

## Permian Triaplids (Coleoptera, Triaplidae), Yet Another Group of Mesozoic Beetles from the Terminal Permian

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Received May 23, 2020; revised September 28, 2020; accepted October 6, 2020

**Abstract**—The systematic position of *Tomiaplus* gen. nov., *T. sibiricus* (Volkov, 2013), *T. minimus* sp. nov., *Tunguskagyryus* Yan, Beutel et Lawrence, 2018, *T. planus* Yan et al., 2018, *T. yani* sp. nov. described from deposits around the Permian–Triassic boundary of the Tunguska and Kuznetsk basins is revised, and their assignment to the family Triaplidae, previously only known from the Upper Triassic, is proposed. The opinion that *Tunguskagyryus* does not belong to the family Gyrinidae (Kirejtshuk and Prokin, 2018) is upheld. The synonymy of the families Triaplidae and Coleocatinidae (Kirejtshuk and Prokin, 2018) is not supported. A beetle previously considered as a triaplid is here described as *Permocatinus* gen. nov., *P. tomiensis* sp. nov. in the family Coleocatinidae Ponomarenko et Prokin, 2015. The abundance of Permian triaplids supports the view that new groups appeared not as an aftermath of the Permian–Triassic crisis, but prior to it. No diversity drop is recorded on the mountain plateau of Siberian Traps either for plants (Sadovnikov, 2016) or for animals, so mountain barriers were most likely refugia for preserving biodiversity during the crisis.

**Keywords:** Coleoptera, Coleocatinidae, Gyrinidae, new taxa, Permian–Triassic crisis, Siberian Traps

**DOI:** 10.1134/S0031030121050130

### INTRODUCTION

The family Triaplidae was proposed (Ponomarenko, 1977) for new beetles from the Upper Triassic of Madygen (Central Asia). The name reflected a certain similarity between the new beetles and the beetles of the family Haliplidae, which are traditionally regarded as Adephega, although they also have a number of characters typical for Archostemata, especially in the wing morphology (Ponomarenko, 1977). In Haliplidae and Triaplidae, the hind coxae have unusually long medial processes and large coxal plates. It was unexpectedly found that many of the most ancient Adephega, Caraboidea, and Dytiscoidea also had large coxal plates, allowing a re-interpretation of the relationship between Adephega and Archostemata, which was done in the publication above. When the family Triaplidae was established, the higher suborders of beetles, Polyphaga and Adephega were known only from the Late Triassic, and it was assumed that they first appeared in the Triassic (Ponomarenko, 1969). However, this assumption was later shown to be erroneous, and it was demonstrated that the higher suborders already existed in the terminal Permian. The terminal Permian beds (Kuznetsk Basin, Babiy Kamen; Maltsev Formation, Kedrovka Beds), also

contain Haliplidae (Ponomarenko and Prokin, 2015), unfortunately not yet described.

*Triaplus sibiricus* was described by Volkov (2013) from a rather large moderately preserved fossil beetle with large coxal plates. A better-preserved beetle specimen was found at the same locality, of a similar appearance and approximately the same size, and was assigned to the same species, and further discussion of the structure and systematic position of *T. sibiricus* was mainly based on this specimen and not on the holotype. For instance, it was argued that beetles of this species did not have large coxal plates of the hind coxae (Kirejtshuk and Prokin, 2018), while the counterpart imprint of the holotype showed such coxal plates. Electron microscope examination of the holotype showed small (about 0.1 mm long) lines mostly arranged in irregular transverse rows on its elytron. It is assumed that these are partly preserved setae. The same structures can be seen in electronic images of several isolated elytra from the same location. They appear to be located on the same surface as the pyrite frambooids. Preservation of frambooids is more likely beneath the elytron; it is possible that setae were also located on its lower surface. Several large (up to 1 cm) isolated elytra with a smooth upper surface and a longitudinal groove (schiza) on the lateral margin were

found in the same locality. Since large beetles are very rare in the locality, these elytra were considered to belong to beetles of the same species. The study of the holotype and the additional specimen showed significant differences between them and differences from the type species of the genus *Triaplus* Ponomarenko, 1977. This is suggested by the large transverse anterior coxae, separated in the holotype of *T. sibiricus* by the prothoracic process reaching their apex. In the additional specimen, the contact of the anterior coxae is poorly visible, and it is impossible to decide whether the coxae are divided by the prothoracic process or not. Its hind coxae are shown to be much shorter than those of the holotype. Numerous pyrite framboids are visible on the holotype, while none are present on the second specimen. These two specimens differ in size, frons width, shape of the pronotum and metepisternum, relative length of the last abdominal sternite, and should be described as different species, although part of these differences may depend on taphonomy. The head and pronotum of the holotype are directed prognathously; in the second specimen, they are turned sideways to the right side and the head is slightly bent down, probably partially affecting the shape of these body parts. Both specimens have large, rounded notches on the mesothorax for inserting the anterior coxae; on the imprints there is a significant distance between them and the coxae, so that the lifetime position of the prothorax and head had to be inclined, or even orthognathous. In the new specimen, the coxal plates are incompletely visible; they are often not visible at all if they overlap the abdomen, and their presence can only be discerned from different punctures of the basal abdominal sternites on the right and left sides. Therefore, these beetles are described below as representatives of different species, and *T. sibiricus* Volkov, 2013 is assigned to a new genus, which, nevertheless, can be left in the family Triaplidae, since the differences between *T. sibiricus* and other Triaplidae are no greater than between different genera of the family Schizophoridae. For the second specimen (PIN, no. 4887/348), a new genus is described in the family Coleocatiniidae Ponomarenko et Prokin, 2015 (=Catiniidae Ponomarenko, 1968). Finally, a recent expedition to the Babiy Kamen site (led by A.V. Khramov) assembled a large collection, almost doubling the number of beetles. Among them were two specimens that may belong to beetles of the same genus. They are much smaller in size than the holotype of *T. sibiricus*, so they cannot belong to the same species. Unfortunately, both beetles are incompletely preserved. There is only one character that makes these beetles similar to *Tomiaplus*. These are characteristic short lines (or setae) on the elytra. One (specimen PIN, no. 4887/704) has long median processes of the hind coxae. Large transverse fore coxae, separated by a process, bring it closer to the holotype of *T. sibiricus*. Since the second specimen is much smaller, it is described below as the second species of the genus

*Tomiaplus*. The second specimen (PIN, no. 4887/626) is even smaller, and its underside structures are not clearly visible. The prothorax, which is not notched anteriorly is different from all other Triaplidae. Currently, it is preferable not to classify this species within Triaplidae. Similar beetles were found at the Anakit-3 locality in the Tunguska Basin (Central Siberia, Krasnoyarsk Territory; Upper Permian, Taimyrian Stage, Lebedevskian Horizon). They also have long medial processes of the hind coxae, the length of which is only slightly less than the coxal width. They were described as a new genus and species *Tunguskagyryus planus* Yan, Beutel et Lawrence, 2018 and referred to Gyrinidae (Yan et al., 2018). Even before the publication of this paper, they were re-studied, combined into one genus with *Triaplus sibiricus* Volkov, 2013, and placed in the family Triaplidae, which was transferred to Schizophoridae (Archostemata) by Kirejtshuk and Prokin (2018). At the same time, the interpretation of the structure was radically changed; the characters by which this beetle was classified within Gyrinidae were considered an artifact: the eyes were described as simple, not double, the structure of the basal segments of the antennae, as not corresponding to that of the Gyrinidae, the abdomen was described as having only five visible sternites, legs as walking (Kirejtshuk and Prokin, 2018). The proposed interpretation of the structures differed little from what I proposed based on the same material. There are, however, important differences. In both publications, the head of the holotype is considered to be prognathous, but from the very beginning I considered it to be orthognathous. This is indicated by the fact that the head is transverse, and in my opinion, no structures of either the upper or lower side of the head are visible on the sample. None of the publications reflect the fact that there are several pyrite framboids on the head, very similar to faceted eyes. The latter publication states that the holotypes *Triaplus sibiricus* and *Tunguskagyryus planus* do not have large femoral tepals; however, they are clearly visible on the first of them, which is why it was placed in the genus *Triaplus*. The hind coxae are described as “strongly transverse” (Kirejtshuk and Prokin, 2018, p. 879), but in Fig. 5 in the same work, their length is four-fifths of their width, while in the genus *Hadeo-coleodes* they are less than two-fifths. This difference does not allow *Tunguskagyryus* to be classified within Schizophoridae and supports the assignment of *Triaplus sibiricus* and *Tunguskagyryus planus* to *Triaplus*.

Finally, recently A.S. Bashkuev, among the unsorted material from the Anakit locality, with no specific collection point, found another beetle specimen similar to the holotype of *Tunguskagyryus planus*, but significantly larger and differing in body proportions (specimen PIN, no. 2362/22).

This specimen is better preserved, and its legs are preserved as three-dimensional structures. At the same time, the borders of the sclerites are poorly visible, and in photographs taken under oblique illumina-

tion, the shadow of the sclerites is better visible than its border. The high-magnification SEM images show that the boundary is blurred because the specimen consists of ashy material, the particles of which are flattened into flakes, slightly displaced relative to one another. Because of this, it is not possible to obtain either high-quality photographs or drawings. Even the boundaries of the abdominal sternites, which are usually clearly visible, cannot be accurately determined on the imprint. Along with them, other transverse structures are visible, probably the boundaries of tergites. Depending on the nature of the illumination of the sample, one or the other sets of transverse structures are better visible, which is why the number and proportions of sclerites are difficult to establish. The same difficulties are encountered in determining the number and shape of the tarsomeres. Longitudinal structures are also visible under the elytra, apparently, venation of folded wings, but their structure could not be restored. Only oval structures can be seen, very similar to *oblongum* of Hydradephaga. Since they are visible in the same place under both elytra, and still visible, although poorly, on the holotype; the hypothesis that they are *oblongum* seems highly probable. Some electron microscope images may show structures similar to long bristle-like formations on the hind tibia. Perhaps these are the remains of swimming setae.

The authors of the genus *Tunguskagyryus* published an article (Beutel et al., 2019) containing some new results of the re-examination of the holotype of *T. planus*. Most of Kirejtshuk and Prokin's (2018) proposals were rejected there, and it was claimed that the main drawback of Kirejtshuk and Prokin's (2018) work is that it was not based on cladistic methodology. I cannot agree with this. During 60 years of studying the phylogeny of beetles, I cannot recall a single case when the cladistic methods could have obtained a result significantly superior to the results obtained by traditional methods. The statement that hypotheses obtained using traditional phylogenetic methods cannot be falsified is unfair. The only method for falsifying phylogenetic trees is accumulation of paleontological facts, and this is applicable to phylogenetic hypotheses obtained using any available method. It is necessary once again emphasize the nature of the eyes, whether they are whole or divided, as the authors still claim; I, despite careful searches, could not determine this. However, the legs are indeed present, but they are so poorly preserved that they can only be illustrated approximately. The described remains are interesting not only for providing important material for understanding the evolution of beetles at one of the basal stages, but also as significant evidence of the nature of the Permian–Triassic ecological crisis. Both beetle localities are dated close to the Paleozoic–Mesozoic boundary and were formed during the Permian–Triassic event. At present most researchers believe that the cause of this event was a colossal eruption that produced the volcanics of the Tunguska Traps. The cli-

matic and landscape consequences of this eruption transformed Earth's entire ecosystem, however, a detailed study of intertrap deposits, carried out mainly by G.N. Sadovnikov, showed that on the basalt plateau itself, the picture was not at all apocalyptic and that phytocenoses were quite normal for this time. The abundance and diversity of insect remains also confirms Sadovnikov's conclusions. Deposits of the Tunguska and Kuznetsk basins may have formed as a result of a single vast volcanic event (Svetlitskaya and Nevvolko, 2016): Anakit was formed at the end of the tuffaceous-sedimentary stage of plateau construction, and Babiy Kamen, also containing dikes and basalt covers, was formed somewhat later, before the massive outpouring of basalts, when they spread far from the center of the eruption. It is possible that the dikes and covers of the basalts of the Kuznetsk Basin are also part of the basalts of the Siberian Traps, and they are synchronous. The altitude of the volcanogenic plateau is estimated to have been more than 1.5 km, and conditions on this mountain plateau were acceptable for fairly abundant life even during the thermal maximum in the middle of the Induan time (Sun et al., 2012). Aref'ev et al. (2015) in an important study on carbon and oxygen isotopic compositions of the Permian-early Triassic carbonates of the Russian Platform, questioned the connection between the extinction and the outpouring of basalts, because an episode of significant cooling, rather than warming is recorded near the boundary. However, it follows that at the beginning of the event there was a stage of explosive volcanism with a release of a huge amount of ash and sulfur compounds into the atmosphere, which could only cause a noticeable cooling.

It seems that the formation of volcanic deposits in the Tunguska Basin was a one-time event and was momentary in the geological sense. In itself, a single eruption of such monstrous power outside volcanic regions requires a special explanation. It was proposed that this was an aftermath of the impact of a shock wave in the earth's core after the fall of a large asteroid capable of breaking through the Earth's crust. Suitable astrolems are known in the southern hemisphere. Finds of meteorite matter are known in the Upper Vyatkian deposits of the Russian Platform (Arefiev and Tselmovich, 2017). These considerations are summarized in more detail in a special paper (Ponomarenko, 2017), although new facts and concepts appear so quickly that it is already somewhat outdated.

## MATERIAL AND METHODS

The studied material is housed at in the collection of the Laboratory of Arthropods of the Borissiak Paleontological Institute, Russian Academy of Sciences in Moscow (PIN RAS).

We used a Tescan Vega XMU scanning electron microscope and a Leica M165C light stereoscopic microscope with a Leica DFC420 digital camera (PIN RAS).

Drawings from photographs and plates are made using Corel Draw software. Legend: solid lines – borders of sclerites and body parts, setae; dotted lines – unclear boundaries of sclerites, body parts and furrows, places of damage to the imprint, structures that overlap each other.

## SYSTEMATIC PALEONTOLOGY

### Family Triaplidae Ponomarenko, 1977

#### Genus *Tomiaplus* Ponomarenko, gen. nov.

**E t y m o l o g y.** From the Tom River and the genus name *Triaplus*.

**T y p e s p e c i e s.** *Triaplus sibiricus* Volkov, 2013.

**D i a g n o s i s.** Head weakly transverse, almost prognathous. Fore coxae large, transverse, oblique, separated by a prothoracic segment. Scutellum rounded triangular. Mesothorax rather long, in front with paired rounded notches for entering the apices of the anterior coxae. Middle coxae large and rounded. Metepisternum strongly expanded forward. Metasternum transverse, roundly narrowed anteriorly. Length of medial process of hind coxa almost equal to its width at anterior margin. Tibia and femora with short, sparse setae; swimming setae absent. Elytra smooth, without punctate grooves; at high magnification, with short lines, apparently representing small setae. On some elytra, ring structures are visible, which are usually interpreted as columella openings.

**S p e c i e s c o m p o s i t i o n.** Two or three species from the Babiy Kamen locality, terminal Permian of Kuznetsk Basin. In addition to the two species described below, the locality contains larger elytra with characteristic striae.

**C o m p a r i s o n.** It differs from other genera of the family by an almost prognathous head and coxae separated by a prothoracic process.

#### *Tomiaplus sibiricus* (Volkov, 2013)

*Triaplus sibiricus*: Volkov, 2013, p. 74, text-figs. 1, 2.

**H o l o t y p e.** PIN, no. 4887/72, incomplete part and counterpart distorted imprints of beetle with head and pronotum, without antennae and limbs; sides of the remnant are asymmetric; Kemerovo Region, Novokuznetsk District, right bank of the Tom River, 10 km downstream of the village of Ust-Naryk, Babiy Kamen locality; Maltsevo Formation, Kedrovka Beds.

**D e s c r i p t i o n** (Fig. 1). The head nearly triangular, about 1.5 times as wide as long. The eyes are large, oval, lateral. The pronotum is strongly transverse, the pronotum width three times its length, notched anteriorly, fore angles slightly protruding anteriorly. The prothorax is shorter than the head, its length less than the length of the anterior coxae. The propleura at the posterior margin are twice as wide as at anterior margin. The fore coxae are large, transverse, oblique, twice as wide as long; separated by a prothoracic segment, almost not tapering posteriorad. The scutellum

is rounded triangular. The mesothorax is rather long. The middle coxae are large, rounded, spaced apart. The metepisternum is strongly expanded forward. The metasternum is transverse, roundly narrowed anteriorly (width 2.4 its length), with a process between the middle coxae, with a transverse suture at the posterior margin. The hind coxae are slightly narrowed laterally, incised at the posterior margin. The coxal plates are longer than wide. The medial process of the posterior coxa is only slightly shorter than its width. The middle coxae are widened, about the same length as the hind coxae, which are not widened. The hind tibia is the same length as the hind femur, but slightly narrower.

**M e a s u r e m e n t s** in mm. Length 7.1, width 3.4, elytron length 6.4.

**C o m p a r i s o n.** This species differs from *T. minimus* sp. nov. in the shorter metathorax, longer medial processes of the hind coxae, and larger size.

**M a t e r i a l.** Holotype.

#### *Tomiaplus minimus* Ponomarenko, sp. nov.

**E t y m o l o g y.** From the Latin *minimus* (minor).

**H o l o t y p e.** PIN, no. 4887/704; incomplete part and counterpart, distorted imprints of a beetle lacking the head and most of the pronotum, without antennae or fore limbs; due to burial in an inclined position, the sides of the specimen are asymmetrical, the right elytron is a quarter wider than the left; Kemerovo Region, Novokuznetsk District, right bank of the Tom River, 10 km downstream of the village of Ust-Naryk, Babiy Kamen locality; Maltsevo Formation, Kedrovka Beds.

**D e s c r i p t i o n** (Fig. 2). The anterior coxae are large, transverse, oblique, separated by a prothoracic segment, almost not tapering posteriorly. The scutellum is longitudinal, round-triangular. The mesothorax long, only slightly shorter than metathorax. The middle coxae are rounded, spaced apart. The metepisternum is not very widened forward. The metasternum transverse, slightly roundly narrowed anteriorly; its length is one-fifth less than its width. The metepisternum is three times as wide at the anterior margin than at the posterior margin. The hind coxae are slightly narrowed laterally, their posterior processes are slightly shorter than the width of the coxae. The coxal plates are longer than wide. The middle femora are widened, about the same length as the tibiae; the first segment of the middle tarsus is a third of the length of the second. The hind tibia is as long as the hind coxa, widened at the apex; the first hind tarsomere is a third of the length of the second.

**M e a s u r e m e n t s** in mm. Elytron length 3.97.

**C o m p a r i s o n.** This species differs from the type species in the longer metathorax, shorter medial processes of the hind coxae, and smaller size.

**M a t e r i a l.** Holotype.

#### Genus *Tunguskagyrus* Yan, Beutel et Lawrence, 2018

*Tunguskagyrus*: Yan et al., 2018, p. 2.



**Fig. 1.** *Tomiaplus sibiricus* (Volkov, 2013), holotype PIN, no. 4887/72: (a) counterpart, (b) part imprints; (c, d) drawing, upper view and lower view; (e) elytron with characteristic structures: serrations or setae and fr—pyrite framboids; Babiya Kamen; Upper Permian, Vyatkian Stage. Scale bar 1 mm.

**Type species.** *Tunguskagyryrus planus* Yan et al., 2018, by primary monotypy; Krasnoyarsk Region, Tunguska Basin; Upper Permian, Taimyrian Stage, Lebedevskian Horizon.

**Diagnosis.** Medium-sized beetles with streamlined body, orthognathous head, prothorax bent downward, elytra without traces of venation, rather long legs. Pronotum strongly transverse, notched in



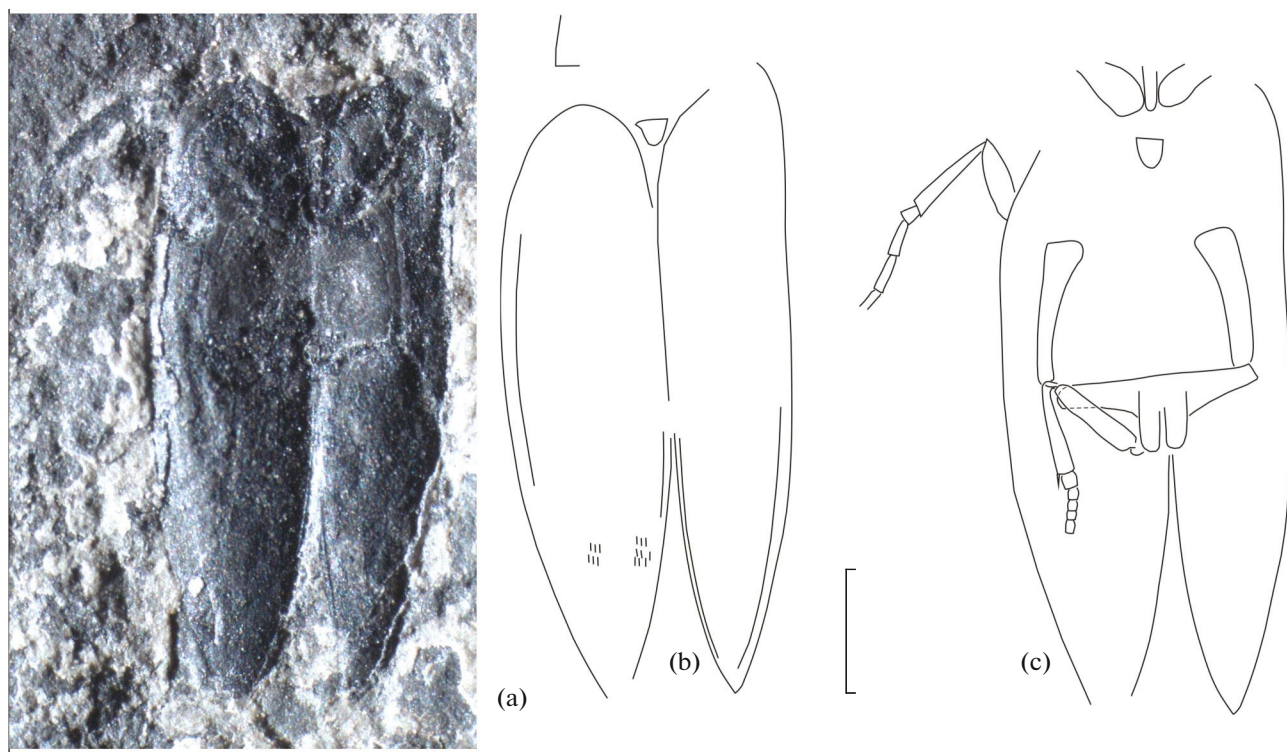


Fig. 2. *Tomiaplus minimus* sp. nov., holotype PIN, no. 4887/704: (a, b) upper view, (c) lower view; Babiy Kamen; Upper Permian, Vyatkian Stage. Scale bar 1 mm.

front, anterior angles projecting anteriorly. Scutellum rounded triangular. The prothorax is shorter than the head. The fore coxae are large, entering the rounded fossa on the mesothorax. Mesothorax rather long, in front with paired rounded notches for entering the apices of the anterior coxae. Middle coxae are large and rounded. Metepisternum is extended forward. Metathorax transverse, roundly narrowed anteriorly, bears process with rounded anterior margin between middle coxae, at posterior margin with transverse suture. Hind coxae slightly narrowed laterally, notched at posterior margin. Length of the medial process of the posterior coxa not less than its width at the anterior margin. Coxal plates smaller in length than in width. Legs relatively long. Tibiae and femora almost equal in length, with short, sparse setae. Elytra smooth, without punctate grooves; at high magnification, short lines visible on them, apparently, representing small setae. On some elytra, concentric structures visible, which are usually interpreted as columella openings.

**Species composition.** Two species from the Anakit-3 locality.

**Comparison.** This genus differs from other genera of the family in the wide and short contiguous anterior coxae.

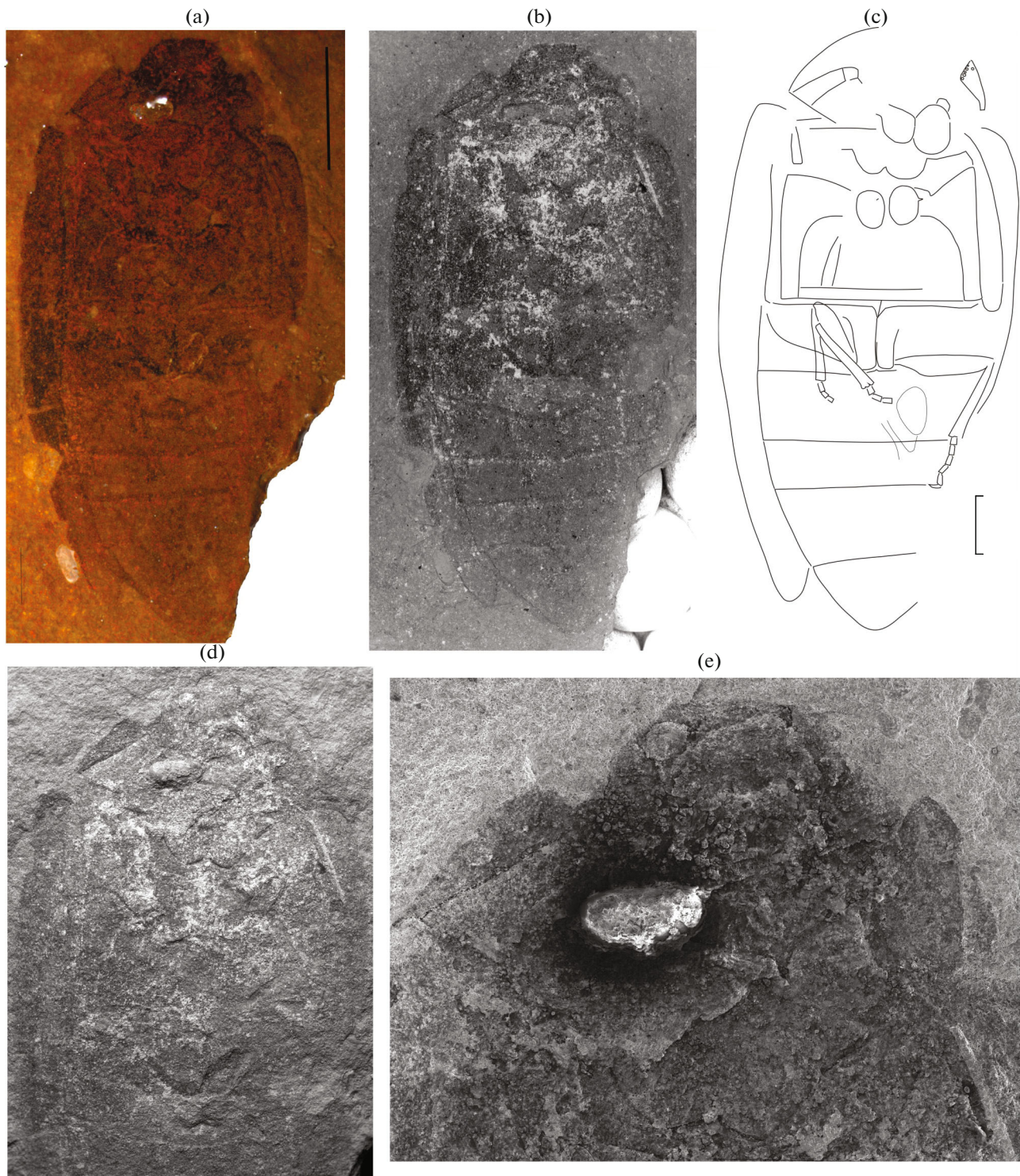
*Tunguskagyrus planus* Yan et al., 2018

*Tunguskagyrus planus*: Yan et al., 2018, p. 2, text-figs. 1–3.

**H o l o t y p e.** PIN, no. 3381/32, part and counterpart imprints of the beetle without antennae and most of the legs, the prothorax and head are shifted forward and turned to the left, so that the prothorax appears asymmetrical; Krasnoyarsk Region, Tunguska Basin, Anakit-3; Upper Permian, Taimyrian Stage, Lebedevskian Horizon.

**Description** (Fig. 3). Oval beetle, more narrowed posteriorly. The length of the beetle is twice its width. The pronotum is equal in length to the head thickness, strongly transverse, incised anteriorly, anterior angles projecting anteriorly. The fore coxae large, transverse, oblique, with length approximately their width. The mesothorax lacks a transverse suture. The middle coxae are large and rounded. The metepisternum at the anterior margin is 5 times wider than at the posterior margin. The length of metasternum between the coxae one third of width at the posterior margin; width of anterior margin equal to  $3/4$  of posterior margin. The anterior process between the middle coxae is almost triangular, the transverse suture does not reach the borders of the metathorax. The hind coxae are strongly narrowed laterally, the length of the medial process is approximately equal to the width of the coxa at the anterior margin. The coxal plates are approximately equal in length to the medial process. The last ventrite of





**Fig. 3.** *Tunguskagyryrus planus* Yan et al., 2018, holotype PIN, no. 4887/72: (a) photograph; (b, d, e) SEM image, object on the prothorax is an ostracoda shell; (c) drawing, lower view; Anakit-3; Upper Permian, Vyatkian Stage. Scale bar 1 mm.

the abdomen is twice as long as the penultimate one. The hind legs, extended backward, do not reach the apex of the abdomen. The hind femora are long, extending beyond the boundaries of the body, the tibiae are shorter

than the femora, the first and fifth tarsomeres are longer than the other tarsomeres, which are almost equal in size. The elytra are thin, through which the bases of the wing veins, including *oblongum*, are visible.

Measurements in mm. Length 9.48, width 4.66, elytron length 7.1.

Comparison. The species differs in smaller size, wider body; the metepisternae more extended anteriorly, and shorter legs.

Material. Holotype.

*Tunguskagyryus yani* Ponomarenko, sp. nov.

**Etymology.** In honor of paleoentomologist Evgeniy Yan.

**Holotype.** PIN, no. 2362/22, part and counterpart imprints of a beetle lacking antennae and parts of legs; head and pronotum are incurved; Krasnoyarsk Region, Tunguska Basin, Anakit; Upper Permian, Taimyrian Stage, Lebedevskian Horizon.

**Description** (Fig. 4). Oval beetle, narrowed posteriorly. The length of the beetle is 2.5 times its width. The pronotum is strongly transverse, notched in front, the anterior angles project anteriorly. The anterior coxae are broad and long. The sternum has a transverse suture. The middle coxae are large and rounded. The metepisternum at the anterior margin is twice as wide as at the posterior margin. The length of the metasternum between the coxae is 0.45 of its width at its posterior margin; the width of the anterior margin of the metathorax is half that of the posterior margin. The anterior process between the middle coxae is almost triangular, a transverse suture reaches the borders of the metathorax. The hind coxae are strongly narrowed laterally, the length of the medial process is almost 0.75 times the width of the coxa at the anterior margin. The coxal plates are longer than the medial process. The last abdominal ventrite is longer than the penultimate one. The hind legs, extended backward, extend beyond the apex of the abdomen. The hind femora are long, reaching the border of the body, the tibiae are longer than the thighs, the first and fifth tarsal segments are longer than the second to fourth segments, which are of equal size. The elytra are thin, and through them the bases of the wing veins, including the *oblongum*, are visible.

Measurements in mm. Length 12.5–13.3, width 5.0–5.26, elytron length 9.6–10.7.

Comparison. The species differs from the type species in its larger size, more elongated body, weaker metepisterna widened forward, and longer legs.

Material. Holotype and possibly, specimen PIN, no. 3381/110, Anakit-3, with the head turned forward.

**Family Coleocatiniidae Ponomarenko et Prokin, 2015**  
(=Catiniidae Ponomarenko, 1968)

**Genus *Permocatinus* Ponomarenko, gen. nov.**

**Etymology.** From the Permian Period and the generic name *Catinus*; masculine gender.

**Type species.** *Permocatinus tomiensis* sp. nov.

**Diagnosis.** Medium-sized beetles with an oval flattened body, protractile head, slightly bent downward prothorax, rather long legs. Head transverse, slightly narrowed anteriorly. Eyes small, lateral. Pronotum strongly transverse, roundly narrowed anteriorly, incised anteriorly, anterior angles projecting anteriorly. Scutellum transverse triangular. Prothorax much longer than head, roundly narrowed anteriorly. Anterior coxae large, transverse. Mesothorax rather short, in front with paired rounded notches for the entry of apices of anterior coxae, with transverse suture. Middle coxae large, rounded, spaced apart. Metepisternum is strongly expanded forward. Metasternum transverse, roundly narrowed anteriorly, bears process with rounded anterior margin between the middle coxae, at the posterior margin with a transverse suture interrupted in the lateral part. Hind coxae slightly narrowed laterally, incised at posterior margin. Medial process of the posterior coxa wide and short. Tibiae and femora with short, sparse setae; swimming setae absent. Abdomen with five ventrites; last ventrite narrow and long.

**Species composition.** Monotypical.

**Comparison.** It differs from other genera of the family in its drop-like body shape, pronotum roundly narrowed anteriorly and large transverse anterior coxae.

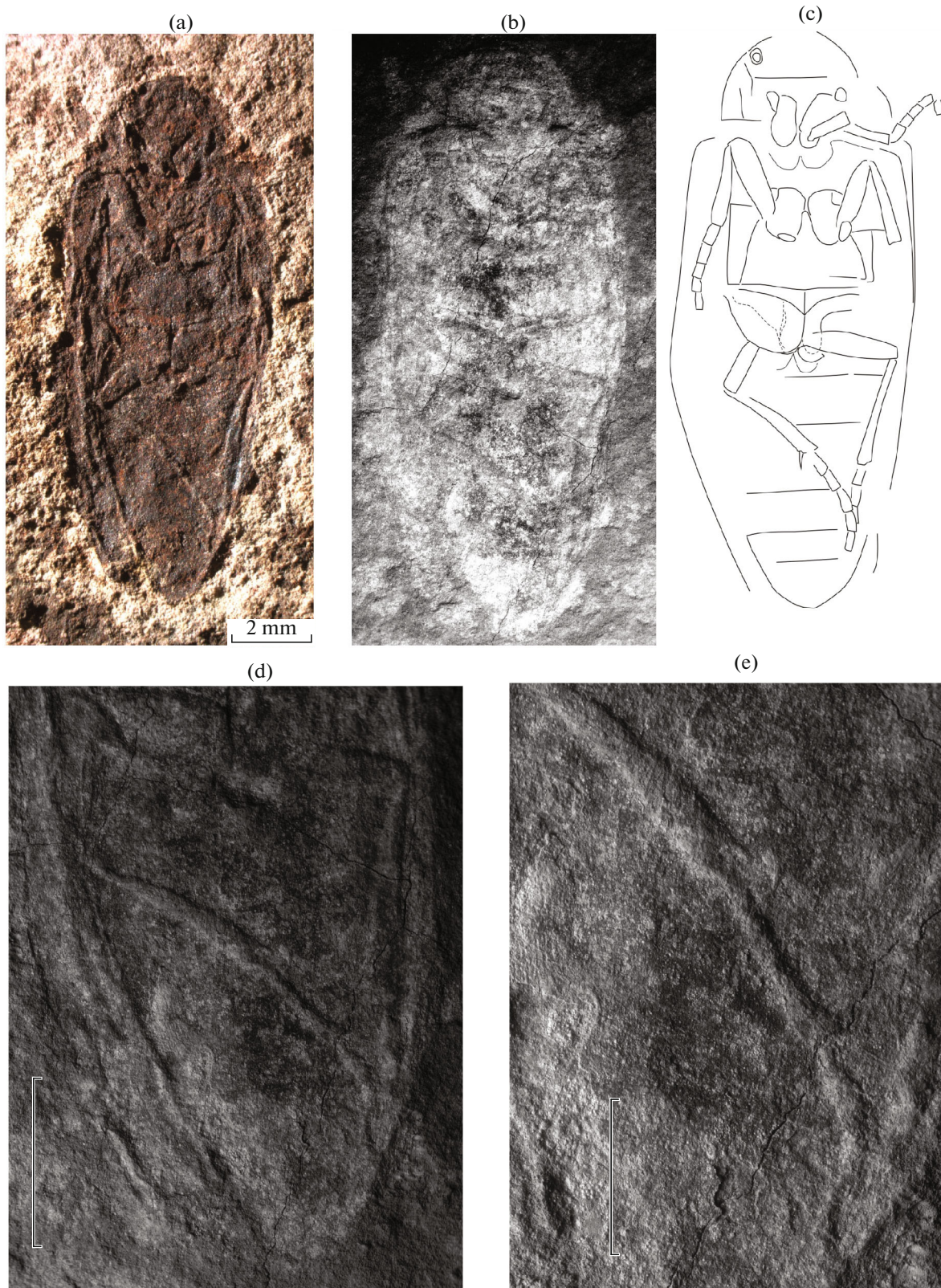
*Permocatinus tomiensis* Ponomarenko, sp. nov.

**Etymology.** From the Tom River.

**Holotype.** PIN, no. 4887/348, part and counterpart imprints of a beetle without elytra and most of the legs; Kemerovo Region, Novokuznetsk District, right bank of the Tom River, 10 km downstream of the village of Ust-Nary, Babiy Kamen Locality; Maltsevo Formation, Kedrovka Beds.

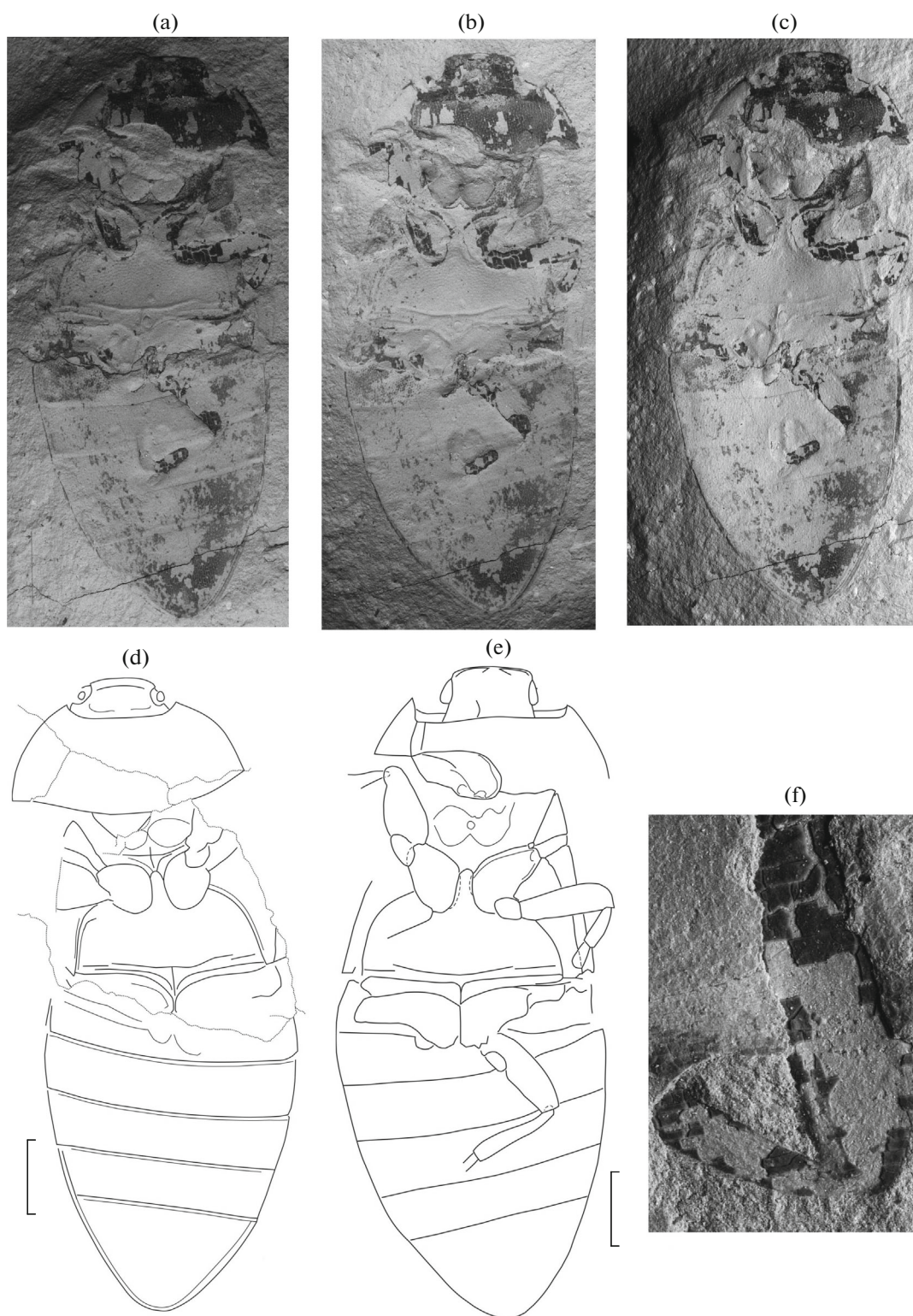
**Description** (Fig. 5). Medium-sized beetles with an oval flattened body, a protractile head, slightly bent downward prothorax, rather long legs. The head is transverse, slightly narrowed anteriorly. The eyes are small, lateral. The pronotum is transverse, strongly roundly narrowed anteriorly, notched anteriorly, the anterior angles projecting anteriorly. The scutellum is transverse triangular. The prothorax is much longer than the head, roundly narrowed anteriorly. The anterior coxae are large, transverse. The mesothorax is rather short, anteriorly with paired rounded notches for the entry of the apices of the anterior coxae, with a transverse suture. The middle coxae are large, rounded, spaced apart. The metepisternum is strongly expanded anteriorad. The metasternum is transverse, roundly narrowed anteriorly, bears a process with a rounded anterior margin between the middle coxae, at the posterior margin with a transverse suture interrupted in the lateral part. The hind coxae are slightly narrowed laterally, incised at the posterior margin. The medial process of the posterior coxa is short and wide. The femora and tibiae with short, sparse setae.





**Fig. 4.** *Tunguskagyruy yani* sp. nov., holotype PIN, no. 2362/22: (a) photograph; (b, d, e) SEM image; (c) drawing, lower view; Anakit-3; Upper Permian, Vyatkian Stage. Scale bar 1 mm.





**Fig. 5.** *Permocatinus tomiensis* sp. nov., holotype PIN, no.3446/348: (a–c, f) SEM image; (d, e) drawings, lower view; (f) middle leg; Anakit-3; Upper Permian, Vyatkian Stage. Scale bar 1 mm.

The abdomen has five visible ventrites; the last ventrite is long and narrow.

**M e a s u r e m e n t s** in mm. Length 7.1, width 3.4, elytron length 6.4.

**M a t e r i a l.** Holotype.

## DISCUSSION

In modern taxonomy, two approaches methodologically and ideologically different, coexist. The mainstream is the cladistic approach, i.e., positive nominalism. Characters (as many as possible) are assembled, coded and analyzed using phylogeny programs, which determine the degree of similarity of characters. Adaptive and correlation analyzes are usually not used. The advantage of this approach is its formalization and unambiguous results. However unambiguity and consistency within the framework of a particular program does not provide verification of the results obtained, and more so does not necessarily correspond to the real evolutionary process. However, cladistic methods are treated as the ultimate truth. Using cladistic methods, it was established that Gyrinidae should be considered the sister group to the rest of the Adephaga. At the same time, the previous hypothesis that Haliplidae were the first to split off (Ponomarenko, 1977) was simply not considered or renounced. It was based on the similarity between Haliplidae and schizophoroid Archostemata in the structure of the hind wings and the specific structure of the hind coxae and the base of the abdomen. In the fossil state, it is rarely possible to see the hind coxae with large coxal plates covers. They are clearly visible on the holotype of *Triaplus macroplatus*, since its abdomen is torn off. But about the paratype of the same species, it was argued that it does not have coxal plates and cannot be considered to belong to triaplids (Kirejtshuk, Prokin, 2018). In fact, it has coxal plates, but, apparently, during burial they were bent and positioned at an angle. They are visible as a narrow strip in Fig. 10 (p. 67) in the work of Kirejtshuk and Prokin. During burial of three-dimensional objects, we usually see not the real shape of sclerites, but its projection onto the burial plane. The conspecificity of the holotype and paratype of *T. macroplatus* is demonstrated by the presence of long medial processes of the hind coxae. A detailed study of the holotype of *Tunguskagyryus planus* Yan et al., 2018 did not provide any evidence of its belonging to the Gyrinidae. The head is in fact orthognathous, which is not the case in the Gyrinidae. I managed to find only two eyes, and they are lateral and not of the same structure as in *Spanglerogyryus*. Inside the head, the contours of a large mandible, unlike those of the Gyrinidae, are vaguely visible.

Coxal plates of the hind coxae are often found in Adephaga, in Caraboidea and Dytiscoidea, and in Polyphaga (Mesocinetidae), from the Terminal Permian to the Late Jurassic. Later, including in modern

beetles, they are much less common. They are known in both aquatic beetles and beetles with a terrestrial appearance. In Coptoclavidae and Eudromeinae, it can be seen that almost all Triassic and Jurassic taxa have enlarged hind coxae; beetles with or without medium-sized plates predominate in the Cretaceous. Elongation of the medial processes of the hind coxae and the extension of the first visible (second true) abdominal sternites from under them was considered as a device for increasing the forward movement of the coxa with an increase in stroke amplitude (Ponomarenko, 1977). It is unlikely that the appearance of large coxal plates is associated with their use for air storage, since they are also present in land forms. Triaplidae were considered as a possible ancestor of Haliplidae, linking the latter with schizophoroid Archostemata. However, the most ancient Haliplidae have now been found in Babiy Kamen, the same locality as the beetles under consideration, so they should all be considered as different lines of the process of adaptation of beetles to the aquatic lifestyle. Due to significant differences in size, Triaplidae and Haliplidae had to colonize different ecological niches. The increase in the diversity of beetles with long hind coxae and large coxal plates did not alleviate the difficulties of their classification; rather, on the contrary, these difficulties increased. Not only do Triaplidae and Haliplidae not belong to the same phylogenetic lineage, but Triaplidae are also only parallel forms with the newly described beetles. Apparently, in the late Permian, and possibly only in the Vyatkian time, Polyphaga and Adephaga evolved not in two main lineages, but as a whole “evolutionary lawn” representing archaic diversity. Of course, it is not only the evolution of the hind coxae and the base of the abdomen that evolves in this way. Similarly, the formation of smooth elytra and elytra with punctate grooves occurs in numerous parallel lineages.

The taxonomic position of the beetles described above as *Tomia plus* cannot be precisely determined. In paleontological practice, there is a tendency to place forms that combine features of archaic and advanced groups in the latter. By following it, *Triaplus* can be placed among Adephaga, just like Triaplidae and Haliplidae. They could be considered as Archostemata, but in that case Haliplidae should also be moved there, which would lead to a significant change in taxonomic concepts in Adephaga.

At the same time, Ponomarenko’s (1977) hypothesis of the aquatic lifestyle of *Triaplus* is not without grounds, since the medial processes of the hind coxae and large coxal plates, elongated along the midline of the body, could indeed provide the forward movement of the hind legs for a more efficient stroke, similar to that of Haliplidae.

The abundance of Permian Triaplidae confirms the idea that new groups appear not after and as a result of the Permian-Triassic crisis, but before it. On the mountain plateau of the Siberian Traps, no drop in the



diversity of either plants (Sadovnikov, 2016), or animals has been recorded, and in fact the mountains were the most likely biodiversity refugia during the crisis.

### CONCLUSIONS

Triaplidae are a group of beetles with long medial processes of the hind coxae, and their attribution to schizophorids is impractical. A study of the base of the abdomen on better preserved material is required to determine whether the Triaplidae belong to Archostemata or to Adephaga.

### ACKNOWLEDGMENTS

The author thanks R.A. Rakitov for electron microscopic examination of the remains, and E.V. Yan and A.A. Prokin for help in preparing the publication.

### FUNDING

This work was financially supported by the Program I.22P of the Presidium of the Russian Academy of Sciences “Evolution of the organic world and planetary processes”.

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*Translated by S. Nikolaeva*