

Description of *Caenoephemera shangyuanensis*, gen.nov., sp.nov. (Ephemeroptera), from the Yixian Formation

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Abstract—A fossil mayfly nymph *Caenoephemera shangyuanensis*, gen.nov., sp.nov., discovered in the lower part of the Upper Jurassic – Lower Cretaceous Yixian Formation of Jianshangou, Beipiao district, West Liaoning, China, is described. It has several archaic features typical of Paleozoic mayfly nymphs, such as 5 tarsal segments and hind wing pads not covered by fore wing pads, but also exhibits specialized modern features, such as a short metathorax, abdominal tracheal gills, and cerci. It appears to be intermediate in structure between Paleozoic and extant mayfly nymphs.

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Résumé—On trouvera ici la description de *Caenoephemera shangyuanensis*, gen.nov., sp.nov., à partir d'une larve d'éphémère fossile découverte à la base de la formation Yixian (Jurassique supérieur – Crétacé inférieur, Jianshangou, district de Beipiao, Ouest Liaoning, Chine). Ce fossile présente non seulement plusieurs caractères archaïques typiques des éphémères paléozoïques comme des tarse à 5 articles et des fourreaux d'ailes postérieures non couverts par ceux des ailes antérieures, mais également des structures nettement "modernes" comme un métathorax court, des branches abdominales et des cerques. Ce fossile semble être "intermédiaire" entre les éphémères paléozoïques et modernes.

Introduction

The widely spread Jehol biota is one of the most important fossil faunas in northern China and dates from the latest Jurassic – earliest Cretaceous periods. It contains abundant animal and plant remains, including plant macrofossils, alynomorphs, charophytes, dinoflagellates, conchostrans, ostracods, shrimps, insects, bivalves, gastropods, fishes, turtles, lizards, pterosaurs, crocodiles, dinosaurs, birds, and mammals (Chen *et al.* 1998).

The insect fauna include *Ephemeropsis trisetalis* Eichwald (Ephemeroptera: Hexagenitidae) (Lin and Su 1994; Ren 1994) and *Caenoephemera* (gen.nov.); *Pseudosamarura largina* Lin, *Yxiangomphus labius* Lin, and *Chrysogomphus beipiaoensis* Ren (Odonata: Gomphidae and Liassogomphidae) (Lin and Su 1994; Ren 1994); *Baissoptera liaoningensis* Ren, *Liaoaphidia fornicata* Ren, *Alloraphidia longistigmata* Ren, *A. Bliquivenatica* Ren, and *Archeraphidia shangyuanensis* Ren (Raphidioptera: Baissopteridae) (Ren *et al.* 1995); *Karatavoblatta formosa* Ren (Blattaria: Mesoblattinidae) (Ren 1994) and *Mesolygaeus laiyangensis* Ping

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(Hemiptera: Enicocoridae) (Lin and Su 1994; Ren 1994); and *Coptoclava longipoda* Ping (Coleoptera: Coptoclavidae), *Sinocupes validus* Lin, and *Tetraphelus laetus* Ren (Coleoptera: Cupidae) (Lin and Su 1994; Ren 1994). The fauna contain representatives of archaic types and of many advanced forms.

The nymph herein described was collected from the same bed as *Sinosauropteryx prima* Ji and Ji, 1996 in the Yixian Formation of Jianshangou, Beipiao district, West Liaoning (120°9'N, 41°9'E). This formation consists of andesites, andesitebreccia, agglomerates, and basalts but has 4 fossil-bearing sedimentary intercalations rich in tuffaceous materials. The Jianshangou intercalated bed comprises the basal part of this volcanic sedimentary formation and consists of greyish-white, greyish-yellow, and greyish-black sandstones, siltstones, mudstones, and shales. Its geological age is assigned to the late Jurassic – Early Cretaceous, although we are inclined to date it as the Early Cretaceous (Neocomian). Terminology follows that of Carpenter (1992), Kukalova-Peck (1985), and Riek (1979).

Systematics and descriptions

Family uncertain.

***Caenoephemera* gen.nov.**

Type species: *Caenoephemera shangyuanensis* sp.nov.

Etymology

The generic name comes from the Greek "Caen"(rare) and "ephemera" (short-lived).

Diagnosis

Head rounded, triangular; mandibles well developed, with 2 apical teeth; pterothorax large, with 2 pairs of wing pads curved posteriorly; the hind pads not covered by the anterior pads and reduced in size, both articulated beside each other to the pterothorax; legs strong, each with 5 tarsal segments and 1 apical pretarsal claw; abdomen with 7 pairs of gills, the first 6 pairs narrow and the 7th pair greatly enlarged, broad, and elliptical-elongate; 3 caudal filaments shorter than body, the median filament bearing setae on both sides and the cerci with setae only on their inner surfaces.

Species includes only the Type specimen.

Geographic and geologic distribution

Liaoning, China; Late Jurassic – Early Cretaceous.

***Caenoephemera shangyuanensis* sp.nov.**

(Figs. 1–2)

Material examined

Holotype: Collection of the Nanjing Institute of Geology and Palaeontology, Academia Sinica, Field No. Ncp 66. A single complete nymphal specimen with head, pterothorax with 2 pairs of wing pads, 3 pairs of legs, an abdomen with a median filament, and 2 cerci. The nymph was preserved in shales from Changbodianzi village.

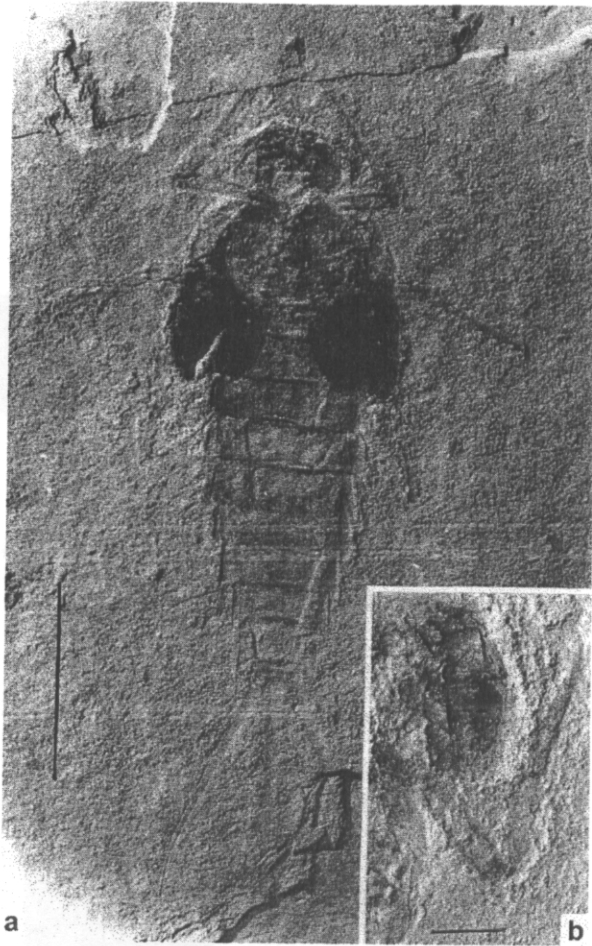


FIGURE 1. (a) *Caenoephemera shangyuanensis* nymph, Ncp 66 (holotype, dorsal view). The specimen is housed in the Nanjing Institute of Geology and Palaeontology, Academia Sinica. Scale bar = 1 cm. (b) Enlargement of left foreleg of the holotype, showing the 5 tarsal segments. Scale bar = 0.2 cm.

Shangyuan, Beipiao County, Liaoning Province, China, in the Upper Jurassic – Lower Cretaceous Yixian Formation.

Etymology

Species epithet from the Chinese “Shangyuan,” which is a local name for West Liaoning Province, China.

Description

Nymph. Dimensions: body length 28.5 mm (excluding caudal filaments), width 10 mm (at pterothorax); head length about 3 mm, width 4.7 mm; prothorax length about 1.5 mm, width 7 mm; mesothorax length 4 mm, width 10 mm; metathorax length 1.5 mm, width 8 mm; abdominal length about 18.5 mm (excluding caudal filaments); caudal filament length about 12 mm, length of gill pairs: 1 = 2 mm, 2–6 = 2.9–3 mm, and 7 = 3.9 mm. **Head:** rounded and wider than long, eyes well developed and set

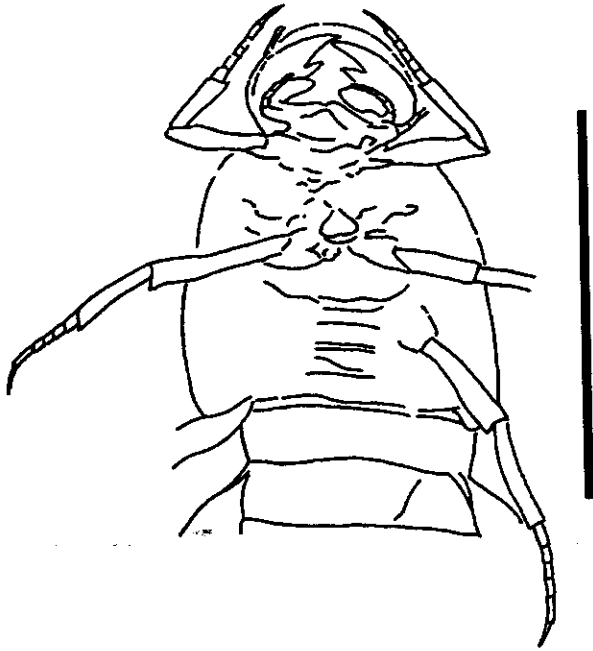


FIGURE 2. Anterior part of the holotype of *Caenophemera shangyuanensis*. Scale bar 1 = cm.

dorsolaterally on the posterior margin of either side of the head, antennae short and slender, similar to those of hexagenitid nymphs. Mouthparts prognathous, mandibles powerful and well sclerotized and each with 2 teeth. Maxillae large, palpi apparently 5-segmented; labium with well-developed, apparently 5-segmented, palpi. **Thorax:** prothorax short, about half the length of the head and 1.6 times wider; pterothorax carrying 2 pairs of wing pads, both pairs beside each other and independently attached to the articular area and strongly curved backwards, the hind wing pads smaller than the fore wing pads. Fore legs distant from middle legs, their coxae large; trochanters more narrow but longer than the coxae; femora stout, about 3 times the length of the trochanters; tibiae nearly as long as but more narrow than the femora; each of 5 tarsomeres subequal in length and gradually narrowing from 1st to 5th, 1 pretarsal claw curved; middle legs similar to fore legs, mid-coxae inserted adjacent to metathoracic coxae. **Abdomen:** about 1.85 times as long as head and thorax together, 9 visible segments, their posterolateral angles not spine-like; the 1st segment the shortest; the 2nd–5th segments subequal and with the width of each exceeding its length by 3.5 times, slowly diminishing in width from the 6th to the 9th; 7 gill pairs, each pair inserted posterolaterally on each side of each of segments 1–7, each gill with a sclerotized rib running along its anterior and inner margins; anterior 6 gill pairs narrow lamelliform, gill pair 7 broad, elliptical–elongate, and strikingly larger than gill pairs 1–6; median filament and cerci half the length of the body; the median filament bearing setae on both sides; the cerci on their inner sides only, median filament shorter than cerci.

Horizon and locality

Lower part of the Upper Jurassic – Lower Cretaceous Yixian Formation in Jianshangou, Beipiao district, Liaoning, China.

TABLE 1. Comparison of nymphal characters in the genera *Caenophemera*, *Ephemeroptis*, and *Protigoneuria*.

Character	Genus		
	<i>Caenophemera</i>	<i>Ephemeroptis</i>	<i>Protigoneuria</i>
Head	Head narrower than prothorax (about 1.6 times wider than head)	Head nearly as wide as prothorax	Head narrower than prothorax (about 1.3 times wider than head)
Mandible	With 2 teeth, unforked at the apex	With 2 teeth, both forked at the apex	Unknown
Palp of maxilla	Palp multisegmented (5 palp segments can be seen)	With 3 palp segments (Meshkova 1961)	Unknown
Wing pad	Hind wing pad includes articulation not covered by anterior, anterior articulation far from hind articulation; the vena CuA straight, no forks or loop-like veinlets	Hind wing pad entirely covered by anterior; CuA curved with forks and a series of weak loop-like veinlets (Lin and Su 1994)	Hind wing pad entirely covered by anterior
Leg	3 pairs of legs, strongly developed, long, and nearly equal, with 5 tarsal segments	3 pairs of legs, narrow and short, with 1 tarsal segment	3 pairs of legs, narrow and short, with 1 tarsal segment
Abdominal gill	7 pairs of gills, with sclerotized rib running along anterior and inner margins, gill 7 enlarged	7 pairs of gills, with sclerotized ribs running along anterior and inner margins, gill 7 not enlarged	7 pairs of gills, with sclerotized rib running along anterior, gill 7 enlarged and more strongly developed than the others

Discussion

The nymph described here was originally identified as *Ephemeropsis trisetalis* in the field, but is here shown to differ in a series of significant characters from nymphs of the genus *Ephemeropsis*. A comparison indicates that the nymph of the new genus differs from nymphs of *Ephemeropsis* and other hexagenitids in its hind wing pads, tarsal segments, and nymphal wing pad venation (veins straight, CuA without branches and by a series of loop-shaped veinlets) (Table 1). Also, articulations of the anterior wing pads are remote from and more laterally placed than those of the hind wing pads, exposing the hind wing pads. In modern mayfly nymphs, the hind wing pads are hidden under the anterior wing pads. If these nymphs are flattened dorsoventrally, both pairs of pads are distorted and displaced, with the hind wing pads exposed and extending anteriorly to the bases of the anterior pads; however, in the fossil nymph described herein, we believe the pads are not displaced, because numerous fossil nymphs of *E. trisetalis* were discovered in the same bed as the fossil nymph described herein and have undergone the same geological trauma (sedimentation, diagenesis, thermal alteration, preservation, duration, etc.). This is why all mayfly nymphs in the bed are preserved in the same state and with similar outlines. Most palaeoentomologists to whom the specimens have been shown believe the nymphs to be in their original state. Therefore, we interpret the hind wing pads of all nymphs in the bed to be in their natural position, including those of *E. trisetalis* and the new genus. That the hind wing pads of the specimen described are not covered by the anterior pads is natural. When a mayfly nymph is flattened, the hind wing pads may extend anteriorly; this distortion is accompanied by extension of the conjunctival membrane between meso- and meta-thorax and this is not observed in the fossil described herein. One can see the conjunctival membrane of the meso- and meta-thorax but it is not so extended. Thus, we believe the positions of both pairs of wing pads to be as in their natural state.

The earliest record of the order Ephemeroptera is of a single adult from the Upper Carboniferous, and fossil representatives of 5 extinct families are known from elsewhere in the Palaeozoic. These fossils share the following characteristics: adults: fore and hind wings similar in form and venation, mandibles strongly sclerotized and dentate, mouthparts functional; nymphs: well-developed mandibles, fore and hind wing pads projecting obliquely, independently of each other, and inserted into the thorax at articulation points equivalent to those of the adult.

In nymphs of all extant and Tertiary and most Mesozoic species, the hind wing pads are reduced and covered by the fore wing pads and the tarsi of all legs are 1-segmented. How the Palaeozoic type evolved into the modern type is not clear.

The following features of the nymph of the genus *Caenoephemera* are pertinent to this discussion.

In the genus *Caenoephemera*, the mandibles of the nymph are well developed, sclerotized, and have 2 teeth; this state is similar to that in nymphs of the genus *Ephemeropsis* from the Late Jurassic – Early Cretaceous. The mandibles of nymphs of the genus *Ephemeropsis* bear 2 apical teeth that fork apically (Demoulin 1956; Meshkova 1961). In the nymph of the genus *Caenoephemera*, such forks are missing from the teeth. In the nymph of the new genus, maxillary palpi are 5-segmented but, in nymphs of the genus *Ephemeropsis*, they are 3-segmented.

In all recent and Tertiary mayfly nymphs, as well as in those from the Mesozoic, the hind wing pads are covered by the fore pair and, in representatives of some genera, are completely absent. Their legs have only 1 tarsal segment. Known Palaeozoic nymphs have well-developed mandibles, legs subequal in length and each with 5 tarsal segments, and 2 pairs of wing pads similar in size and venation. For example, nymphs of *Protereisma americanum* Demoulin, the 2 pairs of wing pads are

independent of each other and are articulated one in front of the other. Nymphs of *Bojophlebia prokopi* Kukulova-Peck have 3 pairs of wing pads equally shaped and curved strongly backwards, with the prothoracic wing pads slightly smaller than those of the pterothorax (Kukulova-Peck 1985). In addition, the largest thoracic segment in these nymphs is the metathorax, which carries the largest wing pads; the mesothorax is slightly smaller, and the prothorax is smallest. In modern mayfly nymphs, the largest segment is the mesothorax, the metathorax is reduced, and the prothoracic wing pads have been lost. The most remarkable features of the nymph of the genus *Caenoephemera* are the pterothoracic wing pads, with the metathoracic wing pads not covered by the mesothoracic wing pads, just as in bojophlebid and syntonopterid nymphs, but with the metathoracic wing pads reduced in size, inserted medial to the mesothoracic pads, and curved backwards. The mesothoracic segment is the largest, unlike the case in nymphs of the genus *Ephemeroopsis* and others.

The above 2 features might assist us in tracing the evolutionary history of these mayflies: from the Palaeozoic type, the metathoracic wing pads of descendant nymphs might have reduced in size and moved forward to the inner margins of the mesothoracic wing pads, in which position, at first, they would still have been entirely exposed and curved backwards as in the genus *Caenoephemera*. In the genus *Caenoephemera*, the location of the pads is intermediate between that seen in the Palaeozoic and that in modern mayfly nymphs.

Nymphs of most known Mesozoic, Tertiary, and extant species have simple 1-segmented tarsi. However, in the genus *Mirawara* (Ephemeroptera: Baetidae, Siphonurinae), the nymphs are unusual in that mature nymphs have 4-segmented tarsi and younger nymphs 3-segmented tarsi (Riek 1979). The nymphs and adults of Palaeozoic mayflies have 5 tarsal segments. Nymphs of the genus *Caenoephemera* have 5 tarsal segments, as do those of the Palaeozoic genera *Bojophlebia* Kukulova-Peck (Kukulova-Peck 1985) and *Lithoneura* Carpenter (Carpenter 1992).

The nymphs of most extant mayflies molt into a subimago stage before molting again to the adult, a molt accompanied by loss of the functional nymphal mouthparts and abdominal gills; the subimago has 4-5 tarsal segments. The presence of strongly developed mouthparts and well-developed abdominal gills indicates that the nymph we describe is not a subimago.

The metathorax of the nymph of *Caenoephemera* is distinctly shorter than the mesothorax. Palaeozoic nymphs with 3 thoracic segments subequal in size are known, whereas in modern nymphs, the pro- and meta-thorax are much shorter than the mesothorax. The nymph described herein is modern in this respect.

Based on the discussion presented above, we conclude that this nymph differs from those of all known genera of Ephemeroptera. A new family should probably be erected for it, but we prefer to wait until more specimens (we hope including adults) are discovered.

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