

New fossil mayflies (Insecta: Ephemeroptera) from the Middle Jurassic of Daohugou, Inner Mongolia, China

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Abstract *Jurassonurus amoenus*, a new genus and species of Siphonuridae *s. l.* is described from the Middle Jurassic Jiulongshan Formation of the Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China. The new species is established by more than 20 imago and subimago specimens in relatively good condition. Detailed description and illustration of the specimens along with a review of fossil Siphonuridae *s. l.* are given. Comparing with two known dominant nymph species *Fuyous gregarious* Zhang and Kluge, 2007 and *Shantous lacustri* Zhang and Kluge, 2007 from the same locality, we could not find any relationship among them. The new species is another dominant species in Daohugou beds.

Key words new genus, new species, Ephemeroptera, Siphonuridae, fossil, Daohugou, Middle Jurassic, China

Introduction

The mayfly family Siphonuridae Bank, 1900 is accepted in its broader sense. Now such taxon is regarded to be paraphyletic and is rejected by most ephemeropterologists (McCafferty, 1991; Kluge *et al.*, 1995; Kluge, 2004). In the last publications (Studemann *et al.*, 1992; McCafferty, 1991; Kluge, 2004) on recent mayflies the family Siphonuridae *s. l.* is divided into several smaller families. However, McCafferty (1991) pointed out two by-products of splitting Siphonuridae: it is more difficult in differentiating the adults of the resultant new families; and the smaller size of the resultant families in their composition. Moreover, modern phylogenetic classifications cannot be applied to fossils, because many features (genitalia, tarsi and other important characters), which are used in recent taxonomy of the family, are unknown in the fossils. So here we use the name of “family Siphonuridae” to represent

a plesiomorphon-family Siphonuridae in a broader sense; instead of the family Siphonuridae which is accepted in modern classifications of recent mayflies. It is considered only temporary to use the old broad definition of the family Siphonuridae, at least for the extinct groups, until their new systematics is resolved (Kluge, 1993).

The most ancient representative of the fossil family Siphonuridae *s. l.* is *Triassonurus doliiformis* Sinitshenkova (Sinitshenkova *et al.*, 2005) which was collected from the Vosges in France (early Middle Triassic). The fossil Siphonuridae originally included the following genera (Huang *et al.*, 2007a): *Siphonurus* Eaton, 1868, *Cronicus* Eaton, 1871, *Mesobaetis* Brauer *et al.*, 1889, *Siphurites* Cockerell, 1923, *Mesonetopsis* Ping, 1935, *Sinoephemera* Ping, 1935, *Aphelophlebodes* Pierce, 1945, *Stackelbergisca* Tshernova, 1967, *Baltameletus* Demoulin, 1968, *Balticophlebia* Demoulin, 1968, *Olgisca* Handlirsch, 1906, *Cretoneta* Tshernova, 1971, *Proameletus* Sinitshenkova, 1976, *Mogzonurella* Sinitshenkova, 1985, *Mogzonurus* Sinitshenkova, 1985, *Promirara* Jell and Duncan, 1986, *Australurus* Jell and Duncan, 1986, *Dulcitimanna* Jell and Duncan, 1986, *Albisca* Sinitshenkova, 1989, *Bolbonyx* Sinitshenkova, 1990, *Siphgondwanus* McCafferty, 1990, *Costalimella* Martins-Neto, 1996, *Siphangarus*

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Sinitshenkova, 2000 and *Multiramificans* Huang et al., 2007. However, many members of these genera and species have unclear systematic positions and were described on plesiomorphic characters only (Kluge, 2004). The systematic position of Upper and Middle Jurassic *Stackelbergisca* is not quite clear. McCafferty (1991) has suggested that *Stackelbergisca* cannot be placed into any family, but undoubtedly should be regarded as Pisciforma incertae sedis. Zhou and Peters (2003) have placed this fossil genus provisionally in Siphonuridae Zhou and Peters, 2003, and Kluge (2004) has attributed it to Anteritorna incertae sedis. Kluge (2004) has placed the following genera in Anteritorna incertae sedis: *Cronicus*, *Siphurites*, *Balticophlebia*, *Baltameletus*, *Olgisca*, *Cretoneta* and *Proameletus*, and taken genera *Mesobaetis*, *Mogzonurus*, *Mogzonurella*, *Australurus*, *Dulcimanna*, *Albisca*, *Siphogondwanus*, *Bolbonyx* and *Costalimella* into Euplectoptera incertae sedis. In addition, the two genera *Mesonetopsis* and *Sinoephemera* are probably not mayflies (Hubbard, 1987). So these genera placements need to be further studied.

The age of the Jiulongshan Formation in Daohugou area is still controversial, ranging from early Middle Jurassic to Early Cretaceous by various authors (Ren et al., 2002; Shen et al., 2003; Chen et al., 2004; Liu et al., 2004; Rasnitsyn et al., 2004; Wang et al., 2005; Gao & Ren, 2006). We consider that the age of the Jiulongshan Formation is the Middle Jurassic.

Some new and unique imago specimens from the Daohugou beds allow us to carry out detailed studies because of their excellent preservation. We establish a new genus and species *Jurassonurus amoenus* gen. et sp. nov. of the Siphonuridae s. l. Morphological terms used here are explained by Kluge (2004).

Material and methods

The fossil specimens were recently collected from the Middle Jurassic Daohugou beds, Jiulongshan Formation, Ningcheng County, Inner Mongolia in China, about 165Ma (Ren et al., 2002; Chen et al., 2004; Gao & Ren, 2006).

The specimens were examined with a Leica MZ12.5 dissecting microscope and illustrated with the aid of a drawing tube attached to the microscope. Line drawings were made with CorelDRAW 12 graphic software. Type specimens studied here are housed in the Key Lab of Insect Evolution and Environmental Change, College of Life Sciences, Capital Normal University, Beijing, China.

Systematic paleontology

Order: Ephemeroptera Hyatt et Arms, 1891

Infraorder: Anteritorna Kluge, 1993

Family: Siphonuridae Bank, 1900

Jurassonurus Huang, Ren & Sinitshenkova, gen. nov.

Type species *Jurassonurus amoenus* sp. nov., Middle Jurassic, Jiulongshan Formation, Daohugou beds, Shantou Township, Ningcheng County, Inner Mongolia in China.

Etymology Generic name combining the Jurassic age and part of the type-genus name *Siphonurus* Eaton. The gender is masculine.

Diagnosis Imago and subimago. Antennae filiform short, about two-thirds of head length. Prothorax relatively large, about one-third of pterothorax length; basisternum (BS) well-developed, round; more or less wide furcasternal impression (FSi) exists between the furcasternal protuberances (FSp); all legs with vestige of patella-tibial suture; femora of middle and hind legs evidently stronger than tibiae and tarsi; forewing triangular with fairly obtuse tip, short hind margin, few short intercalate veins at the wing margin. Hindwing shorter than half of forewing, long oval with slightly developed costal projection. Forceps with two apical segments, styliger plate slightly V-shaped incisor between forceps bases and penis bifurcated in its apical part. Rudiment of paracercus shortened with several segments, cerci length about 1.2 times as long as the abdomen.

Composition The type species only.

Comparison Based on the shape and venation of forewing, *Jurassonurus* gen. nov. is somewhat similar to *Proameletus* Sinitshenkova (Sinitshenkova, 1976) from the Lower Cretaceous of Transbaikal, *Olgisca* Handlirsch (Demoulin, 1970) from the Jurassic of Bavaria and *Multiramificans* Huang et al. (Huang et al., 2007b) from the same formation with new genus, and differs from *Olgisca* by simple A_1 and the presence of an intercalary vein between RSa_1 and RSa_2' , and from *Proameletus* and *Multiramificans* by the vestige of patella-tibial suture and the shape of hindwing. *Jurassonurus* gen. nov. differs from these genera by relatively short hindwing. In addition, this new genus is very similar to recent *Siphonurus* Eaton in characters of fore- and hindwings and legs, but differs from the latter by relatively long prothorax.

Remark The combined characters of this new genus allow an allocation of it to the family Siphonuridae s. l.: tarsi five-segmented, with first segment fused with tibia; on forewing CuA and CuP connecting basally forming acute angle; cubital area of forewing relatively narrow, with series of veinlets arising from CuA towards posterior margin of wing.

Jurassonurus gen. nov. possesses a peculiar combination of characters: prothorax relatively long; a furcasternal impression (FSi) appears between the furcasternal protuberances (FSp); all legs with vestige of patella-tibial

suture; femora evidently stronger than tibiae and tarsi; hindwings small, long oval, with costal projection; forceps with two apical segments and penis bifurcated in its apical part; paracercus shortened, cercus length about 1.2 times as long as the abdomen. These characters allow formal separation of this new genus from other known genera of the Siphonuridae *s. l.* established by mayfly adults, extant or in fossil records.

Jurassonurus amoenus Huang, Ren & Sinitshenkova, sp. nov. (Figs. 1–9)

Etymology From Latin *amoenus* (lovely).

Holotype Male subimago, ventral view. CNU-E-DHG-2006006-1(Figs. 1, 5, 8B, 9B), CNU-E-DHG-2006006-2. Well-preserved part and counterpart of body with complete antennae, forelegs, shape of forewings, ventral structure of thorax, male genitals and with incomplete middle and hindlegs and only left hindwing. The venation is not clear, right hindwing is not preserved.



Fig. 1 Photograph of *Jurassonurus amoenus* sp. nov. Subimago male. Holotype, No. CNU-E-DHG-2006006-1.



Fig. 2 Photograph of *Jurassonurus amoenus* sp. nov. Imago female. Paratype, No. CNU-E-DHG-2006002.

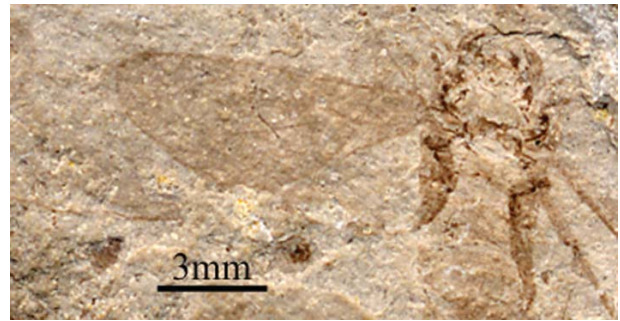


Fig. 3 Photograph of *Jurassonurus amoenus* sp. nov. Subimago female. Paratype, No. CNU-E-DHG-2006043.

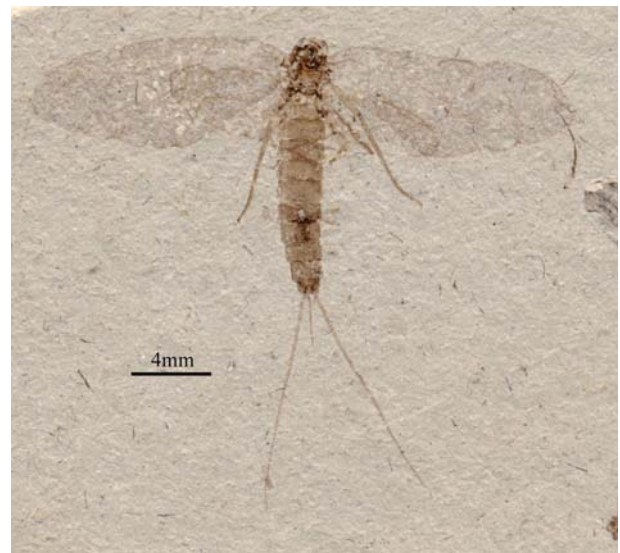


Fig. 4 Photograph of *Jurassonurus amoenus* sp. nov. Subimago male. Paratype, No. CNU-E-DHG-2006038-1.

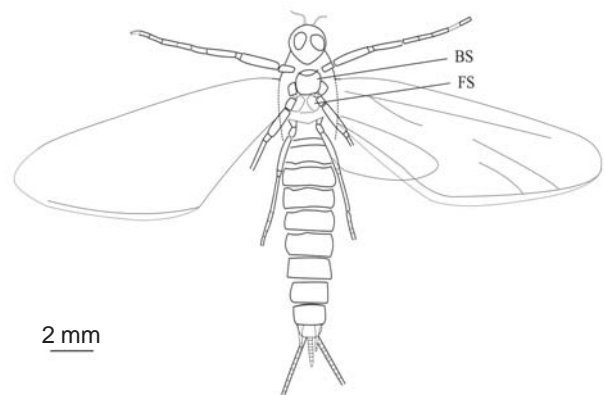


Fig. 5 Line drawing of *Jurassonurus amoenus* sp. nov. Subimago male. Holotype, No. CNU-E-DHG-2006006-1.

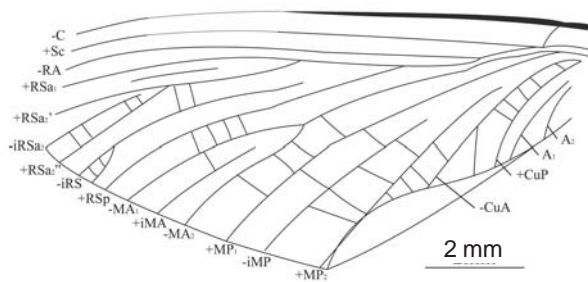


Fig. 6 Forewing of *Jurassonurus amoenus* sp. nov. Imago female. Paratype, No. CNU-E-DHG-2006002.

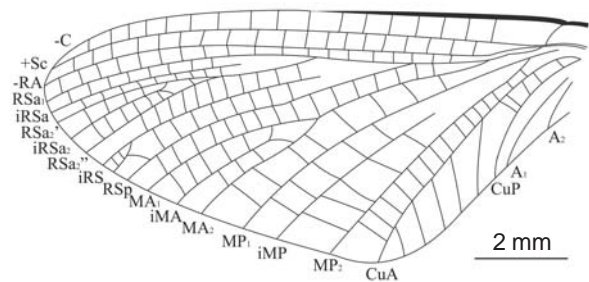


Fig. 7 Reconstruction of forewing of *Jurassonurus amoenus* sp. nov. Imago female. Paratype, No. CNU-E-DHG-2006002.

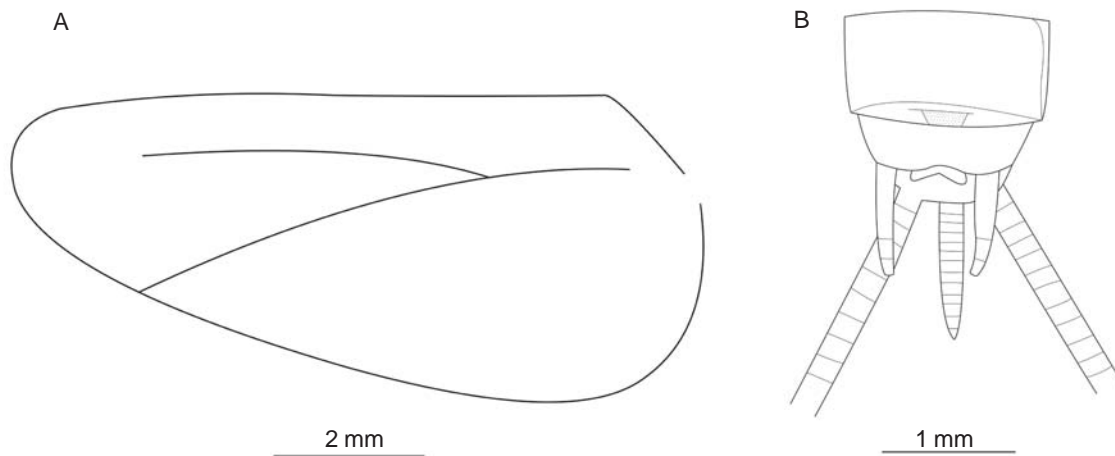


Fig. 8 *Jurassonurus amoenus* sp. nov. A. subimago female, paratype, No. CNU-E-DHG-2006043, hindwing; B. subimago male, holotype, No. CNU-E-DHG-2006006-1, genital.

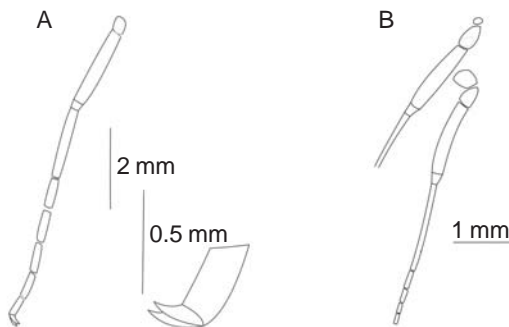


Fig. 9 *Jurassonurus amoenus* sp. nov. A. subimago male, paratype, No. CNU-E-DHG-2006038-1, foreleg and claws of middle leg; B. subimago male, holotype, No. CNU-E-DHG-2006006-1, middle and hind legs.

Material Besides holotype there are 28 paratypes from the same locality: female imago, CNU-E-DHG-2006002 (Figs. 2, 6, 7), ventral view, well-preserved body with relatively complete venation of forewings and middle and hindlegs; female subimago CNU-E-DHG-2006043 (Figs. 3, 8A), ventral view with complete shape of hindwing; male subimago CNU-E-DHG-20060038-1 (Figs. 4, 9A), CNU-E-DHG-2006038-2, part and counterpart with relatively complete legs and cerci; female subimago CNU-E-DHG-2006039-1, CNU-E-DHG-2006039-2, part and counterpart with the body of large size (body length 16.5 mm excluding cerci and antenna); CNU-E-DHG-2006040, with the body of small size (body length 9.5 mm excluding cerci and antenna). Male subimagos: CNU-E-DHG-2006008, CNU-E-DHG-2006028, CNU-E-DHG-2006032, CNU-E-DHG-2006041, CNU-E-DHG-2006042, CNU-E-DHG-2006044, CNU-E-DHG-2006045, CNU-E-DHG-2006050, CNU-E-DHG-2006052. Female subimagos: CNU-E-DHG-2006025, CNU-E-DHG-2006027-1, CNU-E-DHG-

2006027-2, CNU-E-DHG-2006031, CNU-E-DHG-2006043, CNU-E-DHG-2006046-1, CNU-E-DHG-2006046-2, CNU-E-DHG-2006047, CNU-E-DHG-2006049, CNU-E-DHG-2006051-1, CNU-E-DHG-2006051-2. Unknown gender subimagoes: CNU-E-DHG-2006024, CNU-E-DHG-2006036, CNU-E-DHG-2006048, CNU-E-DHG-2006053.

Locality and horizon Daohugou beds, Jiulongshan Formation, Ningcheng County, Inner Mongolia in China, Middle Jurassic.

Description Male subimago (ventral view) (Figs. 1, 4, 5, 8B, 9A, B). Head rounded; eyes relatively large, contiguous; antenna filiform, short only about two-thirds of head length.

Thorax with clear basisternum (BS) and furcasternal protuberances (FSp) of mesothorax; BS round between fore- and middle legs; a more or less wide furcasternal impression (FSi) appeared between the furcasternal protuberances (FSp).

Wing opaque; only the outline of fore- and hindwings preserved. Forewing triangular with fairly obtuse tip. Hindwing long oval, shorter than half of forewing.

All legs with vestige of patella-tibial suture; foreleg obviously longer than middle and hindlegs, little more than abdomen; middle and hindlegs, similar; femora of middle and hindlegs evidently stronger than tibiae and tarsi; all tarsi five-segmented; first tarsal segment is the longest, fused with tibia; fourth segment is the shortest; joint between fourth and fifth segments of middle and hind legs, oblique; two claws similar, pointed.

Styliger plate has slightly V-shaped incisor between forceps bases. Forceps are with two apical segments. Penis is short, slightly V-shaped bifurcation in its apical part. Rudiment of paracercus is short. Cerci are very long, about 1.2 times as long as abdomen length (Fig. 4).

Female imago and subimago (Figs. 2, 3, 6, 8A) Eyes are relatively small, separated. Only longitudinal veins of forewings and some crossveins are visible; convex and concave veins are alternating; MA branched after middle area of wing; cubital area strongly narrowed apically, with few simple veinlets arising from CuA; A_1 is unforked. Hindwing opaque, slightly developed costal projection pointed apically. Other characters are same as in male.

Measurement (mm) CNU-E-DHG-200606-1: body length 13.5; forewing length 12.7, its width 4.5; hindwing length 6.0; foreleg length 6.9; middle leg length 6.0. CNU-E-DHG-200602: forewing length 14.0, its width 5.0; middle leg length 7.0; hindleg length 6.8. CNU-E-DHG-200604: forewing length 13.5; hindwing length 6.0. CNU-E-DHG-200605: cerci length 9.0; abdomen length 7.0. CNU-E-DHG-2006038-1: body length (excluding the antenna and cerci) 16.5. CNU-E-DHG-200607: body length 9.5.

Discussion

In recent mayflies, the subimago has the same shape and size as the imago and differs from the imago in cuticle structure, setation and the wing membrane. Besides these, male subimagoes have less expressed sexual characters in structures of eyes, forelegs, genitals and caudalii. The subimaginal cuticle in most part is covered with microtrichia and the posterior margin of the wing always has a row of setae (Kluge, 2004). However, in fossils, tiny microtrichiae and setae on subimaginal wings could not be preserved. The imago and subimago can be distinguished by the wing membrane. In the subimago the membrane is thick and not transparent, that is why the veins are not well visible, but on the imago wings the veins are very clear because the wing membrane is very thin and transparent. To our surprise, there are many subimagoes but very few imagoes of the winged specimens collected so far (28 subimagoes and 1 imago). Normally, the percent of subimagoes in a mayfly assemblage is similar to imagoes.

Jurassonurus amoenus sp. nov. is established by more than 28 subimago and one imago specimens. Such mass burial of winged mayflies is very peculiar, because the winged mayflies survive for only between about an hour and a few days; moreover in forming the fossils the adult specimens cannot be easily preserved. The great number of specimens indicates that this new species is probably taphonomically autochthonous and one of the dominant species there. Another two dominant species reported from the same locality, *Fuyous gregarious* (family: Fujoidae) Zhang and Kluge, 2007 and *Shantous lacustri* (family: Hexagenitidae) Zhang and Kluge, 2007, are described for nymphs (Zhang & Kluge, 2007). Studying fossil stoneflies, Sinitshenkova (1987) put forward three useful criteria to resolve the association between nymphs and adults: first, nymph and adult fossils occur together at the same site; second, both belong to the same high-level taxon basing on the available characters; third, both sizes are compatible. Only when nymph and adult meet all the three criteria, they might be conspecific. These criteria should be applied to fossil mayflies (Sinitshenkova *et al.*, 2005, Huang *et al.*, 2007c). However, the above criteria have not indicated any relationship among *Jurassonurus amoenus* sp. nov., *Fuyous gregarious* and *Shantous lacustri*. Therefore *Jurassonurus amoenus* sp. nov. is another dominant species of mayfly fauna in Daohugou beds.

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