New genus and species of Hexagenitidae (Insecta: Ephemeroptera) from Yixian Formation, China

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Abstract

A new genus and two new species of the extinct family Hexagenitidae, Epicharmeropsis hexavenulosus gen. et sp. nov. and Epicharmeropsis quadrivenulosus sp. nov., are described from the Late Jurassic-Early Cretaceous Yixian Formation, Hebei and Liaoning Provinces in China. Detailed description and illustration of the specimens along with a brief review of Hexagenitidae are given. By comparing with the imago specimens of so-called Ephemeropsis which were previously reported from China, we believe these Ephemeropsis-like specimens should be placed into Epicharmeropsis gen. nov. and Ephemeropsis Eichwald could be absent in China.

Key words: Ephemeroptera, Hexagenitidae, Epicharmeropsis gen. nov., Ephemeropsis, fossil, Yixian Formation, China

Introduction

The family Hexagenitidae Lameere, 1917 which was proposed for the genus Hexagenites Scudder, 1880 from the remains of imago in the Late Jurassic of Solnhofen, Germany, is an extinct group. As the number of dentisetae and other important infraordinal characters are unknown, Hexagenitidae is temporarily classified to Anteritorna incertae sedis (Kluge, 2004). Toward the Early-Middle Jurassic boundary Hexagenitidae had appeared in Transbaikalia and Mongolia (Siberiogenites Sinitshenkova, 1985), to become common in Solnhofen (Hexagenites Scudder). In the Early Cretaceous, where it was widespread and often forming mass burial, Hexagenitidae was usually the only dominant family in mayfly assemblages (Kluge and Sinitshenkova, 2002). They have been recorded in Ukraine and Algeria (Hexameropsis Tshernova and Sinitshenkova, 1974), Transbaikalia (Ephemeropsis Eichwald, 1884), Mongolia (Ephemeropsis and Mongologenites Sinitshenkova, 1986), China (Caenoephemera Lin and Huang, 2001) and Brazil (Protoligoneuria Demoulin, 1955; Palaeobaetodes Brito, 1987; Cratogenites and Cratogenitoides Martins-Neto, 1996). Kluge (2004) believes that Siberiogenites cannot be placed to any family (including Hexagenitidae), but undoubtedly should be regarded as Euplectoptera incertae sedis.

Recently we discovered 14 well-preserved adult fossil mayfly specimens from the Yixian Formation, in Jianshangou and Huangbanjigou, Chaomidian Village, Shangyuan Township, Beipiao City, Liaoning Province; Dakangpu Village, Liulongtai Township, Yixian County, Liaoning Province; and Shimen Village, Yangshuling Township, Pingquan County, Hebei Province, China. Two new species of a new genus are established and described in this paper.

The geological age of the Yixian Formation is still contentious, considered to be the Late Jurassic (Ren et al. 1997, Zheng et al. 2003), the transition from the Late Jurassic to the Early Cretaceous (Chen et al. 2004,
Wang et al. (2004), and the Early Cretaceous (Swisher et al. 1999, Zhou et al. 2003). Recently, Wang et al. (2005) summarized and analyzed the geological age of the Yixian Formation by abundant fossil data and isotope data, and finally considered that the synthetic age of the Yixian Formation may be determined as the Late Jurassic to the Early Cretaceous. We accept this opinion and consider the age of the Yixian Formation as the transition from the Late Jurassic to the Early Cretaceous (Late Tithonian to the Berriasian).


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

Ephemeroptera Hyatt et Arms, 1891

Euplectoptera Tillyard, 1932

Hexagenitidae Lameere, 1917

Genus Epicharmeropsis Huang, Ren & Shih, gen. nov.

Type species. Epicharmeropsis hexavenulosus Huang, Ren & Shih, sp. nov.

Etymology. Greek prefix Epichar- (beautiful) and meropsis (a suffix taken from genus Ephemeropsis).

Diagnosis. Imago. Moderate to good-sized species; mesonotal suture (MNs) in anterior part of mesonotum strongly stretched backwards medially, not transverse; paired medioparapsidal sutures (MPs) anastomosed at middle area of mesonotum, not parallel; lateroparapsidal suture (LPs) curved laterally; metanotum relatively long. Forewing about 2.4 times as long as its width; membrane thickened at distal part of the field between C and RA; RS forking about 10mm from base of forewing, RSA formed two triads, RSp non-branched; distinct intercalary veins existing between MP_2 and CuA_1; CuA_1 with 4–6 triads (loop-shaped veinlets) leading to wing margin; numerous crossveins and intercalary veins between longitudinal veins. Hindwing more or less than half as long as forewing, broad, about 1.6 times as long as its width with fairly obtuse tip.

Composition. The type species and Epicharmeropsis quadrivenulosus.

Comparison. Epicharmeropsis gen. nov. is very similar to Ephemeropsis Eichwald from the Early Cretaceous of Transbaikalia and Mongolia in the shape and venation of fore and hind wings; but it differs from Ephemeropsis by membrane thickened at distal part of the field between C and RA, unforked RSp, and the distinct intercalary veins existing between MP_2 and CuA_1 of forewing. The later two features of wing venation are present in Late Jurassic genus Hexagenites Scudder, 1880 and Lower Cretaceous genus Cratogenites Martins-Neto, 1996, but in contrast to them, hind wing of Epicharmeropsis is more or less than half as long as forewing.

Remark. The combined characters of this new genus allow an allocation of it to the family Hexagenitidae: moderate to large size; vein CuA of forewing forked, one of its branches with a series of triads (loop-shaped veinlets) leading to wing margin.

Epicharmeropsis gen. nov. possesses a peculiar combination of characters: mesonotal suture (MNs) in anterior part of mesonotum strongly stretched backwards medially, not transverse; paired medioparapsidal sutures (MPs) jointed at middle area of mesonotum, not parallel; forewing less than 2.5 times as long as its width; RSp non-branched; the presence of intercalary veins between MP_2 and CuA_1; hindwing broad, about 1.6 time as long as its width, with fairly obtuse tip. These characters allow formal separation of this new genus from other known genera of the Hexagenitidae established by mayfly adults, extant or in fossil records.
**Epicharmeropsis hexavenulosus** Huang, Ren & Shih, sp. nov.

(Fig. 1–4.)

**Etymology.** Latin prefix *hexa-* (six) and *venulosus* (veinlet).

**Holotype.** CNU-E-YX-2007001-1, CNU-E-YX-2007001-2 (Fig. 1–3). Well preserved part and counter-part of imago; antennae and tarsi of middle and hind legs are not preserved; the Late Jurassic to the Early Cretaceous, Yixian Formation, Shimen Village, Yangshuling Township, Pingquan County, Hebei Province, China.

**Material.** Holotype and from the same locality, paratypes: male imago, No. CNU-E-YX-2007021-1, No. CNU-E-YX-2007021-2; male imago, No. CNU-E-YX-2007023; male imago, No. CNU-E-YX-2007024; male imago, No. CNU-E-YX-2007025-1, No. CNU-E-YX-2007025-2; female imago, No. CNU-E-YX-2007004 (Fig. 4.).

**Diagnosis.** In addition to the diagnosis for the new genus, the species can be diagnosed as follows: CuA₁ of forewing with 6 triads (loop-shaped veinlets) leading to wing margin.

**Description.** Male imago (dorsal view) (Fig. 1–3.).

Eyes relatively large, contiguous. Pterothorax well-developed; mesonotal suture (MNs) in anterior part of mesonotum strongly stretched backwards medially, not transverse; paired medioparapsidal sutures (MPs) jointed at middle area of mesonotum, not parallel; metanotum long, with evident scutum.

Forewing: broad and triangular with costal brace; costal margin slightly curved; tornoapical (outer) margin longer than basitornal (anal) margin; costal area relatively wide, narrowing toward tip; RA subparallel to SC; membrane slightly thickened at distal part of the field between C and RA; RSa formed two triads, RSp non-branched; MA branched after middle area of wing; MA₁ and MA₂ uniformly diverging; iMA approximated MA₁; MP₁ and MP₂ diverged at an angle of approximately 30 degree; distinct intercalary veins existing between MP₂ and CuA₁; CuA bifurcated to CuA₁ and CuA₂, from the bifurcation a vein iCu formed 6 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.

Hind wing: broad with fairly obtuse tip; venation relatively profuse; the base of C strongly arched, far from SC; subcostal area broad, more than 3 times as wide as costal area; RA terminated near wing apex; RS formed triad RS₁-RSp₁; MA₁ and MA₂ non-branched; MA branched near middle; RSp non-branched; MA bifurcated near middle; MP bifurcated near the base of wing; iMP approximated with MP₁; CuA and CuP un-forked; more than 4 A present; anal area broad; numerous crossveins and intercalary veins near wing margin.

Legs (preserved): relatively sturdy and long; femora longer than tibia; three-segmented tarsi of fore legs preserved, slender; tarsi of middle and hind legs absent.

Abdomen: the posterolateral projections of the ninth segment, very long and sharp, nearly as long as the tenth abdominal tergum.

Paracercus, very short; cerci, long.

Female imago (Fig. 4.). Eyes relatively small, separate; mouth apparatus vestigial, only anterior margin of the frons forming a projected lamella; coxa, trochanter and femur of fore and middle legs preserved, sturdy; the posterolateral projections of the ninth segment not extended posterolaterally. Other characters are as in male.

Male and female subimagoes, and nymph are unknown.

**Measurements** (mm). Holotype: body length (excluding caudalii) 31.0 (head length 3.0, pronotum length 0.5, pterothorax length 9.5, abdomen length 18.0); forewing length 34.0, its width 14.0; hind wing length 18.0, its width 11.0; length of fore leg fragment 27.0 (femur 9.0, tibia 7.0, first tarsus 4.0, second tarsus 5.0, third preserved tarsus 2.0); femora of middle and hind legs preserved, slender; tarsi of middle and hind legs absent.

Abdomen: the posterolateral projections of the ninth segment, very long and sharp, nearly as long as the tenth abdominal tergum.

Paracercus, very short; cerci, long.

Female imago (Fig. 4.). Eyes relatively small, separate; mouth apparatus vestigial, only anterior margin of the frons forming a projected lamella; coxa, trochanter and femur of fore and middle legs preserved, sturdy; the posterolateral projections of the ninth segment not extended posterolaterally. Other characters are as in male.

Male and female subimagoes, and nymph are unknown.

*Epicharmeropsis quadrivenulosus* Huang, Sinitshenkova & Ren, sp. nov.
(Fig. 5–7.)

**Etymology.** Latin prefix *quadri-* (four) and *venulosus* (veinlet)

**Holotype.** Male imago, No. CNU-E-YX-2007002 (Fig. 5–6.). Well preserved fore and hind wings as well
as head and thorax, other parts of the specimen not preserved, the Late Jurassic to the Early Cretaceous, Yixian Formation, Jianshangou, Chaomidian Village, Shangyuan Township, Beipiao City, Liaoning Province, China.

**Paratype.** Male imago, No.CNU-E-YX-2007014 (Fig. 7.) from Yixian Formation (the Late Jurassic to the Early Cretaceous), Dakangpu Village, Liulongtai Township, Yixian County, Liaoning Province; male imago, No.CNU-E-YX-2007020 from Yixian Formation, Shimen Village, Yangshuling Township, Pingquan County, Hebei Province; male imago, No.CNU-E-YX-2007007 from Yixian Formation, Jianshangou, Chaomidian Village, Shangyuan Township, Beipiao City, Liaoning Province; male imago, No. CNU-E-YX-2007008 from Yixian Formation, Huangbanjigou, Chaomidian Village, Shangyuan Township, Beipiao City, Liaoning Province, China.

**Diagnosis.** In addition to the diagnosis for the new genus, the species can be diagnosed as follows: CuA₁ of forewing with 4 triads (loop-shaped veinlets) leading to wing margin.

**Description.** Male imago (Fig. 5–7.). CuA₁ of fore wing with 4 loop-shaped veinlets leading to wing margin; left hind wing is not completely same with right hind wing, RSa of left hind wing branched and iRSa absent, however, RSa of right hind wing unforked and iRSa present. Other characters are similar to those of male *E. hexavenulosus*.

Female imago, male and female subimagoes, and nymph are unknown.

**FIGURE 2.** *Epicharmeropsis hexavenulosus* gen. et sp. nov., male imago, holotype CNU-E-YX-200701-1: A, photograph of head and thorax in dorsal view; B, photograph of cubital area on forewing. Without scale.
FIGURE 4. *Epicharmeropsis hexavenulosus* sp. nov., female imago, paratype CNU-E-YX-2007004: A, photograph of paratype; B, body with wings on lateral view; C, forewing.
Comparison. *E. quadrivenulosus* sp. nov. can be distinguished from *E. hexavenulosus* sp. nov. by 4 triads (loop-shaped veinlets).

**FIGURE 5.** *Epicharmeropsis quadrivenulosus* sp. nov., male imago, holotype CNU-E-YX-2007002: A, photograph of part; B, forewing; C, left hind wing.
Measurements (mm). Holotype: forewing length 38.5, its width 15.5; hindwing length 21.0, its width 13.0; pronotum length 1.0; mesonotum 10.0. Paratype: male imago No.CNU-E-YX-2007014, body length 30.0 (excluding caudalii), forewing length 32.0, its width 13.0; male imago No.CNU-E-YX-2007011-1, forewing length 37.0, its width 15.5; hindwing length 17.0, its width 13.0.

FIGURE 6. Epicharmeropsis quadrivenulosus sp. nov., male imago, holotype, CNU-E-YX-2007002: A, photograph of head and thorax; B, photograph of cubital area on forewing. Without scale.

FIGURE 7. Epicharmeropsis quadrivenulosus sp. nov., male imago, paratype, CNU-E-YX-2007014: A, photograph of part; B, body with wings.
FIGURE 8. A, forewing of *Ephemeropsis trisetalis* Eichwald (after Tshernova and Sinitshenkova, 1974); B, hindwing of *Ephemeropsis trisetalis* Eichwald (after Tshernova, 1961); C, fore- and hind wings of *Ephemeropsis trisetalis* Eichwald (after Hong, 1982).

Discussion

We collected 14 adult specimens of *Epicharmeropsis gen. nov.*, including 10 male, 1 female and 3 gender unknown (due to poor preservation No. CNU-E-YX-2007006, No. CNU-E-YX-2007012 and No. CNU-E-YX-2007013) from Northern China. Evidently *Epicharmeropsis* is one of dominant groups in Yixian Formation and probably taphonomicaly autochthonous.
The relatively large hind wings of *Epicharmeropsis* gen. nov., which are more or less than half length of forewings and complex venation, especially numerous intercalary veins are plesiomorphic features. Evolution of mayfly has shown the reduction of hind wings and their venation. But the character of vestigial mouth apparatus, i.e. only anterior margin of the frons forming a projected lamella, is obvious synapomorphic. Therefore, *Epicharmeropsis* gen. nov. might have been a transitional group. Its taxonomic position in *Anteritorna* is worthy of further study.

Some Chinese paleoentomologists attributed most of the specimens of Hexagenitidae, which are similar to *Ephemeropsis* from China, especially Northern China, to so-called *Ephemeropsis trisetalis* Eichwald (Fig. 8A, 8B.). Hong (1982) published a line drawing (Fig. 8C.) of imago based on a specimen from Yixian Formation, Heishangou Village, Chifeng County, Liaoning Province, China. The line drawing shows the same character of new genus *Epicharmeropsis*: distinct intercary veins existing between MP1 and CuA1, which is obviously different from *Ephemeropsis* although the drawing itself had some mistakes. So we think the species of *Ephemeropsis*, which only occurred in Transbaikalia of Russia and Mongolia, was not present in China. The *Ephemeropsis*-like imagos specimens reported before from China, which was classified as *Ephemeropsis trisetalis*, should be placed into this new genus. Of course, as the nymph specimens of Hexagenitidae from China have not been described in detail and the association between nymphs and adults has not been established, our opinion should be considered as preliminary.

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Reference


