Paleontological Journal, Vol. 36, No. 3, 2002, pp. 270–276. Translated from Paleontologicheskii Zhurnal, No. 3, 2002, pp. 43–48.
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New Late Mesozoic Mayflies from the Shar-Teeg Locality, Mongolia (Insecta, Ephemerida=Ephemeroptera)

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Received February 22, 2001

Abstract—New taxa of mayflies from the Upper Mesozoic Shar-Teeg locality in Mongolia are described. These are *Furvoneta lucida* sp. nov.; *F. sobria* sp. nov. (Mesonetidae); *Epeoromimus umbratus* sp. nov. (Epeoromimidae); and *Siberiogenites mongolicus* sp. nov. (Hexagenitidae), all based on nymphs; and *Sharephemera cubitalis* gen. et sp. nov. (Sharephemeridae fam. nov.), based on a wing. A new specimen of the rare species *Clavineta cantabilis* is found, which is supposed to be a filter feeder. Peculiarities of the Shar-Teeg mayfly fauna are discussed.

INTRODUCTION

The material described below comes from the Shar-Teeg (Shara-Teeg) locality, which represents a series of outcrops of the Mesozoic and, most probably, the Upper Jurassic lacustrine sediments southeast of the Adzh-Bogdo Mountain Ridge, south of Shar-Teeg Mountain, Gobi-Altai Aimak, Mongolia (Gubin and Sinitza, 1996). Earlier, one species of mayflies, *Clavineta cantabilis*, was described from Shar-Teeg, outcrops 423/6, 434/2, 441/4, and 443/1. An extensive new collection from this locality created by the Joint Soviet–Mongolian Paleontological Expedition in 1989 and deposited at the Paleontological Institute of the Russian Academy of Sciences (PIN) contributes to our knowledge of the Mesozoic fauna of mayflies.

This collection contains 82 nymphs and two winged stages. Twenty nymphs and one adult come from outcrop 434/2 (cyclite 7, after Gubin and Sinitza, 1996); the remaining 60 nymphs and one adult come from outcrop 443/1 (cyclite 3). Despite the fine granulation and pale color of imbedding sediments (gray claystone), the preservation is generally poor, which is mainly due to incompleteness of most specimens. Possibly, they represent mainly fragments of molting skins. As a result, 32 specimens, including one imago, cannot be identified closer than to the order.

The Shar-Teeg Mayfly Fauna is rather rich. Identifiable nymph specimens belong to five species of four genera that are referred to three families. Among other Asian localities known, Shar-Teeg is inferior in this respect only to the Chernovskie Kopi (eight species) and Khutel-Khara (six species) localities (Sinitshenkova, 1989, 2000). Each species is represented by at least several specimens. This allows one to hypothesize that all species are taphonomically autochthonous in a broad sense; i.e., they developed in the same lake where insect-bearing sediments accumulated, although they did not necessarily inhabit exactly the zone of accumulation. All species are endemic, although they belong to the genera known from other localities as well. The only identifiable specimen of imago cannot be allocated to any previously known families of mayflies. For three families represented by nymphs, winged stages are known only for the Hexagenitidae, which is why conspecifity of the imago with one of mesonetid or epeoromimid species cannot be excluded. This question may be answered only by the finding of imago in one-species nymph assemblages, which would allow one to associate aquatic and winged stages. Unless such a record is made, it is wise to describe winged stages under separate names, as is commonly accepted in paleoentomology (Sinitshenkova, 1987).

Regarding the generic composition, the fauna of Shar-Teeg is quite similar to other Asian faunas of the Jurassic and, partially, the Early Cretaceous; however, the combination of these genera is unique and has not been found in any other locality. The genera *Epeoromimus* and *Siberiogenites* occur in Siberia and Mongolia from the end of the Early Jurassic to at least the beginning of the Early Cretaceous (Sinitshenkova, 1985, 1989), but they appear sporadically and have been found together only in the Lower Cretaceous Tsagan-Tsab Formation of southeastern Mongolia (Khutel-Khara locality). The genus *Furvoneta* is common in Transbaikalia in sediments of the Glushkovo, Ukurei, and Ust'-Kara formations (Sinitshenkova, 1990), whereas, in Mongolia, it was found only in the Bayan-Hoshu locality (Sinitshenkova, 1991). The age of all these findings is still debatable from the Late Jurassic to the Early Cretaceous. In some Transbaikalian localities, *Epeoromimus* is found in association with *Furvoneta*, although it is rather scarce, whereas *Furvoneta* and *Siberiogenites* have not been recorded together earlier. Finally, *Clavineta* is a pretty rare genus, being found, besides Shar-Teeg, only in the Chernovskie Kopi local-

ity in the Chita Region (Sinitshenkova, 2000), where *Siberiogenites* is found as well, but neither *Furvoneta* nor *Epeoromimus* occur. Judging from the mayfly fauna, insect-bearing deposits of Chernovskie Kopi are presumably referred to the Upper Jurassic, but their Early Cretaceous age cannot be excluded (Sinitshenkova, 2000). The complete absence of representatives of the family Siphlonuridae, which are very common in most of the Asian Jurassic or debatable Jurassic/ Early Cretaceous localities where *Siberiogenites, Epeoromimus, Furvoneta*, or *Clavineta* are found, is a rather unusual feature. As a whole, the generic composition of mayflies strongly suggests the Late Jurassic age of the Shar-Teeg sequence. In this respect, the data on mayflies disagree with the data on Shar-Teeg stoneflies, which are most likely of the Middle Jurassic appearance (Sinitshenkova, 1995).

The mayfly fauna of Shar-Teeg is also unusual in quantitative composition. *S. mongolicus* sp. nov. (22 specimens, 26.8% of all identifiable nymphs) is a dominant, whereas *F. lucida* sp. nov. (14 specimens, 17.1%) and *E. umbratus* sp. nov. (ten specimens, 12.2%) are subdominants. *Siberiogenites* does not numerically dominate over other mayflies in any other assemblage. In the Khutel-Khara locality, *S. medius* Sinitsh. is only one of two codominants alongside the siphlonurid *Albisca tracheata* Sinitsh. [each species is represented by 11 individuals, 39.3% of all identifiable nymphs (Sinitshenkova, 1989)]. In a small collection from the Lower or Middle Jurassic sediments of the Zhargalan Formation in northwestern Mongolia (Oshin-Boro-Udzyur-Ula locality), *S. rotundatus* Sinitsh. takes the second place among mayfly nymphs (five specimens, 23.8%) and is substantially inferior to the dominant mesonetid *Mesoneta antiqua* Br., Redtb. et Ganglb. (nine specimens, 42.9%) (Sinitshenkova, 1985). In other localities where *Siberiogenites* is recorded, i.e., the Lower or Middle Jurassic Ichetui Formation in Buryatia and Chernovskie Kopi (Sinitshenkova, 1985, 2000), it is extremely scarce. Subdomination of *Epeoromimus* is also unusual. To date, it has been found in large numbers only in the locality of Chernyi Etap in the Kemerovo Region (Abashevo and Osinovka formations, Lower or Middle Jurassic), where *E. kazlauskasi* Tshernova clearly dominate over other mayflies (Sinitshenkova, 1985). In other faunas (Khutel-Khara, Glushkovo Formation), nymphs of *Epeoromimus* are singular.

It should be emphasized that the composition of assemblages from outcrops 434/2 and 443/1 is nearly the same. Dominants are found in both outcrops and their ratio (*S. mongolicus* sp. nov.: *F. lucida* sp. nov.: *E. umbratus* sp. nov.) is similar, viz., 5 : 3 : 2 in 434/2 and 17 : 11 : 8 in 443/1. Rare *F. sobria* sp. nov. and *C. cantabilis* are found in the more representative collection from the 443/1 outcrop only. It is interesting, however, that a considerably smaller, older collection from Shar-Teeg contains three nymphs of *C. cantabilis*, which is represented in the new collection by a single specimen. This may reflect certain changes in the composition of the assemblage along the section. Regrettably, the precise stratigraphical position of the first findings of *Clavineta* is unknown. A fragmentary nymph of siphlonuroid appearance that has been found together with *C. cantabilis* (Sinitshenkova, 1991) may belong to *S. mongolicus* sp. nov.; however, its certain identification is impossible. Both layers, where the new material comes from, refer to the stage of maximum transgression of Shar-Teeg Lake (Sinitshenkova, 1995; Gubin and Sinitza, 1996).

The bizarreness of the Shar-Teeg mayfly fauna may be explained by ecological, as well as biogeographic, reasons. Zherikhin and Kalugina (1985) pointed that the most of the Jurassic faunas from Siberia and Mongolia, which are characterized by the dominance of the Siphlonuridae; Mesonetidae; and, rarely, Epeoromimidae, are associated with deposits of either oxbow lakes or relatively small and presumably oligotrophic mountain dam lakes without clear evidence of stratification, whereas the Cretaceous faunas of this region, usually dominated by the Hexagenitidae of the genus *Ephemeropsis* Eichw., are connected mainly with sediments of large plane or intermontane lakes with well-pronounced stratification of their limnion. The authors also surmised that large Jurassic lakes might contain assemblages, which resemble Early Cretaceous ones, including, in particular, hexagenitids as a dominant. The domination of *Siberiogenites* in Shar-Teeg could be considered as evidence in favor of this opinion. However, hexagenitids are not only a dominant in the Cretaceous faunas but, as a rule, the only group of mayflies, even in the deposits of small lakes (Sinitshenkova, 1990), whereas, in Shar-Teeg, they are found in association with other families. Khutel-Khara, where *Siberiogenites*, one of the dominants, refers not to a large plane lake but to an oligotrophic mountain lake; hexagenitids are extremely rare in such Jurassic lakes. On the contrary, in the Upper Jurassic deposits of Khoutiin-Khotgor, Dund-Gobi Aimak, which originated under the condition of a large stratified lake, mayflies are represented exclusively by mesonetids, whereas hexagenitids are absent (Sinitshenkova, 1989). All these findings demonstrate that Zherikhin and Kalugina's hypothesis, at beat, greatly simplifies the real situation and cannot satisfactorily explain the observed pattern of the distribution of mayflies.

From a biogeographical point of view, considerable differences of the Shar-Teeg fauna from previously known faunas are not surprising, since the locality is situated in southeast Mongolia, i.e., in the region that belonged to the European rather than to Siberian Biogeographic Region, where the overwhelming majority of Jurassic localities occurred (Zherikhin and Kalugina, 1985). However, similar to the case of stoneflies (Sinitshenkova, 1995), one may be surprised by the diversity of species, since large lakes in the warm climatic zone have a deficiency of dissolved oxygen, which restricts the diversity of aquatic gill-breathing insects.

Plate 3


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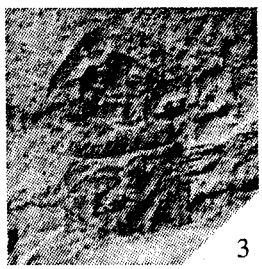
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Explanation of Plate 3

Fig. 1. *Furvoneta lucida* Sinitshenkova, sp. nov., holotype PIN, no. 4270/322, ×13.
Fig. 2. *Furvoneta sobria* Sinitshenkova, sp. nov., holotype PIN, no. 4270/358, ×10.3.
Fig. 3. *Clavineta cantabilis* Sinitshenkova, 1991, specimen PIN, no. 4270/375, ×6.2.
Fig. 4. *Epeoromimus umbratus* Sinitshenkova, sp. nov., holotype PIN, no. 4270/353, ×7.3.
Fig. 5. *Siberiogenites mongolicus* Sinitshenkova, sp. nov., holotype PIN, no. 4270/373, ×5.8.
Fig. 6. *Sharephemera cubitalis* Sinitshenkova, sp. nov., holotype PIN, no. 4270/357, ×11.5.
Fig. 7. Ephemerida fam. indet., specimen PIN, no. 4270/313, ×9.2.

Comparison with previously studied stoneflies from Shar-Teeg allows one to notice that the peculiarity of the mayfly fauna is expressed weaker. Whereas no mayfly genus based on nymphs is endemic to Shara-Teeg, two stonefly genera based on nymphs, *Sharaperla* Sinitsh. and *Bestioperlisca* Sinitsh., and two genera based on imagoes, *Sharaperla* and *Mongolonemoura* Sinitsh., are endemic to this locality; moreover, *Sharaperla* dominates numerically (Sinitshenkova, 1995).

As for the probable ecology of the Shar-Teeg mayflies, nearly all of them appear to be benthic collectors of fine detritus and, probably, algivorous (as a rule, it is impossible to distinguish these two trophic guilds in fossils from the structure of their mouthparts). *Epeoromimus* is the only large-gilled genus in the assemblage. Nymphs of *Clavineta* were free-living filter feeders, judging from the structure of their forelegs furnished with long hairs. This living form of mayflies needs rather rapidly flowing water and rarely occurs in lakes. The low number of *C. cantabilis* allows one to surmise that its nymphs inhabited the near-shore zone with more intensive currents and wind-induced intermixing of water and only occasionally were buried in the sediments of the more quiet and deep parts of the lake.

SYSTEMATIC PALEONTOLOGY

Family Mesonetidae Tshernova, 1969

Genus *Furvoneta* Sinitshenkova, 1985

Furvoneta lucida Sinitshenkova, sp. nov.

Plate 3, fig. 1

Etymology. From the Latin *lucidus* (bright).

Holotype. PIN, no. 4270/322, imprint and counterpart of nearly complete nymph without caudal filaments; Mongolia, Shar-Teeg locality, outcrop 443/1; Middle–Upper Jurassic.

Description (Figs. 1a and 1b). Nymph. The head is rounded with small lateral eyes. The labrum is widely rounded; the mandibles have acute teeth on the narrow apex. The pronotum is short and broad, five times as wide as long. The abdomen is twice as long as broad. The mesothorax is massive and has long oval wing sheath that reaches the third abdominal segment. The legs are short and narrow. The abdominal segments nearly five times as broad as long; the third segment is longest, five times as broad as long. A dark pattern on the abdominal tergites forms pale medial spots, which are rounded on middle segments.

Measurements, mm. Nymph body length, 9–10.

Comparison. The new species is most similar to *F. lata* (Sinitsh., 1976), well differing by the smaller size, wider abdomen, and by the presence of a pattern on the abdominal tergites.

Remarks. Nearly all nymph specimens lack gills. Two gills are discernible only in the holotype, although they are very pale. All specimens lack caudal filaments.

Material. In addition to the holotype, paratypes PIN, nos. 4270/295, 297, and 298, imprints and counterparts of nymphs from outcrop 434/2; and PIN, nos. 4270/326±, 327±, 351±, 355±, 363, 366, 367, 372, 379, and 380, nymphs from outcrop 443/1.

Furvoneta sobria Sinitshenkova, sp. nov.

Plate 3, fig. 2

Etymology. From the Latin *sobrius* (moderate).

Holotype. PIN, no. 4270/358, imprint of abdominal segments 5–10 with gills and bases of caudal filaments; Mongolia, Shar-Teeg locality, outcrop 443/1; Middle–Upper Jurassic.

Description (Fig. 1c). Nymph. The abdomen is almost three times as long as broad, the segments are 3.2 times as broad as long, and segment 10 is two times shorter than segment 9.

Measurements, mm. Length of fragmentary abdomen (holotype), 6; entire nymph length, ca. 11; complete length of abdomen (paratype PIN, no. 4270/314), 8.5; entire nymph length, ca. 13.

Comparison. This species is closest to *F. undina* (Sinitsh., 1976), from which it differs by the greater size and by the narrower and longer abdominal segments.

Material. In addition to the holotype, paratypes PIN, nos. 4270/314±, 369, and 371, nymph fragments from outcrop 443/1.

Genus *Clavineta* Sinitshenkova, 1991

Clavineta cantabilis Sinitshenkova, 1991

Plate 3, fig. 3

A new specimen of *C. cantabilis*, PIN, no. 4270/375, was found in outcrop 443/1. The specimen (Fig. 1d) has a head, forelegs, pronotum, and a fragmentary mesothorax. Although the hairs on the inner face of the fore tibiae are nearly indiscernible, there is no doubt about the assignment of this specimen to *C. cantabilis*,

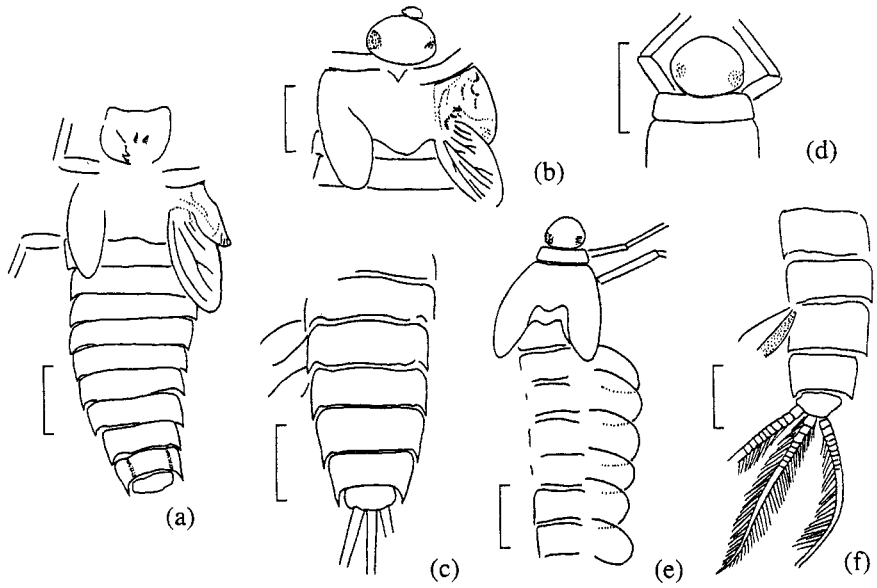

Fig. 1. Mayfly nymphs of the families (a–d) Mesonetidae, (e) Epeoromimidae, and (f) Hexagenitidae: (a, b) *Furvoneta lucida* sp. nov.: (a) nymphal molting skin, holotype PIN, no. 4270/322, (b) fragment of nymphal molting skin, paratype PIN, no. 4270/298; (c) *F. sobria* sp. nov., fragment of abdomen of nymph, holotype PIN, no. 4270/358; (d) *Clavineta cantabilis* Sinitsh., specimen no. 4270/375, fragment of anterior part of nymph body; (e) *Epeoromimus umbratus* sp. nov., nymph, holotype PIN, no. 4270/353; and (f) *Siberiogenites mongolicus* sp. nov., fragmentary nymph abdomen, holotype PIN, no. 4270/373. Scale bar, 2 mm.

since its forelegs are clearly close to the head, i.e., in the position specific for filter feeders. The short and thickened femurs and long tibiae are characteristic of *C. cantabilis* only, whereas other species from this locality have different structures of their legs.

Family Epeoromimidae Tshernova, 1969

Genus *Epeoromimus* Tshernova, 1969

***Epeoromimus umbratus* Sinitshenkova, sp. nov.**

Plate 3, fig. 4

Etymology. From the Latin *umbratus* (covered with shadow).

Holotype. PIN, no. 4270/353, imprint and counterpart of a nymph with well-preserved gills; Mongolia, Shar-Teeg locality, outcrop 443/1; Middle–Upper Jurassic.

Description (Fig. 1e). Nymph. The head is rounded, not broader than the pronotum. The pronotum is short, has slightly prominent anterior corners, approximately four times as broad as long. The wing sheaths are narrow. The legs are narrow and long. The femurs are not broader than the tibiae. The gills are large, rounded, and overlapping; the first gill is elongated and markedly shorter than the second gill; the subsequent gills gradually become smaller, although they are longer than the segment, which they are attached to. The abdominal segments are long, only slightly broader than longer. The length of the caudal filaments is less than one-third of the body length.

Measurements, mm. Body length of the latest instar nymph lacking the last abdominal segments (holotype), 13; entire body length, ca. 15.

Comparison. By the presence of the rounded gills and long abdominal segments, the new species is most similar to *E. infractus* Sinitsh., 1989 from the Lower Cretaceous of Mongolia and *E. cretaceous* Sinitsh., 1976 from the Upper Jurassic–Lower Cretaceous Glushkovo Formation of Transbaikalia, being different from them in its larger size, the shape of the pronotum, and broader first gills.

Material. In addition to the holotype, paratypes PIN, nos. 4270/296± and 311, nymph specimens from outcrop 434/2; and PIN, nos. 4270/317±, 318±, 319±, 342±, 347±, 356±, and 360, nymph specimens from outcrop 443/1.

Family Hexagenitidae Lameere, 1917

Genus *Siberiogenites* Sinitshenkova, 1985

***Siberiogenites mongolicus* Sinitshenkova, sp. nov.**

Plate 3, fig. 5

Holotype. PIN, no. 4270/373, imprint of a nymph fragment with well-preserved caudal filaments; Mongolia, Shar-Teeg locality, outcrop 443/1; Middle–Upper Jurassic.

Description (Fig. 1f). Nymph. The legs are narrow and short. The gills are narrow, and their thickened anterior margin and the inner rib form an acute angle. The abdominal segments are long, not more than 1.5 times as broad as long. The caudal filaments are

thick, furnished with a dense pubescence, which is well visible in the imprints. The paracercus is slightly shorter than the cerci and longer than one-third of the body length.

Measurements, mm. Length of nymph body fragments, 9–11; complete nymph length, ca. 12.

Comparison. The nymph differs strikingly from other known species by its narrow gills and by the long, thickened, and densely pubescent caudal filaments.

Remarks. Nearly all nymph specimens are poorly preserved, and many of them are represented by jammed molting skins. Several fragments are assigned to this genus on the basis of the characteristic caudal filaments.

Material. In addition to the holotype, paratypes PIN, nos. 4270/300±, 302±, 303±, 305±, and 309, nymph specimens from outcrop 434/2; and PIN, nos. 4270/320±, 324±, 325±, 328±, 334±, 338±, 341±, 343±, 344±, 350±, 354±, 362, 364, 376±, 383±, and 2778, nymph specimens from outcrop 443/1.

Family Sharephemeridae Sinitshenkova, fam. nov.

Type genus. *Sharephemera* gen. nov.

Diagnosis. Anterior wing. Fore margin slightly concave. Wing length more than two times as long as broad; wing base broad with well-developed anal area; cubital region narrow; posterior margin broadly rounded so that tornus only weakly developed. MA branching in basal third of wing; MP branching near wing base. CuA with long fork, CuP simple, A1 with long fork, and cubital and anal veins nearly straight.

Composition. Type genus.

Comparison. Strongly differs from known families in the shape of wing, having a broad basal part, narrow cubital region, and nearly straight cubital and anal veins.

Genus *Sharephemera* Sinitshenkova, gen. nov.

Etymology. From Shar-Teeg Mountain and the generic name *Ephemera*.

Type species. *Sh. cubitalis* sp. nov.

Diagnosis. As for family.

Specific composition. Type species.

***Sharephemera cubitalis* Sinitshenkova, sp. nov.**

Plate 3, fig. 6

Etymology. From the Latin *cubitalis* (cubital).

Holotype. PIN, no. 4270/357, imprint and counterpart of anterior wing jammed in MP region; Mongolia, Shar-Teeg locality, outcrop 443/1; Middle–Upper Jurassic.

Description (Fig. 2a). Anterior wing. At the wing base, the costal area is three times as broad as the subcostal area; these areas are nearly equal in breadth

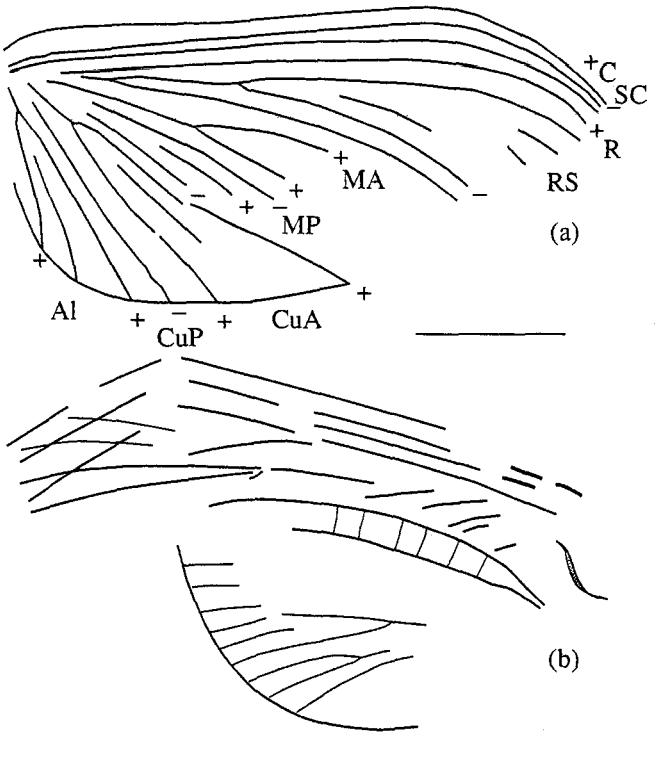

Fig. 2. Mayfly wings from the Shar-Teeg locality: (a) *Sharephemera cubitalis* gen. et sp. nov., anterior wing, holotype PIN, no. 4270/357; (b) Ephemerida fam. indet., specimen PIN, no. 4270/313, fragments of anterior and posterior wings. Scale bar, 2 mm.

at the wing apex. The pterostigma is well pronounced. The radial area is broad. The anterior branch of RS is simple; the posterior branch ramifies twice; the first bifurcation is near the base, and the second is almost at the midlength of the wing. MA bifurcates somewhat basal to the second fork of the posterior branch of RS, its fork is considerably longer than the stem. CuA bifurcates somewhat basal to the first fork of the posterior branch of RS; its fork is more than four times longer than the stem.

Measurements, mm. Anterior wing length, 8.

Remarks. The small size of the wing does not allow one to associate it with the previously described nymphs. It most likely represents a separate species, of which the preimaginal stages are still unknown.

There is another imprint of imago, PIN, no. 4270/313, outcrop 434/2, which has fragments of the anterior and posterior wings. In spite of its rather poor preservation with a jammed anterior wing, wing venation being obscure and taxonomical position being uncertain, we have found appropriate to figure and discuss this specimen (Fig. 2b, Pl. 3, fig. 7), taking into account the rarity of imagoes. The uniqueness of this specimen is that both anterior and posterior wings are found together. The posterior wing is rounded and less than half as long as the anterior wing. Judging from the measurements

(the length of the anterior wing fragment is 10 mm, its complete length is about 12 mm, and the posterior wing length is 4.5 mm), this wing is somewhat larger than those of *S. cubitalis* sp. nov. and may be compared to those of nymphs of *F. lucida* sp. nov. or *S. mongolicus* sp. nov.

Material. Holotype.

ACKNOWLEDGMENTS

I express my sincere thanks to A.V. Mazin (Paleontological Institute of the Russia Academy of Sciences) for producing photos.

This work was supported by the Russian Foundation for Basic Research, project no. 01-05-64741.

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