorax 1.3 times as long as

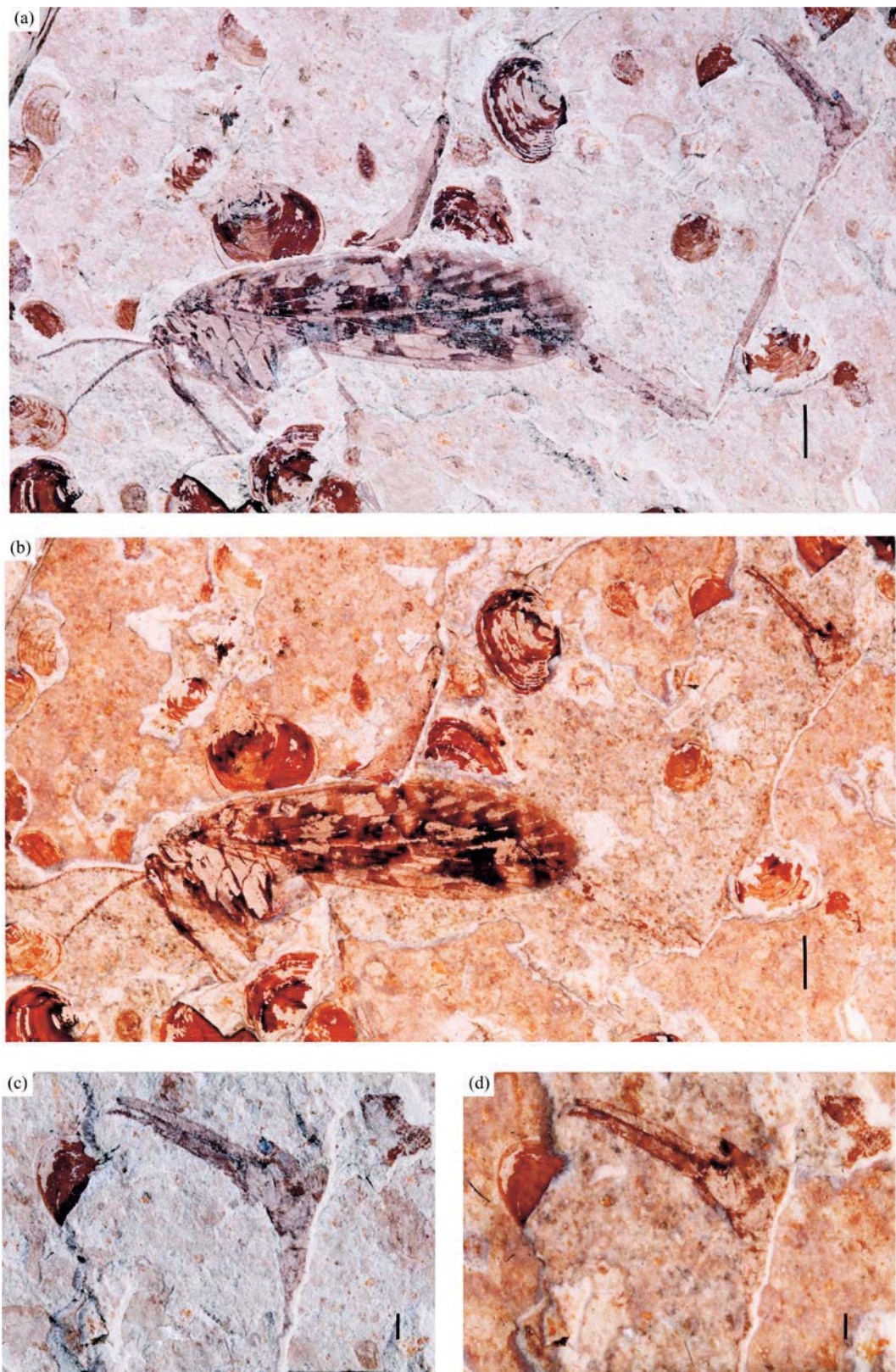


Fig. 2. Photographs of *Conicholcorpa stigmosa* gen. et sp. nov., holotype, CNU-NN-MEC-2015023. (a), Photo of the holotype without alcohol; (b), Photo of the holotype under alcohol; (c), Photo of the genitalia; (d), Photo of the genitalia under alcohol; Scale bars represent 2 mm in a and b; 1 mm in c and d.

mesothorax. The fore legs well preserved with coxa, trochanter, femur, tibia and part of tarsi. Tibia of right mid leg visible while the other three legs missing.

Forewing. Oval, long and relatively broad, apical margin rounded, 21.5 mm long, 5.7 mm wide. The Sc long, almost reaching midsection of pterostigma. Vein R unforking, originating from the Sc, curving just before pterostigma and reaching C on anterior wing margin well before apex. The Rs forking from R at two seventh of the wing, and then forking into Rs_{1+2} and Rs_{3+4} at two fifth of the wing. The Rs_{1+2} has 4 branches, the Rs_{3+4} has 2 branches, the stem of Rs_{1+2} 1.3 times as long as that of Rs_{3+4} . The stem of M parallel with R and forking into M_{1+2} and M_{3+4+5} just distal to Rs forking. The M_{1+2} forking at the same level with Rs_{1+2} forking. The stem of M_{3+4+5} 0.2 time as long as the stem of M_{1+2} while the stem of M_{4+5} as long as that of M_{3+4+5} . The Cu_1 curving basally, then straight, terminating on the posterior margin of mid-wing. The Cu_2 close to Cu_1 at base, then parallel with Cu_1 to the posterior margin just before mid-wing. The A_1 , A_2 , A_3 veins long, reaching the anal margin and parallel with each other.

Hind wing. Similar to the forewing but slightly smaller, 19.6 mm long, 5.4 mm wide. The Sc is short, reaching the middle of the anterior margin. The stem of Rs_{3+4} 2 times as long as that of Rs_{1+2} . The part of A veins indiscernible.

Abdomen. A_1 – A_5 7.7 mm long, A_6 4.7 mm long, no spurs at the terminal part of A_6 , A_7 9.5 mm long. A_8 14.5 mm long, 1.5 times as long as that of A_7 .

Genitalia. Genital bulb distinctively enlarged, hypovalva

and two gonocoxites well preserved. Gonostyli long and straight like tweezers, 4.4 mm long, 2.5 times as long as the genital bulb, curving inward at distal part (Fig. 3).

5 Discussion

Conicholcorpa stigmosa gen. et sp. nov. is the earliest holcorpidae hitherto, extending its existence from the Early Eocene to the Middle Jurassic by 114 million years and providing one more early case of presenting exaggerated male body parts for sexual display and/or selection.

Holcorpidae is a sister group of Orthophlebiidae, with similar wing venation. For example, the media veins (M) in both families have 5 branches with almost the same structure. But according to the previous studies, holcorpids, especially the male and “sex-unknown” specimens of *Holcorpa maculosa*, show significant differences from orthophlebiids, i.e., their length of Rs_{3+4} is much longer (vs. shorter in Orthophlebiidae) and their Rs_{3+4} forking is more distal than Rs_{1+2} forking (vs. more proximal in Orthophlebiidae) (Scudder 1878, Archibald 2010). On the contrary, *Conicholcorpa* gen. nov. has a different type of venation, its Rs_{3+4} forking more proximal than Rs_{1+2} forking, the same as the Rs_{3+4} forking of the genus *Mesopanorpa* in Orthophlebiidae (Hong et al. 2007, Qiao et al. 2012). Therefore, the new genus might be basal to *Holcorpa* and might have closer phylogenetic relationship with Orthophlebiidae than *Holcorpa*, thus, providing an additional evidence to support that

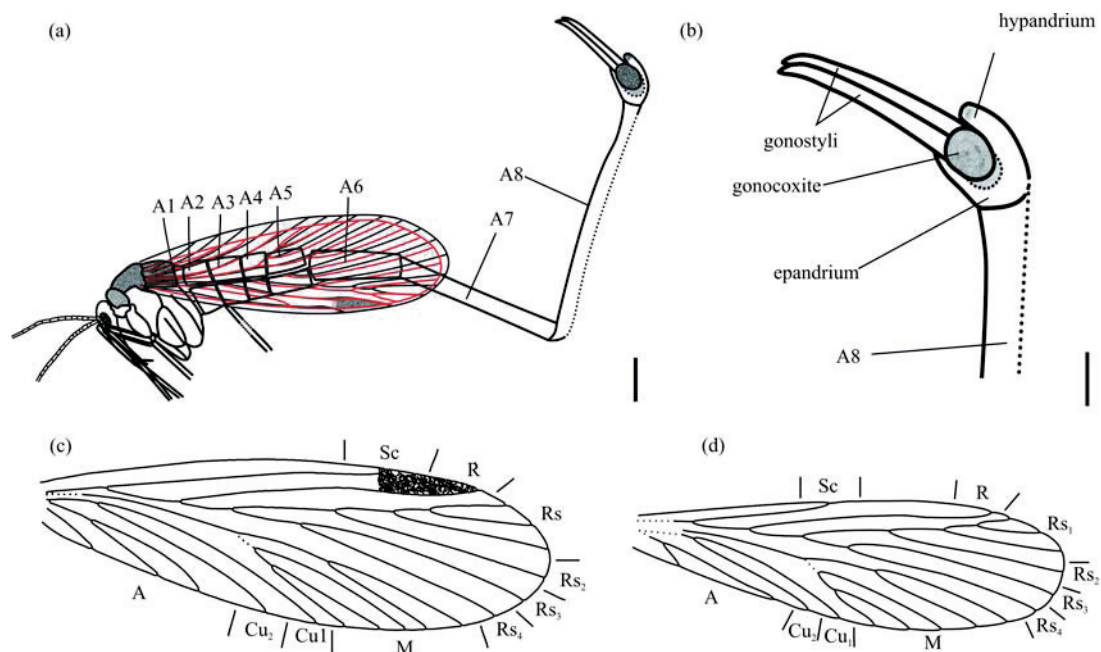


Fig. 3. Interpretive drawings of *Conicholcorpa stigmosa* gen. et sp. nov., holotype.

(a), The habitus of holotype; (b), The genitalia; (c), The left forewing (flipped upside down); (d), The left hind wing (flipped upside down). Scale bars represent 2 mm in a, c and d; 1 mm in b.

Holcorpidae is a sister group of Orthophlebiidae.

Apart from the special venation, species of Holcorpidae have unique characters of the extremely elongate A6 to A8 segments and the enlarged male genitalia that are different from all other mecopterans, and even from all other insects. In 2013, Wang, Shih et Ren reported two scorpionfly species, as Family Incertae sedis, with the extremely elongate A6 to A8 segments and the enlarged male genitalia. They compared the lengths of A6–A8 and the length ratios of the abdomen segments among some extinct and extant scorpionflies (Wang et al. 2013). To add new and more detailed morphological data of *C. stigmosa* gen. et sp. nov. and to provide a more systematic analysis of the extremely elongate male abdominal segments of mecopterans, we update their data Table and list the total lengths of A7–A8, A6–A8, A1–A6 and A1–A5 respectively, while calculating length ratio data of A7/A6, A7–A8/A1–A6 and A6–A8/A1–A5 in Table 1.

Table 1 shows that the *Conicholcorpa stigmosa* gen. et sp. nov. has significantly elongate abdominal segments and male genitalia. The length of the last two segments (A7–A8) of *C. stigmosa* is 24 mm, similar to those of other species in Holcorpidae (from 21.8 to 26.3 mm), shorter than *Fortiholcorpa paradoxa* (42.9 mm), but longer than *Miriholcorpa forcipata* (11.6 mm), both were deemed as Family Incertae sedis as aforementioned, and longer than those in Orthophlebiidae (from 6.5 to 13.7 mm). A key difference between *Holcorpa* and *Conicholcorpa* gen. nov. is the ratio of A7/A6. The A7 of *Conicholcorpa* is almost two times as long as the A6, while the A7 of *Holcorpa* is as long as or shorter than the A6 (with ratios of A7/A6, 1.0 and 0.81). It is interesting to note that the ratio of A7/A6 for *C. stigmosa* (with a ratio of 2.02) is similar to those of the two species, *M. forcipata* (with 1.27) and *F. paradoxa* (with 3.01), that is, all three have longer A7 than A6. Length Ratio of A6–A8 / A1–A5 ranges from 2.7 to 3.8 for two species of *Holcorpa*, 3.7 for *C. stigmosa*, while 4.7 for *F. paradoxa* and 2.0 for *M. forcipata*.

Besides, the A7's of *C. stigmosa* and *M. forcipata* are preserved as a straight tubular shape without bending, while A7 of *F. paradoxa*

Table 1 Comparison of fossil scorpionfly species with extremely elongate male abdominal segments A6 to A8

Family	Genus	Material ID number	Length of A6 (mm)	Length of A7 (mm)	Length Ratio of A6/A7	Length of A8 (mm)	Total length of A7–A8 (mm)	Total length of A1–A6 (mm)	Length Ratio of A7–A8 / A1–A6	Total length of A6–A8 (mm)	Total length of A1–A5 (mm)	Length Ratio of A6–A8 / A1–A5
Holcorpidae Willmann, 1989	<i>Holcorpa</i> Scudder, 1878											
	<i>H. maculosa</i> Scudder, 1878	AMNH 18887 (part) and UCM4494 (counterpart)	10.0	10.0	1.0	16.3	26.3	19.5	1.4	36.3	9.5	3.8
	<i>H. dillhoffi</i> Archibald, 2010	RBCM-EH-2008-018-0001 (part only) ^{1*}	ca. 10.4	8.4	1.2	13.4	21.8	ca. 22.2	ca. 1.0	ca. 32.2	ca. 11.8	ca. 2.7
	<i>Conicholcorpa</i> gen. nov.											
	<i>Conicholcorpa stigmosa</i> sp. nov.	CNU-MEC-NN-2015023 (part only)	4.7	9.5	0.5	14.5	24	12.4	1.9	28.7	7.7	3.7
Family Incertae sedis	<i>Fortiholcorpa</i> gen. nov.	Wang, Shih et Ren, 2014										
Family Incertae sedis	<i>F. paradoxa</i> sp. nov.	Wang, Shih et Ren, 2014	7.0	21.1	0.3	21.8	42.9	17.7	2.4	49.9	10.7	4.7
	<i>Miriholcorpa</i> gen. nov.	Wang, Shih et Ren, 2014										
Orthophlebiidae Handlirsch, 1906	<i>M. forcipata</i> sp. nov.	Wang, Shih et Ren, 2014	3.7	4.7	0.8	6.9	11.6	11.3	1.0	15.3	7.6	2.0
	<i>Orthophlebia</i> Westwood, 1845											
Orthophlebiidae Handlirsch, 1906	<i>O. nervulosa</i> Qiao, Ren, 2012	Shih et CNU-MEC-NN-2009617 (part only)	3.9	3.7	1.1	2.8	6.5	12.7	0.5	10.4	8.8	1.2
	<i>O. riccardii</i> Petrulevičius et Ren, 2012	CNU-MEC-NN2011001 p/c	11.0	6.6	1.7	3.0	9.6	21.9	0.4	20.6	10.9	1.9
	<i>O. longicauda</i> Willmann et Novokshonov, 1998	PIN RAN 2997/280] ^{2*}	ca. 5.3	5.6	0.9	8.1	13.7	14.7	0.9	ca. 19.0	ca. 9.4	ca. 2.0

^{1*} The abdomen of the specimen is disarticulated between the 5th and 6th segments. For length of A1 to A5, it is measured to the ending of the 5th segment. "ca." denotes "approximately".
^{2*} The 5th and 6th abdominal segments are not clearly marked in Fig. 23 of [1]. It is assumed that the 6th segment starts at the point of sudden narrowing of abdomen, "ca." denotes "approximately".

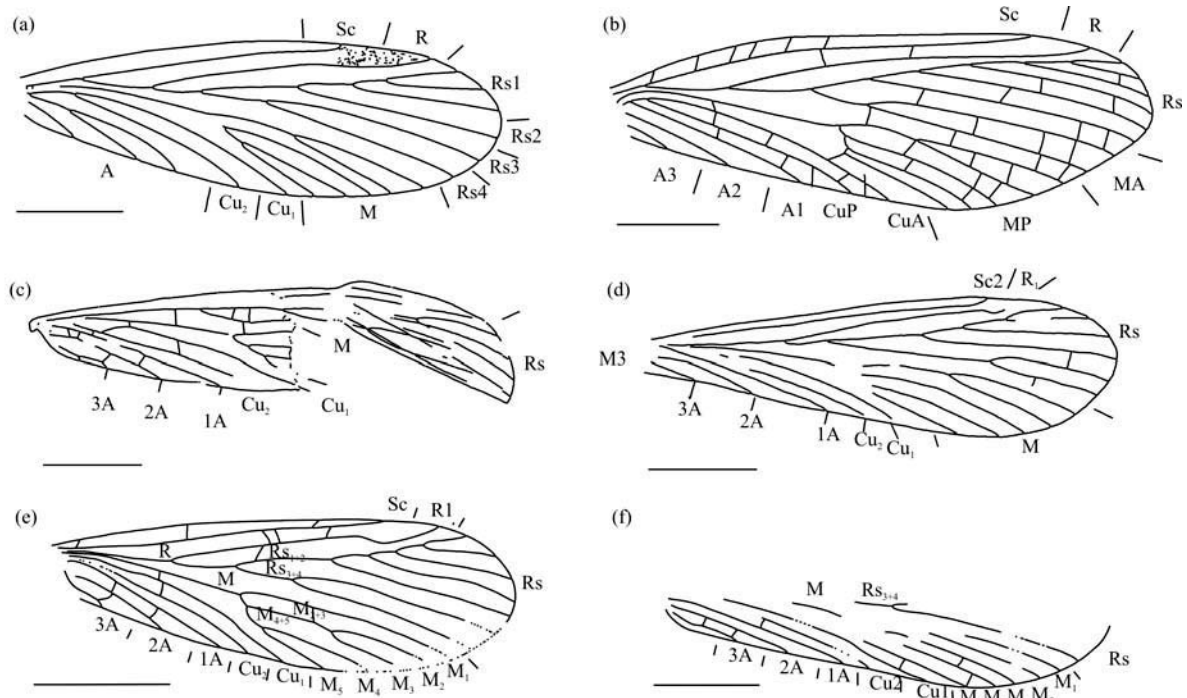


Fig. 4. Comparison of the venation in forewings of some fossil scorpionflies. (a), Line drawing of the left forewing of *Conicholcorpa stigma* gen. et sp. nov. (flipped upside down); (b), Line drawing of the right forewing of *Orthophlebia nervulosa* (from Qiao et al. 2012); (c), Line drawing of the forewing of male *Holcorpa dillhoffi* (from Archibald 2010); (d), Line drawing of the forewing of male *Holcorpa maculosa* (from Archibald 2010); (e), Line drawing of the right forewing of *Miriholcorpa forcipata* (from Wang, Shih et Ren 2013); (f), Line drawing of part of the right forewing of *Fortiholcorpa paradoxa* (from Wang, Shih et Ren 2013). Scale bars represent 5 mm.



Fig. 5. Reconstruction drawing of *Conicholcorpa stigma* gen. et sp. nov.

paradoxa also has a straight tubular shape with a slight bending at one fourth length from the base of A7, which might be caused by the preservation. This linear shape is different from the two male specimens of *Holcorpa* with clearly and strongly curved A7 (Scudder 1878). We are not sure what is the significance or implication of straight A7 vs. curved A7, pending future finding of more fossil specimens.

In addition to the afore-mentioned similarity of abdominal segments of A6 to A8 among *C. stigmosa*, *M. forcipata* and *F. paradoxa*, the *M. forcipata* also has Rs_{3+4} forking more proximal than Rs_{1+2} forking, the same as that of *C. stigmosa*. Furthermore, the *F. paradoxa* has Rs_{3+4} forking at the same level as Rs_{1+2} forking, presenting a transition from *C. stigmosa* and *M. forcipata* to *H. maculosa*. These similar morphological characters suggest affinities of *M. forcipata* and *F. paradoxa* with *C. stigmosa*, a new species of Holcorpidae. However, due to limited number (only one) of new specimen, it is prudent for us not to draw any conclusions on the family assignment of *M. forcipata* and *F. paradoxa* pending future discoveries and studies of new specimens (Fig. 4).

6 Conclusions

Conicholcorpa stigmosa gen. et sp. nov. is the first holcorpidae documented from the Daohugou locality, albeit two previously reported species with extremely elongate male organs but deemed by our Team as Family Incertae sedis, providing one more early case of presenting exaggerated male body parts for sexual display and/or selection. Our results also support the sister relationship between Holcorpidae and Orthophlebiidae by its unique wing venations (Fig. 5).

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References

Archibald, S.B., 2010. 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 America*, 46 (1–2): 173–182.
- Archibald, S.B., Rasnitsyn, A.P., and Akhmetiev, M.A., 2005. The ecology and distribution of Cenozoic Eomeropidae (Mecoptera), and a new species of Eomerope Cockerell from the Early Eocene McAbee locality, British Columbia, Canada. *Annals of the Entomological Society of America*, 98: 503–514.
- Bode, A., 1953. Die Insektenfauna des Ostniedersächsischen oberen Lias[J]. *Palaeontographica*, 103(4): 1–375.
- Byers, G.W., and Thronhill, R., 1983. Biology of the Mecoptera. *Annual Entomology*, 28: 203–228.
- Carpenter, F.M., 1931. Affinities of *Holcorpa maculosa* Scudder and other Tertiary Mecoptera, with descriptions of new genera. *Journal of the New York Entomological Society*, 39: 405–414.
- Carpenter, F.M., 1992. Treatise on Invertebrate Paleontology—Arthropoda. *The Geological Society of America*, 3: 79–88.
- Crampton, G.C., 1931. The genitalia and terminal structures of the male of the archaic Mecopteran, *Nothiothauma reedi*, compared with related Holometabola from the standpoint of phylogeny. *Psyche*, 38: 1–21.
- Gao Taiping, Ren Dong and Shih Chungkun, 2009. *Abrotaxyela* gen. nov. (Insecta, Hymenoptera, Xyelidae) from the Middle Jurassic of Inner Mongolia, China. *Zootaxa*, 2094: 52–59.
- Grimaldi, D., and Engel, M.S., 2005. *Evolution of the Insects*. New York: Cambridge University Press, New York, 755.
- Hong Youchong and Xiao Zongzheng, 1997. New fossil Blattodea, Coleoptera and Mecoptera (Insecta) from Houcheng formation of Yanqing country, Beijing. *Journal of Beijing Geology*, 3: 1–10.
- Hong Youchong and Zhang Zhijun, 2004. New taxonomy of Orthophlebia. *Geological Bulletin of China*, 23: 803–808.
- Hong Youchong and Zhang Zhijun, 2007. Reclassification of Fossil Orthophlebiidae (Insecta: Mecoptera). *Entomotaxonomia*, 29(1): 26–36.
- Hu Haijing, Yao Yunzhi and Ren Dong, 2014. New Fossil Procercopidae (Hemiptera, Cicadomorpha) from the Early Cretaceous of Northeastern China. *Acta Geologica Sinica (English Edition)*, 88(3): 725–729.
- Lieftinck, M.A., 1936. Studies in Oriental Mecoptera I. The genus *Leptanorpa* in Malaysia. *Treubia*, 15: 271–320.
- Li Shu, Shih Chungkun, Wang Chen, Pang Hong and Ren Dong, 2013. Forever Love: The Hitherto Earliest Record of Copulating Insects from the Middle Jurassic of China. *PLoS ONE*, 8: e78188. doi:10.1371/journal.pone.0078188.
- Martynov, A.B., 1927. Jurassic fossil Mecoptera and Paratrachoptera from Turkestan and Ust-Balei (Siberia). *Bulletin of the Academy of Sciences of the USSR*, 21: 651–666.
- Martynova, O.M., 1948. Materials on evolution Mecoptera. *Bulletin of the Academy of Sciences of USSR*, 14: 1–76.
- Martynova, O.M., 1956. Scorpionfly from Turgai Basin. *All-USSR Paleontological Society*, 15: 266–273.
- Martynova, O.M., 1962. Order Mecoptera. Scorpion flies. In: Rohdendorf, B.B. (ed.), *Fundamentals of paleontology: reference book for paleontologists and geologists of the U.S.S.R. 9, Arthropods, tracheates and chelicerates [English translation of: Osnovy Paleontologii: Spravochnik Spravochnik dlya paleontologov i geologov SSSR 9, Chlenistonogie, Tracheiny i Khelitserovyie. Izdatel'stvo*