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JURASSIC LARVAE OF MAYFLIES (EPHEMEROPTERA) FROM THE DAOHUGOU FORMATION IN INNER MONGOLIA, CHINA

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ABSTRACT. Two mayfly larvae from the Callovian or Oxfordian (uppermost Middle Jurassic or lowermost Upper Jurassic) Daohugou Formation in Inner Mongolia, China are described as *Fuyous gregarius,* gen. et sp. nov. (family Fuyoidae, fam. nov.) and *Shantous lacustris,* gen. et sp. nov. (family Hexagenitidae). These larval forms were previously identified as *Mesoneta antiqua* Brauer, Redtenbacher & Ganglbauer, 1889 and *Mesobaetis sibirica* Brauer, Redtenbacher & Ganglbauer, 1889, respectively. The both Lower Jurassic species *Mesoneta antiqua* and *Mesobaetis sibirica* lack not only in the Daohugou Formation, but elsewhere in China. The taxonomic placements of all the mayfly records earlier from the Mesozoic of China are questionable, and are briefly reviewed and reassessed.

Key words: Ephemeroptera, larva, Fuyoidae, fam. nov., *Fuyous,* gen. nov., *Fuyous gregarius,* sp. nov., Hexagenitidae, *Shantous,* gen. nov., *Shantous lacustris,* sp. nov., *Mesoneta*, *Mesobaetis*, *Stackelbergisca*, Jurassic, China.

Introduction

The Ephemeroptera in the widest sense, or Panephemeroptera Crampton, 1928, besides true mayflies, include the Carboniferous taxon Protephemeroidea Handlirsch, 1906 (*Triplosoba* Handlirsch, 1906). Sometimes the Carboniferous families Syntonopteridae Handlirsch, 1911 and Bojophlebiidae Kukalova-Peck, 1985 (Kluge & Sinitshenkova, 2002) are also included. The relationships of these taxa are unclear, and possibly Panephemeroptera is a plesiomorphon. Ephemeroptera in a narrower sense, or Euephemeroptera Kluge, 2000, are known since Permian. All known Permian representatives belong to a plesiomorphon Permoplectoptera Tillyard, 1932, which differs from all Recent mayflies by homonomous wings and some other features (Kluge, 2000, 2004). The taxon Ephemeroptera in the narrowest sense, or Euplectoptera Tillyard, 1932, includes all Recent, Coenozoic and most Mesozoic mayflies; it is known for certain since Jurassic. Reports about Triassic representatives of Euplectoptera are not clearly established (Kluge, 2004). Euplectoptera are characterized, first of all, by anteromotoric wing specialization: hind wings are reduced, with modified venation (Kluge, 2004) and at flight are coupled with fore wings. The species described in this paper, undoubtedly belong to Euplectoptera, as their larval hind protoptera are twice shorter than fore protoptera.

The findings of the Jurassic and Early Cretaceous mayflies (Euplectoptera) are correspondingly poor in number of species but usually abundant in the number of individuals. Most of them are immature larvae, and imagoes and subimagoes are very rare.

From the Jurassic and latest Jurassic – earliest Cretaceous of China, 10 species referable to seven genera have been recorded (Lin, 1980, 1986; Lin & Huang, 2001; Hong, 1983; Hong et al., 1995; Wang, 1980, 1987; Ren et al., 1996; Ren et al., 2002; Tan & Ren,

2002). Among them, two species, *Caenoephemera shangyuanensis* Lin & Huang, 2001 and *Ephemeropsis trisetalis* Eichwald, 1864, belong to an extinct Jurassic – Cretaceous taxon Hexagenites/fg1 within Euplectoptera-Anteritorna Kluge, 1993 (Kluge, 2004); the giant mayfly, *Ephemeropsis trisetalis*, represents a geographically widespread species distributed in southern and northern China, Mongolia and Russian Transbaikalia, but some of these reports are of a related species – *E. melanurus* Cockerell, 1924 (Sinitshenkova, 1990). Five species attributed to the artificial genera *Mesobaetis* and *Mesoneta* – *Mesobaetis sibirica* Brauer, Redtenbacher & Ganglbauer, 1889, *Mesoneta antiqua* Brauer, Redtenbacher & Ganglbauer, 1889, *Mesoneta beipiaoensis* Wang, 1980, *Mesobaetis maculata* Hong, Liang & Hu, 1995 and *Mesobaetis sanjianfangensis* Hong, Liang & Hu, 1995 – have a doubtful position within Euplectoptera. Two species, *Clephemera clava* Lin, 1986 and *Palinephemera densivena* Lin, 1986, originally recognized as a larva of Ephemerellidae and a single wing of Mesephemeridae respectively, should be considered either belonging to an unplaced Euplectoptera (Kluge & Sinitshenkova, 2002), or even unplaced Euephemeroptera (Kluge, 2004). The tenth species, *Huizhougenia orbicularis* Lin, 1980, mistakenly regarded as the member of Siphlonuridae, most likely belongs to Aeschnidiidae within Odonata (Kluge & Sinitshenkova, 2002).

The age of the Daohugou Formation is debatable. It has been at range from early Middle Jurassic to Early Cretaceous. Probably, the Daohugou, Haifanggou and Karabastau (Karatau, Kazakhstan) entomofaunas could be correlated and are synchronous or nearly so, belonging to Callovian or Oxfordian (latest Middle Jurassic or earliest Late Jurassic) based on the biostratigraphical correlation and isotope dating (Zhang, 2004, 2006a).

Some terms used here are explained in the monograph on mayfly systematics (Kluge, 2004); these are: **plesiomorphon** (plural **plesiomorphons**) – a taxon characterized by plesiomorphies only (either paraphyletic, or such holophyletic, whose holophyly is not proven); **maxillary canine** – apical denticles on maxilla (primitively three in number); **tergalius** (plural **tergalii**) – peculiar movable paired abdominal appendage of larval Ephemeroptera, often called "abdominal tracheal gill" (not homologous to abdominal tracheal gill of other insects); **costal** and **anal ribs** – two thickened sclerotized longitudinal strips on tergalius (reduced in some taxa); **caudalius** (plural **caudalii**) – cercus or paracercus; **primary swimming setae** of caudalii – long setae forming a regular row on inner margin of each cercus and each lateral margin of paracercus. One more term – **protopteron** (plural **protoptera**) – is introduced in the paper for complete metamorphosis (Kluge, 2005); protoptera exist in pupae and nymphs, being that external outgrowths of pterothoracic terga, from which develop subimaginal wings (in Ephemeroptera) or imaginal wings (in Metapterygota). Protoptera are called either "wing buds", "wing rudiments", "wing cases", or "wing pads". Unlike true wing bud (or rudiment), protopteron has its own cuticle, which is different from the wing cuticle; unlike true wing case, protopteron has own living tissues inside; shape of protopteron can be not pad-like.

Systematics

Order EPHEMEROPTERA Hyatt & Arms, 1891
EUEPHEMEROPTERA Kluge, 2000
EUPLECTOPTERA Tillyard, 1932

Family FUYOIDAE Zhang & Kluge, fam. nov.

Type genus: Fuyous, gen. nov.

Diagnosis: Larva. Larva retains primary siphlonuroid swimming specialization, i.e. with thorax and legs relatively small, abdomen relatively large, caudalii bearing dense

primary swimming setae. Head nearly prognathous (unlike primary hypognathous), with tips of mouthparts directed forward. Maxilla seems to have strongly elongate, arched, pointed canines at apex (as can be assumed from the specimen DHG 0505 – Figs. 1E, 3E). Fore protoptera (buds of fore wings) widely separated from bases; hind protoptera (buds of hind wings) large, as long as one half of fore protoptera, in mature larva terminate at the same level as fore protoptera. Legs short and thick. Fore leg with femur thicker than those of middle and hind legs; inner margin of fore femur, tibia and tarsus covered with long hairs. On all legs claw bears a broad-based, dactyl-like appendage arising from claw base (visible on some legs of specimens DHG 0501, DHG 0504, DHG 0505). Abdomen not widened, long; posterolateral projections on abdominal segments first–ninth prominent. All tergalii first–seventh present; each tergalius unilamellate, broad-oval, with rounded tip; costal rib locates on fore (costal) margin, anal rib absent or invisible (some tergalii are retained on specimen DHG 0501). Caudalii subequal; each inner margin of cerci and lateral margin of paracercus with a regular row of long dense primary swimming setae.

Subimago and imago (basing on details visible on mature larva ready to moult to subimago). Hind wing as long as one half of fore wing (condition plesiomorphic for Euplectoptera). Tarsus five-segmented; on fore leg of female (well visible through larval cuticle on specimens DHG 0501, DHG 0502, DHG 0505, DHG 0506) first segment longest, about 1.3 times longer than fifth, and twice longer than second; third a little shorter than second, and slightly longer than fourth (Figs. 1D, 3F). Paracercus vestigial; this conclusion is based on the fact that in mature larvae ready to moult to subimago (DHG 0501, DHG 0504, DHG 0505) larval cuticular cerci are dark, being filled with subimaginal cerci, while larval cuticular paracercus is lighter, being empty (Figs. 1A, G).

Includes a gingle genus, *Fuyous,* gen. nov.

Genus *Fuyous* Zhang & Kluge, gen. nov.

Type species: *Fuyous gregarius,* sp. nov. from the Daohugou Formation in the vicinity of Daohugou, Ningcheng, Chifeng, Inner Mongolia, China.

Etymology: The generic name refers to Chinese "mayflies".

Diagnosis: As for family.

Composition: Single species only – *Fuyous gregarius,* sp. nov.

***Fuyous gregarius* Zhang & Kluge, sp. nov. (Figs. 1A–I, 3A–H)**

Mesoneta antiqua: Ren, Gao, Guo, Ji, Tan & Song, 2002: pl. II, fig. 2A (non Brauer, Redtenbacher & Ganglbauer, 1889).

Etymology: The specific refers to gregarious, alluding to the behaviour of this species.

Holotype and paratypes: Holotype: DHG 0501 – mature larva ready to moult to subimago, dorsal view. Paratypes: DHG 0502 – mature larva, dorsal view; DHG 0503 – mature larva, left view; DHG 0504 – mature larva moulting to subimago, dorsal view; DHG 0505 – mature larva ready to moult to subimago, right view; DHG 0506 – mature larva, dorsal view. All six specimens are larvae of the last instar and so mature that their protoptera are dark, being filled with crumpled subimaginal wing buds. The uppermost Middle Jurassic (Callovian) or lowermost Upper Jurassic (Oxfordian) Daohugou Formation in the vicinity of Daohugou, Ningcheng, Chifeng, Inner Mongolia, China. Deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Description: Body brown. Head relatively small and short, its length less than its width and height (Figs. 1A–C, 3A–C). Eyes small, suboval. Antenna, as preserved, nearly as long as head, at least 10-segmented, gradually thinned and shortened apically (Figs. 1C, 3D). Anterior margin of clypeus slightly wider than posterior margin, and nearly twice wider than long (Figs. 1B, 3B, C). Mandibles poorly preserved, only incisors visible (Figs. 1F, 3B, C). Pronotum short, some five times wider than long. Pterothorax nearly as long as wide (Figs. 1A, 3A). Femur of fore leg clavate, with two or three longitudinal furrows, tibia and tarsus cylindrical, nearly equaling in length, joint between them oblique; claw about one half as long as tarsus, appendage some one half of length of claw (Figs. 1D, I, 3F). Abdomen 2.2 times longer than head and thorax combined, with basal five abdominal segments nearly equal in width, remainder segments gradually tapering terminally, their posterior margins straight, anterior margins W-like (Figs. 1A, 3A). Tergalii with costal margins (armed by ribs) smoothly arched, anal margins strongly convex; usually light, or with base brown (right fourth tergalius of DHG 0501) (Figs. 1A, 3A, G, H). Caudalii somewhat longer than one half of length of abdomen, unicolour, swimming setae light (Figs, 1A, G, 3A).

In the holotype, DHG 0501, body length 25.0 mm including, and 20.2 mm excluding paracecus; head length, as preserved, 1.3 mm, width 2.0 mm; prothorax length 0.6 mm, width 3.1 mm; pterothorax length 3.7 mm, width 3.5 mm; femur of fore leg length 1.7 mm, tibia length 1.0 mm, tarsus length 1.1 mm; abdomen length 14.2 mm, width 3.6 mm; fourth tergalius length 2.3 mm, width 1.7 mm; paracercus length, as preserved, 4.5 mm; circus length, as preserved, 2.8 mm.

Comparison: From most other mayflies *Fuyous* differs by presence of long straight subbasal projection on larval claw. Similar projection is fond only in the Recent species *Siphluriscus chinensis* Ulmer, 1920 (Zhou & Peters, 2003) and the Jurassic larvae ascribed to *Stackelbergisca* Tshernova, 1967. The monospecific Recent Chinese taxon Siphluriscus/fg(1) (i.e., the family Siphluriscidae Zhou et Peters, 2003, or the genus *Siphluriscus* Ulmer, 1920) and the Recent Amphinotic taxon Nesameletus/f2=Metamonius/g2 are united in a taxon Nesameletus/f1 = Metamonius/g1 (Kluge, 2004). Larval *Fuyous* differs from all Nesameletus/f1=Metamonius/g1 by presence of setation on fore legs and possibly by structure of maxillae. About relation between *Fuyous* and *Stackelbergisca* see below.

If our interpretation of mouthparts of specimen DHG 0505 is correct, maxilla has some similarity with that of Ameletopsis/fg1, but is not so greatly enlarged. The taxon Ameletopsis/fg1 (i.e., family or subfamily Ameletopsidae or Ameletopsinae) occurs only in Notogea (Australia, New Zealand and Chile) since Cretaceous till Recent (Kluge, 2004). Larval *Fuyous* well differs from all Ameletopsis/fg1 by non-enlarged head.

Family HEXAGENITIDAE Lameere, 1917

Hexagenitidae, Tshernova, 1961: 589.
Hexagenites/fg1, Kluge, 2004: 353.

Diagnosis: Larva.Tergalii of last (seventh) pair enlarged: either larger than others, or have better developed anal rib (unique apomorphy). On each tergalius, anal rib, if developed, locates at a distance from anal margin (the same in some other taxa). Caudalii subequal, retain well-developed primary swimming setae.

Imago and subimago. On fore wing CuA bifurcates to CuA_1 and CuA_2; from the bifurcation a vein iCu arises, which forms several (three–five) triads following one another: anterior branch of each triad forms next triad; each of these triads has anterior branch

arched by its convexity anteriorly; all branches of these triads go to basitornal margin of wing.

Composition: Jurassic of Europe: *Hexagenites* Scudder, 1880 (= *Paedephemera* Handlirsch, 1906 = *Stenodicranum* Demoulin, 1954).

Jurassic–Cretaceous of Asia: *Ephemeropsis* Eichwald, 1864 (= *Phacelobranchus* Handlirsch, 1906); *Hexameropsis* Tshernova et Sinitshenkova, 1974; *Mongologenites* Sinitshenkova, 1986; and *Caenoephemera* Lin et Huang, 2001.

Cretaceous of South America: *Protoligoneuria* Demoulin, 1955; *Palaeobaetodes* Brito, 1987; *Cratogenites* Martins-Neto, 1996; and *Cratogenitoides* Martins-Neto, 1996.

The genus *Siberiogenites* Sinitshenkova, 1985 also was placed in the family Hexagenitidae. It is known as larvae of four species; their tergalii seventh are not enlarged, so the placement of these larvae in Hexagenitidae is not confirmed (see discussion below).

Genus *Shantous* Zhang & Kluge, gen. nov.

Type species: Shantous lacustris, sp. nov.

Etymology: The generic name refers to Shantou – township, where is situated village Daohugou, the locality of mayfly-bearing rocks.

Diagnosis: Larva. Unlike other Hexagenitidae, tergalii first–sixth very long (not shorter than tergalius seventh) and lack anal ribs. Tergalius seventh widened, retains anal rib near middle of tergalius. Each tergalius first–seventh has well-developed costal rib on costal margin.

***Shantous lacustris* Zhang & Kluge, sp. nov. (Figs. 2A–G, 4A–G)**

Mesobaetis sibirica: Ren, Gao, Guo, Ji, Tan & Song, 2002: pl. II, fig. 4. (non Brauer, Redtenbacher et Ganglbauer, 1889)

Etymology: The specific refers to lacustrine, alluding to the habitat of this species.

Holotype and paratypes: Holotype: DHG 0508 – mature larva, dorsal view. Paratypes: DHG 0507 – mature larva, dorsal view; DHG 0509 – mature larva, dorsal view (paler impression); DHG 0510 – larva, dorsal view (tergalii missing); DHG 0511 – larva, dorsal view (tergalii missing); DHG 0512 – larva, right view; DHG 0513 – larva, dorsal view (tergalii missing). For locality and repository, see under *Fuyous gregarius* sp. nov.

Description: Body darkish brown or brown. Head large, wider than long (dorsoventral aspect) (Figs. 2A, B, 4A) or higher than long (lateral aspect) (Fig. 2F). Eyes correspondingly small, suboval. Antenna, as preserved, at least eight-segmented, gradually thinned and elongated apically (Fig. 4D). Anterior margin of clypeus 1.4 times wider than posterior margin, and nearly twice wider than long (Figs. 2D, 4C). Mandible elongate, with incisor slender (visible on specimen DHG 0509 – Figs. 2C, 4B). Pronotum quite short, five times wider than long. Pterothorax clearly wider than long (Figs. 2A, B, 4A). Fore protoptera triangular, with basitornal margin fused with notum (Figs. 2A, B, 4A). Femur somewhat clavate, tibia and tarsus cylindrical, tibia covered with dense hairs; claw slightly arched, about four times shorter than tarsus (Figs. 2E, 4E). Abdomen short and wide, some 2.2 times longer than head and thorax combined; first five abdominal segments nearly equaling in width, each of them 3.3–3.5 times wider than long; remainder segments gradually tapering terminally, their posterior margins straight, anterior margins W-like (Fig. 2B); posterolateral projections on abdominal segments first–ninth developed into small, sharp spines; tergum 10 with slightly curved posterior margin. Tergalii very long and directed

laterally; their fore margins (armed by costal ribs) slightly arched; hind margins (not armed by ribs) strongly curved near base so that basal portion sub-parallel to side of abdomen, and terminal portion straight; tips pointed; on anterior abdominal segments tergalii nearly as long as segments width, on posterior abdominal segments tergalii longer than segments width; basal pairs of tergalii brown, terminal portions more or less lighter (Figs. 2A, B, 4A); tergalii first–sixth lack anal ribs; tergalius seventh widened, has anal rib at a distance from anal margin (Figs. 2A, 4G). Caudalii (cerci and paracercus) subequal, with primary swimming setae; caudalii and their primary swimming setae pale (Figs. 2A, B, G, 4F) (in most specimens setae invisible because of poor preservation).

In the holotype, DHG 0508, body length 13.6 mm including, and 10.5 mm excluding caudalii; head length 1.5 mm, width 2.3 mm; prothorax length 0.4 mm, width 2.6 mm; pterothorax length ca. 1.3 mm, width ca. 2.6 mm; femur of middle leg length (specimen no. DHG 0511) 1.6, tibia length 0.8 mm, tarsus length 1.0 mm; abdomen length ca. 7.3 mm, width 3.2 mm; 1st abdominal tergalius length 1.8 mm, width 0.7 mm; 7th abdominal gill length 1.9 mm, width 0.7 mm; terminal filament length, as preserved, 2.4 mm; circus length, as preserved, 3.1 mm.

Comparison: *Shantous* is presumably attributed to the extinct Jurassic – Cretaceous family Hexagenitidae (or Hexagenites/fg1) basing on the single known larval character of Hexagenitidae: seventh tergalii are larger than others (Kluge, 2004). *Shantous* differs from other Hexagenitidae (and from all other known mayflies) by the fact, that only the seventh tergalii have well-developed anal ribs. In other Hexagenitidae, whose larva are known, anal ribs are well-developed on all tergalii; in other mayflies anal ribs are either well-developed on all tergalii, or reduced on all tergalii, or on 7th tergalii are weaker than on previous ones.

By very long tergalii directed laterally, *Shantous* resembles Epeoromimidae Tshernova, 1969; unlike Epeoromimidae, *Shantous* has seventh tergalii not smaller than others and bearing anal ribs.

Discussion

Mesoneta, Mesobaetis, Fuyous and *Shantous*

Brauer et al. (1889) established two genera – *Mesoneta* (with a single species *Mesoneta antiqua*) and *Mesobaetis* (with a single species *Mesobaetis sibirica*), basing on fossil larvae from the Lower Jurassic Cheremkhovo Formation in Ust-Bailey (Siberia, Russia). Demoulin (1954) and Tshernova (1962a) placed *Mesobaetis* into the extant family Leptophlebiidae, that was not argued. Tshernova (1962a) placed *Mesoneta* into the extant family Ephemerellidae and gave such diagnoses for Ephemerellidae and *Mesoneta*, which contradicted one another. Later (Tshernova, 1969), she established for *Mesoneta* an extinct family Mesonetidae Tshernova, 1969. After this (Tshernova, 1971), she transferred the subfamily Mesonetinae into the extant family Leptophlebiidae, that was based on a wrong diagnosis of Leptophlebiidae. Sinitshenkova (1985) transferred *Mesobaetis* into the extant family Siphlonuridae s.l., which in that sense represented a plesiomorphon ancestral for other Euplectoptera-Anteritorna. Kluge (1989, 1993) demonstrated that both *Mesoneta* and *Mesobaetis* undoubtedly belong to a plesiomorphon Costatergalia Kluge, 1989, which includes Siphlonuridae s.l. and some other taxa, but does not include neither Leptophlebiidae, nor Ephemerellidae. Nevertheless, some Chinese researchers persisted in the old classificatory positions that *Mesoneta* and *Mesobaetis* belong, respectively, to the families Ephemerellidae and Leptophlebiidae (Hong, 1983; Hong et al., 1995; Ren et al., 1996; Ren

et al., 2002; Tan & Ren, 2002; Wang, 1980, 1987). In the modern phylogenetic classification, where plesiomorphons Costatergalia and Siphlonuridae s.l. are not accepted, *Mesoneta* and *Mesobaetis* should be regarded as unplaced Euplectoptera (Kluge, 2004).

Mesoneta antiqua has a distinct apomorphy – strongly widened abdomen whose greatest width is near the middle (Brauer et al., 1889, fig. 2b; Tshernova 1962a, fig. 79; Ponomarenko & Schultz, 1988, fig. 1). Unlike Ephemerellidae and some other mayflies with widened larval abdomen, in *Mesoneta* bases of tergalii are located just on lateral margins of the abdomen, being not shifted dorsally (Tshernova, 1962a, fig. 79). At the same time, caudalii of *Mesoneta* retain plesiomorphic structure, with well-developed primary swimming setae (these setae are not drawn by Brauer et al., but well visible on the photo by Ponomarenko & Schultz and on the drawing by Tshernova – see fig. 5A in this paper). Combination of these two features allows to separate larvae of the *Mesoneta antiqua* from other mayfly larvae.

The original description of *Mesobaetis sibirica* was based on five specimens and contained only plesiomorphic characters. Body size was indicated as 20 mm with caudalii and 14.4 mm without caudalii. Possibly, the original description of *Mesobaetis sibirica* was based on larvae which belong to two or more non-related species. Unlike *Mesoneta*, these larvae have plesiomorphically slender abdomen. Sinitshenkova (1985) described adults and larvae, which she attributed to *Mesobaetis sibirica*. These larvae have caudalii about three times shorter than the body, that is usual for many mayfly larvae. Ponomarenko & Schultz (1988) designated a lectotype of *Mesobaetis sibirica*, which is the single specimen preserved in the Naturhistorischen Museums in Wien. Judging by their photograph (Ponomarenko & Schultz, 1988, fig. 2 – see fig. 5D in this paper), this lectotype is a young larva about 9 mm long (instead of 14.4 mm in the original description); its head is especially large, as wide as thorax; its caudalii are unusually short, about four times shorter than the body. This means that the description of *Mesobaetis sibirica* made by Sinitshenkova, belongs not to the species which should bear this name, but to one or several other species. The genus, for which the name *Mesobaetis* should be reserved, differs from most mayflies by enlarged larval head and shortened larval caudalii.

Wang (1980, 1987) described remnants of larval Ephemeroptera from Haifanggou Formation (= Guojiadian Formation) in Chaoyang, Liaoning, China. He described a new species *Mesoneta beipiaoensis* Wang, 1980 (Wang, 1980, p. 131, pl. 65, fig. 1; 1987, p. 204, fig. 1, pl. 2, fig. 10) and reported a single fragment of larva as "*Mesobaetis sibirica*" (Wang, 1980, p. 132, pl. 66, fig. 3). Larva of *beipiaoensis* [*Mesoneta*] has slender body (Fig. 5C), so there are no any reasons to attribute it to the genus *Mesoneta*. Taxonomic relationships of these species are uncertain, and worthy of further restudy.

Hong (1983) described remains of larval Ephemeroptera from the Jiulongshan and Haifanggou formations, in Heibei and Liaoning provinces, China and determined them as "*Mesobaetis sibirica*" and "*Mesoneta antiqua*". The specimens determined by him as "*Mesoneta antiqua*" (Hong, 1983, p. 22, fig. 7, pl. 2, figs. 6–8) have slender body, triangular protoptera and very large, suboval tergalii (Fig. 5B); they have no any common features with *Mesoneta*, much more the *Mesoneta antiqua* (Fig. 5A). The taxonomic placement of these specimens has been reassessed; it represents a new species referable to *Clavineta* Sinitshenkova, 1991 (within Eusetisura incertae sedis), but not related to *Fuyous* gen. nov. or *Shantous* gen. nov. (Zhang, 2006b).

The specimen determined as "*Mesobaetis sibirica*" (Hong, 1983, p. 21, fig. 6; pl. 6, fig. 5) later were described as a new species, *Mesobaetis sanjianfangensis* Hong, Liang et Hu, 1995 (Hong et al., 1995, pp. 434–435, fig. 3A–B; pl. I, figs. 1, 2). These authors attributed to the genus *Mesobaetis* also remnants of mayfly larvae from the Sanjianfang Formation in the Tuha Basin, Xingjiang Uigur Autonomous Region, China: four fragments of larvae were reported as "*Mesobaetis sibirica*" (Hong et al., 1995, 435–436, fig. 4; pl .I, fig. 3), and one poorly preserved print was described as *Mesobaetis maculata* Hong, Liang et Hu, 1995. Judging from the original photographs and illustrations (Figs. 5E–G), these larvae have no derived features of *Mesobaetis*.

Ren et al. (2002) reported two forms of larval remnants from the Daohugou Formation as the two species: they determined larvae with more slender abdomen as "*Mesoneta antiqua*", and larvae with wider abdomen as "*Mesobaetis sibirica*" (while actually, vice versa, *Mesoneta* is characterized by strongly widened abdomen, and *Mesobaetis* – by slender abdomen).

Recently, one of us (J. Zhang) collected several dozens of impressions of larvae from the same locality and same beds in the vicinity of Daohugou Village. These specimens share, respectively, the identical features to those images provided by Ren et al. (2002, pl. II, figs. 2A, 4), and then can be assigned into the same species; here we describe these species as *Fuyous gregarius* gen. et sp. nov. and *Shantous lacustris* gen. et sp. nov. The both new species can be distinguished from *Mesoneta antiqua* by more slender abdomen, and from *Mesobaetis sibirica* – by longer caudalii and smaller head.

To sum up, we can conclude that, to date, *Mesoneta antiqua* (and other true representatives of *Mesoneta*) and *Mesobaetis sibirica* (and other true representatives of *Mesobaetis*) are not found outside Siberia, Russia of the Jurassic times.

Stackelbergisca, Siberiogenites* and *Fuyous

The genus *Stackelbergisca* Tshernova, 1967 was described from the Uda Formation (Middle–Upper Jurassic of Buryatia) as fragments of imaginal wings and larvae. All these fossils were attributed to a single species *S. sibirica* Tshernova, 1967; holotype is one of the wing fragments, and 25 larvae are paratypes (Tshernova, 1967). Wing venation of the holotype is common for many primitive siphlonuroid Mesozoic and Recent mayflies. All that larval paratypes which are well-preserved, have typical siphlonuroid primary swimming specialization, with long abdomen and long dense primary swimming setae on caudalii. In older classifications, all mayflies with such characters were united in a plesiomorphon Siplonuridae, so *Stackelbergisca* was also included into this family (Tshernova, 1967; Sinitshenkova, 1985; Carpenter, 1992). Currently, this plesiomorphon is not recognized, being divided to a number of holophyletic taxa within Anteritorna Kluge, 1993 (McCafferty, 1991; Kluge et al., 1995; Kluge, 2004); so systematic position of *Stackelbergisca* can be determined now as unplaced Anteritorna. Among the larval paratypes of *Stackelbergisca sibirica*, there are representatives of at least two different taxa.

The first taxon is represented by the specimen 2022/719/4 – an empty moulting larval skin (exuviae), from which subimago emerged. The published drawing of this specimen (Tshernova, 1967, fig. 2a) contains many errors: pronotum and mesonotum are drawn as being integral, while actually they are broken by median line, and their right halves overlap their left halves; metanotum with hind protoptera is not drawn; tergalii are drawn and described as represented by median tracheae only, while actually each tergalius has a strong costal rib on costal margin (this rib was taken for a median trachea) and a strong anal rib at

a distance from anal margin (this rib was overlooked by Tshernova). Some of these details are visible on photo (Tshernova, 1967, fig. 2). Structure of claws of this specimen is unknown. Among Jurassic mayflies, the same structure of tergalii occurs in *Siberiogenites* Sinitshenkova, 1985. Originally, the genus *Siberiogenites* was attributed to the family Hexagenitidae (Sinitshenkova, 1985), whose larvae also have anal rib at a distance from anal margin of tergalius. However, *Siberiogenites* has seventh tergalii not enlarged, so its placement to Hexagenitidae is not grounded. Besides Hexagenitidae and *Siberiogenites*, prominent anal rib located at a distance from anal margin occurs in various non-related Recent taxa (Kluge, 2004), so this character is not enough to characterize a natural taxon. Until other taxonomic features of these Mesozoic larvae are known, we can attribute all siphlonuroid larvae with such structure of tergalii to the genus *Siberiogenites*.

The second taxon is represented by the specimens 2022/720/2, 2022/720/3 and 2022/720/5. They have claws with a peculiar long straight sub-basal projection (as in *Fuyous*). Among them, specimens 2022/720/2 and 2022/720/3 have preserved tergalii, which have a costal rib, but no anal rib (as in *Fuyous*). Besides these paratypes, there is a specimen 353/198, whose claws also have projections. Possibly, these specimens are congeneric or even conspecific with *Fuyous gregarius* sp. nov.

It is impossible to determine now, which larval form (*Siberiogenites*, *Fuyous*, or some other) should bear the older name *Stackelbergisca*, because wing venation of all larval specimens is unknown, and holotype of *Stackelbergisca sibirica* has such plesiomorphic wing venation, which can be identical to that of many non-related mayflies.

Inhabitancy of Jurassic mayfly larvae

Ren et al. (1996) claimed that Mesozoic mayflies *Ephemeropsis trisetalis*, *Mesobaetis sibirica* and *Mesoneta antiqua* are lotic. On the contrary, Sinitshenkova (1976, 1984, 1999) deemed all known Jurassic and Early Cretaceous larvae of mayflies being lacustrine rather than rheophilous.

This question is rather difficult, because sometimes morphological features do not allow to distinguish lacustrine and rheophilous mayfly species. For example, larvae of *Baetis macani* Kimmins, 1957 inhabit only stagnant waters of tundra lakes, but nearly identical larvae of a closely related species *Baetis feles* Kluge, 1980 inhabit only running waters of small mountain streams; larvae of *Ephemera vulgata* Linnaeus, 1758 often inhabit stagnant waters of lakes and ponds, while identical larvae of the closest species *Ephemera romantzovi* Kluge, 1988 inhabit rapid mountain rivers of the Caucasus.

The dense primary swimming setation of caudalii, which was retained in many known Jurassic mayfly larvae, is more characteristic for lacustrine forms, than to rheophilous ones (while there are exceptions: many Recent species of *Ameletus* and *Baetis* inhabit mountain steams, having well-developed primary swimming setation). Among the Recent mayflies, most rheophilous forms are found among Radulapalpata (or Heptageniidae s. str.); this taxon did not exist in Jurassic – Early Cretaceous, being known as fossils only in Late Cretaceous (adults in New Jersey amber), Palaeogene (adults of several species in Baltic amber) and Miocene (larvae of several species in Europe and Asia) (Tshernova, 1962b; Zhang, 1989; Kluge, 2004).

The fact that a great number of Jurassic larvae referable to a few species appeared in a single horizon, indicates that they lived, in fact, in that lake. The rheophilous larvae, on the other hand, would be able to be transported into lake only by chance; if so, their relics can

be found rarely among the true lacustrine larvae (Sinitshenkova 1976, 1984). Up to now, thousands of fossil limnic larvae referable to several dozens of mayfly species have been recorded. For this reason, it is most probable that all larvae of mayflies from the Jurassic and Early Cretaceous of China (including the *Ephemeropsis trisetalis*, *Fuyous gregarius,* gen. et sp. nov. and *Shantous lacustris,* gen. et sp. nov.) may be lacustrine rather than lotic.

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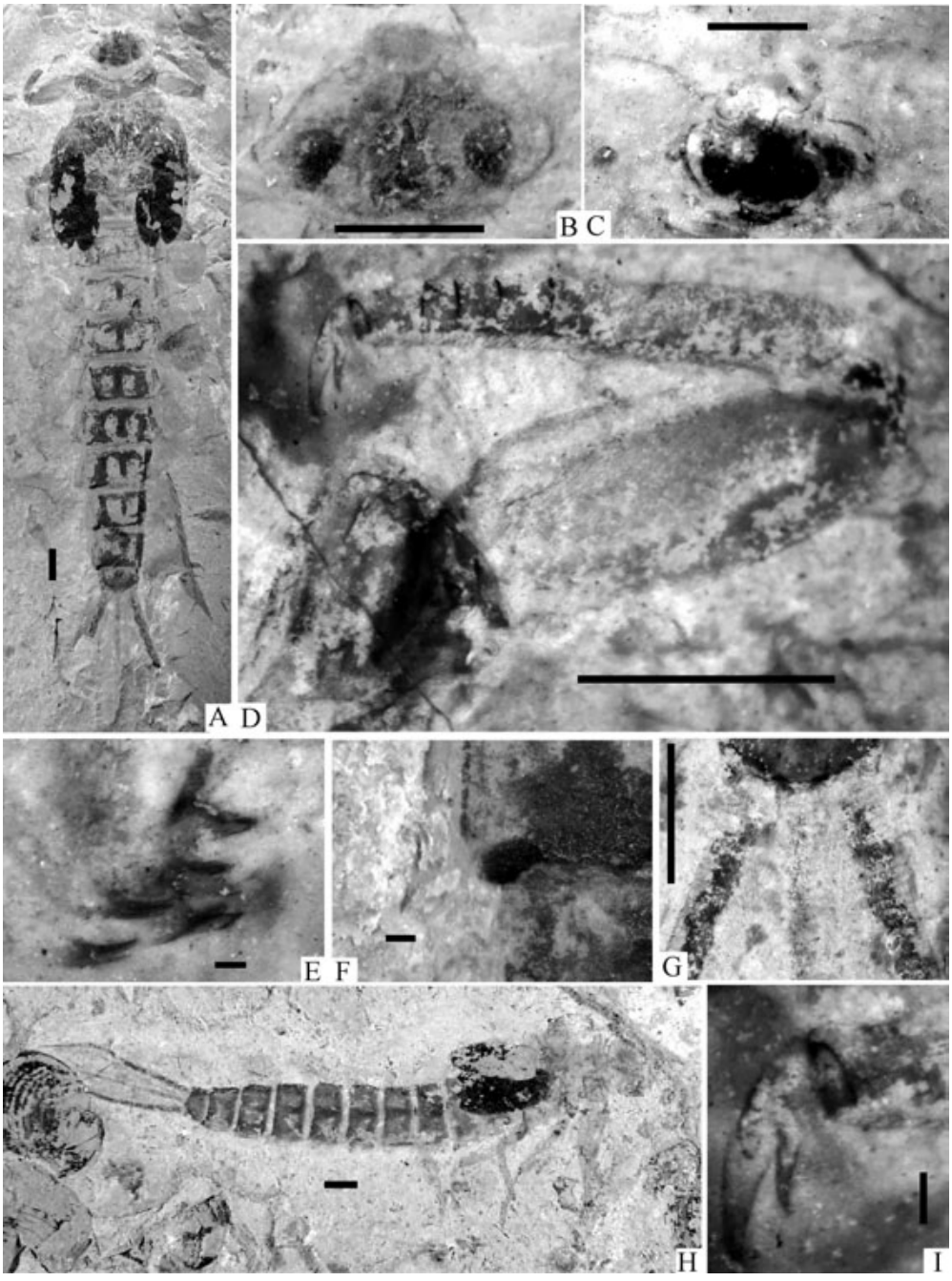

Figure 1

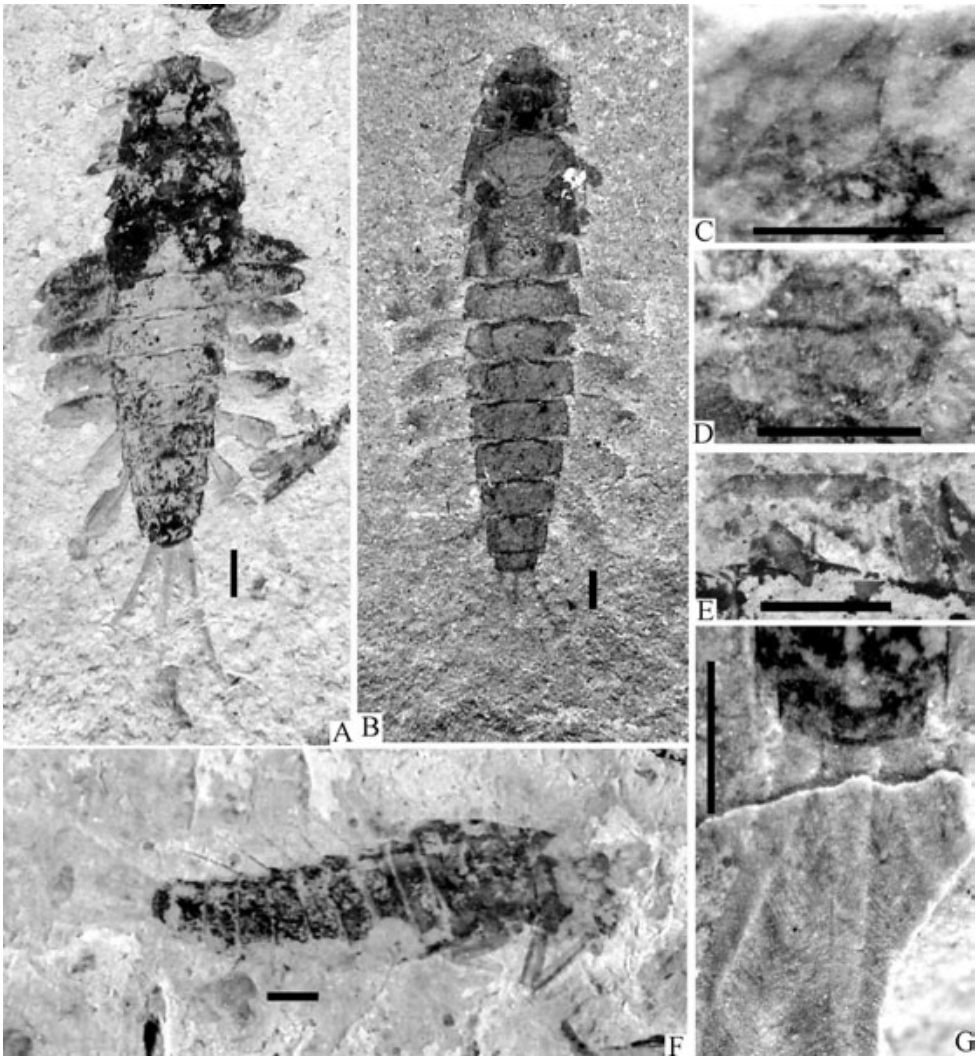

Figure 2

Fig. 1. *Fuyous gregarius,* gen. et sp. nov. (larvae; photographs); A, general view, holotype, no. DHG 0501, dorsoventral aspect; B, head, paratype, no. DHG 0502, dorsoventral aspect; C, head (including antennae), paratype, no. DHG 0504, dorsoventral aspect; D, right fore leg, holotype, no. DHG 0501, lateral aspect; E, incisors of mandibles and canines of maxillae of mouthparts, paratype, no. DHG 0505, lateral aspect; F, left projection of 9th abdominal segments, holotype, no. DHG 0501, dorsoventral aspect; G, basal portion of caudalii, holotype, no. DHG 0501, dorsoventral aspect; H, general view, paratype, no. DHG 0505, lateral aspect; I, claw of right foreleg, holotype, no. DHG 0501, lateral aspect.

All the specimens are from the Daohugou Formation in the vicinity of Daohugou, Ningcheng, Chifeng, Inner Mongolia, China. Scale bars represent 1 mm with exception of figs. E, F and I, on which scale bars represent 0.1 mm.

Fig. 2. *Shantous lacustris* gen. et sp. nov. (larvae; photographs); A, general view, holotype, no. DHG 0508, dorsoventral aspect; B, general view, paratype, no. DHG 0507, dorsoventral aspect; C, left mandible, no. DHG 0509; D, clypeus, no. DHG 0510; F, left middle leg, no. DHG 0511; G, general view, paratype, no.

DHG 0512, lateral aspect; H, paracercus and cerci (covered with dense hairs), no. DHG 0513, dorsoventral aspect.

All the specimens are from the Daohugou Formation in the vicinity of Daohugou, Ningcheng, Chifeng, Inner Mongolia, China. Scale bars represent 1 mm with exception of figs. C and D, on which scale bars represent 0.5 mm.

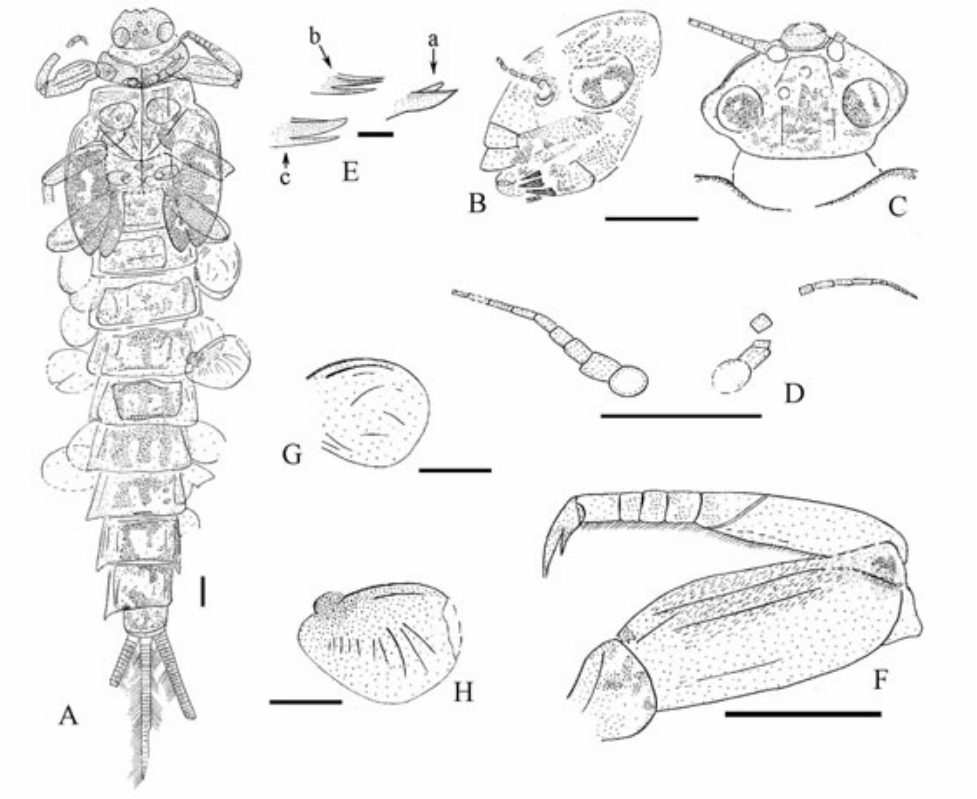

Figure 3

Fig. 3. *Fuyous gregarius* gen. et sp. nov. (larvae; camera lucida line drawings); A, general view, dorsoventral aspect, specimen no. DHG 0501; B, head, lateral aspect, specimen no. DHG 0503; C, head, dorsoventral aspect, specimen no. DHG 0502; D, antennae, dorsoventral aspect, specimen no. DHG 0504; E, a, incisor of left mandible, b, canines of left maxilla, c, canines of right maxilla, lateral aspect, specimen no. DHG 0505; F, right foreleg, lateral aspect, specimen no. DHG 0501; G, right first tergalius, specimen no. DHG 0501; H, right fourth tergalius, specimen no. DHG 0501.

Scale bars represent 1 mm with exception of fig. E, on which scale bar represents 0.1 mm.

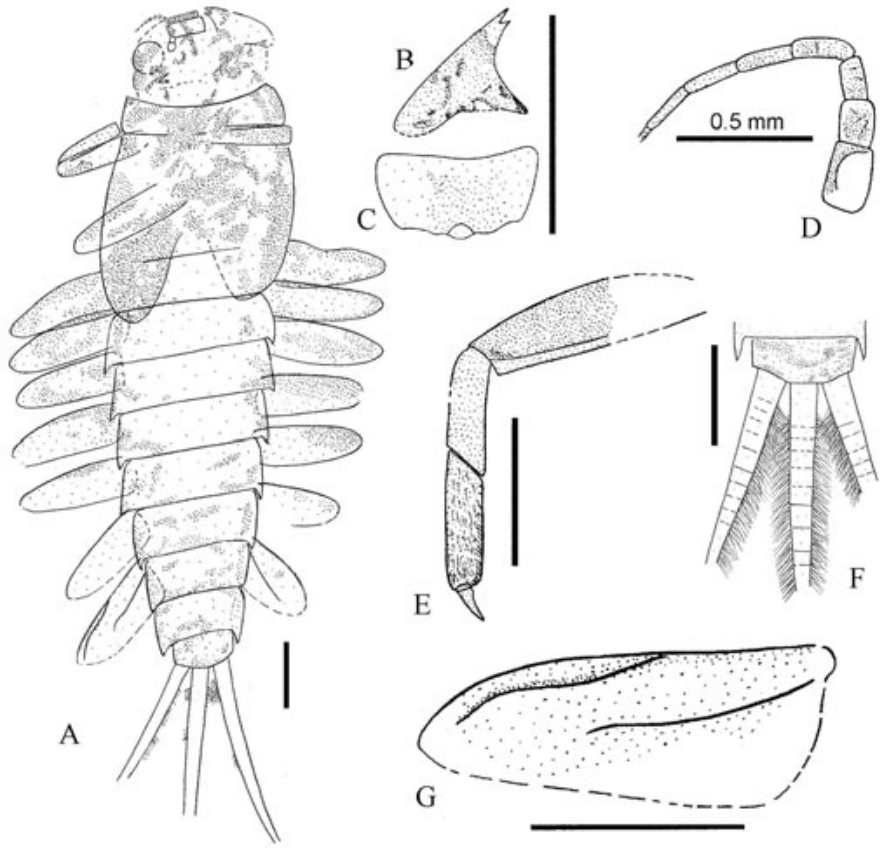

Figure 4

Fig. 4. *Shantous lacustris* gen. et sp. nov. (larvae; camera lucida line drawings): A, general view, dorsoventral aspect, specimen no. DHG 0508; B, left mandible, dorsoventral aspect, specimen no. DHG 0509; C, clypeus, dorsoventral aspect, specimen no. DHG 0510; D, left antenna, dorsoventral aspect, specimen no. DHG 0508; E, left middle leg, lateral aspect, specimen no. DHG 0511; F, tenth abdomen segment and caudalii (cerci and paracercus), dorsoventral aspect, specimen no. DHG 0513; G, left seventh tergalius, dorsoventral aspect, specimen no. DHG 0508.

All scale bars represent 1 mm with exception of fig. D, on which scale bar represents 0.5 mm.

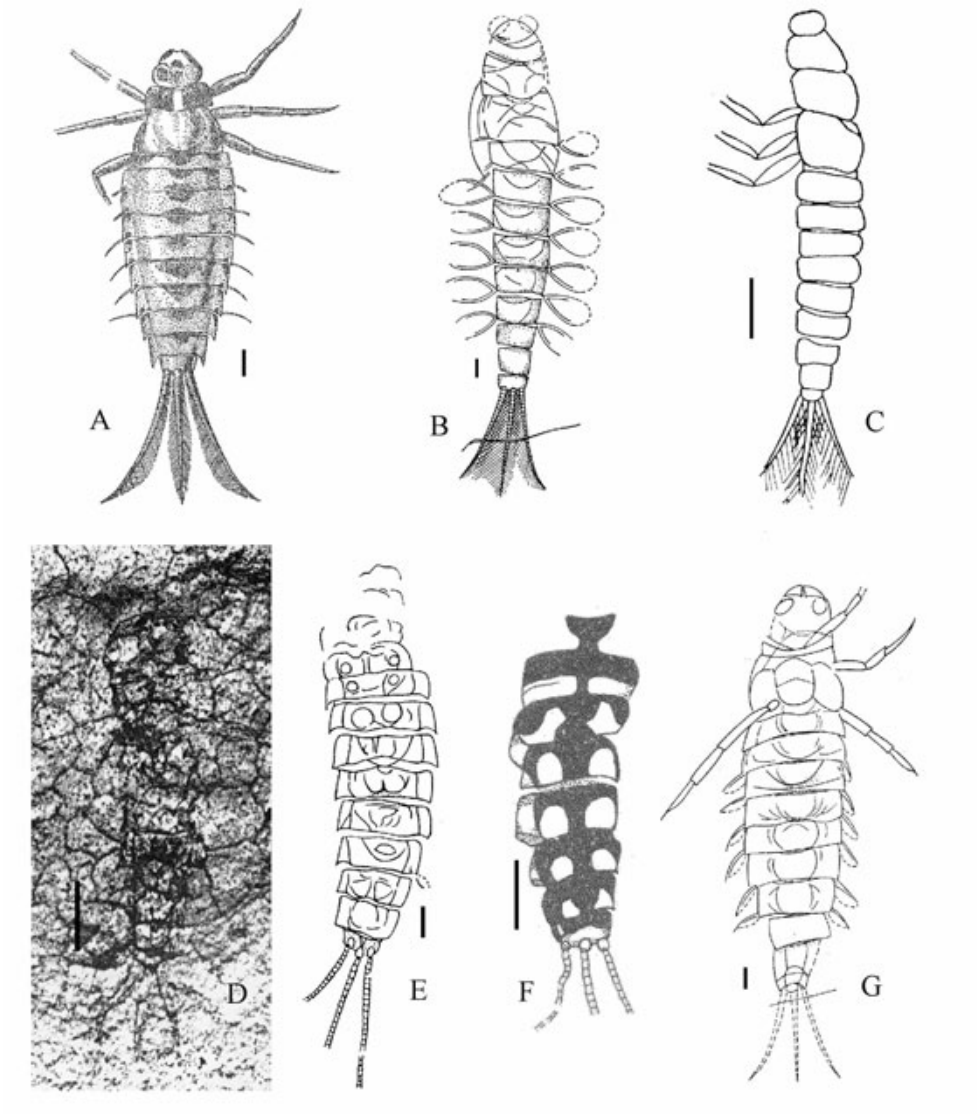

Figure 5

Fig. 5. Larvae of Jurassic mayflies; A, *Mesoneta antiqua* Brauer, Redtenbacher et Ganglbauer, 1889 (after Tshernova, 1962a); B, *Mesoneta antiqua* sensu Hong, 1983 (non Brauer, Redtenbacher et Ganglbauer, 1889) (after Hong, 1983); C, *Mesoneta beipiaoensis* Wang, 1980 (after Wang, 1987); D, *Mesobaetis sibirica* Brauer, Redtenbacher et Ganglbauer, 1889 (photograph of lectotype, after Ponomarenko & Schultz, 1988); E, *Mesobaetis sibirica* sensu Hong, Liang et Hu, 1995 (non Brauer, Redtenbacher et Ganglbauer, 1889) (after Hong et al., 1995); F, *Mesobaetis maculata* Hong, Liang et Hu, 1995 (after Hong et al., 1995); G, *Mesobaetis sanjianfangensis* Hong, Liang et Hu, 1995 [originally *Mesobaetis sibirica* sensu Hong, 1983 (non Brauer, Redtenbacher et Ganglbauer, 1889)] (after Hong, 1983).