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New Mayflies from the Upper Mesozoic Transbaikalian Locality Chernovskie Kopi (Insecta: Ephemerida = Ephemeroptera)

N. D. Sinitshenkova

Paleontological Institute, Russian Academy of Sciences, ul. Profsoyuznaya 123, Moscow, 117868 Russia

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Abstract—Seven new species and a new genus, *Clavineta transbaikalica* sp. nov., *C. citima* sp. nov., *Mesoneta deusta* sp. nov. (Mesonetidae), *Siberiogenites recticostalis* sp. nov. (Hexagenitidae), *Mesobaetis amplectus* sp. nov., *Siphangarus rotundus* gen. et sp. nov., and *Stackelbergisca clara* sp. nov. (Siphlonuridae), are described based on nymphs. The mayfly assemblage of the Transbaikalian locality Chernovskie Kopi is analyzed. This assemblage is unique for the Mesozoic of Asia, but generally more similar to Jurassic rather than to Cretaceous assemblages.

INTRODUCTION

The material described below came from the locality Chernovskie Kopi (Chita Region, Chita District, Chita-Ingoda Depression, the left bank of the Ingoda River, 18–20 km southwest of Chita) that was briefly characterized elsewhere (Sinitshenkova, 1998). All the impressions but one were collected by S.M. Sinitsa from Outcrop 9, beds 1, 2, 3, 10, and 16 (hereafter 9/1, 9/2 etc. respectively). One impression (no. 4626/252) was found by N. Berdnikov in Outcrop 1006/3. All mayfly specimens are represented by larval impressions on burned mudstone. The organic matter was not preserved because of fire, and some characters are obscure. Moreover, the vast majority of remains are incomplete. Nevertheless, the material in question is of great interest. The material studied, including the types, is housed in the collection of the Paleontological Institute of the Russian Academy of Sciences (PIN).

RESULTS AND DISCUSSION

Only 39 of 56 specimens were identified at species level. They belong to seven species of seven genera, which may be allocated to the families Siphlonuridae (*Mesobaetis amplectus* sp. nov., *Stackelbergisca clara* sp. nov., *Siphangarus rotundus* gen. et sp. nov.), Hexagenitidae (*Siberiogenites recticostalis* sp. nov.), and Mesonetidae (*Mesoneta deusta* sp. nov., *Clavineta citima* sp. nov., *C. transbaikalica* sp. nov.). Specimen no. 4626/238, an impression of a nymph from Outcrop 9/16, was identified as *Proameletus* (Siphlonuridae). It is impossible to identify this species precisely because of poor preservation of the specimen that is represented by incomplete remains of the abdomen with tail filaments. The specimen differs from the only known species *P. caudatus* Sinitsh. (Sinitshenkova, 1976) in the narrower abdominal segments. Sixteen specimens of mayflies are not identified with greater precision.

The mayfly fauna of Chernovskie Kopi may apparently be considered as a single assemblage, although there may be differences between different beds that cannot be recognized because of insufficiently preserved material. For instance, two specimens of *S. recticostalis* sp. nov. come from the same bed 9/3, where none of *M. deusta* sp. nov. appear, although the latter are found in beds 9/1, 9/2, 9/10, and 9/16.

The fauna of the locality is peculiar in many aspects. Unlike any other Mesozoic fauna it shows high taxonomic diversity, an unusual generic fauna, and dominant taxa.

Chernovskie Kopi exceeds any other Mesozoic locality in Asia in the absolute number of species (eight) and genera (eight) found, although considerably more remains have been collected in many sites. In the Jurassic deposits mayflies are represented by three to four species of two or three genera (Sinitshenkova, 1985), while only one species of the genus *Ephemeropsis* is recorded in the majority of the Lower Cretaceous localities. The only exception is the locality Hutel-Hara in southeastern Mongolia (Tsagaan-Tsav Formation, the Upper Jurassic–Lower Cretaceous) where five species of five genera belonging to five families have been discovered (Sinitshenkova, 1989). Nevertheless, this locality shows lesser generic and species diversity compared to Chernovskie Kopi. There is only one Lower Cretaceous locality outside Asia, in Brazil (Santana), with a more diverse mayfly fauna than in Chernovskie Kopi. Not less than 11 species in 11 genera of nine families are recorded from there (McCafferty, 1990; Martill, 1993).

All families represented in Chernovskie Kopi, viz. the Siphlonuridae, Hexagenitidae, and Mesonetidae, are usual in Mesozoic assemblages in Asia. Fossorial mayflies and Epeoromimidae found in some other localities are not recorded. All genera except for endemic *Siphangarus* gen. nov. have previously been

recorded in the Asian Mesozoic, and some of them are widespread. However, their associations are unique. Both genera *Mesobaetis* and *Mesoneta* are found in many Jurassic localities, but their association with *Siberiogenites* is recorded only in Novospasskoe (Buryatiya, the Ichetui Formation) and Oshin-Boro-Udzuur-Uul (Western Mongolia, the Jargalant Formation) (Sinitshenkova, 1985, 1991), whereas *Stackelbergisca*, *Clavineta*, and *Proameletus* have not previously been recorded in association or with any of above genera (Sinitshenkova, 1985, 1989, 1990a). All the species found in Chernovskie Kopi are endemic.

The pattern of domination is also unique. Three of the most abundant species are represented by nearly equal numbers of specimens, i.e. 12 specimens of *S. rotundus* gen. et sp. nov., 11 specimens of *S. clara* sp. nov., and 10 specimens of *M. deusta* sp. nov. The species *S. recticostalis* sp. nov. and *M. amplectus* sp. nov. are represented in the collection by two individuals, and *Proameletus* sp. and both species of *Clavineta* are represented by a single individual each. In other localities species of *Mesobaetis* and *Proameletus* are always among the dominants. Although siphlonurids often dominate by the number of individuals in Mesozoic faunas, they are usually represented by a single genus with one or two species, whereas in Chernovskie Kopi two species of two genera are recorded in equal proportions. Mayflies of the family Hexagenitidae often dominate in the Lower Cretaceous beds (Sinitshenkova, 1986, 1990b; McCafferty, 1990), except for a few occurrences, e.g., the Koonwarra Locality in Australia (Jell and Duncan, 1986).

Since Chernovskie Kopi is situated in the region where many other Mesozoic mayfly localities have been discovered, the peculiarity of the mayfly fauna may be explained by either taphonomic, or ecological, or stratigraphic reasons.

The majority of the species found apparently developed in the same lake where the insect-bearing sediments were deposited. Thus these species are autochthonous in a broad sense. It is true for the most common species mentioned above as well as for *M. amplectus* sp. nov., *Proameletus* sp., *S. recticostalis* sp. nov., which are superficially similar to other limnetic species and belong to genera found in other lacustrine deposits. The small quantity of their remains may be explained by either a low number of the insects or their preference for other parts of the lake. Similar to nymphs of both *Clavineta* species, they might be allochthonous and have been transported here from flowing water bodies. Their morphological features are not characteristic of mayflies from stagnant water and indicate a possible filter-feeding diet. However, filtrators need flowing water with seston. Hence, the burial of Chernovskie Kopi does not differ taphonomically from the majority of others burials in Transbaikalia and Mongolia.

The fact that nymphs are found in the beds containing leaf and seed floras may explain ecological reasons for the peculiarity of the mayfly assemblage from Chernovskie Kopi. Mayflies remains are accompanied by numerous plant remains. Only few Jurassic localities in the region of lake Baikal (Cheremkhovo Formation) and western Mongolia (Jargalant Formation) resemble Chernovskie Kopi in this respect. It is noteworthy that *Mesobaetis*, *Mesoneta*, and *Siberiogenites* are recorded together in the deposits of the Jargalant Formation as well. In contrast, in Transbaikalia, in central and western Mongolia nearly all burials occur in beds where the macroremains of plants are much scarcer. Only in the deposits of the Bukachacha Formation, the Bukachacha Locality, nymphs of hexanitid *Ephemeropsis* were found directly in coal measures (Sinitshenkova, 1990a). Since plant detritus, both large- and small-sized, is the main diet of nymphs of many mayflies, its abundance and composition influence the fauna significantly. Hence, the peculiarity of the mayfly assemblage of Chernovskie Kopi may at least partly be explained by this.

The large amount of plant debris may influence the fauna indirectly, through the presumable bactericidal effect of Mesozoic plants. Existence of so-called hypotrophic lake ecosystems in the Mesozoic is supposed be connected with such an effect (Zherikhin and Kalugina, 1985; Sinitshenkova, 1983; Sinitshenkova and Zherikhin, 1996). The main source of this debris are gingoaceous plants. It is of great interest, in this respect, that these plants are poorly represented in the Jurassic insect-bearing beds (Zherikhin and Kalugina, 1985), and Lower Cretaceous insects have been known mainly from the deposits of large lakes which were not affected strongly by hypotrophic conditions (Zherikhin and Kalugina, 1985; Sinitshenkova and Zherikhin, 1996). The high diversity of mayflies may reflect considerable oxygenation of water body.

All presumed autochthonous nymphs found in Chernovskie Kopi are benthic detrivores judging from their morphological features. There are two groups among them, viz. with large gills, *Siberiogenites*, and with small gills which comprise all the others genera. Fossorial forms are absent. Such a set of morphoecotypes generally resembles the assemblage which is characteristic for the Jurassic hypotrophic lakes of southern Siberia, but the forms with large gills, mainly the Epeoromimidae, are often more abundant in those lakes. The causes for the relative abundance of small- and large-gilled nymphs in different assemblages are not yet clear. Presumably allochthonous nymphs of *Clavineta* have long and dense setation of the fore legs, a characteristic of recent filter-feeders, and consequently may be referred to this type.

The age of the locality Chernovskie Kopi is disputable (Sinitshenkova, 1998). It is possible to compare the fauna with other assemblages only at generic level since all the species of the mayflies are endemic. All the genera, except for the endemic *Siphangarus* gen. nov., have been known from either Jurassic or debatable

Explanation of Plate 11

Fig. 1. *Clavineta transbaikalica* Sinitshenkova, sp. nov.; holotype PIN, no. 4626/200, ×5.3.
Fig. 2. *Clavineta citima* sp. nov. Sinitshenkova, sp. nov.; holotype PIN, no. 4626/252, ×10.
Fig. 3. *Mesoneta deusta* Sinitshenkova, sp. nov.; holotype, PIN, no. 4626/244, ×12.
Fig. 4. *Siberiogenites recticostalis* Sinitshenkova, sp. nov.; holotype PIN, no. 4626/221, ×6.3.
Fig. 5. *Mesobaetis amplectus* Sinitshenkova, sp. nov.; holotype, PIN, no. 4626/201, ×6.
Fig. 6. *Stackelbergisca clara* Sinitshenkova, sp. nov.; holotype PIN, no. 4626/232, ×8.6.
Fig. 7. *Siphangarus rotundus* Sinitshenkova, gen. et sp. nov.; holotype PIN, 4626/202 ×4.

Jurassic or Cretaceous beds. *Mesobaetis* and *Mesoneta* are characteristic mostly for the faunas of the Early and Middle Jurassic. In the younger assemblages they are rare and represented by much larger species (Sinitshenkova, 1989). The species of *Mesoneta* and *Mesobaetis* from Chernovskie Kopi are small and resemble the Early–Mid Jurassic ones. In contrast, representatives of the genus *Stackelbergisca* were found in large numbers only in the Upper Jurassic of Transbaikalia whereas they are quite rare in the older beds (Sinitshenkova, 1991). The genus *Clavineta* has been known until now only from the Locality of Shara-Teg in western Mongolia (Sinitshenkova, 1991). Insect-bearing deposits of Shara-Teg may most likely be referred to the Upper Jurassic, although the Lower Cretaceous can not be excluded with certainty. Besides the Lower–Middle Jurassic, *Siberiogenites* are found in the Tsagaan-Tsav Formation in southeastern Mongolia which is considered as the basalmost Lower Cretaceous (Sinitshenkova, 1989). And finally, the genus *Proameletus* has been known until the present only from the Glushkovo Formation and its analogues in eastern Transbaikalia, the age of which is estimated to be the Late Jurassic to Albian (Sinitshenkova, 1990a). In those beds *Proameletus* is nearly always recorded together with the genus *Furvoneta* which is absent from Chernovskie Kopi. To summarize, the general appearance of the mayfly assemblage of Chernovskie Kopi testifies to a Jurassic, probably Late Jurassic, age although its peculiarity makes its comparison with other faunas difficult. Such a dating agrees with the data obtained from the other aquatic insects, the stoneflies (Sinitshenkova, 1988).

SYSTEMATIC PALEONTOLOGY

Family Mesonetidae Tshernova, 1969

Genus *Clavineta* Sinitshenkova, 1991

***Clavineta transbaikalica* Sinitshenkova, sp. nov.**

Plate 11, fig. 1

Etymology. From Transbaikalia.

Holotype. PIN, no. 4626/200, anterior part of nymph body; locality Chernovskie Kopi, outcrop 9/1; Upper Jurassic.

Description (Fig. 1a). Nymph. The head is elongate and little narrowed anteriorly, its length is almost 1.5 times greater than its width at the hind margin. The maxillary palps have two short basal segments and the long apical one is densely covered with long hairs, the palps are protruding from the head sides. The

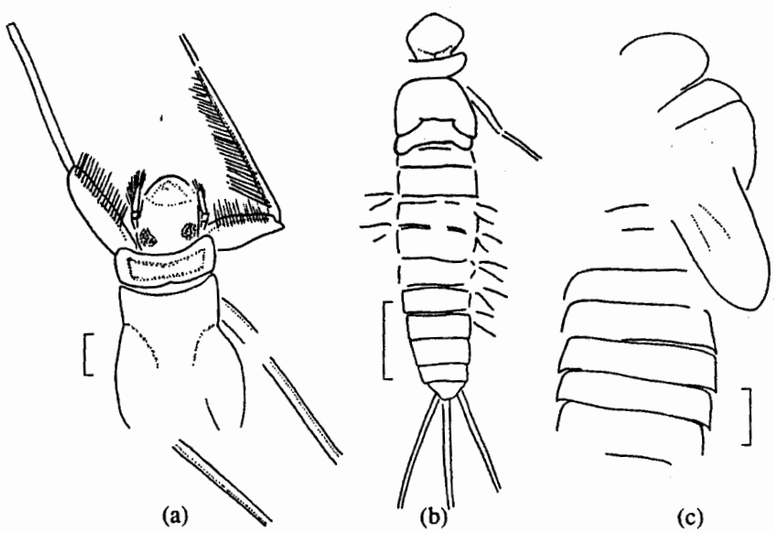

Fig. 1. Nymphs of mayflies of the family Mesonetidae: (a) *Clavineta transbaicalica* sp. nov., holotype PIN, no. 4626/200; (b) *C. citima* sp. nov., holotype PIN, no. 4626/252; (c) *Mesoneta deusta* sp. nov., holotype PIN, no. 4626/244. Scale bar 1 mm.

Plate 11


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pronotum is transverse, 3.2 times as wide as long, and 0.4 times the length of the head. The wing sheaths are narrow and close to each other. The fore femora are twice as wide but 0.625 times the length of the tibiae. There are long hairs, not in fascicles, along the inner side of the femora and tibiae.

Measurements (mm): the length of the impression is 6.6, the complete length of the nymph body is approximately 13.

Comparison. Differs from *C. cantabilis* Sinitsh., 1991 in that the head and fore tibiae are longer, and in the smaller size.

Remarks. The genus *Clavineta* was originally described in the family Leptophlebiidae, where it was placed close to *Furvoneta* Sinitsh. based on the similarity of the gill structure (Sinitshenkova, 1991). The recent revision of fossil mayflies showed that the genus *Furvoneta* and the genus *Mesoneta* Br., Redtb. et Ganglb., closely similar to *Furvoneta*, are not related to the Leptophlebiidae and should be assigned to the superfamily Siphlonuroidea (Kluge, 1993).

Clavineta differs substantially from the genus *Colocrus* McCaff. (Oligoneuriidae) from the Lower Cretaceous of Brazil (McCafferty, 1990) in the more primitive structure of the filtering apparatus, *Clavineta* has dense hairs on the fore femora and tibiae along their inner side rather than arranged in broad fascicle like in oligoneuriids.

It is known that typical morphological features of larvae, the presence of long hairs on the inner side of the fore femora and tibiae connected with a filter-feeding diet, appear among various mayfly groups (Oligoneuriidae, Behningiidae, Heptageniidae, Isonychiidae) that are not always phylogenetically close.

A nearly complete nymph of the stonefly *Trianguliperla volucris* Sinitsh., 1998 (no. 4626/237) is preserved besides the impression of the mayfly.

Material. The holotype.

***Clavineta citima* Sinitshenkova, sp. nov.**

Plate 11, fig. 2

Etymology. From Latin *citimus* (proximate).

Holotype. PIN, no. 4626/252, almost complete young nymph (part and counterpart); Chernovskie Kopi Locality, outcrop 1006/3; Upper Jurassic.

Description (Fig. 1b). Nymph. The head is rounded, a little narrower and twice as long as the pronotum. The pronotum has beveled hind angles; the front angles are widely rounded and somewhat prominent. Wing sheaths are short. Abdominal segments have short indentations on the latero-posterior position. The abdominal segments are 2–2.5 times as wide as long. The gills have thickened outer and inner margins. The length of each gill does not exceed the width of a segment. Tail filaments are half as long as the body length.

Measurements (mm): body length 5, the length of the tail filament 2.5.

Comparison. Differs from known species in the shape of the pronotum and smaller size.

Remarks. The fore legs with characteristic setation are not preserved, but the gills with typical *Clavineta*-type structure allow referal of *C. citima* to this genus. *Furvoneta* has gills of similar structure, but its representatives are characterized by wide abdominal segments and long indentations latero-posteriorly. These features are absent from the new species.

Material. The holotype.

Genus *Mesoneta* Brauer, Redtenbacher et Ganglbauer, 1889

***Mesoneta deusta* Sinitshenkova, sp. nov.**

Plate 11, fig. 3

Etymology. From Latin *deustus* (burnt).

Holotype. PIN, no. 4626/244, part and counterpart of the nymph without the tip of the abdomen; Chernovskie Kopi Locality, outcrop 9/16; Upper Jurassic.

Description (Fig. 1c). Nymph. The head is oval shaped, prognathous, and twice as long as the pronotum. The pronotum is short, three times as wide as long. The body is approximately 3.4 times as long as the abdomen is wide. The abdomen is three times as long as thorax and nearly twice as long as wide. The width of segments in the middle part of the abdomen is 3.5 times their length.

Measurements (mm): the holotype length 6.9, the full length of the nymph approximately 8.

Comparison. The new species is close to *M. utriculata* Sinitsh., 1985 in size and abdominal segment width, but differs in the shorter body.

Remarks. Up to now all species of *Mesoneta* have been found in the Jurassic localities of Siberia and Mongolia: *M. antiqua* Br., Redtb. et Ganglb., 1889 (Abashevo, Osinovka, Cheremkhovo, Ichetui, and Jargalant Formations, the Lower–Middle Jurassic), *M. utriculata* (Osinovka, Cheremkhovo, Ichetui, and Jargalant Formations, Lower–Middle Jurassic), *M. magna* Sinitsh., 1985 (Uda Formation, Upper Jurassic), *M. zolensis* Sinitsh., 1990 (Bokhto Formation, upper part of the Lower Jurassic), *M. mongolica* Sinitsh., 1989 (Ulaan-Ereg Formation, the Upper Jurassic), and *M. tushilgae* Sinitsh., 1989 (Hamar-Huburin Formation, the Lower–Middle Jurassic).

Material. Besides the holotype, paratypes PIN, nos. 4626/227 (outcrop 9/10), 4626/246, 248, 250 (outcrop 9/16), 4626/251 (outcrop 9/2), 4626/253, 255, 260, 271 (outcrop 9/1), fragments of nymphs.

Family Hexagenitidae Lameere, 1917

Genus *Siberiogenites* Sinitshenkova, 1985

***Siberiogenites recticostalis* Sinitshenkova, sp. nov.**

Plate 11, fig. 4

Etymology. From Latin *rectus* (straight) and *costa* (rib).

Holotype. PIN, no. 4626/221, part and counterpart of nymph abdomen with gills; Chernovskie Kopi Locality, outcrop 9/3; Upper Jurassic.

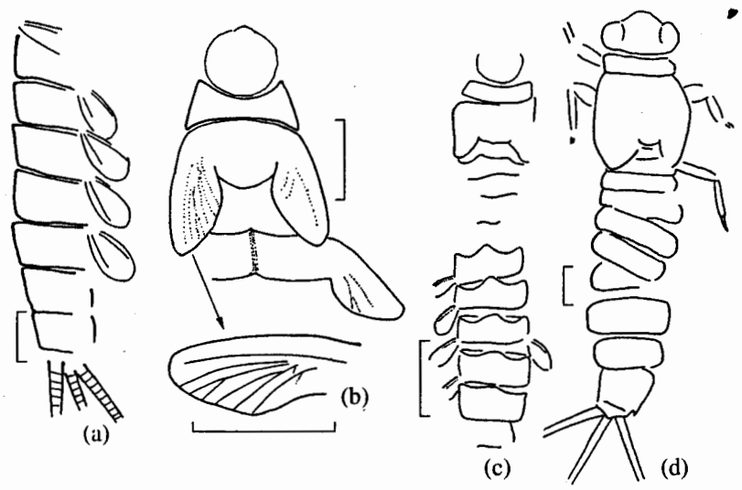

Fig. 2. Nymphs of mayflies of the families Hexagenitidae and Siphlonuridae: (a) *Siberiogenites recticostalis* sp. nov., holotype PIN, no. 4626/221; (b) *Mesobaetis amplectus* sp. nov., holotype, no. 4626/201; (c) *Stackelbergisca clara* sp. nov., holotype PIN, no. 4626/232; (d) *Siphangarus rotundus* sp. nov., holotype PIN, no. 4626/202. Scale bar 2 mm.

Description (Fig. 2a). Nymph. Abdominal segments are rectangular. Segments in the middle part of abdomen are twice as wide as long. The inner ribs on the gills run close to each other at the base and diverge at a significant angle; the inner rib is straight.

Measurements (mm): the length of abdomen is 13, the complete length of the nymph near 18.

Comparison. Differs considerably from known species in the straight inner rib on the gills.

Material. Besides the holotype, paratype PIN, no. 4626/212, a fragment of a nymph from the same bed.

Family Siphlonuridae Ulmer, 1920

Genus *Mesobaetis* Brauer, Redtenbacher et Ganglbauer, 1889

***Mesobaetis amplectus* Sinitshenkova, sp. nov.**

Plate 11, fig. 5

Etymology. From Latin *amplectus* (embracing).

Holotype. PIN, no. 4626/201, impression of the head and thorax; Chernovskie Kopi Locality, outcrop 9/1; Upper Jurassic.

Description (Fig. 2b). Nymph. The head is rounded, 0.7 times the width of the pronotum. The pronotum has a deeply concave front margin and a notably concave hind margin. The pronotum is 2.6 times as wide as long. The mesonotum has rounded front angles. Distinct three-branched RS and simple MA, MP, CuA, and CuP on the fore wing sheath are present. The hind wing sheaths are rounded.

Measurements (mm): the length of the holotype is 5.5, the full length of the nymph approx. 20, and the length of middle instar nymph (paratype) 16.2.

Comparison. In the shape of the pronotum with the concave front margin the new species resembles *M. sibirica* Br., Redt. et Ganglb., 1889, but differs in the rounded angles of the mesonotum and large size.

Material. Besides the holotype, paratype PIN, no. 4626/240, a complete poorly preserved nymph (outcrop 9/16).

Genus *Stackelbergisca* Tshernova, 1967

***Stackelbergisca clara* Sinitshenkova, sp. nov.**

Plate 11, fig. 6

Etymology. From Latin *clarus* (clear).

Holotype. PIN, no. 4626/232, part and counterpart of nearly complete nymph with gills; Chernovskie Kopi Locality, outcrop 9/3; Upper Jurassic.

Description (Fig. 2c). Nymph. The head is rounded with a smoothly convex hind margin, a little narrower and nearly 3 times as long as the pronotum. The pronotum is short, 4 times as wide as long, with nearly straight sides. The abdomen is almost 4.5 times as long as the thorax. The abdominal segments have an undulate front margin. The mid part of the eighth segment is slightly convex, that of the sixth and seventh is strongly convex, widely rounded at the tip, the tip of the middle outgrowth of the fourth and fifth segments is nearly acute. Segments of the middle part of the abdomen are nearly twice as wide as long. The gills are oval-shaped, with the mid-rib placed nearer to the outer margin.

Measurements (mm): the length of the holotype is 10.4, the body length approx. 10.

Comparison. In size and gill structure the new species is close to *S. shaburensis* Sinitsh., 1991, from which it differs considerably in the undulate bases of the abdominal segments.

Material. Besides the holotype, paratypes PIN, nos. 4626/206, 209 (outcrop 9/1), 4626/214, 231, 232, 274, 275 (outcrop 9.3), 4626/229 (outcrop 9/10), 4626/235 (part and counterpart), 4626/236 (outcrop 9/16), nymphs.

Genus *Siphangarus* Sinitshenkova, gen. nov.

Etymology. From the genus *Siphlonurus* and Angara-land.

Type species. *S. rotundus* sp. nov.

Diagnosis. Nymph. Large mayflies with large lateral eyes and short legs. Sides of abdominal segments convex and rounded, angles of segments rounded. Gills lamellate, oval-shaped.

Composition. Monobasic.

Comparison. Differs sharply from other genera in the rounded sides of the abdominal segments.

***Siphangarus rotundus* Sinitshenkova, sp. nov.**

Plate 11, fig. 7

Etymology. From Latin *rotundus* (rounded).

Holotype. PIN, no. 4626/202, nearly complete and well preserved nymph of the final instar (part and counterpart); Chernovskie Kopi Locality, outcrop 9/1; Upper Jurassic.

Description (Fig. 2d). Nymph. The head has a convex fore margin. The pronotum is short, not wider than the head. The metathorax is short, hind wing sheaths are hidden under the fore wing sheaths. The middle femora are short and broad, 2.5 times as long as wide. The tibiae 0.6 times as wide and 1.37 times as long as the femora. The tarsus is 0.56 times the length and halt the width of the tibia, the claw is long 0.8 times the length of the tarsus. Abdominal segments are short, the fourth segment, which is widest, is 2.83 times as wide as long. The ninth abdominal segment has no indentations latero-posteriorly.

Measurements (mm): the length of the holotype 20.6.

Material. Besides the holotype, paratypes PIN, nos. 4626/205, 254, 266 (outcrop 9/1), 4626/211, 213, 215, 272 (outcrop 9/3), 4626/216, 223 (outcrop 9/2), 4626/233, 242 (outcrop 9/16), fragments of nymphs.

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