

A Revision of the Jurassic Stonefly Genera *Dobbertiniopteryx* Anson and *Karanemoura* Sinitshenkova (Insecta: Plecoptera), with the Description of New Species from the Daohugou Locality, China

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Abstract—The stonefly genera *Dobbertiniopteryx* Anson and *Karanemoura* Sinitshenkova are revised. Based on new material from the Middle Jurassic of Daohugou, China, two new species, *D. juracapnia* sp. nov. and *K. manca* sp. nov., are described and *Karanemoura abrupta* Sinitshenkova, 1987 is redescribed. *K. desiliens* Sinitshenkova, 1987 is excluded from *Karanemoura*; its position within the family Perlariopseidae remains uncertain. The placement of *Dobbertiniopteryx* in the modern family Capniidae is confirmed. The perfect state of preservation of the nearly complete adult stonefly remains from China made it possible to improve and extend the diagnoses of the Perlariopseidae and *Dobbertiniopteryx*. The geological background of the Daohugou deposits is briefly discussed.

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INTRODUCTION

The fossil stoneflies described below were collected in the Jiulongshan Formation of the Daohugou locality in northeastern China, at the junction between Inner Mongolia and the Liaoning and Hebei provinces. In the Late Mesozoic, this was a volcanic area with mountain streams (Ren and Lu, 1996). The age of the Daohugou beds remains controversial, with estimates by different authors, varying from the Middle Jurassic to Early Cretaceous. The absolute age of the volcanic rocks overlaying the Daohugou fossil-bearing strata (41°18.979' N, 119°14.318' E) has been recently estimated with the Ar–Ar and SHRIMP U–Pb methods as approximately 164–165 Ma. Thus, the age of the Daohugou beds containing fossil insects does not exceed 165 Ma (Chen et al., 2004). Analyses of the strata of the Daohugou section (41°23.10' N, 119°09.6' E) indicated an approximate age of 162 ± 2 Ma (Liu et al., 2006). This estimate is corroborated by the composition of conchostracans and insects, strongly suggesting a Middle Jurassic age (Bathonian) (Gao and Ren, 2006).

The lacustrine deposits of the Jiulongshan Formation in the Daohugou locality contain fossils of various insect groups: mayflies (Huang et al., 2007), dragonflies (Zhang et al., 2006a), stoneflies (Liu Y.-s. et al., 2006, 2007), cockroaches (Wang et al., 2007a), orthopterans (Li et al., 2007), true bugs (Yao et al., 2006),

neuropterans (Ren and Yin, 2003), scorpion flies (Sun et al., 2007), homopterans (Wang et al., 2007b), dipterans (Zhang et al., 2006b), beetles (Tan et al., 2006), and hymenopterans (Rasnitsyn and Zhang, 2004). In addition, descriptions of fossil Phasmatodea, Dermaptera, Grylloblattodea, Trichoptera, and Raphidioptera, found among the large collection of insect remains discovered at this locality, have not yet been published.

The fossil stoneflies described below were collected from the Middle Jurassic deposits of the Jiulongshan Formation in the Daohugou locality, Inner Mongolia, northeastern China.

The abundant remains of stoneflies discovered in Daohugou are dominated by fossil families, with only a few belonging to the Recent family Taeniopterygidae (Liu et al., 2007). The genera *Dobbertiniopteryx* Anson, 1993 and *Karanemoura* Sinitshenkova, 1987 were previously known only from isolated wings, but, recently, nearly complete adult specimens from these genera were discovered in Daohugou. Their excellent state of preservation allowed examination of additional important taxonomic characters of these genera. Based on these data and on the reexamination of the holotypes, we give improved and extended diagnoses for the genera *Dobbertiniopteryx* and *Karanemoura* and the family Perlariopseidae.

The taxonomy and systematics of fossil stoneflies are often complicated since most of these fossils are isolated wings and, therefore, their species and, sometimes, even generic affinities are hard to determine (Sinitshenkova, 1987). Ansoerge (1993) created the monotypic genus *Dobbertiniopteryx* based on a single isolated forewing, collected from the Upper Jurassic of Dobbertin (Mecklenburg, Germany), and placed it in the Recent family Capniidae. That placement has since been questioned by Sinitshenkova (1997), who suggested that *Dobbertiniopteryx* could be placed in the extinct family Baleyopterygidae, since, at that time, no Recent stonefly family had been reported from any unquestionably Jurassic deposits. The nearly complete specimen of *D. juracapnia* sp. nov. from Daohugou, described below, is excellently preserved. The characters of its body and cerci do not contradict the placement of *Dobbertiniopteryx* in the Recent Capniidae. The relatively long, multisegmented cerci are indeed typical of the Capniidae, while in representatives of the Baleyopterygidae the cerci are very short and three-segmented. Unfortunately, the structure of the tarsi, one of the main characters in the diagnostics of stonefly families, still remains unknown for *Dobbertiniopteryx*.

The genus *Karanemoura* comprises eight species from the Jurassic to Early Cretaceous of southern Kazakhstan, Central Asia, Yakutia, Transbaikalia, and Mongolia (Sinitshenkova, 1987, 1992, 1995, 1998). Several specimens of stoneflies from this genus were found in Daohugou. These include specimens belonging to *K. abrupta* Sinitshenkova, 1987 (as indicated by their wing venation) and a new species, *K. manca* sp. nov., which is close to *K. appropinquata* Sinitshenkova, 1987 from the Upper Jurassic of the Ulan-Ereg Formation of Khoutiin-Khotgor in Mongolia. *K. desiliens* Sinitshenkova, 1987, also described from the Khoutiin-Khotgor locality, must be excluded from *Karanemoura*; its taxonomic position within the family Perlarioseidae remains uncertain.

The genitalia of the almost complete remains of *Karanemoura abrupta* and *K. manca* sp. nov. resemble those in the Recent Leuctridae: the tenth male tergite with sclerotized processes; male paraprocts with a long, pointed specillum; the eighth female sternite with a subgenital plate; and the cerci short, single-segmented. The structure and venation of the wings in *Karanemoura* is, in general terms, also similar to those of the Recent Leuctridae. Yet, many characters of *Karanemoura* are more primitive than in the Recent Leuctridae. Fossil *Karanemoura* differ sharply from the Recent Leuctridae in the second tarsomere being long (in Leuctridae very short, not longer than wide), the male abdominal segments only weakly modified, and the female abdominal segments not membranous. The characters shared by the genus with the Recent Leuctridae may indicate its close relationship with the ancestors of this family.

The first and so far the only known case of the same fossil stonefly species (here *K. abrupta*) being found at localities so distant from one another as southern Kazakhstan and northeastern China is remarkable. The conspecificity of the fossils was determined based on the forewing venation. This case justifies the use of venation characters in descriptions of the fossil stonefly taxa, because apparently the intraspecific variation of venation does not affect its functionally important elements. At the same time, Recent species may have similar venation and yet differ in the fine structure of their genitalia, which are almost impossible to study in the fossil material. Therefore, it should be kept in mind that the fossil stonefly species described based on the wing venation alone differ somewhat in their taxonomic scope from the species described based on Recent material.

The material was examined under a Leica MZ12.5 microscope. The drawings were prepared using a camera lucida and the CorelDraw 12 graphics editor software.

All the types and original specimens are deposited in the Capital Normal University in Beijing, China (CNU).

SYSTEMATIC PALEONTOLOGY

Family Capniidae Klapalek, 1905

Genus *Dobbertiniopteryx* Ansoerge, 1993

Type species. *Dobbertiniopteryx capniomimus* Ansoerge, 1993; Late Jurassic; Dobbertin, Germany.

Diagnosis. Adults. Small stoneflies. Prothorax transversely rectangular, wider than long, slightly narrower than mesothorax. Wings considerably longer than abdomen. Forewing with c-r absent; Sc almost as long as half of wing length; Rs branching near apex of Sc, its branches long and straight, except at their bases; M divided noticeably basad of Rs fork. CuA and CuP simple, CuA entering wing margin slightly basad of its middle. M and CuA connected by three crossveins, CuA and CuP connected by single crossvein. Three anal veins present; A2 branching. Hindwings capable of folding; M divided distinctly posterad of Rs fork. Abdomen long, with middle segments wider than segments at base or apex; cerci relatively long, multisegmented.

Species composition. In addition to the type species, *D. juracapnia* sp. nov.

Comparison. The new genus differs from other genera in the absence of c-r, in CuA being shorter and entering the wing margin slightly basad of the wing midlength, and in the shorter cerci.

Dobbertiniopteryx juracapnia Liu, Sinitshenkova et Ren, sp. nov.

Plate 11, fig. 1

Etymology. From the Jurassic Period and the stonefly genus *Capnia*.

Holotype. CNU, no. NMDHG183, adult with the venation on the forewings and a fragment of the

hindwing, abdomen, and legs, well preserved; Dao-hugou locality; Middle Jurassic.

Description. An adult (Fig. 1). The prothorax is slightly narrower and almost three times shorter than the mesothorax; the mesothorax and metathorax are equally well developed. The wings extend beyond the apex of the abdomen by a quarter of their length. In the forewings, Sc is slightly longer than half of the wing length, the crossvein c-sc is well developed, relatively long. Rs deviates from R in the basal quarter of the wing and bifurcates slightly basad of the apex of Sc and r-rs; r-rs is nearly vertical, connecting the apex of Sc with the base of the anterior branch of Rs; M branches slightly basad of the Rs fork; rs-m connects the base of the posterior branch of Rs with M at its branching point; Cu is divided near the wing base; CuP is very short, m-cu connects the base of MP with CuA at approximately the midlength of CuA; there are three crossveins between M and CuA and one crossvein between CuA and CuP. In the hindwings, Sc is half as long as the wing; c-sc and r-rs are as in the forewings, Rs is divided slightly basad of, or even with r-rs; M divides noticeably distad of the Rs fork. The abdomen is fusiform, almost twice as long as the thorax, with the basal and distal segments both narrow, with segments 4–6 almost three times as wide as long, and the distal segments with fine pubescence. The cerci are thin, relatively long, and multisegmented.

Measurements, mm: body length, ca. 6; forewing length, 6.8; maximum forewing width, 2.0.

Comparison. *D. juracapnia* sp. nov. differs from the type species in having c-cs longer, M branching more distally, and rs-m entering M at its branching point (in *D. capniomimus* (Fig. 2), rs-m connects the base of the posterior branch of Rs with the base of MA).

Material. Holotype.

Family Perlariopseidae Sinitshenkova, 1985

Diagnosis. Adults. Large or medium-sized stoneflies, with normally developed or partly reduced wings. When normally developed, wings at rest extending considerably beyond abdomen apex. Second tarsomere shortened, approximately half as long as first, twice as long as wide. Both forewings and hindwings with complete set of longitudinal veins and small number of crossveins. Costal field without supernumerary crossveins. Anal region with two anal veins; A2 bifurcating. Cerci short, multisegmented or single-segmented.

Remarks. The fact that some characters of the Perlariopseidae are subject to considerable variation (for example, an oblique crossvein in the pterostigmal area of the wing can be present or absent, and the cerci can be single-segmented or multisegmented) is not surprising because this family is ancestral to various families of Nemourina. Different genera of Perlariopseidae can be close to ancestral forms of different Recent

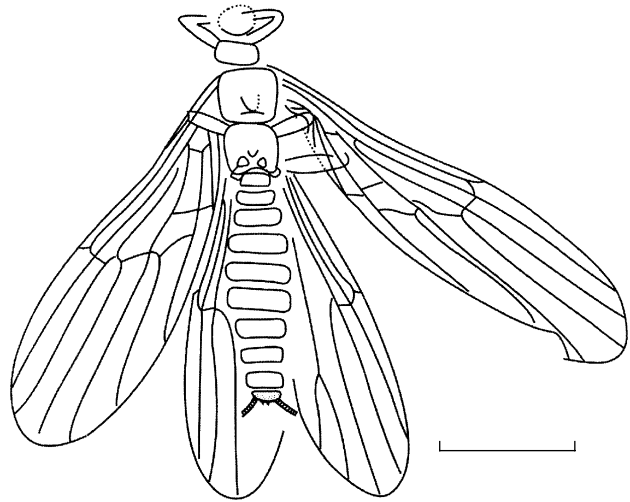


Fig. 1. *Dobbertiniopteryx juracapnia* sp. nov., holotype CNU, no. NMDHG183, general view. Scale bar, 2 mm.

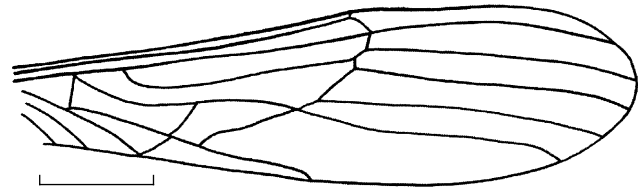


Fig. 2. *Dobbertiniopteryx capniomimus* Ansoerge, 1993, forewing (after Ansoerge, 1993). Scale bar, 2 mm.

families. Therefore, their representatives may have acquired characters typical of those families independently and at different geological times. It is possible that, in the future, the Perlariopseidae will be divided into several families, but it is expedient to consider it as a single taxon until more data become available.

Genus *Karanemoura* Sinitshenkova, 1987

Type species. *Karanemoura abrupta* Sinitshenkova, 1987; Late Jurassic, Karabastau Formation; Karatau, southern Kazakhstan.

Diagnosis. Adults. Medium-sized stoneflies. Head large, antennae long, prothorax narrow. Wings at rest extending considerably beyond apex of abdomen. In forewings, c-r absent; Rs bifurcating, usually forked at level of Sc apex. M branching slightly distad of Rs fork; m-cu always connecting base of MP with CuA. Crossveins between M and CuA and between CuA and CuP numerous. CuP straight, entering wing margin approximately at level of M fork. Hindwings with four longitudinal veins in anal area. Legs long and thin. First tarsomere long, almost twice as long as second; second tarsomere shorter than third. Cerci short, single-segmented.



Composition. The type species, *K. appropinquata* Sinitshenkova, 1987 (Upper Jurassic, Ulan-Ereg Formation; Khoutiin-Khotgor, Mongolia), *K. brevis* Sinitshenkova, 1987 (Lower–Middle Jurassic, Sagul Formation; Sai-Sagul, Kyrgyzstan), *K. curvata* Sinitshenkova, 1998 (Upper Jurassic–Lower Cretaceous, Chernovskaya Sequence; Chernovskie Kopi, central Transbaikalia), *K. distalis* Sinitshenkova, 1987 (Lower Jurassic, Dzhil Formation; Sogyuty, Kyrgyzstan), *K. divaricata* Sinitshenkova, 1987 (Upper Jurassic, Karabastau Formation; Karatau, southern Kazakhstan), *K. manca* sp. nov. (Middle Jurassic, Jiulongshan Formation; Daohugou, China), *K. perpropinqua* Sinitshenkova, 1995 (Middle–Upper Jurassic; Shara-Teeg, Mongolia), *K. probata* Sinitshenkova, 1992 (Upper Jurassic–Lower Cretaceous; Kempendyai, Yakutia (Sakha)).

Comparison. *Karanemoura* is most similar to *Perlariopsis*, from which it differs markedly in the absence of the crossvein c–r in the pterostigmal area of the forewing, and in the cerci being short, single-segmented.

Remarks. Nearly all currently known species of *Karanemoura* have been described based on isolated wings. The only exception is *K. desiliens* Sinitshenkova, 1987, for which a body with multisegmented cerci has been described. However, that species differs markedly from the others in having Rs with three branches. The original description mentioned that this character was uncharacteristic of *Karanemoura* and particularly unexpected given the small size of *K. desiliens*. The author considered the option of creating a separate genus to include *K. desiliens*, but, given the poor state of preservation of the specimen and the lack of additional material at the time, she considered it as premature (Sinitshenkova, 1987, p. 64). The new material from China clearly indicates that *K. desiliens* does not belong to the genus *Karanemoura*. A new genus to include that species will be described elsewhere in the near future.

Karanemoura manca Liu, Sinitshenkova et Ren, sp. nov.

Plate 11, figs. 2 and 3

Etymology. From the Latin *mancus* (incomplete).

Holotype. CNU, no. NMDHG91, well preserved body of an adult female, with the legs, the left forewing (without apex), and a fragment of the hindwing; north-eastern China, Daohugou; Middle Jurassic, Jiulongshan Formation.

Description. An adult female (Fig. 3). The head is large, semicircular, somewhat narrower than the pro-

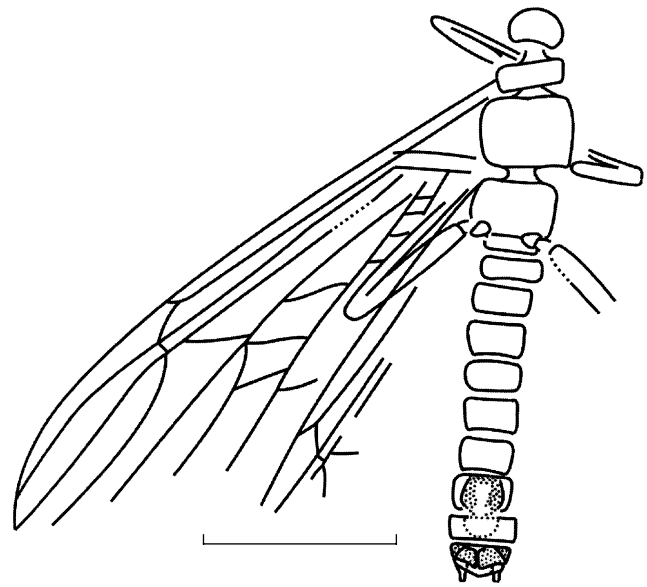


Fig. 3. *Karanemoura manca* sp. nov., holotype CNU, no. NMDHG91, general view. Scale bar, 3 mm.

thorax. The prothorax is transverse, twice as wide as long; the mesothorax and the metathorax are equally well developed. The forewings have the pterostigma not darkened; Sc is approximately two-thirds as long as the wing; c–sc is short, enters C noticeably basad of the apex of Sc; R is slightly convex in the pterostigmal area. Rs bifurcates at the level of the apex of Sc; r–rs is short, connects the apex of Sc with the base of the Rs fork. M bifurcates considerably basad of the Rs fork; rs–m is straight, enters Rs noticeably basad of r–rs and slightly basad of the M fork; m–cu connects the base of MP with CuA. There are no less than three crossveins between M and CuA and no less than five between CuA and CuP. The legs are long and thin, incompletely preserved. The abdomen, with ten visible segments, is almost twice as long as the thorax; the first two segments are short; the middle segments are longer and narrower; the eighth sternite is triangular, with a bilobed subgenital plate. The cerci are short, single-segmented.

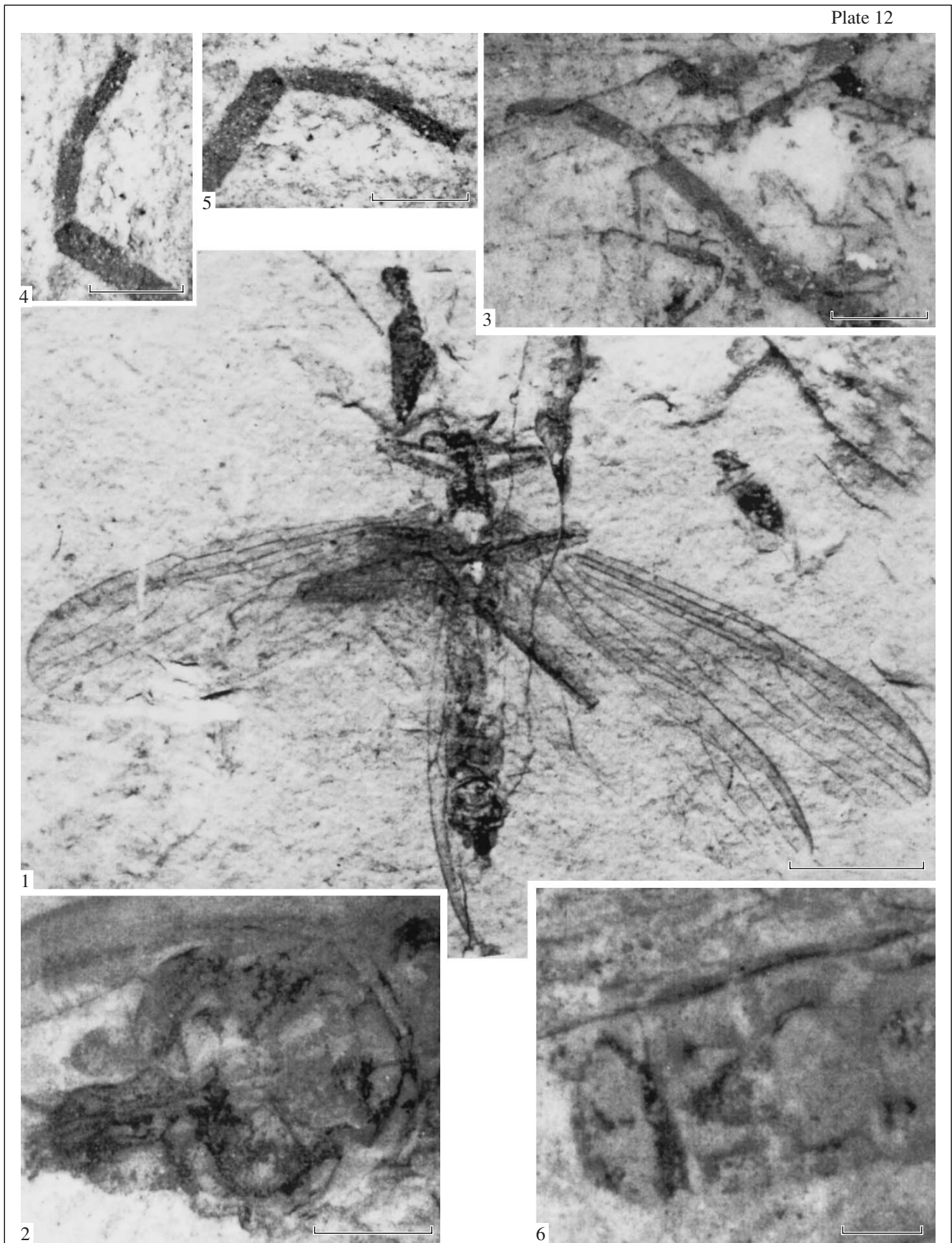
Measurements, mm: body length, 10; forewing length, 10; maximum forewing width, 3–4.

Comparison. In the venation of its forewing, the new species is most similar to *K. appropinquata* Sinitshenkova, 1987, which was described based on a single wing from the Ulan-Ereg Formation in eastern Mongolia (the Khoutiin-Khotgor locality). *K. manca* sp. nov.

Explanation of Plate 11

Fig. 1. *Dobbertiniopteryx juracapnia* sp. nov., holotype CNU, no. NMDHG183. Scale bar, 1 mm.

Figs. 2 and 3. *Karanemoura manca* sp. nov., holotype CNU, no. NMDHG91, female: (2) general view of the adult, scale bar, 3 mm; (3) apex of the abdomen, scale bar, 0.5 mm.



differs from *K. appropinquata* in the c–sc situated more basally, M bifurcating basally, and rs–m entering Rs basally. In addition, in the new species the base of MP is connected with CuA via a single crossvein m–cu, while in *K. appropinquata* there is an additional crossvein between the base of MP and CuA.

Material. Holotype.

Karanemoura abrupta Sinitshenkova, 1987

Plate 12, figs. 1–6

Karanemoura abrupta: Sinitshenkova, 1987, p. 62, text-fig. 62, pl. V, fig. 7.

Holotype. PIN, no. 2384/2367, positive and negative impressions of a forewing; southern Kazakhstan, Karatau; Upper Jurassic, Karabastau Formation.

Description. An adult (Fig. 4). The head is large, triangular, almost as wide as the prothorax, with the antennae exceeding the length of the body; the maxillary palpi are long, with their segments thin. The prothorax is transverse, twice as wide as long; the mesothorax is slightly longer than the metathorax. In the forewings, Sc is approximately two-thirds as long as the wing; c–sc is short, enters C noticeably basad of the apex of Sc; the pterostigma is darkened. Rs deviates from R near the base of the wing and bifurcates almost at the level of the apex of Sc; r–rs short, connects the apex of Sc with the base of the Rs fork. M bifurcates at approximately the wing midlength level, basal of the Rs fork; MA is almost straight; MP is distinctly curved at its base; rs–m is straight or slightly S-shaped, enters R slightly basad of r–rs, enters M at its branching point. CuA enters the wing margin in its distal third; CuP enters the posterior wing margin slightly basad of the M fork. There are 8–9 crossveins between M and CuA and 9–10 between CuA and CuP. The hindwings are distinctly wider than the forewings due to the presence of the anal lobe; their venation is poorly preserved.

The legs are long and thin. The ratios of the mesotarsomere lengths in specimen CNU, no. NMDHG183 (male) are 18 : 13 : 16; the second segment of the metatarsus is two-thirds as long as the first segment; the third segment is incompletely preserved (Pl. 12, fig. 3). In specimens CNU, nos. NMDHG 184 and 185, the second protarsomere is slightly shorter than the third and significantly shorter than the first protarsomere (Pl. 12, figs. 4, 5).

The abdomen, with ten visible segments, is almost twice as long as the thorax. The abdominal segments of male specimen CNU, no. NMDHG183 are poorly preserved, but the apical segments are strongly sclerotized. The styles of the paraproct are thin, with their ventral sides straight, each style bearing a pair of apical setae.

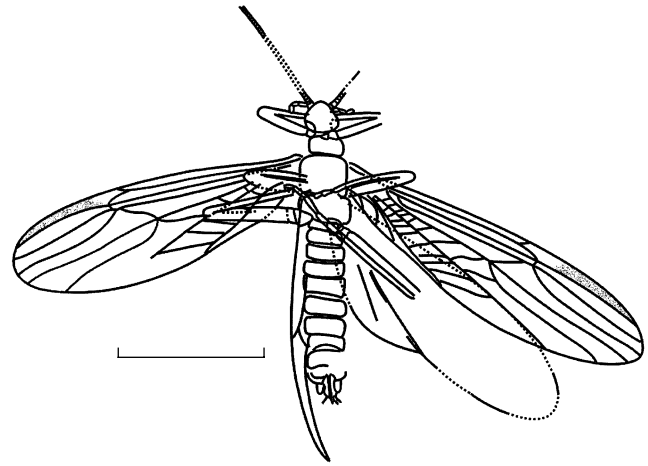


Fig. 4. *Karanemoura abrupta* Sinitshenkova, 1987, specimen CNU, no. NMDHG183, general view. Scale bar, 5 mm.

The cerci are short, single-segmented (Pl. 12, fig. 2). Abdominal sternite VIII of female specimen CNU, no. NMDHG69 has a well developed subgenital plate (Pl. 12, fig. 6).

Measurements, mm: body length, 10–15; forewing length, 12–17; maximum forewing width, 3–4.

Variability. Specimen CNU no. NMDHG183 shows minor variation in the venation between the left and the right wings. In the left wing, the apex of Sc enters R slightly distad of the Rs fork, which is situated slightly basad of r–rs. In the same wing, the rs–m is slightly curved (straight in the right wing).

Comparison. *K. abrupta* differs markedly from other species in having M bifurcating basad of, or even with rs–m and in the larger size.

Material. In addition to the holotype, specimens CNU, nos. NMDHG69, 183, 184, and 185 from the Daohugou locality.

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Explanation of Plate 12

Figs. 1–6. *Karanemoura abrupta* Sinitshenkova, 1987: (1–3) specimen CNU, no. NMDHG183, male: (1) general view; scale bar, 2 mm; (2) apex of the abdomen; (3) mesotarsus and metatarsus; (4) specimen CNU, no. NMDHG184, protarsus; (5) specimen CNU, no. NMDHG185, protarsus; (6) specimen CNU, no. NMDHG69, female, apex of the abdomen; scale bar 0.5 mm.

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