

# The Position of the Palaeozoic Genus *Tunguskagyryus* Yan, Beutel et Lawrence in the Family Triaplidae sensu n. (Coleoptera, Archostemata: Schizophoroidea)<sup>1</sup>

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**Abstract**—Re-examination of the late Permian *Tunguskagyryus planus* Yan, Beutel et Lawrence, 2018 has shown that it does not belong to the family Gyrinidae (Adephaga) but should be placed in the family Triaplidae sensu n. (Archostemata) as a congener to “*Triaplus*” *sibiricus* Volkov, 2013 (*Tunguskagyryus sibiricus* (Volkov, 2013), **comb. n.**). Both these Palaeozoic species, in contrast to the Triassic members of *Triaplus* Ponomarenko, 1977, have no large metacoxal femoral plates and, therefore, would be better placed apart from the Mesozoic representatives of *Triaplus* (in a different genus). The synonymy of the family names Triaplidae Ponomarenko, 1977 (= Catiniidae Ponomarenko, 1968, **syn. n.**, nom. praeocc., non Catiniidae Bocquet et Stock, 1957 (Crustacea, Copepoda), = Coleocatiniidae Ponomarenko et Prokin, 2015, **syn. n.**) is established. Thus, the family now comprises *Avocatinius* Ponomarenko, 1969, *Catinius* Ponomarenko, 1968, *Catinoidea* Ponomarenko, 1969, *Macrocatinius* Ponomarenko, 1969, *Triaplus* Ponomarenko, 1977, *Triassocatinius* Ponomarenko, 1969 and *Tunguskagyryus* Yan, Beutel et Lawrence, 2018.

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## INTRODUCTION

Recently, papers with descriptions and reconstructions of the Palaeozoic and Triassic coleopterous fossils were published that were based on imperfect imprints which caused ambiguities and misinterpretations. In this paper one of these fossils with structural peculiarities intermixed with a certain imperfection of the matrix is re-described. It is *Tunguskagyryus planus* Yan, Beutel et Lawrence, 2018 from Anakit of the late Permian (Krasnoyarsk Territory, Siberia, Russia). This imprint was recently described as the oldest member of the whirligig beetles (Gyrinidae) (Yan et al., 2018). The original diagnosis of this taxon declares “Short, semi-oval head with **completely divided compound eyes**, dorsal ocular subunits smaller than the lateral ones; **short antennae with enlarged, paddle-shaped pedicel** and stout proximal flagellomeres; body streamlined and drop-shaped; pronotum very short, transverse and curved; mesoventrite small, as long as mesocoxae, with small anteromedian groove; metacoxae transverse, without coxal plates; **six completely exposed abdominal ventrites, the terminal one medially divided.**” (Yan et al., 2018: 2—bold ours).

The description of this species on page 3 contains an important addition “terminal ventrite likely represented by medially divided gonocoxosternum VIII; separation along midline distinct posteriorly but not visible on anterior part. Paired, flat female gonocoxae visible posterior to terminal ventrite; with rounded apical part, reaching elytral apices posteriorly.”

Our examination of the holotype has shown that *Tunguskagyryus planus* (Figs. 1–5) indeed has: (1) usual undivided eyes (“dorsal” eyes being absent), (2) basal antennomeres not enlarged, (3) five abdominal ventrites of usual shape and with usual connections, (4) abdominal ventrite 5 not divided, (5) gonocoxites absent. Besides, the holotype has some remains of each of the six legs which can be more or less clearly observed under oblique lighting, and also it is impossible to clearly observe whether the upper integument of the holotype is really completely smooth, although the imprint of the elytra lateral to the body outline and probably the lateral portion of the disc seem to bear distinct dense, diffuse punctures interspaced with microreticulation. The epipleura of the holotype are moderately wide, while the reconstruc-



**Figs. 1–4.** *Tunguskagyrus planus* Yan, Beutel et Lawrence, 2018 (holotype, PIN 5381/32): (1) dry specimen, (2) specimen under alcohol, (3) abdomen under alcohol, (4) head and prothorax under alcohol. Length of specimen 9.8 mm. Scales: to Figs. 1 and 2—2.0 mm; to Fig. 3—1.0 mm; to Fig. 4—0.5 mm. Original.

tion of this beetle by Yan et al. (2018; fig. 3) shows wider epipleura at base, but their drawing reconstruction (Yan et al., 2018; fig. 2) demonstrates moderately wide epipleura. The imprint of *Tunguskagyryrus planus* also possesses the remains of moderately long and narrow legs, as well as small mesoventrite, making questionable the hypothesis of the aquatic mode of life for this species. The pterothoracic sclerites are similar to those in Triaplidae *sensu n.* and Schizophoridae Ponomarenko, 1968 rather than to those in other Palaeozoic and Triassic beetle families. Finally, the characters of “Catiniidae,” “Schizophoridae” and “Triaplidae” given in the original descriptions (Ponomarenko, 1968, 1969, 1977) were re-tested and analyzed. As a result, it was established that *Tunguskagyryrus* and the three above mentioned “families” belong to the same group named by Ponomarenko (1968) as the superfamily Schizophoroidea that is preliminarily treated as consisting of the two families Schizophoridae Ponomarenko, 1978 and Triaplidae Ponomarenko, 1977, *sensu n.* (= Catiniidae Ponomarenko, 1968, *syn. n.*—see below).

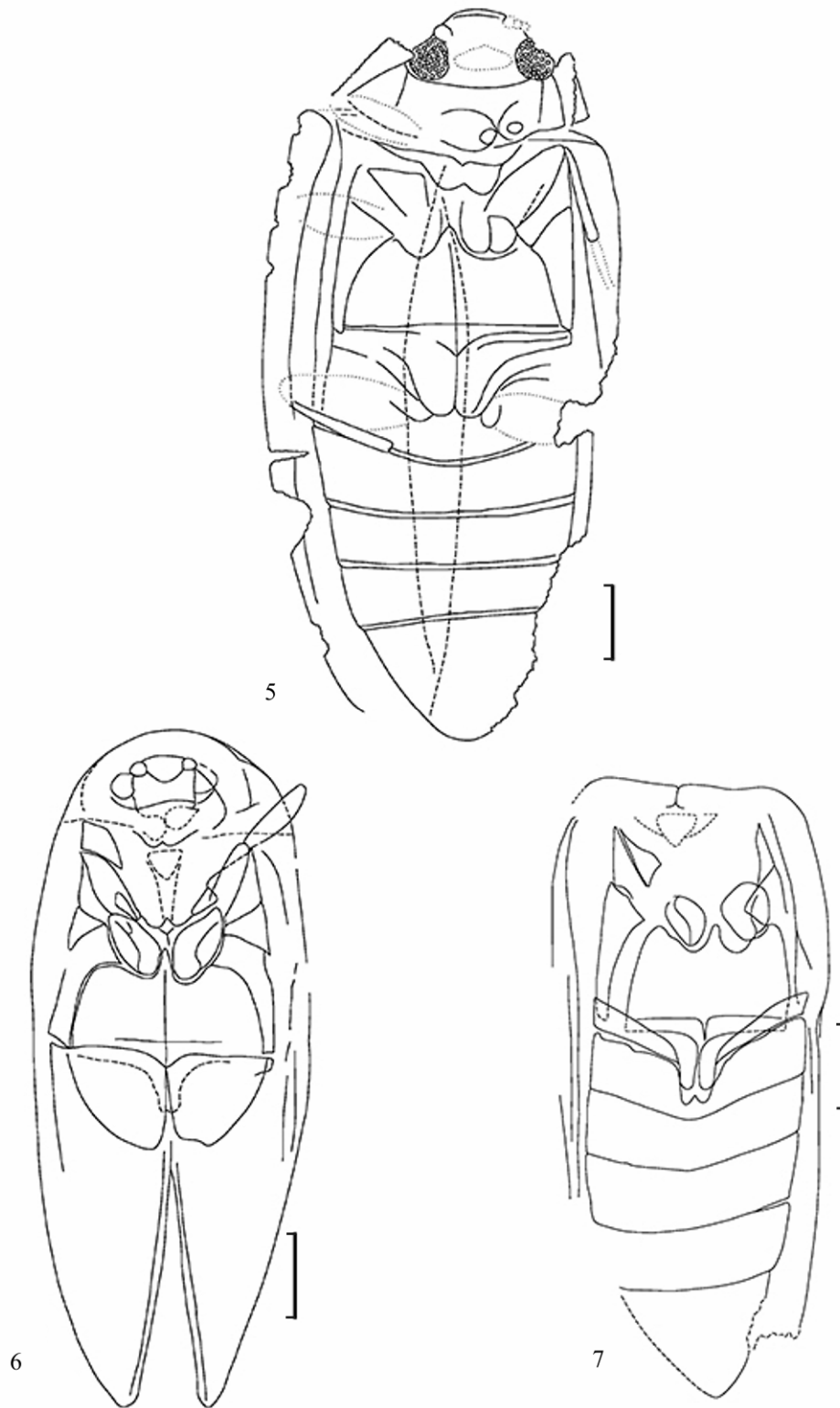
#### MATERIALS AND METHODS

The holotype of *Tunguskagyryrus planus* was studied under a Leica M165c stereomicroscope provided with digital camera Leica DFC420 in the Laboratory of Arthropods at the Borissiak Paleontological Institute, Russian Academy of Sciences (Moscow) (hereafter PIN). Images were generated using Helicon FOCUS 5.3.14 software and enhanced by using PHOTOSHOP CS4. Line drawings were modified for publication in the Autodesk AutoCAD 2015 program. To clarify the position of *Tunguskagyryrus planus* the authors also examined many other specimens from the PIN collection, including several type series of the taxa from the families considered, and they also had an opportunity of examination of the collection of fossils in the Capital Normal University in Beijing (hereafter CNU).

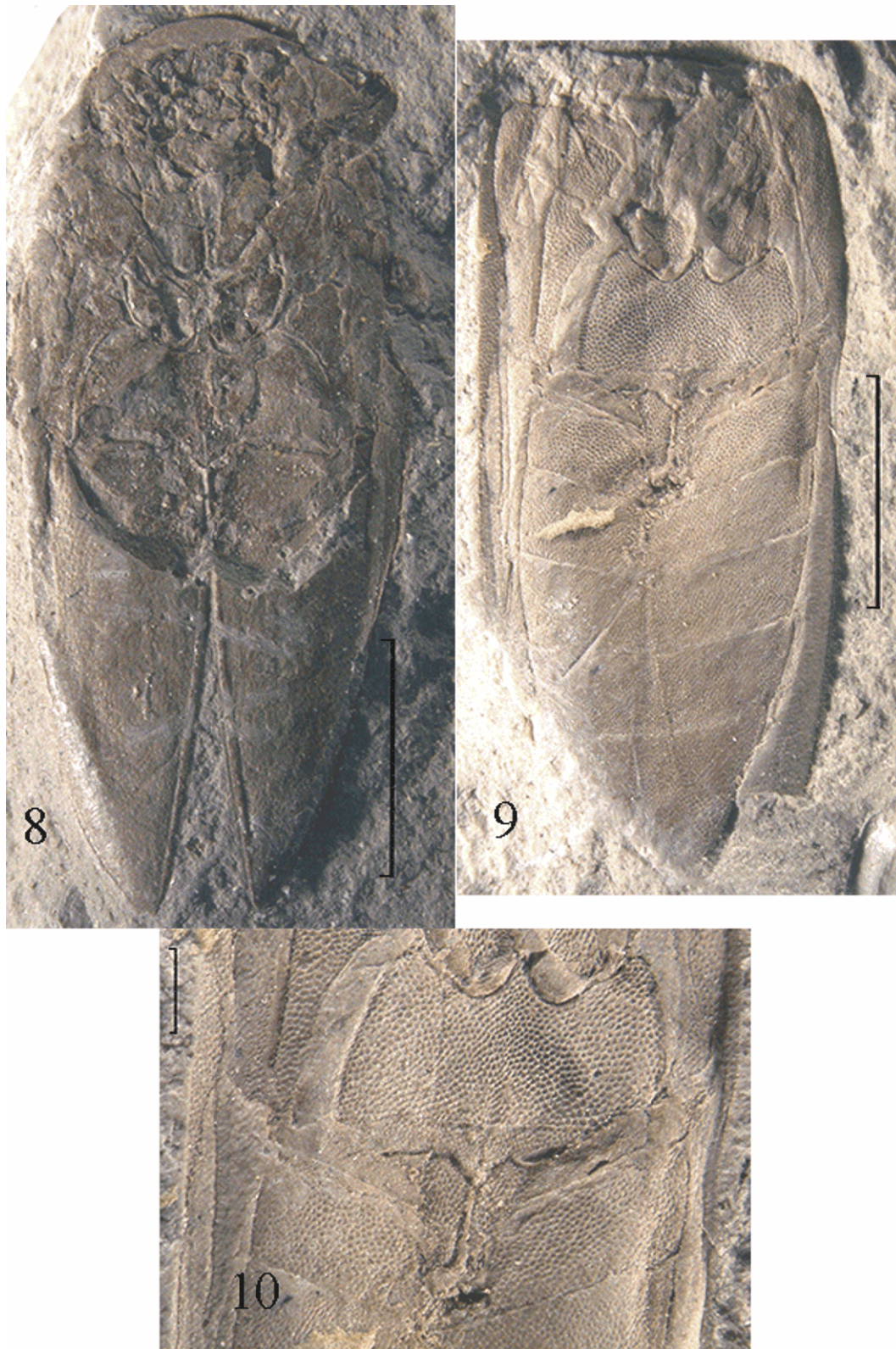
#### THE IDENTITY OF THE FAMILY TRIAPLIDAE SENSU N.

The appearance of an elongate body and the thoracic and abdominal sclerites of *Tunguskagyryrus* are strikingly similar to those of *Triaplus* Ponomarenko, 1977 (Figs. 6–10) in the Triaplidae (established in the Adephaga), *Avocatinius* Ponomarenko, 1969 (Fig. 12) of the “Catiniidae” Ponomarenko, 1968 (Archostemata), and *Hadeocoleodes* Ponomarenko, 1969

(Figs. 15–19) of the Schizophoridae (Archostemata). Attribution of all these taxa to the suborder Archostemata is based on the characteristic structure of their pterothoracic sclerites with a complete set of sutures on the metaventrite, metepisterna (metanepisterna) reaching the mesocoxal cavities, contiguous metacoxae with more or less extended mesal parts, and outlines of abdominal ventrites. Ponomarenko (1977) assigned *Triaplus* to the superfamily Haliploidea (Adephaga) mostly because he considered that the additional imprint (paratype) of *Triaplus macroplatus* (PIN 2905/24) has the remains of ventrite 1 (derivative of sternite 2) separated from ventrite 2 (derivative of sternite 3). However the latter imprint has intact metacoxae and a curved line running parallel to the posterior metacoxal edge (Fig. 9) that was erroneously drawn as a straight suture between “ventrites 1 and 2” by Ponomarenko (1977 : 18) on Fig. 1v, which actually represents the edge of the depression to receive the metacoxa (like that in Fig. 11). *Avocatinius* was initially placed in “Catiniidae” with correct interpretation of all the important visible sclerites. The holotype (PIN 2971/104) and paratype (PIN 2905/24) of *Triaplus macroplatus* belong to different triaplid species both in need of re-description. *Hadeocoleodes* demonstrates characters very similar to those of *Triaplus* but its head is not declined and procoxae are separated by the very narrow prosternal process. Ponomarenko (1968) considered this difference crucial for splitting the related groups into families (Schizophoridae and “Catiniidae”). The prosternal process of *Hadeocoleus gigas* Ponomarenko, 1969 (Fig. 17) is rather narrow, while it is markedly wider in *H. pelopius* Ponomarenko, 1969. Also, some peculiarities of fossilization, i. e. tension and compression of the sediments (tectonic deformation), could have caused a different state of this character in different fossils from the same outcrop. In the authors’ opinion, it would be reasonable to find additional diagnostic characters for separation of the schizophoroid families under consideration. However, a comprehensive revision is necessary to substantiate a new reorganization of the superfamily Schizophoroidea. Yet a significant similarity between *Tunguskagyryrus*, *Triaplus* and *Avocatinius* should be interpreted as a consequence of their close relationships and it is necessary to keep them together in the same family different from Gyridae. Two names, Catiniidae and Triaplidae, are available for this purpose; one of them (Catiniidae) is a junior homonym recently replaced by an invalid name Coleocatiniidae (Ponomarenko and Prokin, 2015), and Triaplidae re-



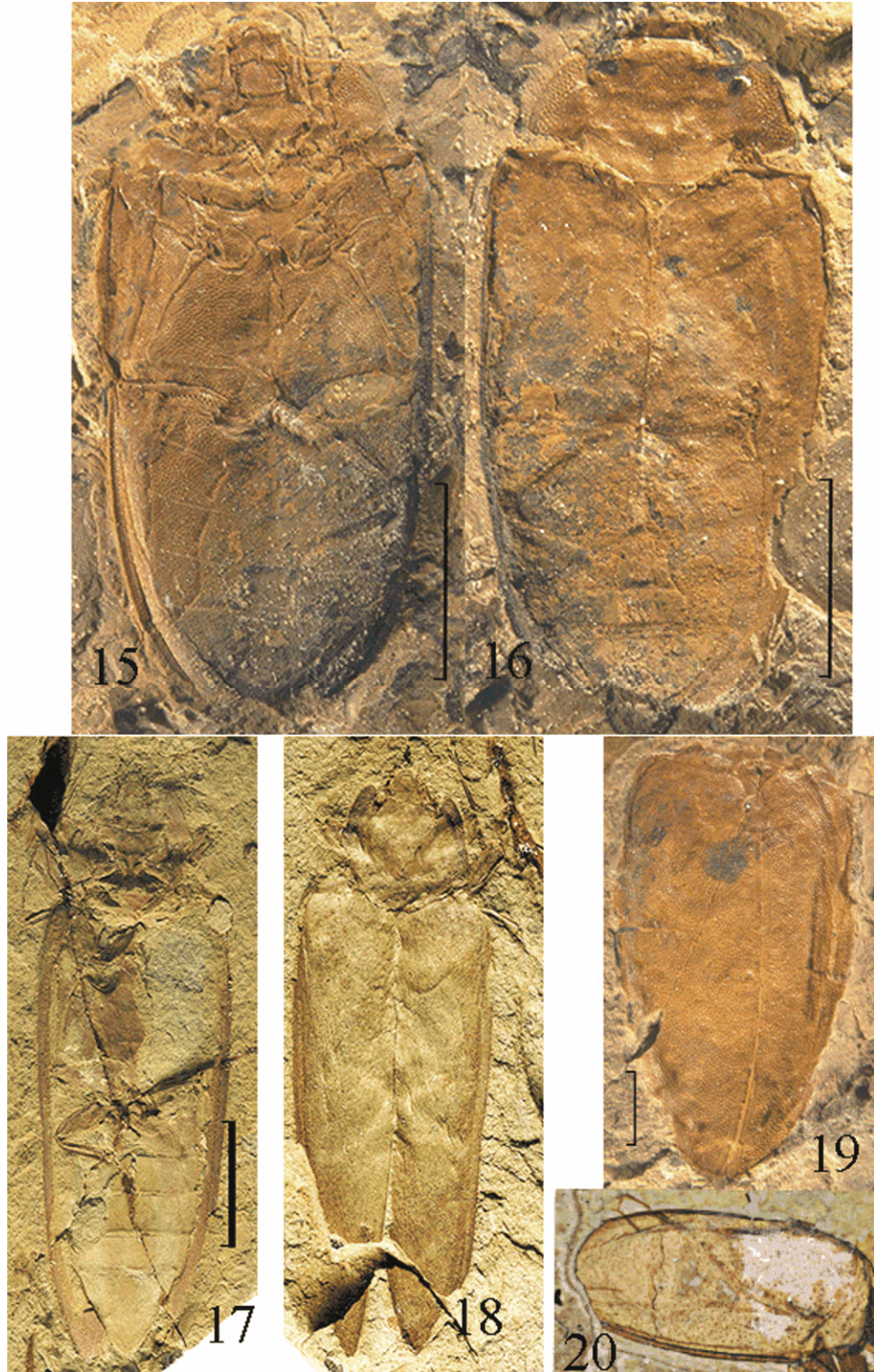
**Figs. 5–7.** Triaplidae, drawing-reconstructions: (5) *Tunguskagyrus planus* Yan, Beutel et Lawrence, 2018, holotype, PIN 5381/32; (6) *Triaplus macroplatus* Ponomarenko, 1977, holotype, PIN 2971/104; (7) gen. et sp. ? (*T. macroplatus*, paratype), PIN 2905/24. Broken lines show outlines of sclerites visible dorsally, and dotted lines show structures not clearly outlined. Scales—1.0 mm. Original.



**Figs. 8–10.** Triaplidae: (8) *Triaplus macroplatus* Ponomarenko, 1977, holotype, PIN 2971/104, dry specimen; (9) gen. et sp. ? (*T. macroplatus*, paratype), PIN 2905/24, dry specimen; (10) idem, dry metaventre and metacoxae. Scales: to Figs. 8 and 9—2.0 mm; to Fig. 10—0.5 mm. Original.



**Figs. 11–14.** Triaplidae: (11) *Macrocatinius brachycephalus* Ponomarenko, 1969, holotype, PIN 2344/256, dry specimen; (12) *Avocatinius elongatus* Ponomarenko, 1969, holotype, PIN 2240/232, dry specimen; (13) *Catinius pelta* Ponomarenko, 1968, holotype, PIN 2384/634, dry specimen; (14) idem, specimen under alcohol. Scales: to Fig. 11—5.0 mm; to Figs. 12–14—2.0 mm. Original.



**Figs. 15–20.** Schizophoridae: (15) *Hadeocoleodes calus* Ponomarenko, 1969, holotype, PIN 1361/20, dry counterpart (underside of body); (16) idem, dry positive imprint (dorsal side of body); (17) *Hadeocoleus gigas* Ponomarenko, 1969, holotype, PIN 2240/322, dry counterpart (underside of body); (18) idem, dry positive print (dorsal side of body); (19) gen. et sp. ? (“*Hadeocoleodes calus*,” additional specimen, PIN 1361/59), photograph of counterpart of elytra; (20) gen. et sp. ?, CNU 2009143, positive imprint of elytra. Scales: to Figs. 15, 16, 19—2.0 mm; to Figs. 17, 18, 20—1.0 mm. Figs. 17, 18 from the web-site “Beetles (Coleoptera) and coleopterists:” [https://www.zin.ru/animalia/coleoptera/rus/hadcol\\_g.htm](https://www.zin.ru/animalia/coleoptera/rus/hadcol_g.htm), Fig. 20 from Ponomarenko and Prokin, 2015, other figures original.

mains the only valid name for the family formerly named as Catiniidae.

Thus, Triaplidae Ponomarenko, 1977 (= Catiniidae Ponomarenko, 1968, syn. n., nom. praecoc., non Catiniidae Bocquet et Stock, 1957 (Crustacea, Copepoda; type genus *Catinia* Bocquet et Stock, 1957), = Coleocatiniidae Ponomarenko et Prokin, 2015, syn. n.).

**Emended diagnosis** (after Ponomarenko, 1968, 1969, 1977). Head more or less retracted into prothoracic segment and more or less covered by pronotum. Pronotum transverse, with anterior angles projecting anteriorly; prosternum significantly shorter than pronotum, propleura distinctly isolated and reaching anterior edge of prothorax. Procoxae transverse, contiguous and projecting. Procoxal cavities open posteriorly. Mesocoxae closed externally and separated mesally. Mesothorax strongly transverse, with clearly isolated sclerites and anterior depressions for receipt of procoxae. Metepisterna widened anteriorly and linked with mesocoxae only by inner anterior angle. Metaventricle narrowed anteriorly, with both discrimen and parametacoxal (katapisternal) lines. Metacoxae strongly transverse and contiguous, mesally more or less extended posteriorly and with distinct trochantin. Abdomen with five ventrites. Elytra with diffuse true punctation but without trace of venation and cells (window punctures).

**Notes.** In the original description of Catiniidae Ponomarenko (1968: 130) also mentioned the microtuberculate integument, “ledge-catch” and indistinct rows of cells on elytra. Later Ponomarenko (1969: 177) pointed out that this group is characterized by the inclined prothoracic segment and head, short and weak legs, presence of the “schiza” (see Discussion below), and lack of elytral cells. Nevertheless, most specimens examined have a more or less smoothed integument with simple diffuse punctures, lacking cells and longitudinal rows on the elytra. Also, the head declination is an occurring but not characteristic feature of this group and elytral “schiza” is usually not visible in the examined specimens. Ponomarenko (1968, 1969) drew “schiza” in his drawing reconstructions of some schizophorids but never in his reconstructions of “catiniids”. Probably the occurrence of this structure as characteristic of the schizophoroids needs to be revised (see below).

#### TAXA INCLUDED

1. *Avocatinus* Ponomarenko, 1969. *A. elongatus* Ponomarenko, 1969 (Dzhailyaicho, Middle–Upper Triassic, Karnian, Madygen Formation) (Fig. 12).

2. *Catininus* Ponomarenko, 1968. *C. pelta* Ponomarenko, 1968 (Karatau, Upper Jurassic, Karabastau Formation); ? *C. artus* Zhang, 1997 (Zhixin, Lower Cretaceous, Dalazi Formation); *ovatus* Zhang, 1997 (Zhixin, Lower Cretaceous, Dalazi Formation) (Figs. 13, 14).

3. *Catinoides* Ponomarenko, 1969. *C. rotundatus* Ponomarenko, 1969 (Dzhailyaicho, Middle–Upper Triassic, Karnian, Madygen Formation).

4. *Macrocatinius* Ponomarenko, 1969. *M. brachycephalus* Ponomarenko, 1969 (Dzhailyaicho, Middle–Upper Triassic, Karnian, Madygen Formation) (Fig. 11).

5. *Triaplus* Ponomarenko, 1977. *T. laticoxa* Ponomarenko, 1977 (Dzhailyaicho, Middle–Upper Triassic, Karnian, Madygen Formation); *T. macroplatus* Ponomarenko, 1977 (Dzhailyaicho, Middle–Upper Triassic, Karnian, Madygen Formation) (Figs. 6–10).

6. *Triassocatinius* Ponomarenko, 1969. *T. glabratus* Ponomarenko, 1969 (Dzhailyaicho, Middle–Upper Triassic, Karnian, Madygen Formation), *T. brachynotus* Ponomarenko, 1969 (Dzhailyaicho, Middle–Upper Triassic, Karnian, Madygen Formation).

7. *Tunguskagyryrus* Yan, Beutel et Lawrence, 2018. *T. planus* Yan, Beutel et Lawrence, 2018 (Anakit, Upper Permian (Changhsingian), Maltsevo Formation); *T. sibiricus* (Volkov, 2013), comb. n. (= *Triaplus sibiricus* Volkov, 2013) (Babiy Kamen, Upper Permian, Maltsevo Formation) (Figs. 1–5)—see below.

#### Genus *TUNGUSKAGYRUS*

Yan, Beutel et Lawrence, 2018

Type species: *Tunguskagyryrus planus* Yan, Beutel et Lawrence, 2018.

**Emended diagnosis.** Body medium-sized, varying in elongate, widest in basal half of elytra. Integument with diffuse, moderately fine and moderately dense subuniform punctures. Head transverse, with rather large (not divided) eyes. Pronotum strongly transverse, widest at base and emarginate at anterior edge. Mesoventricle with excavations for receipt of procoxae. Metaventricle about 1.5 times as wide as long. Metepisterna with gently arcuate inner edge. Metacoxae mesally strongly projecting posteriorly and without femoral plate. Epipleura moderately wide. Abdominal ventrite 1 longer than each of ventrites 2–4; ventrite 5 subtriangular, longest and with rounded



apex. Femora moderately wide. Protibia subtriangular and moderately wide. Meso- and metatibiae very narrow and long.

**Comparison.** This genus is characterized by a short head with very large eyes, very short and strongly transverse prothorax with widely transverse procoxal cavities, well expressed anterior depressions on mesoventrite, short and strongly transverse metaventrite, arcuate inner edge of metepisterna, very long mesal parts of metacoxae, and comparatively narrow and long meso- and metatibiae. It differs from:

—*Catinus* and *Catinoides* in a longer and larger body, shorter and wider pronotum, longer mesal part of the metacoxae, narrower epipleura, longer abdominal ventrite 5 with moderately rounded (not widely rounded) apex; and from *Catinus* also in markedly longer legs;

—*Avocatinus* in a less elongate and larger body, larger eyes, much wider metaventrite, longer mesal part of the metacoxae, wider epipleura, abdominal ventrite 5 with moderately rounded (not widely rounded to subtruncate) apex;

—*Macrocatinius* and *Triassocatinius* in the longer mesal part of metacoxae, less transverse abdominal ventrite 5 with moderately rounded (not widely rounded) apex; from *Macrocatinius* also in markedly longer legs, and from *Triassocatinius* also in a larger body;

—*Triaplus* in a wider and larger body, not strongly declined head, excised anterior edge of pronotum, lack of large femoral plates of metacoxae, and wider epipleura.

**Taxa included.** Two species: type species and *T. sibiricus* (Volkov, 2013), comb. n.

**Notes.** The holotype of *Triaplus sibiricus* is very similar to the members of *Triaplus* in dorsal view (it was the reason for misinterpretation in the original description: Volkov, 2013: 96), but the additional specimen PIN 4887/348 represented by a complete imprint from the same outcrop makes the underside of the body of this species accessible to study. It was discovered that the metacoxal femoral plates in this species are not as large as in the Triassic species of *Triaplus*, and it has five exposed abdominal ventrites (not six as erroneously stated in the original description), and, therefore, its characters fit the above diagnosis of *Tunguskagyus*. This Permian species is dis-

tinct from *Tunguskagyus planus* in the shape of the pronotum and shorter legs and, thus, represents a distinct species *T. sibiricus* comb. n.

### *Tunguskagyus planus*

Yan, Beutel et Lawrence, 2018

Figs. 1–5

**Holotype.** PIN 5381/32, almost complete specimen preserved as an imprint in the rather hard rock matrix. It includes the body with broken or missing outer parts of the right posterior structures (distal part of elytron and abdominal ventrites), apparently right three basal antennomeres and left ultimate palpomere, both protibiae (right one nearly complete and left one with broken apical and outer portions), right middle leg, traceable left mesofemur, right metatrochanter and traceable basal part of both metafemora, traceable left metatrochanter, and left metatibia.

**Description.** Length 9.8, width 4.5 mm. Body subelliptic with gentle outline, apparently rather convex dorsally and moderately convex or subflattened ventrally. Metaventrite, epipleura and apparently elytra with diffuse punctures as coarse as eye facets, separated by about one puncture diameter. Head transverse (somewhat declined downwards as in holotype of *Triaplus macroplatus*), with subpentagonal mentum (triple as wide as long), very large (not divided) eyes with moderately coarse facets, and also with trace of suboval left ultimate palpomere and three small suboval antennomeres of right antenna. Elytra widest at midlength, gently narrowing toward apparently subangular apices (length to width of elytron ratio apparently slightly more than 2). Prothorax very short, widest at base, about 3.5 times as wide as long; posterior angle of pronotum (visible on right side) with distinct top; propleura reaching widely emarginate anterior edge of prothorax. Procoxae strongly transverse. Mesoventrite with very distinct anterior excavations and excised posterior edge (mesoventral process). Mesocoxae moderately large, narrowly separated. Metaventrite with distinct discrimen along its entire length and with parametacoxal sutures. Metepisternum about 2.5 times as long as wide. Each metacoxa about 1.5 times as wide as long mesally. Epipleura at base somewhat narrower than eye and gradually narrowing posteriorly. Abdominal ventrites seemingly somewhat overlapping, ventrite 1 about 1.5 times as long as metacoxa, ventrites 2–4 subequal in length, each markedly shorter than ventrite 1, ventrite 5 longest, about 1.4 times as wide as long, somewhat arcuate at

apex. Protibiae (right one with missing apical part and outer edge and left one with clearly crenulate outer edge) subtriangular, moderately widened apically. Profemur (traceable on left side) about 1.5 times as wide as protibia. Mesotibiae and right metatibia very narrow subparallel-sided. Mesotarsus (right one) nearly as wide as mesotibia. Meso- and metafemora somewhat wider than profemur.

**Emended diagnosis.** This species differs from *Tunguskagyrus sibiricus* comb. n. in a somewhat more robust body with a smaller head with relatively smaller eyes, shorter prothorax and elytra (ratio of length to width of elytron in *T. sibiricus* comb. n. nearly 3), and also longer abdominal ventrite 1. Additionally, the elytra of *T. planus* are widest at midlength while those of *T. sibiricus* are so at base.

## DISCUSSION

From the pre-Jurassic fossil record the only described species *Triadogyrus sternalis* Ponomarenko, 1977 (Adephaga incertae sedis) from Garazhovka of the Upper Triassic could not be considered a potential ancestor of whirligigs (Ponomarenko and Prokin, 2015), although Beutel et al. (2013) and Yan et al. (2018) included this species in Gyrinidae without re-description of the holotype and any supporting evidence. Gyrinidae are known from the Lowermost Jurassic by one questionable fossil (*Mesogyrus sibiricus* Ponomarenko, 1985 (Heterogyrinae): 189.6–182.7 Ma). Nevertheless, according to Gustafson et al. (2017) the time of appearance of the family Gyrinidae could be estimated as the Late Permian or Lower Triassic at 255 Ma (95% highest posterior density 236–271 Ma), although this estimation is extremely premature and needs more support (in particular by fossils).

Ponomarenko (1977) admitted the aquatic mode of life for species of *Triaplus* because of the metacoxae with the mesal portions extended rather far posteriorly and with very large femoral plates which could presumably provide efficient rowing movement in the water. However, one paratype of *Triaplus macroplatus* (PIN 2905/24) considered by Ponomarenko (1977) as missing femoral metacoxal plates apparently never had them because the location of its metacoxae has no trace of damage (Fig. 9) and, furthermore, the specimen belongs to a genus different from *Triaplus*, as, in addition to the lack of femoral plates, it has a different outline of its metaventrite. Another feature treated as adaptation to aquatic life is the presence of the

“schiza” (see above). This term designating a separate longitudinal “short furrow” at the lateral edge of the elytron was introduced by Rohdendorf (1961) for characterization of the Schizocoleidae Rohdendorf, 1961 [Greek σχίζα—splinter, log, block and σχίζω—“I split,” detach], although this term has acquired another meaning in the subsequent literature (for example, Ponomarenko and Prokin, 2015). This “schiza” is usually considered a short additional rib at the inner epipleural edge (Fig. 20), called by other coleopterists as “locking flange” (Crowson, 1981: 44, Fig. 39) and frequently found in Hydrophilidae. The inner long epipleural ridge or flange (not short “schiza”) is an apotypic structural character of Coleoptera (a part of the complex interlocking the abdomen and elytra). It was found in the most archaic representatives of Archostemata (Kirejtshuk et al., 2014, 2016; etc.) and has several kinds of congruence with sclerites of the abdomen (shown by Kasap and Crowson (1975) in Elateriformia). Although the real “schiza” could be present in some Jurassic-Cretaceous archostematans as a short groove in compression imprints. The epipleural ridge or flange of Schizophoroidea could have some association with an aquatic or semiaquatic mode of life, or with a life in moist environment but this character itself can scarcely be an indicator of it. Nevertheless, it is important for this concept that the hindwing venation of Triaplidae (= Catiniidae) to a great extent corresponds to that of Myxophaga (Ponomarenko, 1973). Finally, it can be mentioned that the Jurassic *Chimaerocoleus aenigma* Ponomarenko, 1985 with the sculpture of the dorsal integument similar to that in *Triaplus* has legs with fringes of long swimming hairs (Ponomarenko and Prokin, 2015).

From deposits of the Middle Permian to Upper Triassic larvae are known with characters shared by representatives of the Megaloptera and Coleoptera (Prokin et al., 2015). A long geological existence of such larvae could mean that they belonged to a widespread group which should be represented in the fossil record. The distribution of adults of Schizophoroidea in time rather coincides with the distribution of these larvae that are comparably diverse. Thus, it can be provisionally assumed that Triaplidae sensu n. or schizophoroids as a whole had aquatic larvae, while their adults could live in water or in habitats near basins (like recent representatives of the Myxophaga, which according to Ponomarenko (1973) could be a derivative of the extinct group of beetles considered in this paper) or moist environments, e. g. decaying organic matter.

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