A Review of Triassic Mayflies, with a Description of New Species from Western Siberia and Ukraine (Ephemerida = Ephemeroptera)

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Abstract—The world fauna of Triassic mayflies is reviewed. New mayfly species Mesoneta minuta sp. nov., M. triassica sp. nov. (Mesonetae), Archaeobelvingia mogushevae sp. nov. (Torephemeridae) are described from the Middle Triassic deposits revealed by the ultra-deep borehole TSG-6 in the Tyumen' Region. New species Mesoneta picta sp. nov. and Mesobaetis ornata sp. nov. (Siphlonuridae) are described from the Upper Triassic locality of Garazhovka (Ukraine). Triassomachilis uralensis Sharov, 1948 known from Bashkortostan and originally assigned to Thysanura is synonymized under the genus Mesoneta and redescribed. The changes in composition and role of mayfly fauna in freshwater ecosystems within the Triassic are discussed.

INTRODUCTION

The Triassic was a pivotal turning point in the insect evolution. The set of orders characteristic of the Mesozoic were emerging during that time, and the first Recent families appeared; ecological connections that persisted to the present arose (Gall, 1996; Ponomarenko and Sukacheva, 1998). The mayflies are one of the most ancient insect orders and retain a lot of archaic features that have been lost in other phylogenetic branches. On the other hand, the mayflies have undergone key changes. Their role in aquatic ecosystems has not always been constant. All known Paleozoic mayflies belong to extinct families and had some primitive features that have been lost in other Mesozoic groups and others including burrowing mayfly nymphs characterized by advanced features that are unknown in other Mesozoic mayflies. The remains were collected in the deltaic sediments. The nymphs dwelt most probably in the palatal zone of rivers and delta lakes. This fauna will shortly be studied and described. A similar assemblage appears to be found in the speckled sandstone of Majorca (Balearic Islands, Spain). The Triassic mayflies from Majorca are still undescribed, however, judging from the photographs (Colom, 1988, text-fig. 24; Martinez, 1988, text-fig. 345), they are represented by nymphs belonging to at least two species (one of them is burrowing) that resemble those from Vogses.

A single remnant of a forewing, Thuringopteryx gimmi Kuhn, was described from the Buntsandstein (Anisian) of Germany as Odonata (Kuhn, 1937). Later it was redescribed in detail within the same order (Müller, 1965, text-fig. 1–2). In reality, based on the wing venation, i.e. long SC, RS leaving independently from the wing base, characteristic triads in RS and MA systems, this species should be assigned to the Ephemeroptera. Assignment to family is impossible due to poor preservation, but the basal third of the wing is definitely broadened, and this species does not resemble Permian mayfly species that have wings that are oval and homonomous or nearly so.
A single fragment of the forewing of the mayfly *Montralia muelleri* Via et Calzada assigned to the family Mesephemeridae has been found in the more recent sediments (shelly limestone, Upper Ladinian) of Spain, Tarragona Province (Via and Calzada, 1987, text-fig. 1). Originally this species was allocated to Odonata (Via et al., 1977). It is difficult to comment on this identification since the description is followed by a small photograph and a somewhat inaccurate drawing. The inaccuracy of the drawing and necessity of restudying the holotype have been pointed out by Martínez-Delclòs (1995).

A small fragment of the apical portion of a mayfly wing was found in the Middle Triassic of Cheshire, England (Thompson, 1965). The systematic position of this fossil cannot be clarified, but the find is certainly genuine and testifies to the widespread distribution of mayflies in Europe during the Triassic.

A nearly complete specimen with well preserved wing venation has been discovered by W. Krzeminski in a collection of Middle–Upper Triassic fossils from Switzerland (Meride. Ticino Canton, housed in the Museo Cantonage di Storia Naturale Lugano). The head is not preserved, but the body and long legs are clearly visible. It resembles the mayfly *Lithophlebia* (Lithophlebiidae) from the Triassic of Southern Africa (see below) in the shape of wings and their venation. It is similar also to an undescribed Permian imago from Germany (Völkel, 1959) in the wings being narrow and the legs being long.

As for Eastern Europe, Triassic mayflies are recorded in the locality of Garazhovka, Khar’kov Region, Ukraine, in the sediments of Protopivskaya Formation, Late Carnian–Early Norian. This locality was characterized in general by Stanislavskii (1976) and Dobruskina (1980). Remains were collected in lake deposits and apparently belong to taphonomically autochthonous limnic mayflies. Mayflies from Garazhovka were mentioned elsewhere as presumably close to *Mesoplecotopteron* (Chernova, 1980; Kalugina, 1980). However, in the course of studying this material it was found that this opinion erroneous. There are 19 nymph remains in total. Seventeen individuals belong to new species described below, *Mesoneta picta* sp. nov. (Mesonetidae. 10 specimens) and *Mesobaetis ornata* sp. nov. (Siphlonuridae. 6 specimens). Additionally, two individuals cannot be identified precisely due to their poor preservation, but can tentatively be assigned to the same genera. viz. specimen PIN, no. 3320/62 to *Mesoneta?*, specimen PIN, no. 3320/50 to *Mesobaetis?*. Winged mayflies were not found. It should be noted that fossils form the Garazhovka locality are more clearly visible in polarized light, which reveals some morphological details such as the pattern of the abdominal tergites pattern indistinct under unpolarized lighting.

In European Russia Triassic mayflies have been recorded only in the locality of Nakaz in Bashkortostan, Ladinian, Bukobai Formation (Dobruskina, 1980). Two incomplete nymphs are found here. They were originally described in the order Thysanura under the name *Triassomachilis uralensis* (Sharov, 1948). Later Rasnitsyn (1980) suggested that they were Ephemeroptera. Re-examination of the type material showed them to be mayflies of the genus *Mesoneta*. The specimen PIN, no. 439/3(4) demonstrates a gill on the 7th segment that is thickened along its outer margin. This feature is characteristic of the genus *Mesoneta*. The oblique folds were misinterpreted as styli in the other specimen. Such folds result from the compression of convex abdominal segments during burial. The species is redescribed below. It should be noted that new collections from the type locality and deposits of the Bukobai Formation in the neighboring Orenburg Region did not yield further representatives of this species.

In Asia Triassic mayflies have been recorded in southern Urals, western Siberia, and in Kyrgyzstan. Interestingly, no mayflies are known from the relatively rich, i.e., 97 specimens, collection from the Upper Triassic of Kenderlyk, eastern Kazakhstan.

Martynov (1935, p. 38, text-fig. 1) described a nymph from the Upper Triassic deposits (Group, Rhaetian) of the brown coal field in Chelyabinsk Region near the settlement of Sukhomesovski, borehole 22, depth 234–236.93 m. It is represented by an abdomen impression that is 5.5 mm in length and has a spotted pattern. Martynov assigned it provisionally to the family Mesephemeridae. A generic name was not proposed, the specific epithet is *ornata*. Mesephemerid nymphs are unknown, and this specimen is considerably smaller that was indicated by Martynov. It is likely that this nymph does not belong to this family, and judging from the color pattern on the tergites, this species is not similar to any known mayfly. The second find from the same area (Chelyabinsk Region, Tugai-Kul’ locality, spoil bank of a coal quarry, Korkinskoe Group, Rhaetian) represents the abdomen of a nymph, 4.2 mm in length. It is impossible to identify this specimen precisely, but the similarity of the habitus to *Mesobaetis* nymphs is noteworthy.

In Western Siberia the mayfly remains described below were found in the core of the ultra-deep borehole TSG-6 in Tyumen’ Region (Urengoi District, 65–70 km east-southeastwards of Novyi Urengoi, near the station of Korotcheaev, samples 8402 and 7722) and sent to the PIN by the geologist N.K. Mogucheva in February, 1992. Pollen complexes were preliminary dated as Indian–Early Olenekian in the interval 6439–6457 m (sample 8402) and as Olenekian–Anisian in the interval 6252–6304 m (sample 7722) (Bochkarev and Purtova, 1994). More detail investigation indicates, however, a more recent, Middle Triassic age (Tampesikaya Group, Varengayakhinskaya Formation) (Kirichkova et al., 1999). There are five insect remains in the sample 8402. viz. a well preserved cockroach no. 4683/5, a crushed stonefly nymph no. 4683/4, and three mayfly nymphs.
two of which belong to Mesoneta minuta sp. nov. (Mesonetidae) and Archaeobehningia mogutshevae sp. nov. (Torepheremidae), the third specimen no. 4683/3 could not be identified even at family level. This latter specimen is represented by the part and counterpart of a young nymph 5.7 mm in length and with short legs and a very long narrow abdomen that is 3.6 times as long as the thorax. In general appearance it most resembles mayflies of the genus Albisca. There is one nymph of Mesoneta triassica sp. nov. and an insect fragment of unclear affinity that have been found in the sample 7722. All remains found in the core are carbonized.

Extremely rare mayflies are recorded in the Madygen Formation in two localities in Kyrgyzstan, Osh Region, Batken District. The Madygen Formation was dated differently, now it is considered, however, to be Ladinian–Carnian (Dubruskina, 1980). The collection of insects from the Madygen Formation is very large and includes more than 15000 individuals. The extremely rare occurrence of mayflies proves their allochthonity. The part and counterpart of a forewing sheath and a thorax fragment, specimen PIN, no. 2087/6, have been found in the Madygen locality, Madygen Dale, ca. 1 km eastwards of the river bed Suuk-Tanga. The length of the sheath is 3.7 mm, it is oval, narrow, and relatively long (Fig. 1). The unbroadened basal third suggests that the imaginal wings were comparatively narrow and homonomous as in Paleozoic Prot­ereismatidae and Mithshodotaidae and Triassic Lithophlebiida. The fragment of a nymph abdomen, specimen PIN, no. 2069/40, has been found in the Dzhailoucho locality, Madygen Dale, northern area, 30 km westwards of Shurab. This fragment is 6 mm long and most closer resembles Mesobaetis. The absence of details prevents more precise identification.

Although there are a number of rich Triassic entomo­faunas known in Gondwanaland, mayflies have been recorded only in the Upper Triassic of South Africa, Molteno Formation. The peculiar Lithophlebia optata Riek was described based on a wing fragment within a family of its own. Lithophlebiidae (Riek, 1976; Hubbard and Riek, 1977). As it has been noted above, this family probably appears to occur in the Triassic of Switzerland. Recently, new finds of Lithophle­bia wings have been reported from the same Formation (Anderson et al., 1998). Additionally, seven insect remains identified as Microcorphyia bristletails were found there. Bristletails are extremely scarce in the fossil record, and it is extremely unusual that such a considerable number should be found in one locality. Since the bristletails and mayfly nymphs share a similar habitat, it can be suggested that the bristletails from the Molteno Formation are mayfly nymphs, probably Lithophlebia. Five wing remains of the latter have been found in the same locality Bir 111 (Anderson et al., 1998) buried in the sediments of a flood-plain lake, whereas 42 other outcrops of this formation yield neither Lithophlebia nor Microcorphyia.

All known Triassic mayflies from France and South Africa differ sharply from Jurassic ones. The winged mayflies were dominated by forms with narrow and more or less homonomous Paleozoic-like wings. In contrast, in Ukrainian and Western Siberian material all known nymphs closely resemble those from the Jurassic ones. All families and even genera identified are widespread in the Jurassic of Siberia, Mongolia, and China (Sinitshenkova, 1985, 1989, 1991; Hong et al., 1995). The genus Mesonota is often recorded in association with Mesobaetis in the Lower–Middle Jurassic (Cheremkhovo, Osinovka, and Ichetui Formations) of the Cis-Baikal, Transbaikalia, and China (Hong et al., 1995). The both genera are found in association in the Chernovskie Kopi locality. The age of this locality is debatable, however based on its mayfly and stonefly fauna it should be Jurassic rather than Cretaceous (Sinitshenkova, 1998, 2000). In some Jurassic localities these genera are found separately. Thus, only one species of Mesoneta is recorded in the Lower Jurassic, the Bokhto Formation, of Transbaikalia (Zola locality), Lower–Middle Jurassic, the Hamarhuvuuriin and Jargal­ant Formations, of Mongolia (Tushilga and Oshin­Boro-Udzuur-Uul localities), Upper Jurassic of Trans­baikalia (Uda Formation, Borzhe-2 locality) and Mon­golia (Ulaan-Ereg Fromation, Houtin-Hotgor locality), and one species of Mesobaetis is recorded in the Upper Jurassic–Lower Cretaceous, the ogóln Formation of Mongolia (Hutuliin locality).

No Early Triassic mayflies are known to date. Apparently, the typical Jurassic limnetic mayfly fauna started in the Middle Triassic. In the Middle and Upper Triassic the aquatic insect fauna became more diverse. Besides the mayflies, the dragon-flies, stone-flies, aquatic beetles and bugs are frequently found, and the caddis-flies diversified. In the Mesozoic nymph remains frequently dominate over imagoes, but in the Paleozoic the reverse is true. The existence of water bodies, e.g., oxbow-lakes and delta lakes, with conditions resembling those of Jurassic and Early Cretaceous lakes can be postulated for the Triassic.
In some oryctocoenoses the mayflies clearly dominate over other aquatic insects, but in Triassic oryctocoenoses they occur considerably more rarely than in Jurassic, and only in deltaic sediments. In Vosges odonatans, stoneflies, and megalopteran larvae are found besides the mayflies. The dragonflies are dominant in South Africa, stoneflies in Kazakhstan, and the stoneflies and megalopterans dominate in the Garazhovka locality. The role of rheophilous mayflies in Triassic flowing water bodies it is difficult to estimate due to the scarce material. However, their role in deltaic limnic ecosystems resembling those of the Jurassic became important in the Middle Triassic. In that time water bodies with the ecosystem characteristic of the Mesozoic appeared (Ponomarenko, 1996). Paleozoic mayflies supposedly inhabited flowing waters during the Triassic, which results in only imagoes being preserved. In contrast, in the Jurassic a new fauna started to inhabit stagnant water bodies, and this fauna played a great role in freshwater Jurassic ecosystems.

SYSTEMATIC PALEONTOLOGY

Family Mesonetidae Tshernova, 1969

Genus Mesoneta Brauer, Redtenbacher, Ganglbauer, 1889

Triassomachilis: Sharov, 1948, p. 517. (syn. nov.)

Mesoneta minuta Sinitshenkova, sp. nov.

Plate 4, fig. 1

Etymology. From Latin minuta (small).

Holotype. PIN, no. 4683/1, part and counterpart of complete well preserved nymph; Tyumen’ Region, ultra-deep borehole TSG-6, sample 8402, depth 6447.8–6457.1 m; Middle Triassic, Tampeiskaya Group, Varengayakhinskaya Formation.

Description (Fig. 2a). Nymph. This is a very small mayfly with a transverse oval head. The anterior margin of the head is evenly convex, the head is nearly twice as broad as long. The pronotum is short, 4 times as broad as long. The fourth abdominal segment is the broadest and nearly 5 times as broad as long. The ninth abdominal segment is the longest, 1.5 times longer than the last segment and nearly twice as long as the eighth one. The body is nearly three times the width of the abdomen.

Measurements (mm): nymph body length, 3, abdomen length, 2.5, maximum abdomen width, 1.1.

Comparison. The species clearly differs from all known species in its extremely small size and transverse oval flattened head. In the proportions of the body and abdomen the new species is most similar to M. anti­qua Br., Redt., Ganglb., 1889, which was the smallest known species until recently.

Remarks. There is a clear dependency of body size on the age of the enclosing sediments among the species of Mesoneta. The more ancient species are smaller, the oldest species, M. minuta sp. nov. is the smallest, whereas one of the youngest species, M. mongolica Sinitsh., 1989 from the Ulaan-Ereg Formation of Mongolia (Houtin-Hotgor locality), is the largest, 17–23 cm.

Material. Holotype.

Mesoneta triassica Sinitshenkova, sp. nov.

Plate 4, fig. 2

Etymology. From the Triassic Period.

Holotype. PIN, no. 4683/6, impression of nearly complete well preserved nymph; Tyumen’ Region, ultra-deep borehole TSG-6, sample 7722, depth 6264.1–6277.9 m; Middle Triassic, Tampeiskaya Group, Varengayakhinskaya Formation.

Description. The species clearly differs from all known species in its extremely small size and transverse oval flattened head. In the proportions of the body and abdomen the new species is most similar to M. anti­qua Br., Redt., Ganglb., 1889, which was the smallest known species until recently.

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Material. Holotype.

Mesoneta picta Sinitshenkova, sp. nov.

Plate 4, fig. 3

Etymology. From Latin pictus (colored).
Fig. 2. Representatives of the genus *Mesoneta*: (a) *M. minuta* sp. nov., holotype PIN, no. 4683/1, nymph; (b) *M. triassica* sp. nov., holotype PIN, no. 4683/6, nymph; (c) *M. picta* sp. nov., holotype PIN, no. 3320/51, nymph; (d) *M. uralensis* (Sharov, 1948), lectotype PIN, no. 439/4, nymph.

**Holotype.** PIN, no. 3320/51, part and counterpart of complete well preserved nymph; Ukraine, Khar’kov Region, Izyum District, mouth of the Bereka River, tributary of the Severskii Donets River, right bank between the Garazhovka and Bol’shaya Kamy- shevakha settlements; Upper Triassic, Protopivskaya Formation.

**Description** (Fig. 2c). Nymph. The head is rounded, somewhat broader than long. The pronotum is rectangular, nearly 3 times as broad as long. The
Mesoneta uralensis (Sharov, 1948)

Plate 4, fig. 4

Triassomachilis uralensis: Sharov, 1948, p. 517, text-figs. 1, 2.

Lectotype. PIN, no. 439/3(4), part and counterpart of a nymph without legs; Bashkortostan, Kyrgazin District, left bank of the Nakaz River, the lower part of the outcrop opposite the graveyard near the village of Staraya Mikhailovka; Middle Triassic, Ladinian, Bukobai Formation.

Description (Fig. 2d). Nymph. The head is elongate, just slightly longer than broader. The pronotum is short, more than 5 times as broad as long. The anterior margin is concave, the posterior margin is convex. The abdomen is 3.3 times as long as broad. The fourth abdominal segment is the broadest, 4 times as broad as long.

Measurements (mm): complete nymph length, 6 (lectotype), decapitated nymph length, 7 (paralectotype).

Comparison. The species most closely resembles M. triassica sp. nov. in body size, but differs in the pronotum being shorter.

Remark. The holotype was not originally designated. The syntypes of T. uralensis are labeled with colored marks, as it is accepted in PIN. The specimen no. 439/1 is red labeled that means holotype, and the specimen no. 439/3(4) is green labeled that means...
paratype. It is in accordance with the author's paper labels. However, the specimen no. 439/3(4) is better preserved nymph with the head and is designated here as the lectotype.

**Material.** Besides the lectotype, the paralectotype PIN, no. 439/1, impression of the nymph without head.

**Family Siphlonuridae Ulmer, 1920**

**Genus Mesobaetis Brauer, Redtenbacher, Ganglbauer, 1889**

*Mesobaetis ornata* Sinitshenkova, sp. nov.

Plate 4, fig. 5

**Etymology.** From Latin *ornatus* (ornamented).

**Holotype.** PIN, no. 3320/44, part and counterpart of well preserved complete nymph; Ukraine, Khar'kov Region, Izum District, mouth of the Berekia River, tributary of the Severskii Donets River, right bank between the Garazhovka and Bol'shaya Kamyshevakha settlements; Upper Triassic, Protopivskaya Formation.

**Description (Fig. 3a).** Nymph. The head is rounded. The anterior margin of the pronotum is concave, the anterior corners are acute, the posterior corners are smooth, the lateral sides are beveled. The forewing sheaths reach the midlength of the first abdominal segment. The abdominal tergites have a medial triangular patch that is broadened at the fore margin, the gill bases at the posterior edge of each tergite are darkened. The tail filaments are darkened in their apical third.

**Measurements (mm):** nymph length, 12.6 (holotype), tail filament length, 4.

**Comparison.** The new species resembles *M. allata* Sin. in the tail filaments being darkened, however it clearly differs from the latter in the anterior margin of the pronotum being concave, the color pattern of the abdominal tergites, and the larger size.

**Material.** Besides the holotype, paratypes PIN, nos. 3320/45–49, nymph fragments from the same locality.

**Family Toheroheremidae Sinitshenkova, 1989**

**Genus Archaeobehningia Tshernova, 1977**

*Archaeobehningia modesthesae* Sinitshenkova, sp. nov.

Plate 4, fig. 6

**Etymology.** After geologist N.K. Mogutcheva.

**Holotype.** PIN, no. 4683/2, part and counterpart of well preserved nymph fragment; Tyumen' Region, ultra-deep borehole TSG-6. sample 8402, depth 6447.8–6457.1 m; Middle Triassic, Tampeiskaya Group, Varengaykhniska Formation.

**Description (Fig. 3b).** Nymph. The head in profile. The antenna is inserted on a small prominence near the anterior edge of the head. The pronotum is rectangular, 3 times as broad as long. The mesothorax is somewhat longer than the prothorax, the forewing sheath overlaps the anterior margin of the first abdominal segment. The metathorax is short, the hindwing sheath is completely concealed under the forewing sheath. The fore legs are better developed than the middle and hind ones, the hind legs are notably shortened. The ventral surface of the abdominal segments have longish pubescence.

**Measurements (mm):** total length, 13, complete nymph length, ca. 19.

**Comparison.** The species differs from *Archaeobehningia edmundsi* Tshern., 1977 in the antennae being inserted on a small prominence near the anterior edge of the head.

**Remarks.** The longish pubescence of the ventral surface of the abdomen may refer to the tergalia that are not preserved. Usually, burrowing mayflies have tergalia densely covered with long hairs.

**Material.** Holotype.

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**REFERENCES**


A REVIEW OF TRIASSIC MAYFLIES


Sinitshenkova, N.D., Jurassic Mayflies (Ephem erida = Ephemeroptera) from Southern Siberia and Western Mongolia, in Yurskie nasekomye Sibiri i Mongolii (Jurassic Insects of Siberia and Mongolia), Moscow: Nauka, 1985, pp. 11-23.


Sinitshenkova, N.D., New Mesozoic Mayflies from Transbaikalia and Mongolia, Paleontol. Zh., 1991, no. 1, pp. 120-123.


