



## 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 (*Caenophemera* 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).

Morphological terms used here follow those by Kluge (1994, 2004).

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<sub>2</sub> and CuA<sub>1</sub>; CuA<sub>1</sub> 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<sub>2</sub> and CuA<sub>1</sub> 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<sub>2</sub> and CuA<sub>1</sub>; 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 counterpart 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:  $CuA_1$  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; tornopical (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;  $MA_1$  and  $MA_2$  uniformly diverging;  $iMA$  approximated  $MA_2$ ;  $MP_1$  and  $MP_2$  diverged at an angle of approximately 30 degree; distinct intercalary veins existing between  $MP_2$  and  $CuA_1$ ;  $CuA$  bifurcated to  $CuA_1$  and  $CuA_2$ , 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  $RSa-iRS-RSp$ ,  $RSa$  and  $RSp$  non-branched; MA bifurcated near middle; MP bifurcated near the base of wing;  $iMP$  approximated with  $MP_1$ ;  $CuA$  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.

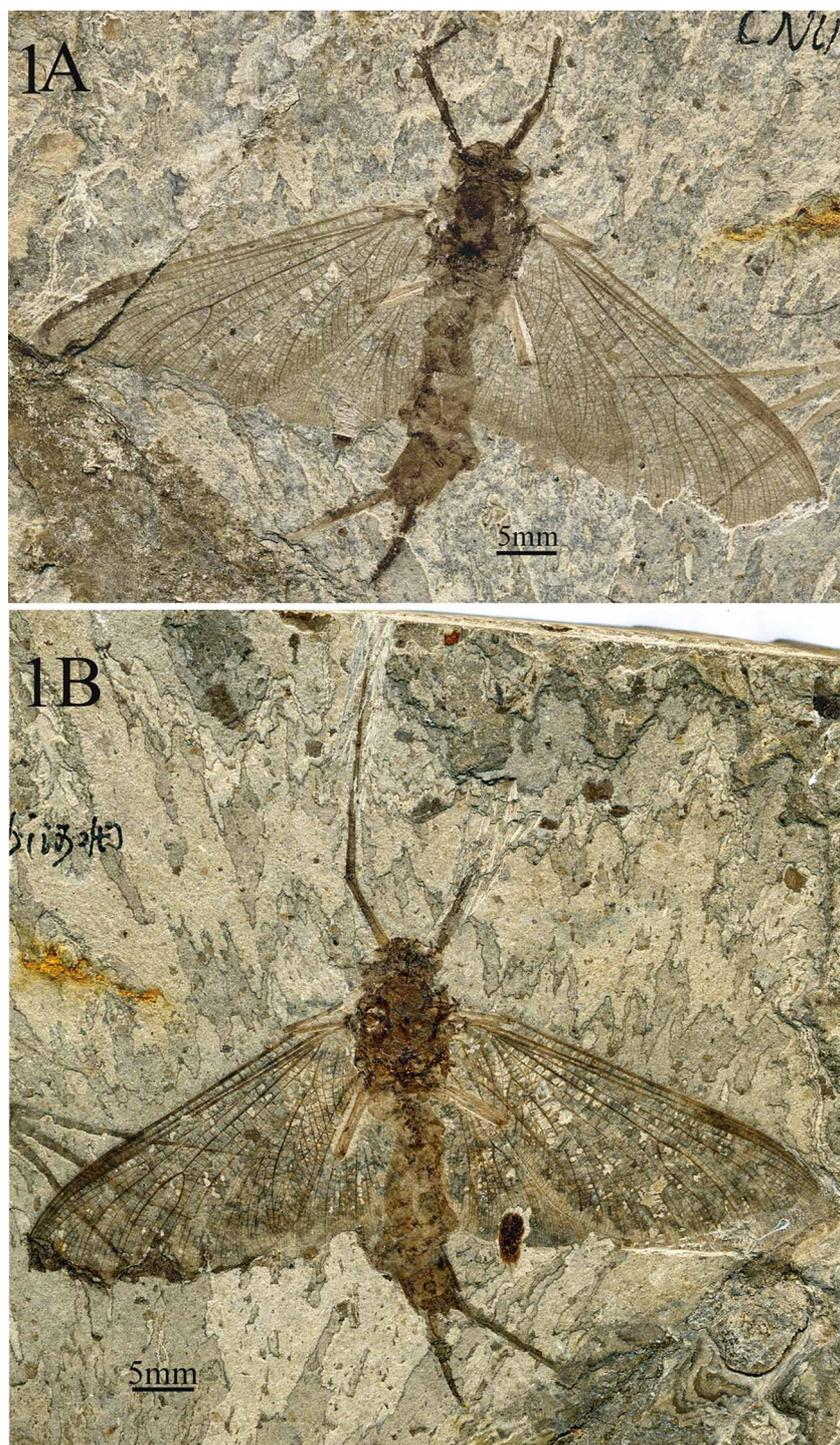
Abdomen: the posterolateral projections of the ninth segment, very long and sharp, nearly as long as the tenth abdominal tergum.

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 6.0; tarsi of middle and hind legs 5.0. Paratype: female imago No. CNU-E-YX-2007004, forewing length 34.0, its width 14.5.



**FIGURE 1.** *Epicharmeropsis hexavenulosus* gen. et sp. nov., male imago, holotype: A, photograph of part CNU-E-YX-200701-1; B, photograph of counterpart CNU-E-YX-200701-2.

*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

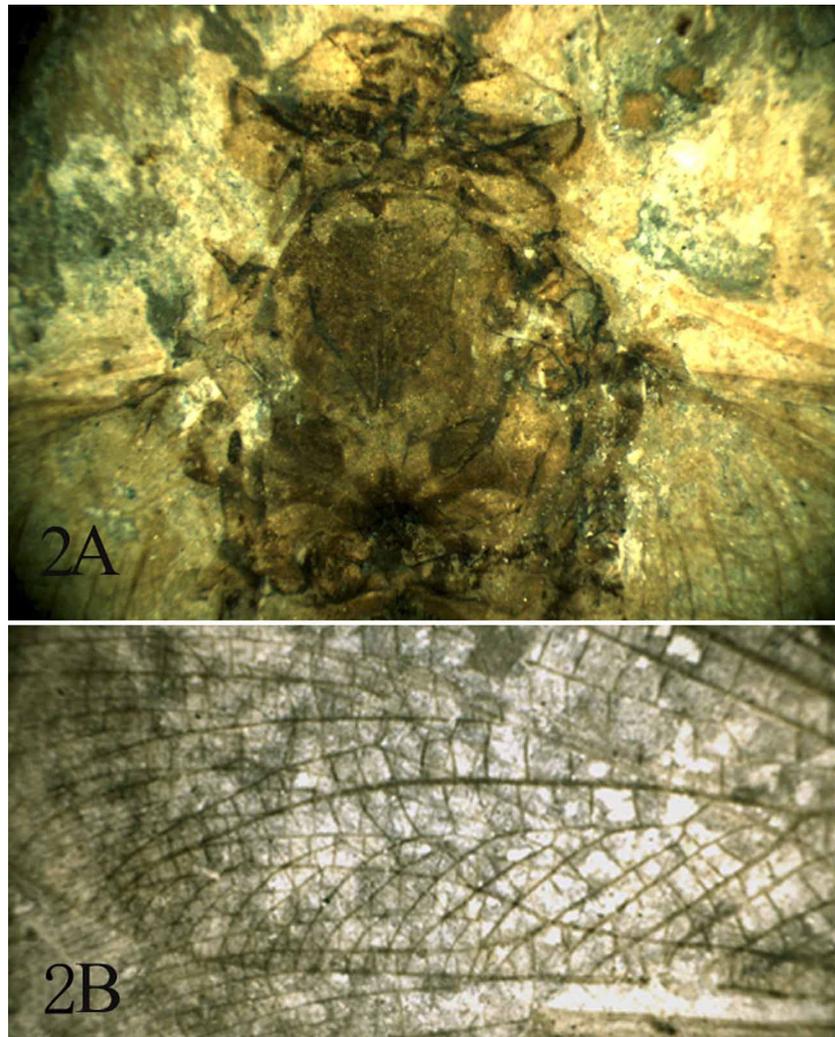
as head and thorax, other parts of the specimen not preserved, the Late Jurassic to the Early Cretaceous, Yixian Formation, Jianshangou, Chaomidian Village, Shangyuan Township, Beipiao City, Liaoning Province, China.

**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.

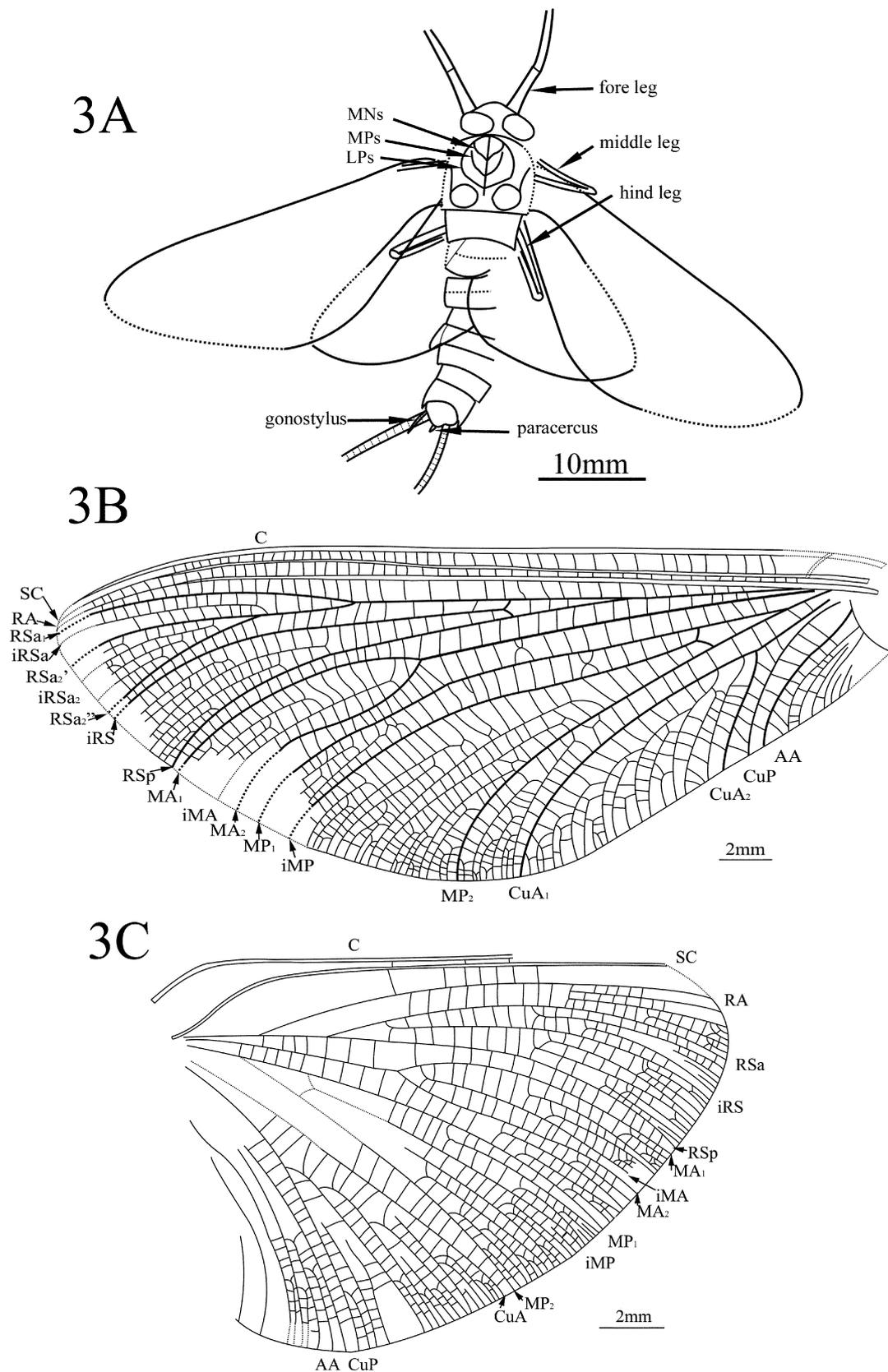
**Diagnosis.** In addition to the diagnosis for the new genus, the species can be diagnosed as follows:  $CuA_1$  of forewing with 4 triads (loop-shaped veinlets) leading to wing margin.

**Description.** Male imago (Fig. 5–7.).  $CuA_1$  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*.

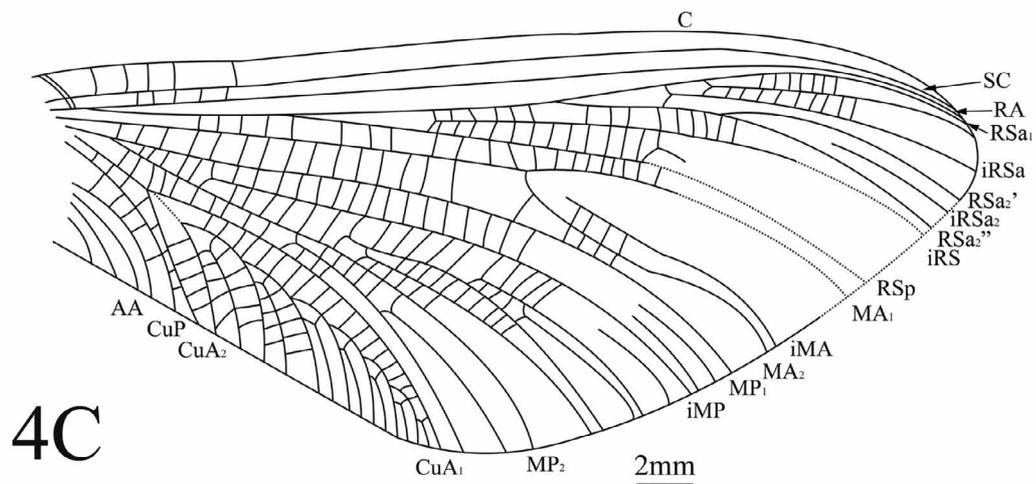
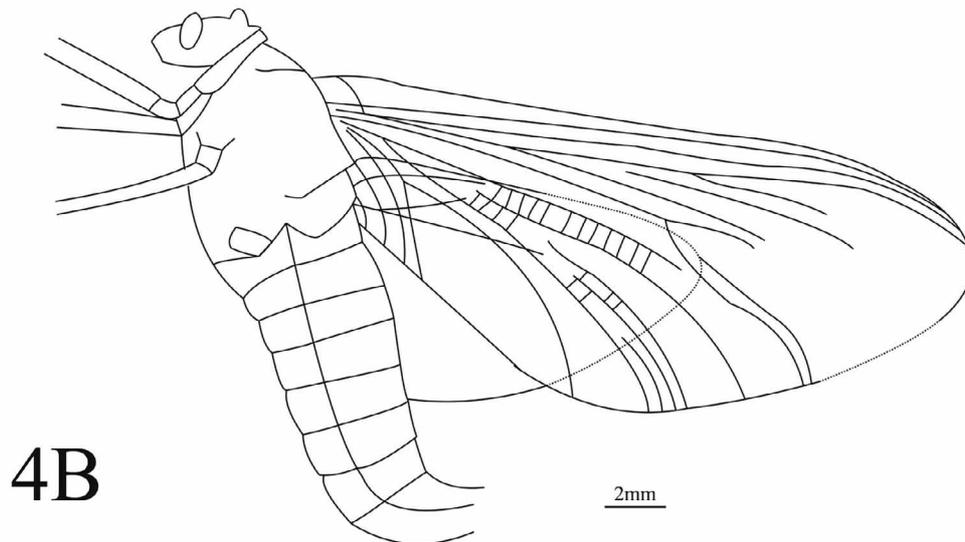
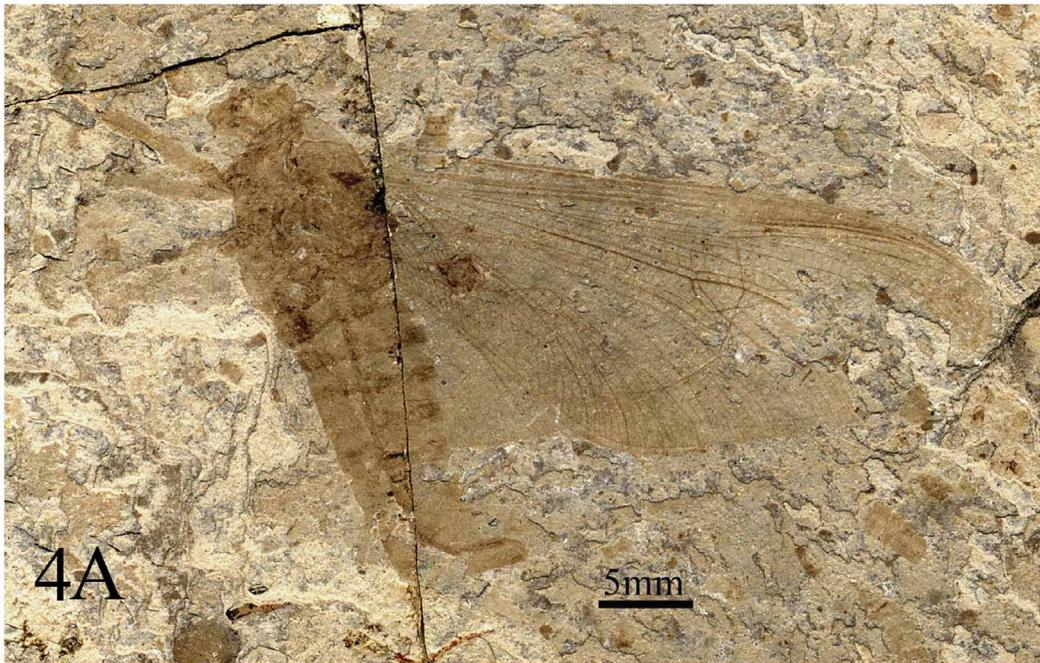
Female imago, male and female subimagoes, and nymph are unknown.



**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.

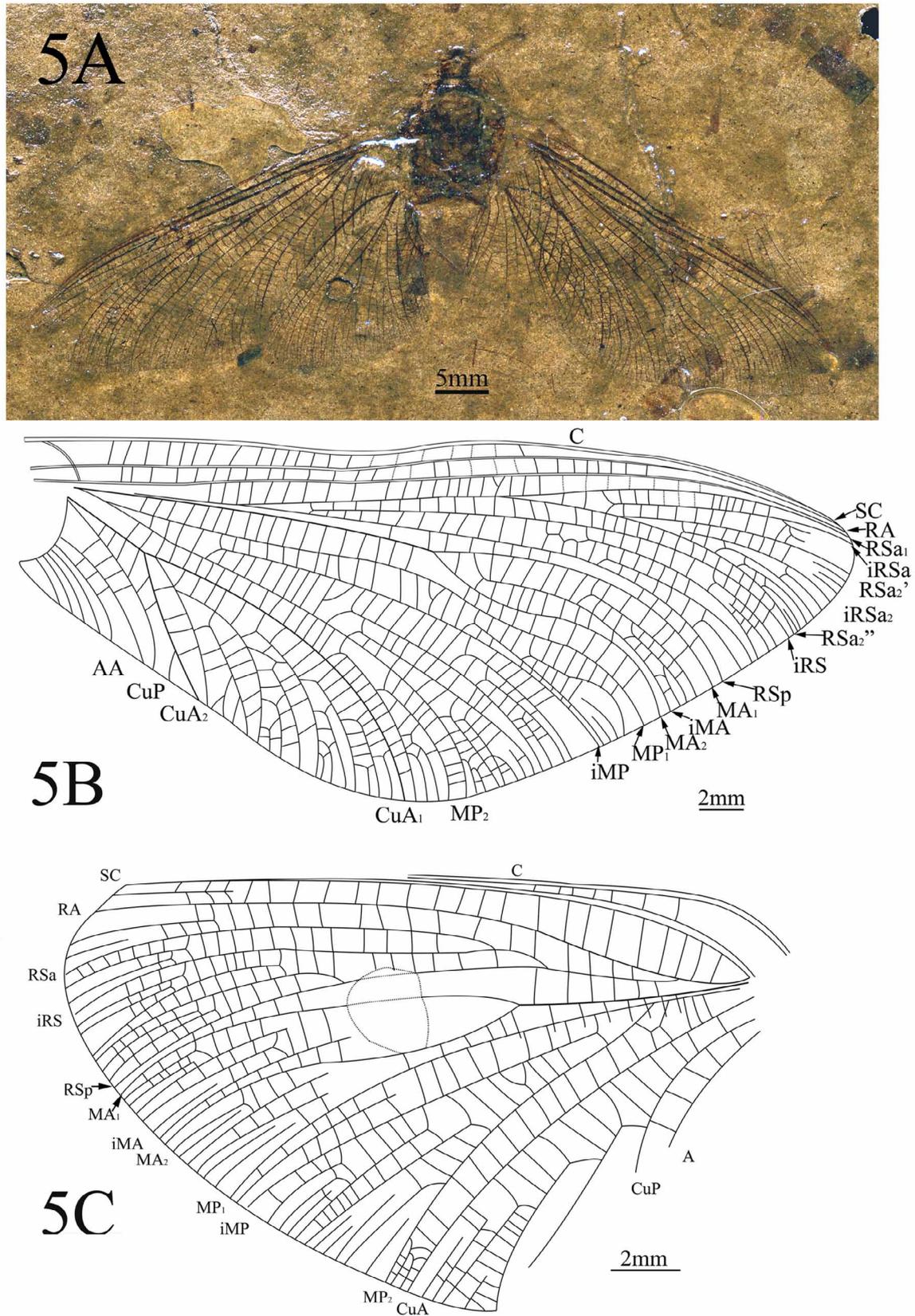


**FIGURE 3.** *Epicharmeropsis hexavenulosus* sp. nov., male imago, holotype: A, body with wings, CNU-E-YX-200701-1; B, forewing, CNU-E-YX-200701-2.; C, hind wing, CNU-E-YX-200701-2. MNs – mesonotal suture, MPs - medio-parapsidal suture, LPs – lateroparapsidal suture.



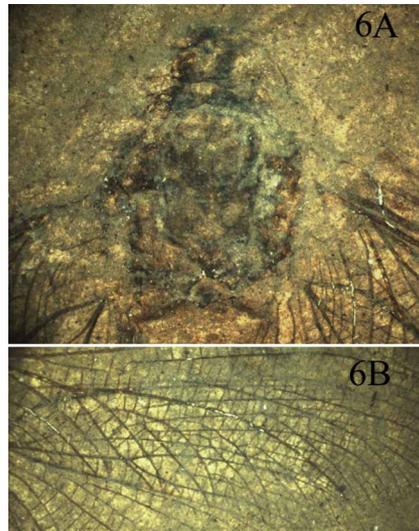
**FIGURE 4.** *Epicharmeropsis hexavenulosus* **sp. nov.**, female imago, paratype CNU-E-YX-2007004: A, photograph of paratype; B, body with wings on lateral view; C, forewing.

**Comparison.** *E. quadrivenulosus* **sp. nov.** can be distinguished from *E. hexavenulosus* **sp. nov.** by 4 triads (loop-shaped veinlets).

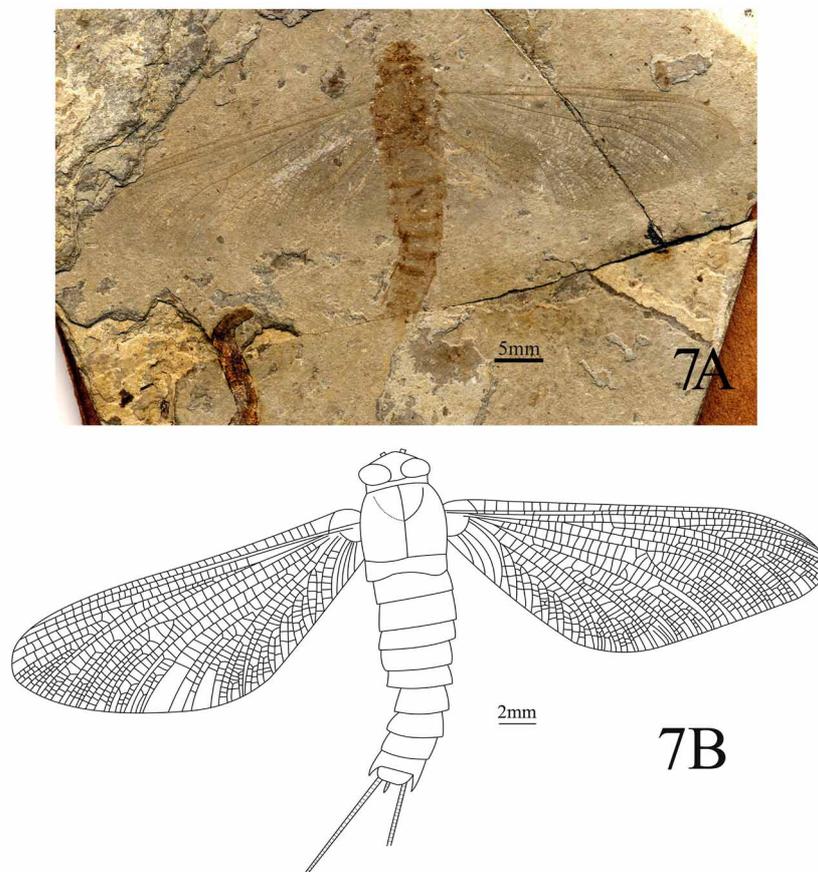


**FIGURE 5.** *Epicharmeropsis quadrivenulosus* **sp. nov.**, male imago, holotype CNU-E-YX-2007002: A, photograph of part; B, forewing; C, left hind wing.

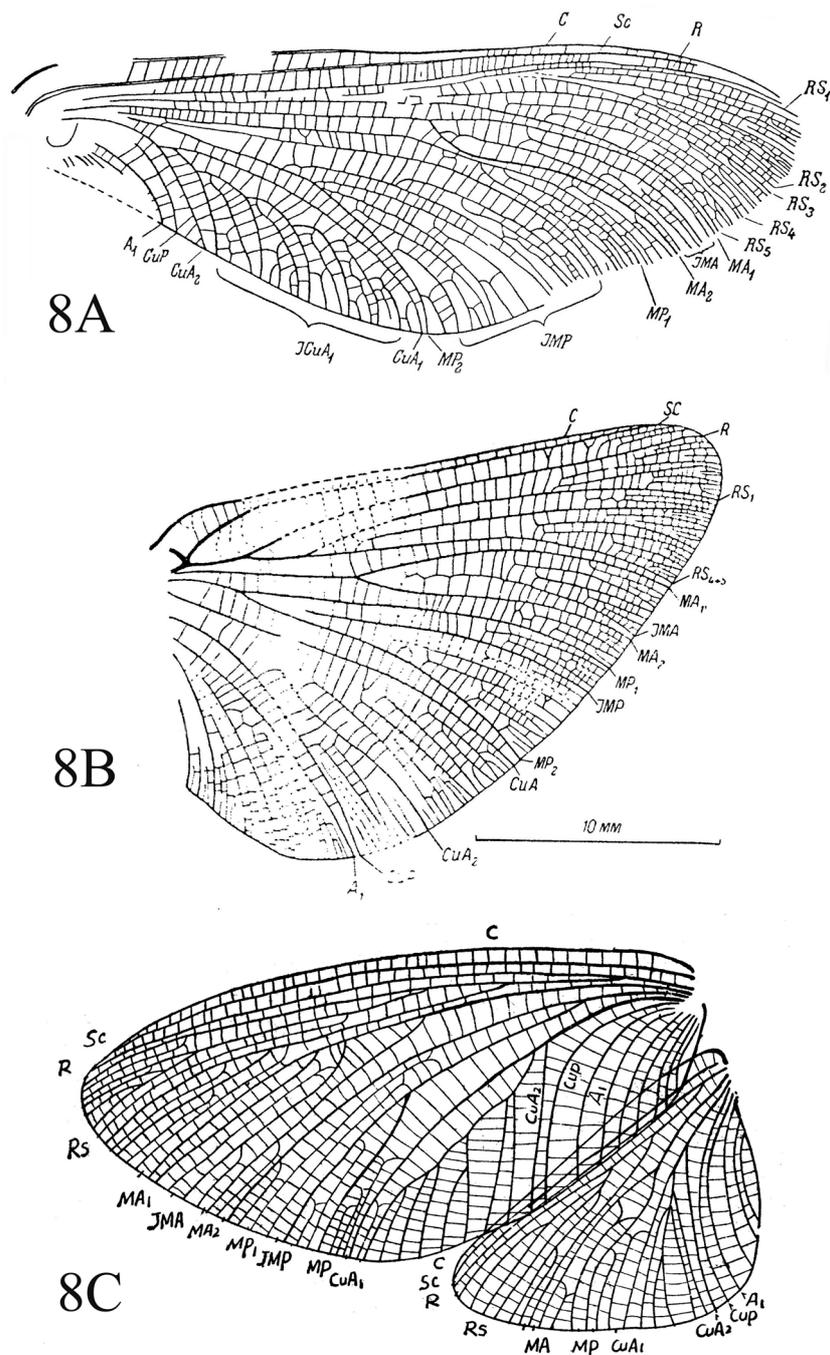
**Measurements** (mm). Holotype: forewing length 38.5, its width 15.5; hindwing length 21.0, its width 13.0; pronotum length 1.0; mesonotum 10.0. Paratype: male imago No.CNU-E-YX-2007014, body length 30.0 (excluding caudalii), forewing length 32.0, its width 13.0; male imago No.CNU-E-YX-2007011-1, forewing 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 *Ephemeroptera trisetalis* Eichwald (after Tshernova and Sinitshenkova, 1974); B, hindwing of *Ephemeroptera trisetalis* Eichwald (after Tshernova, 1961); C, fore- and hind wings of *Ephemeroptera 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 taphonomically 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 intercalary veins existing between  $MP_1$  and  $CuA_1$  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 imago 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.

## Acknowledgements

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