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New Triassic Beetles (Coleoptera) from Northern European Russia

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Abstract—Beetle remains from the Triassic Khey-Yaga locality, Nenets National District, Korotaikha Basin, Nyadeita Formation, Olenekian–Anisian are described. Only isolated elytra have been found. *Tetracoleus tshalyshevi* gen. et sp. nov. and *T. minimus* sp. nov. are described and assigned to Tricoleidae, and six new species are described in formal taxa. *Tetracoleus* is close to Permian tricoleids just found in the Newcastle Group of Australia and the Vyatkian Aristovo locality of northern European Russia. The composition of elytra in the locality is closer to that of Lower Triassic localities than other Middle Triassic localities and characterizes the beginning of a recovery after the Permian–Triassic ecological crisis. *Longxianocupes* Hong in Liu, Liu et Hong, 1985 is shown to be a junior synonym of *Sogdelytron* Ponomarenko, 1969. The species *Palademosyne ovum* Ponomarenko, 2004, *P. elongatum* Ponomarenko, 2004, and *P. latum* Ponomarenko, 2004 are transferred to the genus *Pseudochrysomelites* Handlirsch, 1906.

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Key words: Coleoptera, Permian–Triassic ecological crisis, new taxa, European Russia.

INTRODUCTION

Early and Middle Triassic beetles remain insufficiently studied. However, the lack of data on them, as with fossil insects in general, is not as profound as could be concluded from reading some publications on the restoration of the biota following the Permian–Triassic crisis (Bottjer and Gall, 2005; Béthoux et al., 2005). A few remains of Early Triassic beetles have been previously described (Ponomarenko, 2004). The remains described below have been found at the Khey-Yaga locality, in dark gray argillites containing abundant remains of horsetails. The locality is situated in the southeastern foothills of the Pai-Khoi Range (Polar Ural Mountains), Arkhangelsk Region, Nenets National District, Korotaikha basin, Nyadeita Formation, middle course of Khei-Yaga River, 10 km downstream from the mouth of the Lestan-Shor Creek and 1 km downstream from the mouth of the Grubo-Shor Creek. The locality corresponds to outcrop no. 196 of V.I. Chalyshev, who was the first to find insect remains here (Chalyshev and Varyukhina, 1966). It is slightly upstream of the tetrapod locality Khey-Yaga 3 (Novikov, 1994). Chalyshev considered the locality as Olenekian (Chalyshev and Varyukhina, 1966), and Dobruskina (1980) as Ladinian. According to the modern nomenclature (*Explanatory Notes…*, 1980), these deposits belong to the lower subformation of the Nyadeita Formation and are Anisian. Based on the tetrapod fossils, the locality corresponds to the Donguz Horizon of the more southern areas of European Russia, from which no insect remains are known. Chalyshev has found only a few insect specimens and, in spite of subsequent focused field work by paleoentomologists from the Paleontological Institute of the Russian Academy of Sciences (PIN), headed by I.D. Sukatsheva, the collection of insects from the locality remains small. It contains cockroaches and auchenorrhynchans, but most of the remains, including 12 fairly complete specimens, are of beetles. The actual number of beetle specimens may be higher, but their state of preservation is such that it is not always possible to distinguish beetle fragments from paleoniscid scales. Two specimens are beetles from the family Tricoleidae, one is an elytron fragment with punctate striae, and the remainder are schizophoroids. Therefore, the faunal assemblage studied is intermediate between the purely schizophoroid Early Triassic assemblages and the Ladinian assemblage of the southern Fore-Urals, being closer to the first. The most acceptable age for this assemblage of beetle elytra can be the Late Olenekian, because the Early Anisian assemblage from the Voltzia Sandstone in northeastern France (Papier et al., 2005) has distinctly more advanced features.

The Tricoleidae is one of the least studied extinct beetle families. It was described based on isolated elytra from Late Triassic localities in southern Kazakhstan and Middle Asia (Ponomarenko, 1969). The record of *Tricoleus* from the Early Jurassic stems from a stratigraphic error: the actual age of the Ketmen' locality is Upper Triassic, Carnian. In addition to the genera included in the original description, the family includes *Longxianocupes* Hong (Liu et al., 1985) from the Middle Triassic of China. Judging from the photograph, the only known specimen of this genus belongs to the genus *Sogdelytron* Ponomarenko, 1969. Therefore, *Longxianocupes* Hong (Liu et al., 1985) should be considered as a junior subjective synonym of *Sogdelytron* Ponomarenko, 1969. The synonymy is based on the presence of three principal veins, separated by spaces each containing three rows of cells, and an oblique crossvein extending from the penultimate to the last principal vein. *Sogdelytron*, may in turn be found to be a junior synonym of *Willcoxia* Dunstan, 1924 from the Upper Triassic of Australia. However, because the only specimen placed in that genus is known only from a drawing of an isolated elytron fragment, such a synonymy would be premature until the holotype is reexamined. Photographs of isolated elytra of undescribed tricoleids from the Triassic of Spain (Peñalver et al., 1999) and Poland (Dzik and Sulej, 2004, 2007) have been published. In the last case, the beetles were ascribed to Cupedidae and the reconstruction suggested was utterly monstrous: incorrectly drawn elytra grafted onto the head and pronotum of the Cenozoic beetle genus *Cupes.* Partial study of a large collection of beetles from the Upper Triassic Molteno locality in South Africa has revealed that, in that collection, all the beetles with reticulate venation belonged to Tricoleidae. A complete beetle with reticulate venation was described from this locality as *Moltenocupes townrowi* Zeuner, 1961 and placed in the family Cupedidae. A high quality photograph accompanying the original description shows that it, indeed, belongs to that family. Remains of tricoleids have been found in the terminal Permian Newcastle Coal Measures in Australia (based on a photograph provided by G. Beatty), as well as at the Vyatkian Aristovo locality in the Vologda Region. A beetle recently described from the Jurassic Daohugou locality in northern China was placed in Tricoleidae (Tan et al., in press). Most spaces on the elytra of the beetle described contain four rows of cells, while, in other tricoleids, four cell rows in a space are only known from the most ancient Permian forms and the genus described below. Therefore, modern data suggest that the stratigraphic range of tricoleids extends from the terminal Permian to the terminal Triassic or the Middle Jurassic. While in Induan deposits or in the lower (Rybinsk) Horizon of the Olenekian no tricoleid remains have been found, they are very common in the Middle and Upper Triassic, starting from the Ladinian. During the Permian, they appear together with advanced beetles, having elytra of the permosynid type. These advanced beetles have not been found in the Early Triassic (if the Babii Kamen' locality is considered to be Permian, see Ponomarenko, 2004).

The composition of morphological types of elytra in Khey-Yaga resembles the low-diversity elytral assemblages of the Lower Triassic rather than those of the Ladinian Bukobay Formation. Two specimens, strongly differing in size, belong to tricoleids. Almost all of the others are smooth elytra of the schizophoroid type, as in the Lower Triassic localities. Based on their form and size, they can be assigned to several formal genera and species, also strongly varying in size. They most probably belong to aquatic schizophoroid archostematans and (or) adephagans. Tricoleids, with their grid-like venation, could have been a xylophilous group. The rarity of elytra with few rows of punctures or with punctate striae, some of which might have belonged to polyphagans, is characteristic. They first appear in the terminal Permian of Eurasia and Australia, then disappear from deposits during the Lower Triassic, reappear at the Bukobay Ladinian sites, and are abundant in the Upper Triassic and all younger localities (Ponomarenko, 2004). Only one incomplete specimen has been discovered at Khey-Yaga. Although Dobruskina (1980) assigned these deposits, based on the plant remains, to the Ladinian, the composition of the fossil beetles seems to rather suggest an Anisian or Upper Olenekian age. For beetles it was still a time of decreased diversity after the Permian–Triassic ecological crisis.

The assemblage of beetle elytra from the Anisian localities of the Voltzia Sandstone in northeastern France (Papier et al., 2005) is in stark contrast to the above sequence. Judging from published photographs, it is more similar to assemblages from the Upper Triassic localities. The most characteristic feature is the abundance of cupedids. At the Ladinian Bukobay localities, they are not yet present, although one find is known from the Ladinian of southern Switzerland (Krzeminski and Lombardo, 2001). Cupedids have not been found among elytra from the Anisian or the Ladinian of Germany (Geyer and Kelber, 1987; Brauckman and Schlüter, 1993), and the Early Anisian finds appear more advanced than the beetles from Khey-Yaga. The early restoration of diversity in Europe appears rather strange, because there the disturbance of ecosystems during the Permian–Triassic ecological crisis was more profound (Looy, 2000) than on Angarida and even in the area of the Siberian trap magmatism in the Tungus Basin.

SYSTEMATIC PALEONTOLOGY

Suborder Archostemata

Family Tricoleidae Ponomarenko, 1969

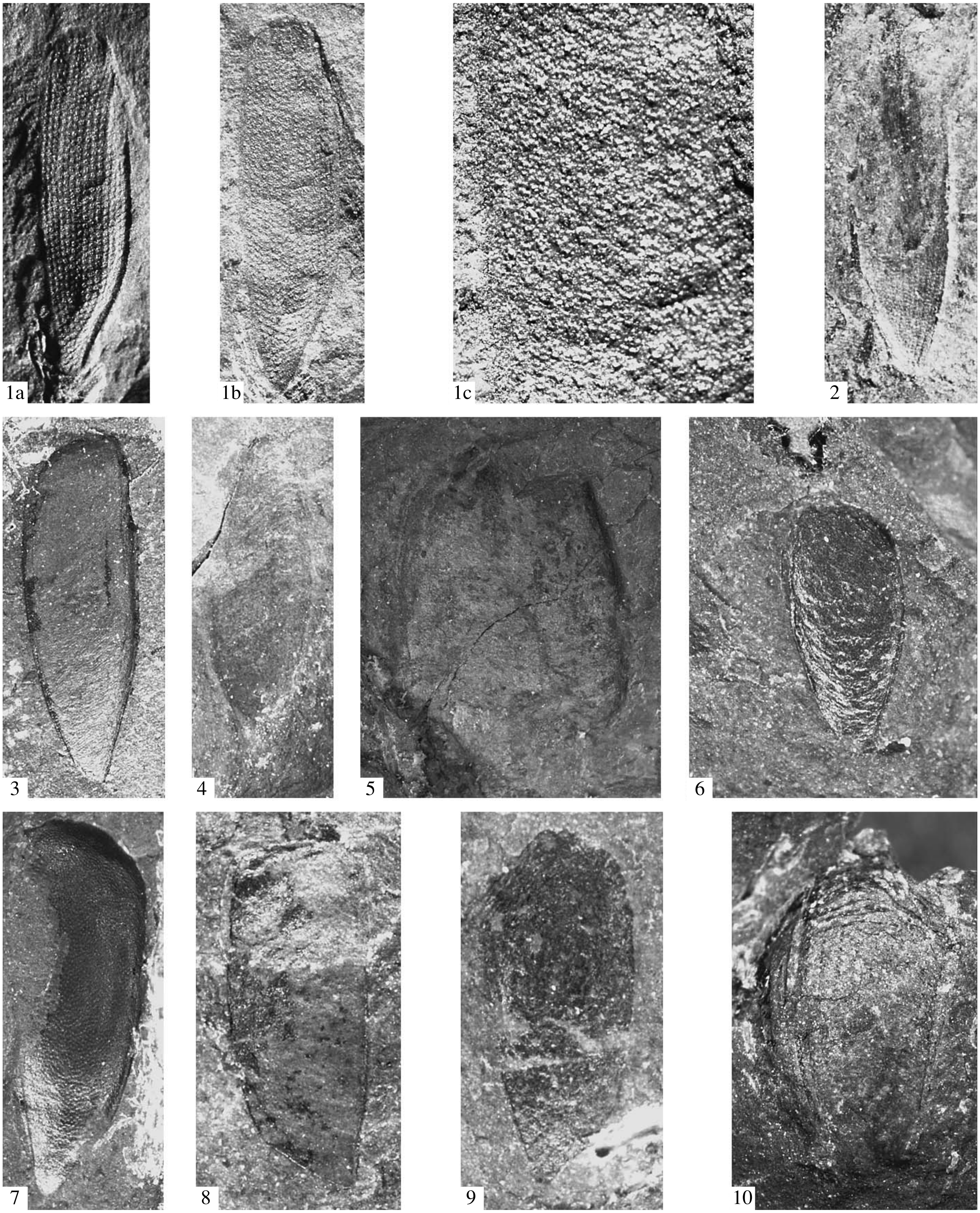
Genus *Tetracoleus* Ponomarenko, gen. nov.

E t y m o l o g y. From the Greek *tetra* (four) and *coleon* (scale).

T y p e s p e c i e s. *Tetracoleus tshalyshevi* sp. nov.

D i a g n o s i s. Elytron convex, with three principal veins and four spaces in between. Principal veins not strongly different from intermediate ones. Marginal vein extended into wing apex, others connect together before apex. Marginal space and third (from the outer margin = adsutural) space with four rows, others with three rows of cells throughout most of their length. Base of second (from the outer margin) space with eight rows of cells and that of sutural space with four. Cells round, conspicuously broader than veins. Tubercles around edges of cells distinct.

Plate 2



S p e c i e s c o m p o s i t i o n. Two species described below.

C o m p a r i s o n. The new genus is distinct from other genera in having four rows of cells in the marginal and adsutural spaces and a larger number of cell rows at the bases of other spaces.

Tetracoleus tshalyshevi **Ponomarenko, sp. nov.**

Plate 2, fig. 1

E t y m o l o g y. In honor of the renowned geologist V.I. Chalyshev, who was the first to find insect remains at the Khey-Yaga locality.

H o l o t y p e. PIN, no. 5252/1, left elytron, negative impression; Khey-Yaga locality; Lower Triassic, Olenekian, or Middle Triassic, Anisian, Nyadeita Formation.

D e s c r i p t i o n (Fig. 1). The elytron is elongate, 3.7 times longer than wide, narrowed in the apical third, with the apex displaced towards the sutural margin, attenuated into a broad "tail," the sutural margin is straight, not bordered. The epipleural border is narrow. Two adsutural principal veins are connected conspicuously proximal of the point where the elytron narrows into the "tail." Each row contains about 50 cells. Tubercles around the edges of cells are distinct. The base of the space posteriad of the middle vein has a short ridge.

M e a s u r e m e n t s (mm): elytron length, 6.6; width 1.7.

M a t e r i a l. Holotype.

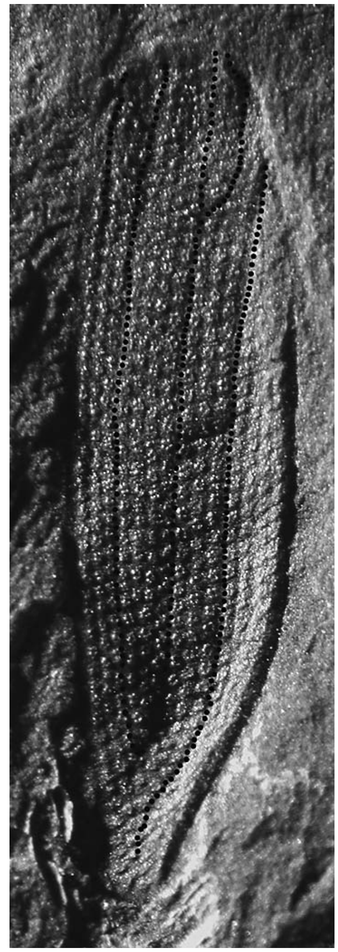


Fig. 1. *Tetracoleus tshalyshevi* sp. nov., holotype PIN, no. 5252/1. Principal veins are shown with dashed lines.

Tetracoleus minimus **Ponomarenko, sp. nov.**

Plate 2, fig. 2

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

H o l o t y p e. PIN, no. 5252/2, right elytron, incomplete positive impression, disc preserved only in the apical third; Khey-Yaga locality; Lower Triassic, Olenekian, or Middle Triassic, Anisian, Nyadeita Formation.

D e s c r i p t i o n. The elytron is elongate, twice as long as wide, tapering in the apical third, with the apex displaced towards the sutural margin, attenuated into a broad "tail," the sutural margin is convex, not bordered. The epipleural border is narrow. The adsutural principal veins are connected together on the "tail." The base of the space posteriad of the middle vein has a short ridge.

M e a s u r e m e n t s (mm): elytron length, 3.2; width 0.8.

C o m p a r i s o n. The new species is distinct from the type species in having the apex of the elytron only weakly narrowed, the adsutural principal veins connected more distally, the sutural margin convex, and in its smaller size.

M a t e r i a l. Holotype.

E x p l a n a t i o n o f P l a t e 2

Fig. 1. *Tetracoleus tshalyshevi* sp. nov., holotype PIN, no. 5252/1: (1a) general view, oblique lighting, ×10; (1b, 1c) vertical lighting: (1b) ×10 and (1c) detail of elytron, ×40.

Fig. 2. *Tetracoleus minimus* sp. nov., holotype PIN, no. 5252/2, general view, ×18.5.

Figs. 3–5. *Schizocoleus septentrionalis* sp. nov.: (3) holotype PIN, no. 2047/1, general view, ×13; (4) specimen PIN, no. 5252/5, general view, ×10; (5) specimen PIN, no. 5252/8, general view, ×12.5.

Fig. 6. *Stegosyne borealis* sp. nov., holotype PIN, no. 5252/6, general view, ×26.

Fig. 7. *Pseudochrysomelites anser* sp. nov., holotype PIN, no. 5252/10, general view, ×21.7.

Fig. 8. *Pseudochrysomelites planus* sp. nov., holotype PIN, no. 5252/3, general view, ×20.

Fig. 9. *Pseudochrysomelites dilatus* sp. nov., holotype PIN, no. 5252/9, general view, ×40.

Fig. 10. *Pseudorhynchophora convexa* sp. nov., holotype PIN, no. 2047/2, general view, ×29.

Coleoptera incertae sedis

Family Schizocoleidae Rohdendorf, 1961

Genus *Schizocoleus* Rohdendorf, 1961

***Schizocoleus septentrionalis* Ponomarenko, sp. nov.**

Plate 2, figs. 3–5

E t y m o l o g y. From the Latin *septentrionalis* (northern).

H o l o t y p e. PIN, no. 2047/1, right elytron, positive impression; Khey-Yaga locality; Lower Triassic, Olenekian, or Middle Triassic, Anisian, Nyadeita Formation.

D e s c r i p t i o n. The elytron is rather broad, convex, three times as long as wide; the base is wide, with the basal two-thirds weakly broadened distally, narrowed in the apical third; the humeral elevation protrudes basally; the apex is acute, displaced towards the outer margin; the sutural margin is weakly convex beyond the elytron base, bordered; the outer margin before the apex is weakly emarginate. The epipleural border is narrow. The "schiza" is one-fifth as long as the elytron, situated proximal of the elytron midlength, at approximately one-fourth of its width. The elytron surface is covered with relatively small tubercles, merging into curved, transverse, obtuse ridges.

M e a s u r e m e n t s (mm): elytron length, 4.8–6.5; width 1.6–2.2.

C o m p a r i s o n. The new species is distinct from the type species in the broader elytron, the conspicuous humeral bump, the outer margin slightly emarginate before the apex, and the tubercles merging into transverse ridges. It differs from *Sch. glabrus* Ponomarenko, 2004 in having a broader elytron, with the sutural margin convex in the basal half.

M a t e r i a l. Holotype and PIN, no. 5252/8, a somewhat larger incomplete left elytron. Additionally, PIN, no. 5252/5, paired elytra of a similar size, have been examined, in which structural details cannot be seen because of the poor preservation. The elytron is approximately 5 mm long and 1.7 mm wide. The elytra possibly belong to the same species, but they are excluded from the type series.

Genus *Stegosyne* Rohdendorf, 1961

***Stegosyne borealis* Ponomarenko, sp. nov.**

Plate 2, fig. 6

E t y m o l o g y. From the Latin *borealis* (northern).

H o l o t y p e. PIN, no. 5252/6, right elytron, positive impression; Khey-Yaga locality; Lower Triassic, Olenekian, or Middle Triassic, Anisian, Nyadeita Formation.

D e s c r i p t i o n. The elytron is broad, convex, slightly more than twice as long as wide, with a broad base; the maximum width is beyond the basal third, narrowing in the apical half, with an acute apex, somewhat displaced towards the outer margin; the sutural margin is more convex than the outer margin, bordered. The epipleural border is narrow. The surface of the elytron has small punctures and tubercles, the latter merging into curved, transverse, obtuse ridges.

M e a s u r e m e n t s (mm): elytron length, 1.7; width 0.7.

C o m p a r i s o n. The new species differs from the type species in the more basal position of the broadest part of the elytron, more convex sutural margin, and sparse transverse, obtuse ridges on the disc.

M a t e r i a l. Holotype.

Genus *Pseudochrysomelites* Handlirsch, 1906

Pseudochrysomelites: Handlirsch, 1906, p. 400.

T y p e s p e c i e s. *Pseudochrysomelites rothenbachi* Handlirsch, 1906, Keuper of Switzerland, by original monotypy.

D i a g n o s i s. Isolated elytra of small beetles. Elytron broad, with outer margin in apical third only slightly convex, usually cut straight. Apex of elytron asymmetrical, sutural margin almost straight. Surface of elytron smooth, without large punctures, with only inconspicuous puncturing. "Schiza" usually not visible.

C o m p a r i s o n. *Pseudochrysomelites* is distinguished by the almost straight posterior margin, which makes the apex of the elytron appear asymmetrical.

S p e c i e s c o m p o s i t i o n. In addition to the type species, in this genus should be placed the described, but not named "species" no. 5, 23, and 25 from the Anisian of northeastern France (Papier et al., 2005); "species" no. 2 has a similar shape of the elytron, but on its disc thin striae have been described. *Palademosyne ovum* Ponomarenko, 2004, *P. elongatum* Ponomarenko, 2004, and *P. latum* Ponomarenko, 2004 also have to be transferred into this genus. These forms have been previously described as representatives of the genus *Palademosyne* Rohdendorf, 1961, but they differ significantly from the type species of that genus in having the sutural margin almost straight, and the apex of the elytron displaced toward it. Elytra of this shape are particularly typical of Early Triassic beetles.

***Pseudochrysomelites anser* Ponomarenko, sp. nov.**

Plate 2, fig. 7

E t y m o l o g y. From the Latin *anser* (goose), indicating the resemblance of the elytron shape to a goose's beak.

H o l o t y p e. PIN, no. 5252/10, right elytron, incomplete positive impression; Khey-Yaga locality; Lower Triassic, Olenekian, or Middle Triassic, Anisian, Nyadeita Formation.

D e s c r i p t i o n. The elytron is convex in the basal part, almost three times as long as wide, expanded near the rounded base, slightly narrowed up to the apical third, then, more strongly narrowed, with the epipleural border expanded at this bend; the apex tapers, the sutural margin is broadly bordered. The "schiza" is inconspicuous, situated near the outer margin. The surface of the elytron has scattered punctures, the spaces between which form transverse ridges.

Measurements (in mm): elytron length, 3.0; width, 1.0.

Comparison. The new species is distinguished by the rounded base of the elytron, conspicuously narrowing beyond the midlength, the epipleural border expanded at the bend of the outer margin outline, and by the larger punctures.

Material. Holotype.

Pseudochrysomelites planus Ponomarenko, sp. nov.

Plate 2, fig. 8

Etymology. From the Latin *planus* (flat).

Holotype. PIN, no. 5252/3, left elytron, positive and negative impressions; Khey-Yaga locality; Lower Triassic, Olenekian, or Middle Triassic, Anisian, Nyadeita Formation.

Description. The elytron is broad and flat, 2.3 times longer than wide, with a wide, almost straight base; the humerus protrudes, the elytron up to the midlength is only inconspicuously narrowed, and then narrowed up to the apical one-sixth, then very strongly narrowed; the epipleural border is narrow, the apex is pointed, the sutural margin is bordered. The "schiza" is invisible. The surface of the elytron is covered with relatively dense punctures.

Measurements (mm): elytron length, 3.0; width, 1.0.

Comparison. The new species differs in the straight base of the elytron, the elytron very weakly tapering up to the midlength, abruptly narrowing near the apex after the bend in the outline of the outer margin, and in the small dense punctures.

Remarks. *Angarogyrus minimus* Ponomarenko, 1977, described as a whirligig beetle (Gyrinidae) from the Jurassic of Siberia has a very similar elytron. The possibility of the Early Triassic beetles having been gyrinids is very small.

Material. Holotype.

Pseudochrysomelites dilatatus Ponomarenko, sp. nov.

Plate 2, fig. 9

Etymology. From the Latin *dilatatus* (expanded).

Holotype. PIN, no. 5252/9, right elytron, positive impression; Khey-Yaga locality; Lower Triassic, Olenekian, or Middle Triassic, Anisian, Nyadeita Formation.

Description. The elytron is broad and flat, 2.3 times wider than long, with a wide, angular base; the humerus protrudes; the elytron expands towards the basal third of the length, then narrows up to the apical quarter, then abruptly narrows; the outer margin here is slightly concave; the epipleural border is narrow; the apex is pointed; the sutural margin is bordered. The "schiza" is not visible. The surface of the elytron is covered with small, widely spaced punctures.

Measurements (mm): elytron length, 1.5; width, 0.7.

Comparison. The new species is very similar to the preceding species and differs in the angular base of the elytron, the longer preapical narrow part of the elytron after the bend in the outline of the outer margin, and the less dense punctures.

Material. In addition to the holotype, paratype PIN, no. 5252/4, left elytron.

Family Permosynidae Tillyard, 1924

Genus *Pseudorhynchophora* Handlirsch, 1906

Pseudorhynchophora: Handlirsch, 1906–1908, p. 402.

Type species. *Pseudorhynchophora olliffi* Handlirsch, 1906, Upper Triassic of Australia, by original monotypy.

Diagnosis. Isolated elytra of small beetles. Elytron rather broad. Apex of elytron asymmetrical, displaced toward sutural margin. Disc of elytron with rows of large punctures embedded in very shallow striae or without the latter.

Comparison. Distinct in having rows of large punctures embedded in very shallow striae or without striae.

Composition. In addition to the type species, the species described below.

Pseudorhynchophora convexa Ponomarenko, sp. nov.

Plate 2, fig. 10

Etymology. From the Latin *convexus* (convex).

Holotype. PIN, no. 2047/2, left elytron, incomplete positive impression; Khey-Yaga locality; Lower Triassic, Olenekian, or Middle Triassic, Anisian, Nyadeita Formation.

Description. The elytron is convex, approximately 2.5 times longer than wide, widest at the rounded base, gradually tapering to the apex; the epipleural border is expanded; the sutural margin is broadly bordered. The surface of the elytron is covered with dense, scattered, very small punctures and with 10–12 rows of rounded, widely spaced punctures, separated by intervals much larger than the puncture size; the rows of punctures are not embedded in striae.

Measurements (mm): elytron length, ca. 3.0; width, 1.2.

Comparison. The new species is distinct from the type species in having the elytron convex, tapering almost from the base on, and the rows of punctures not embedded in striae.

Material. Holotype.

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