ISSN 0031-0301, Paleontological Journal, 2016, Vol. 50, No. 3, pp. 286–292. © Pleiades Publishing, Ltd., 2016.
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New Beetles (Insecta, Coleoptera) from the Lower Triassic of European Russia

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Received May 19, 2015

Abstract—Fossil remains of beetles are described from two Lower Triassic localities: Entala (Induan) and Tikhvinskoe (Olenekian). Only one beetle fossil was previously known from the Lower Triassic of Tikhvinskoe. The fossils are rather few and poorly preserved, but they are worth describing as finds rare for the Lower Triassic. Five fossils from Entala most probably belong to beetles of the same species of the formal genus *Pseudochrysomelites*. Beetles of this genus are especially abundant in deposits close to the Permian–Triassic boundary and can be considered "disaster taxa." There are no known cases, either in the Permian or in the Middle–Upper Triassic, of a random sample of five specimens belonging to a single species. This suggests that in the Entala oryctocenosis the species diversity of beetles is extremely low. All three beetle fossils found in Tikhvinskoe belong to beetles of different species, showing that diversity had already started to increase. However, it remained low, and all fossils belong to the formal family Schizocoleidae, and two of the three belong to the same genus, *Pseudochrysomelites*. The Khei-Yaga locality, which immediately follows Tikhvinskoe in time (topmost Olenekian or early Anisian), already contains beetles of the families Asiocoleidae and Permosynidae. In the Lower Anisian of the Buntsandstein, such typical Mesozoic beetles as Cupedidae and Coptoclavidae have been recorded. The appearance of such advanced beetles as early as the Lower Anisian suggests that the famous Permian–Triassic crisis was not as deep as it is usually believed, and many beetles survived it, disappearing, however, from the fossil record in the Early Triassic.

Keywords: Coleoptera, beetles, Triassic, fossil insects, new taxa

DOI: 10.1134/S0031030116030060

INTRODUCTION

The study of Triassic insects is important and interesting for many reasons. Above all, it is very important to know how the biota adapts to living under the conditions of an ecological crisis and how it regenerates after the crisis. Furthermore, the order-level structure of insects acquires its modern aspect in the Triassic, thus displaying early stages of the formation of the modern living world: extant families start to become widespread in the insect taxocenosis, and even the first extant genera appear. The biota enters the Triassic in a state of strongly decreased diversity observable in the fossil record, which has led to the notion of a huge extinction event that supposedly took place during the Permian–Triassic ecological catastrophe, a crisis that lasted throughout the early Triassic, and subsequent rebuilding of a new world. These notions were developed for the marine biota; however, detailed study of the continental biota, especially insects—the most diverse group of animals—yielded a completely different picture (Rasnitsyn et al., 2013). Since this study is about the order Coleoptera, let us briefly discuss Triassic events using the example of this order. The earliest doubtless coleopterans are known almost from the very basal Permian. The assignment of some Carboniferous insects described as beetles or their closest relatives (Béthoux, 2002; Kirejtshuk and Nel, 2013) to this order cannot be considered proved. The only beetles known from the Lower Permian are xylophilous cupedoid archostematans; they remain dominant until the basal Middle Permian and cease to be dominant by the Middle Permian. Diversity somewhat decreases during this shift, and the average size of beetles decreases almost by half as a result of the disappearance of some larger archostematans. New groups of Adephaga and Polyphaga, most probably aquatic, are completely dominant in the terminal Permian. Families extant to this day appear among them. Therefore, renewal of the beetle fauna preceded the crisis rather than resulted from it. The diversity of beetles in Changhsingian localities remains rather high, and changes in composition are rapid, taking about one million years. Judging by the finds of carbon spherules in the terminal Permian locality Nedubrovo, Siberian traps had already started to erupt. Diversity still decreases in intertrappean deposits of the Tunguska Basin, but abundance does not decrease, and the general picture does not seem to be catastrophic. The composition of beetles in these localities is principally indistinguishable from the composition of beetles in terminal Permian localities.

Lower Triassic localities of European Russia have quite a different aspect. They are very few; the abundance and diversity of the fossils collected are extremely small. Fossil insects collected in the Induan and Olenekian have especially low abundance and diversity; almost all of them are isolated smooth elytra of the formal genus *Pseudochrysomelites* and most probably belong to aquatic adephagans. There are more coleopteran fossils in such localities than those of all other insects together. In the Lower Triassic of Western Europe, no insect fossils have been found, in sharp contrast to the abundance of insect fossils found in the very basal Middle Triassic. Large—and still insufficiently studied—collections of diverse beetles have been accumulated from the Buntsandstein (Lower Anisian) of southern Germany (Bashkuev et al., 2012) and eastern France (Papier et al., 2005). They include both Permian relicts (Permocupedidae) and specific Mesozoic groups (Coptoclavidae, Lasiosynidae), as well as mostly Mesozoic ones (Cupedidae, Trachypachidae); the majority of these beetles are larger than those known from the Permian. Subsequently, the diversity of beetles grows, and their average size increases. Xylophilous cupedoid archostematans appear as early as in the basal Anisian. None of them have been recorded in the Lower Triassic, but most of them should have been present in the Lower Triassic as "Lazarus taxa." Elytra of the type most abundant in the Lower Triassic are also present (*Pseudochrysomelites,* "disaster taxa"), but in these oryctocenoses they are only marginal fossils. In northern European Russia, beetles have been described from the Khei-Yaga locality (Ponomarenko, 2008). Almost all of them are schizophoroids with smooth elytra; in addition to them, there are elytra of some asiocoleid of the Permian type and one permosynid elytron similar to Mesozoic ones. This locality is believed to be Anisian, but judging by the composition of elytra it could belong to the terminal Olenekian, and displays the very beginning of the process of insect diversity regeneration.

The composition of the oryctocenoses of the Australian localities Kockatea (Haig et al., 2015) and Arcadia (Northwood, 2005) has a very different aspect. Rather scant but diverse insect fossils have been collected in these localities; they include no beetles. These oryctocenoses are quite different in diversity from the oryctocenosis of Lower Triassic localities of European Russia. If these localities are correctly dated to the early Olenekian, then Gondwanaland in the Early Triassic could have served as a refugium to pre-crisis insects. Of course, much of the Middle–Late Triassic diversity existed already in the early Triassic, but their abundance was so low that they are not represented in oryctocenoses. One can agree with Wignall and Benton (1999) that it was the low diversity of the crisis oryctocenoses that caused the "Lazarus effect," although the possibility of the existence of refugia cannot be denied.

Triassic insects remain quite insufficiently studied. Beetle fossils have been studied especially poorly, mainly because they are mostly represented by isolated elytra that cannot be classified in a natural system. However, even if they are classified in a formal, imperfect system, they can provide considerable information on diversity and stratigraphic distribution of beetles, and it is therefore reasonable to describe them. Localities of Triassic insects have been found in all continents, both modern and ancient (Laurentia, Angaraland, Cathasia, and Gondwanaland), but all Early Triassic beetle fossils, of which only nine specimens are known, have been collected in two localities of European Russia. These fossils are described below.

MATERIAL AND METHODS

Fossil beetles have been found in two of the three localities of Lower Triassic insects known in European Russia: Entala (Induan) and Tikhvinskoe (Olenekian).

Entala (Anan'ino), right bank of the Yug River 2 km downstream of the Entala River mouth, Kichgorodetskii District, Vologda Region; Lower Triassic, Induan Stage, Vetluga Grup, Vokhma Formation, Krasnye Baki Subformation.

N.S. Kobzoev collected conchostracans in this locality in 1928; an expedition of the Borissiak Paleontological Institute, Russian Academy of Sciences, collected seven insect fossils here; only one incomplete grylloblattid wing has been described as *Yontala camura* Aristov, 2005. The general appearance of the venation of this wing is similar to those found in representatives of the family Chauliodititidae, but it has one character absent in Chauliodititidae and therefore was not assigned to this family in the original description; it is possible that chauliodits are ancestral to *Yontala*, which underwent some reduction of venation. In addition to the grylloblattid, the wing of a cockroach and five fossil beetles have been collected, the latter so poorly preserved that it was initially doubted that they belonged to beetles. The fossils are stored in poorly sorted aleuritic clays, too coarse for the beetles to be well preserved. The shape of the elytra is distorted, which is clearly visible in paired elytra. The remains of beetles were probably trapped in viscous sediment with high water content and fossilized at different angles to the bedding plane rather than parallel to it. As a result, we can see projections of arbitrarily fossilized remains onto a horizontal surface. It can be seen in Figs. 4d, 4e that one beetle elytron is almost twice as long as the other. Only one isolated elytron, shown in Fig. 3, has a shape similar to that normal for beetles of the genus *Pseudochrysomelites*. It is assumed that initially all the beetles had elytra of that shape and belonged to the same species. Similar beetles, possibly also represent-

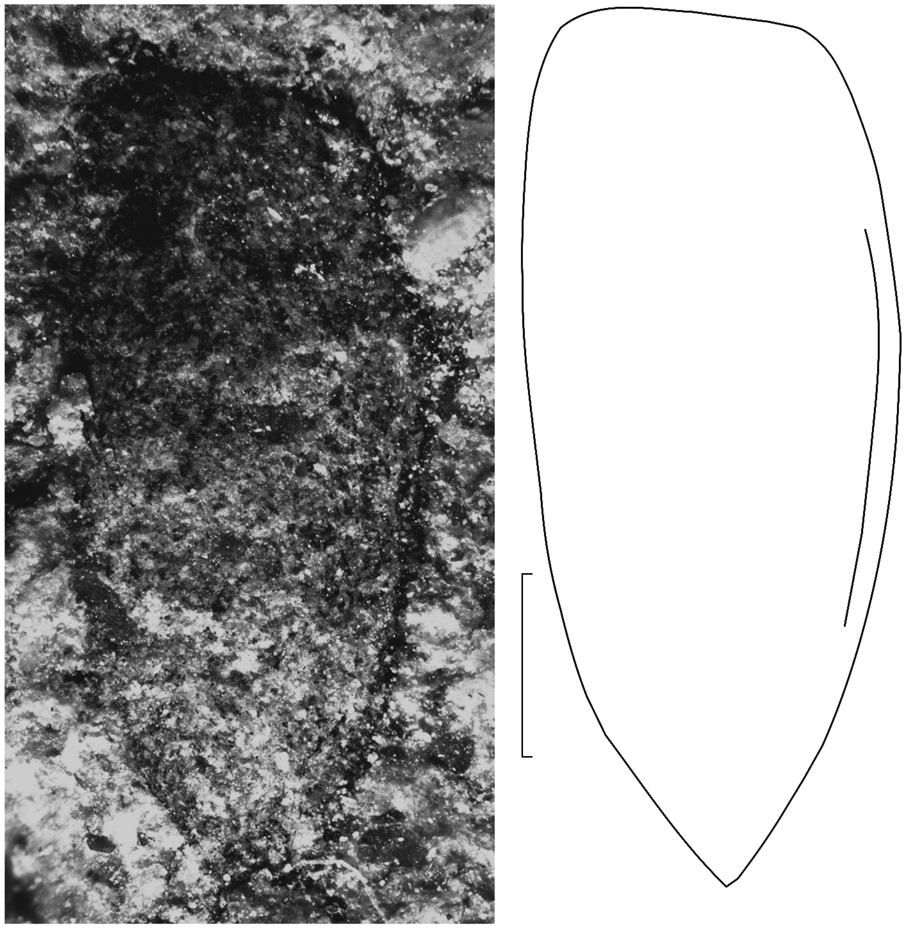

Fig. 1. *Schizocoleus triassicus* sp. nov., holotype PIN, no. 4048/2, photograph and drawing of elytron; Tikhvinskoe locality; Olenekian. Scale bars in Figs. 1–3, 1 mm.

ing a single species, have been found in the Anakit locality, Bugarikta Formation, Tunguska Basin.

Tikhvinskoe, right bank of the Volga near Tikhvinskoe village; Rybinskii District, Yaroslavl Region, Lower Triassic, Olenekian Stage, Rybinskian Horizon, Rybinsk Formation. *Pseudochrysomelites elongatus* (Ponomarenko, 2004) was described from this locality earlier (Ponomarenko, 2004).

The photographs were made using a Leica DFC 425 digital camera under a Leica M165C stereomicroscope. SEM images were made under a Tescan Vega XMU scanning electron microscope. The drawings were made using the program CorelDraw (Corel Co., Ottawa, Canada). The materials are stored in the Borissiak Paleontological Institute, Russian Academy of Sciences (PIN).

SYSTEMATIC PALEONTOLOGY

Order Coleoptera

Family Schizocoleidae Rohdendorf, 1961

The family was proposed for isolated elytra without grooves or series of large punctures on the disc. Such elytra almost invariably have a short impressed groove termed "schiza" (slit) by the author of the taxon. R.A. Crowson pointed to me that the internal surface of the elytron in some aquatic beetles has a protrusion in this place joined with the margin of the abdomen and preventing the rising of the elytra by the air bubble when the beetle is underwater. This is how the groove was subsequently interpreted. Because of its hardness, this structure is usually visible also on the internal surface of fossil elytra, but sometimes it is absent in fossils very similar in all other aspects to elytra with a "schiza." It is possible that it is simply invisible because of fossilization conditions. The surface of the elytron can be smooth, transversely rugose, or punctate. Similar elytra covered with rather dense short hairs are sometimes found. Rather small circular structures, probably sections of internal columns, the columellae, which link the dorsal and ventral surfaces of the elytron, are visible in some rare cases. The outward appearance of the elytron strongly depends on fossilization conditions.

Almost no characters are left for classifying such fossils except for the outline, which strongly depends

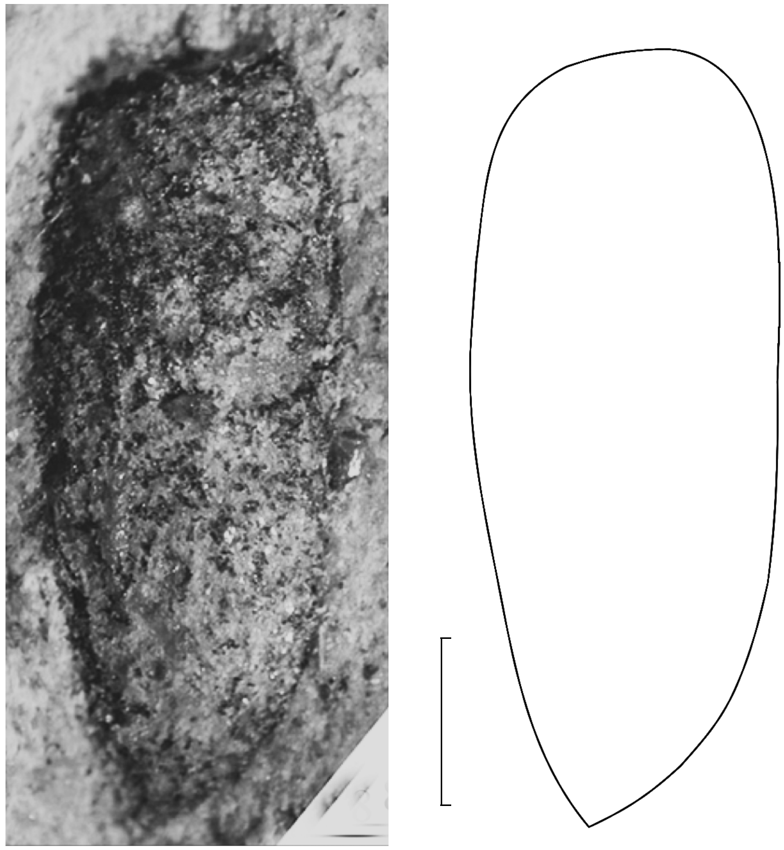

Fig. 2. *Pseudochrysomelites elongatus* (Ponomarenko, 2004), holotype PIN, no. 4048/16, photograph and drawing of elytron; Tikhvinskoe locality; Olenekian.

on the position of the elytron at the time of fossilization. An elytron that lay obliquely during fossilization will have a different shape from an identical elytron that lay parallel to the bedding plane. Elytra that have stayed linked or remained on remnants of the body are often different in shape from isolated elytra. Therefore, the system of schizocoleids, even considered as formal, proves quite unreliable, and has to be used only in the absence of a better system, since analysis of changes in proportions of elytron types in time turns out to be quite informative. For instance, schizocoleids are the only beetle fossils known from the Lower Triassic. Those elytra most probably belonged to representatives of several natural families, possibly even all four suborders of the order Coleoptera.

Genus *Schizocoleus* Rohdendorf, 1961

Schizocoleus triassicus Ponomarenko, sp. nov.

E t y m o l o g y. From the Triassic.

H o l o t y p e. PIN, no. 4048/2, part and counterpart of right elytron; Tikhvinskoe locality; Lower Triassic, Olenekian Stage.

D e s c r i p t i o n (Fig. 1). The elytron is convex, rather wide, only 2.3 times as long as wide, wide, straight, and tilted basally, weakly dilated from the base towards the basal one-third, then weakly and evenly roundedly narrowed; the apex is acute, almost symmetrical, somewhat shifted towards the external margin; the sutural margin is almost straight in the basal half, without beading. The epipleural rim is not broad. The “schiza” is not visible. The surface of the elytron is smooth.

M e a s u r e m e n t s, mm. Elytron length, 4.6; elytron width, 2.0.

C o m p a r i s o n. The widest known representative of the genus, also distinguished from most congeners by the straight and tilted elytral base.

R e m a r k s. The new species is assigned to the genus *Schizocoleus* because of complying with the diagnosis of this genus: weakly convex elytron with almost parallel sides in the basal half.

M a t e r i a l. Holotype.

Genus *Pseudochrysomelites* Handlirsch, 1906

One representative of the genus (Fig. 2) was described earlier from Tikhvinskoe as *Palademosyne elongata* Ponomarenko, 2004 and later transferred to the genus *Pseudochrysomelites* (Ponomarenko, 2013). Another species of the genus is described below; the

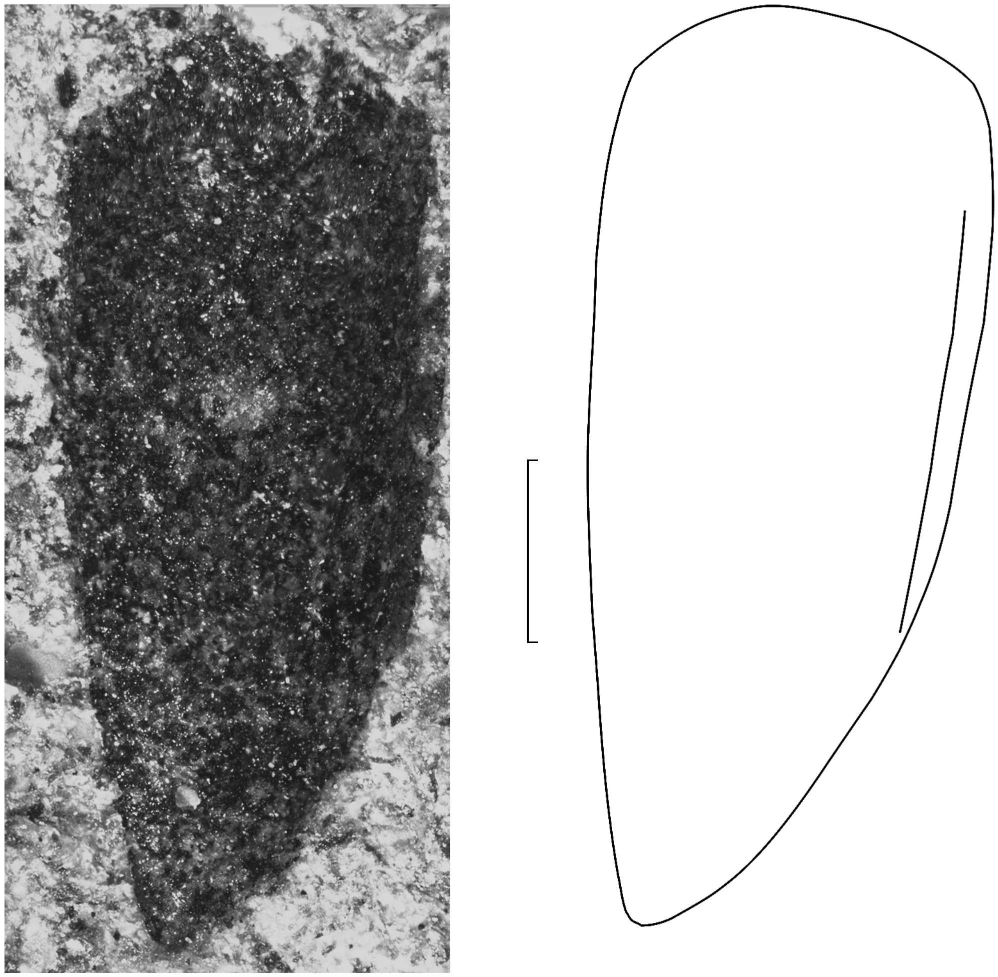

Fig. 3. Pseudochrysomelites humeralis sp. nov., holotype PIN, no. 4048/1, photograph and drawing of elytron; Tikhvinskoe locality; Olenekian.

holotype of this species cannot be assigned to the species described earlier.

The species described below are assigned to the genus *Pseudochrysomelites* because they comply with its diagnosis: convex elytron with sutural margin almost straight and apex shifted towards this margin; external margin convex, often with inflection in apical one-third; elytron strongly narrowed towards apex.

Pseudochrysomelites humeralis Ponomarenko, sp. nov.

Etymology. From the Latin *humerus* (shoulder).

Holotype. PIN, no. 4048/1, part and counterpart of right elytron; Tikhvinskoe locality; Lower Triassic, Olenekian Stage.

Description (Fig. 3). The elytron is rather large, wide, 2.5 times as long as wide at the shoulders, dilated in the basal one-tenth, where it is the widest, then weakly narrowed towards the apical one-third, and more strongly narrowed closer to the middle; the elytral base is rounded; the external margin does not have the characteristic inflection; the apex is subrectangular; the sutural margin is almost straight in the basal one-third, weakly elongate more distally. The epipleural rim is rather broad.

Measurements, mm. Elytron length, 5.5; elytron width, 2.2.

Comparison. The new species is distinguished by the rather large size of the wide elytron and by the smooth outline of the external margin of the elytron, which narrows almost from the shoulder without any sharp inflection in the apical portion. The new species strongly differs from the second species known from the same locality in the shape of the external margin. It is especially similar in the shape of the elytron to *P. sphenoidalus* Ponomarenko, 2013 from the Isady locality and differs from it in the larger size and absence of beading on all elytral margins.

Material. Holotype.

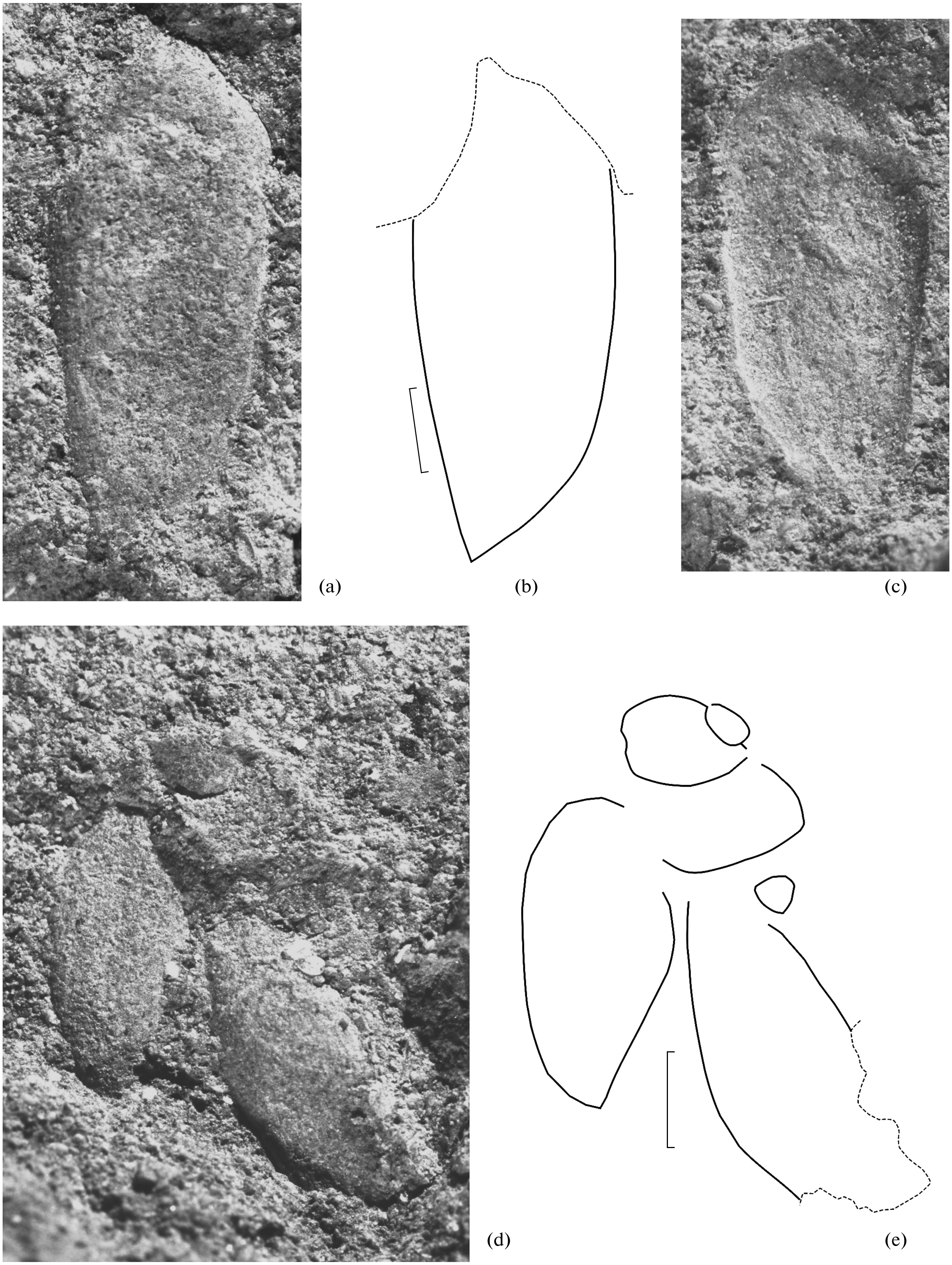

Fig. 4. *Pseudochrysomelites tumidus* sp. nov.: (a, b) holotype PIN, no. 4891/3, photograph and drawing of elytron; (c) specimen PIN, no. 4891/4, photograph; (d, e) specimen PIN, no. 4891/5, photograph and drawing; Entala; Induan.

Pseudochrysomelites tumidus **Ponomarenko, sp. nov.**

Etymology. From the Latin *tumidus* (swollen).

Holotype. PIN, no. 4891/3, direct impression of right elytron; Entala locality; Lower Triassic, Induan.

Description (Fig. 4). The elytron is rather large, not wide, 2.5 times as long as wide; dilated at the basal one-third, then very weakly narrowed to the distal quarter, where it is strongly narrowed, but without any clear inflection; the apex is pointed; the sutural margin is almost straight, beaded.

Measurements, mm. Elytron length, 6.0; elytron width, 2.4.

Comparison. The new species is distinguished by the rather large size of the wide elytron and by the shape of the elytron, which weakly narrows until the apical quarter, where the external margin turns towards the apex sharply but without any sharp bend.

Remarks. The fossil specimen selected as the holotype is the one least distorted in shape. Four other fossils have been collected together with the holotype, two of them isolated elytra, two linked elytra lying on one side, and one partly dismembered beetle with the head, pronotum, and two elytra. The shapes of all fossils have been distorted in the course of consolidation of the sample, but it is assumed that originally they belonged to beetles of the same species. Judging by the distortions of the shape of the sclerites, initially the most completely preserved fossil was fossilized in an inclined position with the anterior end raised. The estimated length of the beetle is 6 mm.

Material. Holotype.

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Translated by P. Petrov