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Description of a Larva of *Kargalarva permosialis* gen. et sp. nov. (Coleoptera: Schizophoromorpha) from the Kargala Fossil Site

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Abstract—An aquatic larva of the holometabolan species *Kargalarva permosialis* gen. et sp. nov. is described from the Upper Permian of the Kargala outcrop (Orenburg Oblast, Russia). This larva was formerly known as *Permosialis* sp. from the preliminary description by A.G. Sharov (1953). It is assigned to the infraorder Schizophoromorpha (Coleoptera). An aquatic lifestyle is assumed for at least a part of the taxa of this infraorder. The larval characters, shared by the orders Coleoptera and Megaloptera, are discussed.

Keywords: Coleoptera, Schizophoromorpha, Kargala, Permian, larvae, holometabolans
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INTRODUCTION

Insects with complete metamorphosis (Holometabola) are the most extensive taxon of the organic world in terms of the number of species. Holometabolan species are more numerous than all other animals and plants. However, Holometabola is not so diverse in the number of genera, and differs little in the number of suprageneric taxa from other taxa of the supraordinal rank. This may indicate a high diversity achieved through subtle adaptations to multiple ecological niches, rather than by abundance of significant morphogenetic transformations. The most important achievement of Holometabola is that during ontogenesis they pass instars of larvae and adults, which are usually completely different in structure and ecology. This makes it possible to split requirements to feeding and distribution into separate stages, while other insects are forced to combine such requirements according to adaptive compromise, and, as a result, adaptations to both remain insufficient. Therefore, studies on the ontogenesis of holometabolans are very important not only for understanding their evolution, but also for general evolutionary problems. It is essential that two different organisms (i.e., larva and imago) appear from the same genome, and this circumstance is very interesting in the light of epigenetic constructions.

Unfortunately, studies of larvae are still far behind descriptions of adults. The lack of attention to ontogeny is vividly illustrated by the indifference, with which the results of A.L. Tikhomirova's works, most important for understanding it, were taken. We know particularly little about the larvae of ancient holometabolans. Very few Palaeozoic larvae are described (Nel et al., 2013; Aristov, Rasnitsyn, 2015; Haug et al., 2016; etc.), while others are only mentioned in the literature (Sharov, 1953; Kukalová-Peck, 1997; etc.). This work contains a redescription of one of them.

The widely known Permian holometabolan larva from the Kargala site (Russia, Orenburg Oblast, Sakmara District; Middle Permian, Urzhumian Stage, Amanak Formation, *Estemmenosuchus uralensis* and *Ulemosaurus svijagensis* zone, ~265 Ma: Shcherbakov, 2008) was indicated by A.G. Sharov (1953) as a larva of the genus *Permosialis* (Martynov, 1928); its brief description, photograph, and drawing were provided, however, without proposing the species taxon. Correlation of the adult and the larva of this genus remained problematic. Subsequently, the genus *Permosialis* Martynov, 1928, originally attributed to Megaloptera, was transferred to Miomoptera, which apparently had terrestrial larvae (Riek, 1976). Thus, it became evident that this larva should not be assigned to Miomoptera, and it was placed in Coleoptera: Gyrinidae (Beutel and Roughley, 1988) or in Schizophoromorpha (?Rhombocoleidae) (Prokin et al.,

2013b). However, neither a redescription of the specimen with its designating as a holotype, nor proposals of a taxon for it have ever been done, which prompted us to this publication.

Kargala is one of the long-known sites where remains of insects were found. It is especially important, because they were found there together with vertebrates. This allows enough accurate correlation. The site represents long-abandoned copper mines, whose rock dumps became a source of paleontological findings. This specimen is more likely to have come from the dumps of the Kuz'minovsky mine. The first insect remains were found here in 1929 by I.A. Efremov and M.N. Chueva; then several other collectors worked at this site. Currently, more than 300 remains of insects from 13 orders, including approximately 10 larvae of three morphological types, are deposited in the collection of the Borissiak Paleontological Institute (PIN), Russian Academy of Sciences. Members of four orders of Holometabola have been recorded from Kargala (Martynov, 1937; Martynova, 1942; Ponomarenko, 1963, 1969, 2013): Neuroptera (*Sialodopsis similis* Martynov, 1937), Mecoptera [*Mesochorista kargalensis* (O. Martynova, 1942), *M. inglora* (O. Martynova, 1942), *Petromantis stigma* O. Martynova, 1942, and *P. mirabilis* (O. Martynova, 1942)], three undescribed impressions of small-sized Miomoptera, and the Coleoptera. As members of the latter order, four species have been described from this site: *Kaltanicupes kargalensis* Ponomarenko, 1963 (Permocupedidae), *Tecticupes martynovi* Ponomarenko, 2013 (Taldycupedidae), *Rossocoleus ellipticus* (Martynov, 1937), and *Rhombocoleites adumbratus* Ponomarenko, 1969 (Rhombocoleidae).

The lack of information on Permian holometabolan larvae does not allow us to confidently attribute the described larva to any order; however, it is assumed to belong to the Coleoptera, in particular, to the infraorder Schizophoromorpha. This assumption is based on numerous finds of holometabolan larvae, which presumably belong to beetles, in outcrops of the Upper Permian–Upper Triassic. These larvae are significantly different from all known ones, and, in accordance with their morphological characters, should belong to a group of beetles widely distributed at that time and with unknown larvae, whose role best suits Schizophoromorpha.

MATERIALS AND METHODS

The photographs presented in this work were taken with a Leica M165C light stereoscopic microscope equipped with a Leica DFC420 digital camera (PIN, Moscow), using the Helicon Focus 5.3.14 and Photoshop CS4 packages. The drawings were adapted for publication in the Autodesk AutoCAD 2015 software.

SYSTEMATIC PALEONTOLOGY

Order Coleoptera

Suborder Archostemata

Infraorder Schizophoromorpha

Family Incertae Sedis

Genus *Kargalarva* Prokin, Ponomarenko et Kirejtshuk, gen. nov.

Etymology. From the Kargala site and Latin *larva* (grub), gender feminine.

Type species. *Kargalarva permosialis* sp. nov.

Diagnosis. Large larvae, weakly tapering posteriorly. Head prognathous, with protruding ocular tubercles and clypeolabral, epistomal (frontoclypeal), Y-shaped ecdysial, and postoccipital sutures. Clypeus transverse, short. Sharp crisscrossing mandibles with denticles on the inner margin. Bases of mandibles partly covered with triangular labrum. Thoracic segments heavily sclerotized, with first segment being narrower that following segments. Pronotal sclerite entire; meso- and metanota with two sclerites, divided by longitudinal ecsuvial suture partly on mesonotum and completely on metanotum. Legs not widened; femur longer than other leg sclerites. Anterior femora and tibiae have long swimming setae. Tarsus with two long, equal, straight claws. Abdomen 10-segmented; each of first nine segments with one pair of lateral processes (probably tracheal gills) pointed at top; segment X with caudal process, possibly homologous to that on dorsal surface of segment X in *Haliplus* (Coleoptera, Haliplidae) (Makarov and Prokin, 2015). Gills with wide base, extending in posterior third of segment, equal to or slightly longer than width of their segment, and twice its length. According to A.G. Sharov (1953), segmentation is discernible at base of some gills.

Species composition. *K. permosialis* sp. nov. from Kargala (Upper Permian, Urzhumian Stage).

Remarks. Larva belongs to Holometabola (=Oligoneoptera), as it lacks wing germs, and sclerotization of thoracic tergites is typical of the group. Among holometabolans, it is most similar to larvae of the orders Coleoptera and Megaloptera. It differs from Megaloptera in the narrow and elongated head, the narrow prothorax, which is smaller than meso- and metathoraces (Achtelig, 1981; Beutel and Roughley, 1988), the body slightly tapering posteriorly, the lack of pleurostomal suture of head capsule, and the protruding ocular tubercles. From Sialoidea, it additionally differs in the large number of tracheal gills—7 pairs in recent Sialinae and 8 pairs in Jurassic Sharasialinae Liu et al., 2014 (*Sharasialis fusiformis* Ponomarenko, 2012 from the Shar-Teg)—and also in the lack of clear segmentation of gills and in the equal claws. Larvae of Corydaloidea are distinguished from *Kargalarva* by the lack of lateral processes on segment IX and by developed appendages of pygopods on segment X; they are also characterized by the cervical "segment" of prothorax and a different structure of

Fig. 1. *Kargalarva permosialis* gen. et sp. nov., PIN holotype, no. 199/213, general view of positive impression, photograph; scale bar 5 mm.

abdominal apex, without long process of segment X. Furthermore, all the described wings of Palaeozoic megalopterans are too small, and the respective adult insects should have been much smaller than the described larva.

Kargalarva differs from all the known beetle larvae in the presence of the "megalopteran" traits: free triangular labrum, transverse short clypeus, and clear postoccipital suture. Furthermore, among larval Polyphaga only some Hydrophiloidea possess tracheal gills, but they are characterized by completely different structure of the terminal segments of abdomen. The described larva is too large for the known adults of Permian and Triassic Adephaga (Prokin et al., 2013a). Larvae of Gyrinidae have one pair of forked appendages of segment IX and segment X with a process bearing 4 hooks, which are probably homologous to the two pairs of hooks of pygopods in corydaloids. At the same time, Gyrinidae are unknown earlier than the Lower Jurassic (Ponomarenko and Prokin, 2015; Gustafson et al., 2017). Among dytiscoids, only larvae of the recent genus *Coptotomus* Say, 1830 (Dytiscidae) have six pairs of lateral tracheal gills, but they are characterized by different structure of the abdominal apex, which is similar to caraboids and dytiscoids (Prokin et al., 2013b), whereas segment IX bears urogomphs (or is represented only by urogomphs). The larva cannot be assigned to Caraboidea either, because the aquatic larvae of the latter, particularly those with tracheal gills, are absolutely unknown to date.

Kargalarva differs from the undescribed Triassic holometabolan larvae of the Sialidae type (Coburger Sandstone, Voltzia Sandstone, Garazhovka, deposits of Mallorca) in the larger number of tracheal gills and protruding ocular tubercles.

Kargalarva is most similar to larvae of Myxophaga, which have eight lateral processes of segments I–VIII and bifid segment IX, protruding ocular tubercles, and head narrower than prothorax. Some authors place the infraorder Schizophoromorpha Ponomarenko, 1968 (Schizophoroidea Ponomarenko, 1968, Asiocoleoidea Rohdendorf, 1961, and Rhombocoleoidea Rohdendorf, 1961) to the suborder Myxophaga (Bouchard et al., 2011). A large-sized beetle, *Rhobocoleites adumbratus* Ponomarenko, 1969 (Rhombocoleidae), was described from Kargala, which suggests attribution of the *Kargalarva* to this family (Prokin et al., 2013a).

***Kargalarva permosialis* Prokin, Ponomarenko et Kirejtshuk, sp. nov.**

Etymology. From the genus *Permosialis*, to which the studied specimen was attributed by Sharov (1953); noun in apposition.

Holotype. PIN, 199/213, positive and negative impressions; Kargala site, Orenburg Oblast; Urzhumian Stage.

Description (Figs. 1–4). Postoccipital suture reaches coronal (epicranial) suture. According to Sharov (1953), the outline of scape preserved at the base of one of mandibles. Pronotum tapering posteriorly, trapezoid, almost completely covered with sclerite. Mesonotum wider and longer than pronotum, rectangular, with sclerite in anterior half partly divided medially. Metanotum of equal width with mesonotum, almost completely covered with sclerite. First two segments of abdomen shorter than the following segments. Widest segments IV and V reach 5 mm (without lateral processes). Segments VIII and IX bear shorter processes than others. Boundary between segments IX and X weakly discernible.

Measurements in mm: length, 24; maximum width, 5.

Material. Holotype.

DISCUSSION

Two lineages of beetle larvae were distributed in the Upper Permian–Upper Triassic. The first lineage ("Sialidae" type: Prokin et al., 2015) includes larvae with the caudal process on segment X and 6–9 pairs of lateral non-segmented tracheal gills, with one tracheal trunk entering each. Among them, the taxa with the larger number of pairs of gills (9–8 pairs) and walking

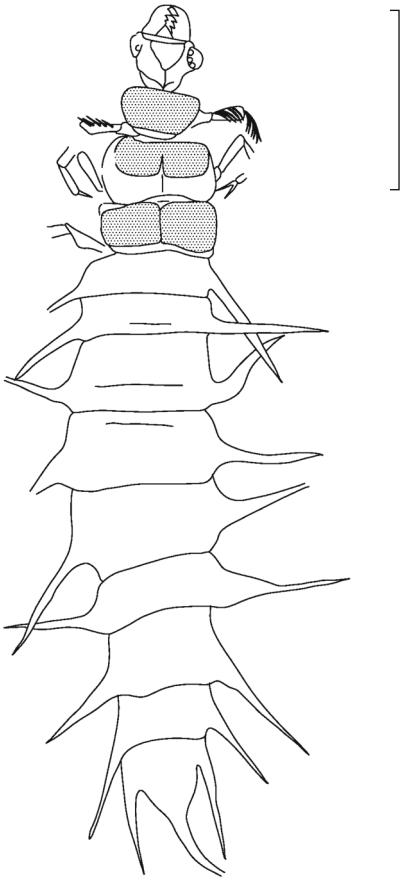

Fig. 2. *Kargalarva permosialis* gen. et sp. nov., PIN holotype, no. 199/213, general view of positive impression, drawing; scale bar 5 mm.

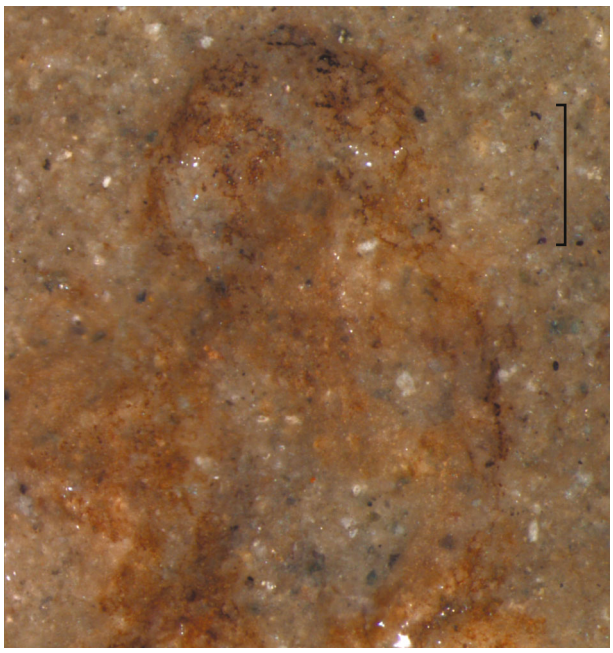

Fig. 3. *Kargalarva permosialis* gen. et sp. nov., PIN holotype, no. 199/213, negative impression, head, photograph; scale bar 0.5 mm.

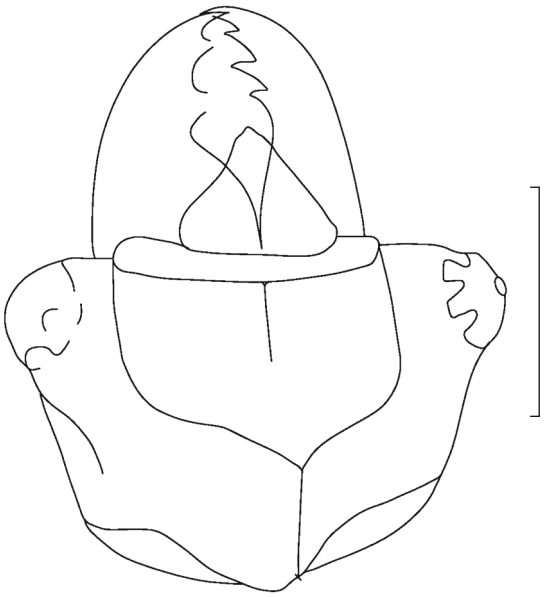

Fig. 4. *Kargalarva permosialis* gen. et sp. nov., PIN holotype, no. 199/213, negative impression, head, drawing; scale bar 1 mm.

legs were known at the beginning of study (*Kargalarva permosialis* gen. et sp. nov.; undescribed larvae from the Coburger Sandstone), and then the taxa with widened swimming legs and the smaller number (six) of gill pairs (undescribed larvae from the Voltzia Sandstone). The second lineage ("Corydalidae" type: Prokin et al., 2015) includes a unique larva from the Voltzia Sandstone, characterized by nine pairs of lateral segmented tracheal gills with paired tracheal trunks running inside and by the abdomen with one pair of pygopods on segment X, the latter having two hooks (like those in Corydaloidea). It is probable that larvae, such as the considered ones, existed at least up to the Middle Jurassic (USA, Sundance Formation), from where the beetle larva with 6–7 pairs of lateral tracheal gills has been depicted (Buatois et al., 2016, p. 207, text-fig. 11.7 m-p).

The long existence and the wide distribution of the larvae under discussion indicate that they belonged to a quite diverse and widespread group of beetles, whose role best suited Schizophoromorpha, in which a part of adults supposedly also lived in water (Ponomarenko and Prokin, 2015). The considerable similarity of these beetle larvae to those of Megaloptera confirms not only the phylogenetic relationship of the orders, but also the wide ontogenetic opportunities for appearance of morphological parallelisms in holometabolans, corresponding to adaptation to a similar (in this case, aquatic) lifestyle.

The attribution of *Kargalarva permosialis* gen. et sp. nov. to the schizophoromorphans but not to gyrinids, as was proposed by R. Beutel with co-author (Beutel and Roughley, 1988; Yan et al., 2018), and the analogous situation with *Tunguskagyrus planus* Yan, Beutel et Law-

rence, 2018, which, in our opinion, also belongs to Schizophoromorpha (Kirejtshuk and Prokin, 2018), do not currently support the hypothesis on the basal position of Gyrinidae among Adephaga. Their larvae, largely similar to those of Corydaloidea and Myxophaga, only illustrate the similar wide ontogenetic opportunities of convergent morphogenesis, which are likely to be characteristic of holometabolans in general.

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REFERENCES

Achtelig, M., Kamelhalsfliegen (Insecta, Raphidioptera) aus der Umgebung von Augsburg, *Ber. Naturwiss. Ver. Schwaben*, 1981, vol. 85, pp. 30–33.

Aristov, D.S. and Rasnitsyn, A.P., New insects from the Kungurian of Tshekarda fossil site in Permian Territory of Russia, *Russian Entomol. J.*, 2015, vol. 24, no. 1, pp. 17–35.

Beutel, R.G. and Roughley, R.E., On the systematic position of the family Gyrinidae (Coleoptera: Adephaga), *Z. Zool. Syst. Evolutionsforsch.*, 1988, vol. 26, pp. 380–400.

Bouchard, P., Bousquet, Y., Davies, A.E., Alonso-Zarazaga, M.A., Lawrence, J.F., Lyal, C.H.C., Newton, A.F., Reid, C., Schmitt, M., Ślipiński, A., and Smith, A.B.T., Family-group names in Coleoptera (Insecta), *ZooKeys*, 2011, vol. 88, pp. 1–972.

Buatois, L.A., Labandeira, C.C., Mángano, M.G., Cohen, A., and Voigt, S., The Mesozoic lacustrine revolution, in *The Trace-Fossil Record of Major Evolutionary Events*, vol. 2: *Mesozoic and Cenozoic*, Topics in Geobiology, vol. 40, Mángano, M.G. and Buatois, L.A., Eds., Dordrecht: Springer-Verlag, 2016, pp. 179–263.

Gustafson, G.T., Prokin, A.A., Bukontaite, R., Bergsten, J., and Miller, K.B., Tip-dated phylogeny of whirligig beetles reveals ancient lineage surviving on Madagascar, *Sci. Rep.*, 2017, vol. 7, art. ID 8619.
https://doi.org/10.1038/s41598-017-08403-1

Haug, J.T., Labandeira, C.C., Santiago-Blay, J.A., Haug, C., and Brown, S. Erratum to: Life habits, hox genes and affinities of 331-million-year-old holometabolan larva, *BMC Evol. Biol.*, 2016, vol. 7, web-p. 169.
https://doi.org/10.1186/s12862-016-0725-x

Kirejtshuk, A.G. and Prokin, A.A., The position of the Palaeozoic genus *Tunguskagyrus* Yan, Beutel et Lawrence in the family Triaplidae sensu n. (Coleoptera, Archostemata, Schizophoroidea), *Entomol. Rev. (Engl. Transl.)*, 2018, vol. 98, no. 7. pp. 872–882.
https://doi.org/10.1134/S0013873818070084

Kukalová-Peck J. Mazon Creek insect fossils: The origin of insect wings and clues about the origin of insect metamorphosis, In: Shabica C.W., Hay A.A. (eds.) *Richardson's Guide to the Fossil Fauna of Mazon Creek*, Chicago: Northern Illinois University Press, 1997, pp. 194–207.

Makarov, K.V. and Prokin, A.A., About homology of *Haliplus* Latreille, 1802 larvae postanal process (Coleoptera, Haliplidae), *Acta Entomol. Mus. Nat. Pragae*, 2015, vol. 55, no. 2, pp. 879–881.

Martynov, A.V., Permian fossil insects of North-East Europe, *Tr. Geol. Muz. Akad. Nauk SSSR*, vol. 4, 1928, pp. 1–118.

Martynov, A.V., The Permian fossil insects of Kargala and their relationships, *Tr. Paleontol. Inst. Akad. Nauk SSSR*, 1937, vol. 7, no. 2, pp. 1–92.

Martynova, O.M., Permian Mecoptera from Chekarda and Kargala, *Izv. Akad. Nauk SSSR, Ser. Biol.*, 1942, nos. 1–2, pp. 133–149.

Nel, A., Roques, P., Nel, P., Prokin, A.A., Bourgoin, T., Prokop, J., Szwedo, J., Azar, D., Desutter-Grandcolas, L., Wappler, T., Garrouste, R., Coty, D., Huang, D., Engel, M.S., and Kirejtshuk, A.G. 2013. The earliest-known holometabolous insects, *Nature*, 2013, vol. 503, no. 14, November 2013, pp. 257–261.
https://doi.org/10.1038/nature12629

Ponomarenko, A.G., The Paleozoic beetles Cupedidea of the European part of the USSR, *Paleontol. Zh.*, 1963, no. 1, pp. 70–85.

Ponomarenko, A.G., *Istoricheskoe razvitie zhestkokrylykh-arkhostemat* (Historical Development of Coleopterans-Archostemate), Rohdendorf, B.B., Ed., Tr. Paleontol. Inst. Akad. Nauk SSSR, vol. 125, 1969.

Ponomarenko, A.G., New beetles (Insecta, Coleoptera) from the latter half of the Permian of European Russia, *Paleontol. J.,* 2013, vol. 47, no. 7, pp. 705–735.

Ponomarenko, A.G. and Prokin, A.A., Review of paleontological data on the evolution of aquatic beetles (Coleoptera), *Paleontol. J.*, 2015, vol. 49, no. 13, pp. 1383–1412.

Prokin, A.A., Makarov, K.V., Ponomarenko, A.G., and Bashkuev, A.S., New beetles larvae (Coleoptera: Coptoclavidae, Carabidae, Polyphaga) from the Upper Triassic of Germany, *Russ. Entomol. J.*, 2013a, vol. 22, no. 4, pp. 259–274.

Prokin, A.A., Petrov, P.N., Wang, B., and Ponomarenko, A.G., New fossil taxa and notes on the Mesozoic evolution of Liadytidae and Dytiscidae (Coleoptera), *Zootaxa,* 2013b, vol. 3666, pp. 137–159.

Prokin, A.A., Kirejtshuk, A.G., and Ponomarenko, A.G., On some Permian and Triassic larvae of Holometabola: beetles or not?, *Acta Entomol. Mus. Nat. Pragae*, 2015, vol. 55, no. 2, pp. 882–884.

Riek, E.F., New Upper Permian insects from Natal, South Africa, *Ann. Natal Mus.*, 1976, vol. 22, pp. 755–789.

Sharov, A.G., The first find of a Permian Megalopteran larva from Kargala, *Dokl. Akad. Nauk SSSR,* 1953, vol. 89, no. 4, pp. 731–732.

Shcherbakov, D.E., On Permian and Triassic insect faunas in relation to biogeography and the Permian–Triassic crisis, *Paleontol. J.,* 2008, vol. 42, no. 1, pp. 15–31.

Yan, E.V., Beutel, R.G., and Lawrence, J.F., Whirling in the late Permian: ancestral Gyrinidae show early radiation of beetles before Permian–Triassic mass extinction, *BMC Evol. Biol.*, 2018, vol. 18, Web-p. 33.
https://doi.org/10.1186/s12862-018-1139-8

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