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A new mayfly species *Triassodotes rasnitsyni* sp. nov. of the family Misthodotidae Tillyard, 1932 (Insecta; Ephemera, Permoplectoptera) from the Triassic deposits of Kuzbass, Russia

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The mayfly sister group family Misthodotidae Tillyard, 1932 includes two genera: *Misthodotes* Sellards, 1909 and *Triassodotes* Sinitshenkova & Papier, 2005. *Misthodotes* species have so far been known only from the Permian, six Early Permian species have been described from North America (Carpenter, 1933, 1979; Tillyard, 1932, 1936), one from Germany (Kinzelbach & Lutz, 1984) and two from the Perm region of Russia (Tshernova, 1965). Only three species are known from the Upper Permian deposits: two from the famous Isady locality in the Vologda Region of Russia (Sinitshenkova, 2013; Sinitshenkova & Vassilenko, 2012) and one from the Urals (Novokshonov *et al.*, 2002). The only *Triassodotes* species was found in the Middle Triassic Grès à Voltzia deposits in France (Sinitshenkova *et al.*, 2005).

In this article a new species, *Triassodotes rasnitsyni* sp. nov. from the Early Triassic deposits of Kuzbass, Russia, is described. Among the mayflies, only the family Misthodotidae survived the Permian/Triassic global crisis, while in the Permian and Triassic it is represented by different, but very close genera.

Material and methods

Part and counterpart of the fossil PIN, No. 4887/140, deposited at the A.A. Borissiak Palaeontological Institute of the Russian Academy of Sciences in Moscow, Russia, were examined using a Leica M165C, both dry and immersed in alcohol. Photographs were taken under alcohol using a Canon camera DFC425. Drawings were made from the enlarged photographs.

Abbreviation of wing veins are given as: C, costal; SC, subcostal; R, radius; RS, radius posterior; MA, median anterior; MP, median posterior.

Systematic palaeontology

Order Ephemera Latreille, 1810

Family Misthodotidae Tillyard, 1932

Triassodotes Sinitshenkova & Papier, 2005

Type species. *T. vogesiacus* Sinitshenkova & Papier, 2005.

Triassodotes rasnitsyni sp. nov.

(Fig. 1)

Holotype. PIN 4887/140, part and counterpart of mayfly imago with four superimposed wings without head and poorly preserved abdomen without cerci. The holotype is stored at the A.A. Borissiak Paleontological Institute RAS, Moscow.

Etymology. Named for the outstanding paleoentomologist Alexandr P. Rasnitsyn.

Diagnosis. Imago. On the fore wing SC does not reach the apex of the wing, flows into C slightly proximal to the middle of the wing; the first RS fork is in the basal third of the wing. Two intercalary veins depart from the posterior branch of RS, the second of them forms a triad, and one intercalary vein departs from the anterior branch. The transverse veins are numerous. The apex of the hind wing is narrowed; the ratio of the length of the fore wing to the length of the hind wing is 1.4.

Type locality and horizon. The specimen was found in the locality Babiy Kamen in the basal Malsevo Group at the Tom' River of Kemerovo Region, Keznetsk Basin, Russia. The age of the deposits is considered to be Early Triassic.

Description. The described specimen 4887/140 is a remnant of an imago with superimposed fore and hind wings, the abdomen is partially preserved, the head is absent, the thoracic region is severely damaged, only some sclerites are preserved. The end of the abdomen with cerci is absent, so determination of the sex of the mayfly is impossible. The basalmost part of the forewing of *T. rasnitsyni* sp. nov. has not been preserved, therefore, it is impossible to speak with certainty about the presence or absence of costal brace. The cubital and anal parts of wings are also absent. On the hind wing, the first fork of RS is located in the basal third of the

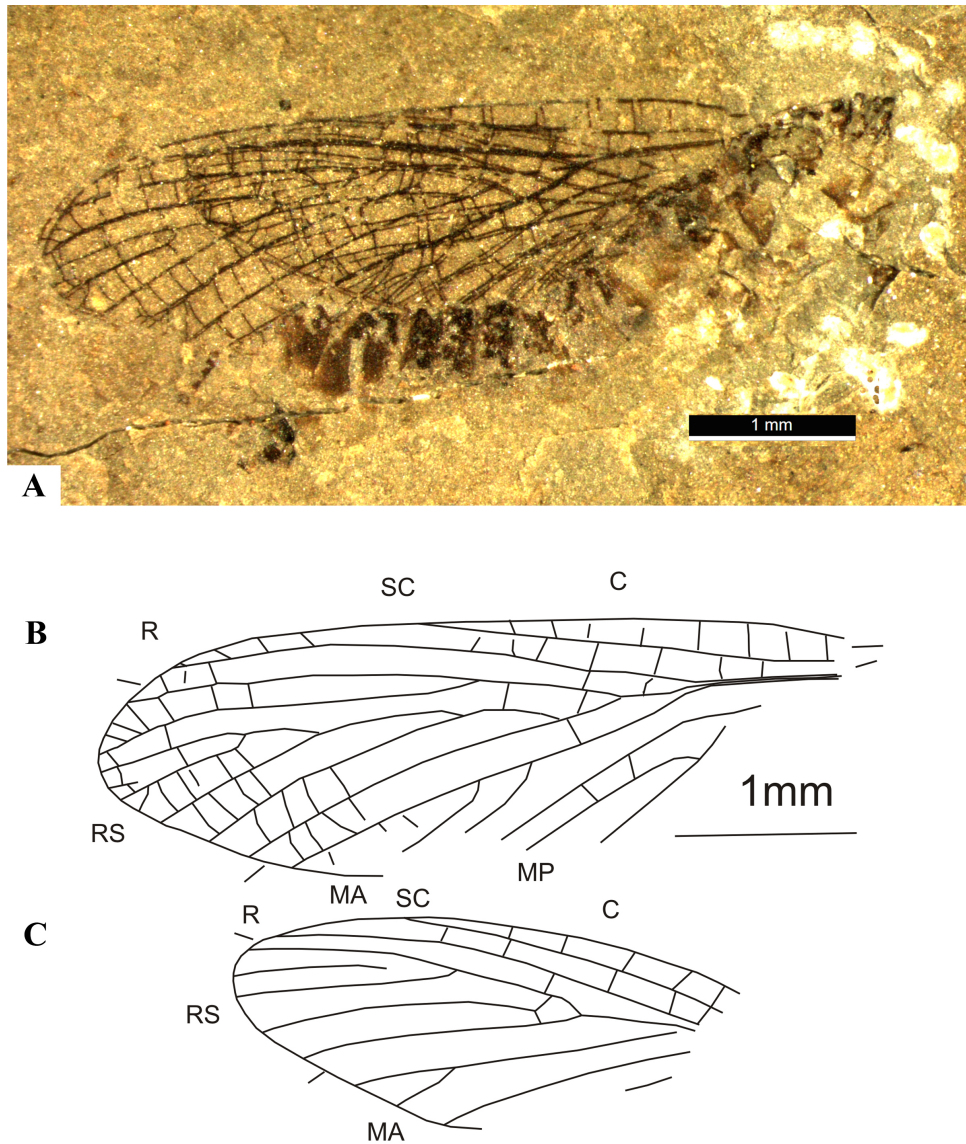


FIGURE 1. *Triassodotes rasnitsyni* sp. nov. Holotype, part PIN N 4887/140. **A**, Photograph. **B**, Fore wing. **C**, Hind wing.

wing, an intercalary vein departs from its anterior branch and forms a triad, and one intercalary vein departs from its posterior branch. MA with short fork near the wing margin. The length of the fore wing is 4.6 mm, its width is about 1.5 mm, hind wing length 3.3 mm, its width 1.2 mm.

The new species differs from *T. vogesiacus* in smaller size (the length of *T. vogesiacus* fore wing is 5.5 mm) and the character of RS branching on the fore wing; in *T. vogesiacus*, its posterior branch is simple, all intercalary branches are separated from the anterior RS branch.

Discussion

By many features of the structure and venation of the wings, the Permian *Misthodotes* and Triassic *Triassodotes* are similar. On the oval forewings, the anterior margin is slightly

convex, the costal, subcostal, and radial fields are wide, the bases of R, RS, and MA stems are closely approximated in the basal quarter of the wing, RS flows into the wing margin with seven branches, MA and MP are three-branched. These similarities leave no doubt that the Triassic genus *Triassodotes* belongs to the family Misthodotidae.

The difference between *Triassodotes* and *Misthodotes* consists in a shorter SC and a shorter hind wing relative to the fore wing in *Triassodotes*. The shortening of the hind wing in Triassic mysthodotids corresponds to the general trend in the evolution of mayflies. In addition, the Triassic species are smaller. The wing length of the smallest Permian species reaches 6 mm—these are the Early Permian *M. delicatulus* (Tillyard, 1936) from Kansas and *M. dubius* Sinitshenkova, 2013 from the Late Permian of the European part of Russia. Other Permian species *Misthodotes* are larger, their wings are from 9 to 15 mm long. The forewing length of *T. vogesiacus* is 5.5 mm, and the new species is the smallest among all

species of the family, the length of its forewing does not exceed 4.3 mm.

Unfortunately, the preservation of the Triassic species does not allow us to confidently judge the presence or absence of such feature important for the phylogeny of the order as costal brace (Sroka *et al.*, 2021). The characters of adults, which can be studied using the available material, make it possible to consider the Triassic representatives of Misthodotidae as more advanced than the Permian ones. A detailed redescription of type specimens of *M. sharovi* Tshernova, 1965 and *M. zaleskyi* Tshernova, 1965 from the famous Early Permian locality of Tsherkarda made it possible to reconstruct their flying apparatus and the lifestyle features of adults and nymphs (Sroka *et al.*, in press). Perhaps the *Triassodotes* species had a better flight ability than the Permian ones. The *Triassodotes* nymphs are unknown, and the *Misthodotes* nymphs had sclerotized ribs on the gills, characteristic of many Mesozoic taxa. Considering the great similarity between the adults of *Misthodotes* and *Triassodotes*, it can be assumed that their nymphs are also similar. If so, then the peculiar features of the gills could give advantages to Misthodotidae nymphs, that allowed them to survive changes in the environment on the Permian/Triassic border.

The families Misthodotidae and Prosopistomatidae Sellards, 1907 occur together in the Early Permian deposits of North America (Tillyard, 1932, 1936; Carpenter, 1933, 1979) and the Late Permian deposits of the European part of Russia (Sinitshenkova & Vassilenko, 2012; Sinitshenkova, 2013). Both families are characterized by almost homonomous wings, longer in Prosopistomatidae and shorter, almost oval in Misthodotidae, while Prosopistomatidae are much larger.

Prosopistomatidae have not yet been found in Triassic sediments. By the end of the Permian period, mayflies with homonomous wings are almost extinct, perhaps one of the reasons was imperfect flight and lifestyle features. The subsequent evolution of mayflies is characterized by a reduction of the hind wing and a change in the wings shape. However, in the Triassic, rare mayflies with homonomous wings are still preserved, as evidenced by the finding of the families Tintorinidae Krzemiński & Lombardo, 2001 in the Middle Triassic of Switzerland (Krzemiński & Lombardo, 2001) and Litophlebiidae in the Triassic of South Africa and Poland (Riek, 1976; Sinitshenkova *et al.*, 2015). Along with them, the modern family Siphonuridae Ulmer, 1920 (*s.l.*) already appears in the Middle Triassic (Sinitshenkova *et al.*, 2005).

Conclusion

The discovery of a new species belonging to the genus *Triassodotes* confirms the earlier statement that the family

Misthodotidae crossed the Permian/Triassic boundary. Paleontological data indicate a change from Paleozoic mayfly groups to Mesozoic ones. The Paleozoic faunas are characterized by mayflies with homonomous wings; in the process of evolution, the hind wing was reduced, and mayflies with homonomous wings are completely absent in the modern fauna. However, in the Triassic and even in the Jurassic, they are found, which can be regarded as a gradual rather than catastrophic change in mayfly groups.

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