ISSN 0031-0301, Paleontological Journal, 2015, Vol. 49, No. 12, pp. 1334–1345. © Pleiades Publishing, Ltd., 2015.

Coptoclavid Beetles (Insecta: Coleoptera: Adephaga) from the Triassic of Lower Franconia, Germany

A. G. Ponomarenko[a], A. A. Prokin[b, c], and A. S. Bashkuev[a]

[a]*Borissiak Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, 117997 Russia*

e-mail: aponom@paleo.ru, fossilmec@gmail.com

[b]*Papanin Institute for Biology of Inland Waters, Russian Academy of Sciences, Borok, Yaroslavl Region, 152742 Russia*

[c]*Venevitinovo Research and Educational Center, Voronezh State University, Universitetskaya pl. 1, Voronezh, 394006 Russia*

e-mail: prokina@mail.ru

Received March 2, 2015

Abstract—Many fossils of water beetles of the family Coptoclavidae have been found unexpectedly among insect fossils from the Middle Triassic (Anisian) and Upper Triassic of Franconia, Germany. Very small (about 3 mm long) beetles with longitudinal dark stripes on the elytra, similar in coloration pattern to beetles of the genus *Holcoptera* Handlirsch, 1906 from the terminal Triassic and Lower Jurassic of England and Lower Jurassic of the United States, have been found in Anisian deposits. Similar but larger beetles (about 5 mm long) have been found in Keuper (Carnian) deposits, in which they occur much more frequently than in Anisian localities, even dominating some of these localities. Unfolded or fragmentary hindwings that also belong to beetles of the same species and match the elytra in size have also been found. There are no known localities in which so many beetle hindwings occur, especially hindwings of the same species. They are described here as wings of Coptoclavidae. A small incomplete larva matching these beetles in size has also been found. The beetles are described as representatives of a new genus of the subfamily Coptoclaviscinae. In addition to them, the larvae of a rather large coptoclavid *Protonectes* Prokin et Ponomarenko, 2013 was described earlier from the same deposits; it is assigned here to the subfamily Timarchopsinae. Only two elytra with numerous fine grooves not bearing any punctures match this larva in the available collection. Similar elytra were described earlier from the Jurassic of Europe and Siberia as *Dinoharpalus* Handlirsch, 1906. A small elytron with many grooves was described in the same genus from the terminal Permian of Eastern Europe. Similar elytra are known in coptoclavids described from the Lower Cretaceous of Spain as *Hispaniclavina*. The presence of such advanced beetles as coptoclavids as early as the Lower Anisian shown that the famous Permian–Triassic crisis was not so deep as it is usually believed, and many beetles survived it, disappearing, however, from the fossil record in the Early Triassic.

Keywords: insects, beetles, Triassic, Germany

DOI: 10.1134/S0031030115120096

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 existing under the conditions of an ecological crisis and how it regenerates following such a crisis. Moreover, in the Triassic the system of insect orders acquires its current aspect, and we can see 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 a strong decrease in diversity observed in the fossil record. This is the source of the notion about an enormous extinction event during the Permian–Triassic ecological catastrophe: the crisis state supposedly encompassed the entire Early Triassic, after which the world was built anew. This notion was developed for the marine biota, but detailed study of the continental biota, especially of the most diverse group of animals, the insects, yielded an entirely different picture. Since this is a study of Coleoptera, let us briefly discuss Triassic events using the example of this insect order.

Early xylophilous Archostemata remain dominant until the beginning of the Middle Permian, but by the middle of the Middle Permian they are not dominant any more. Diversity somewhat decreases in the course of this shift also because of the reduction in large archostematans; the average size of the beetles decreases to less than half. The Late Permian is entirely dominated by new groups of Adephaga and

Polyphaga, most probably aquatic; they include some extant families. Thus, the renewal of the composition at the family level preceded the crisis rather than resulted from the crisis. The diversity of beetles in Changhsingian localities is still rater high, and changes in their composition are rapid, although these transformations take as long as about 1 million years. Judging by finds of carbon spheres in the Nedubrovo locality, terminal European Permian, Siberian traps already started to erupt. In intertrappean localities diversity still continues to decrease, but abundance remains high and the general picture does not seem to be catastrophic. The composition of beetles in these localities does not differ principally from the composition of beetles in localities of the terminal Permian. Localities of the Lower Triassic have a quite different aspect. These localities are few, and the abundance and diversity of fossils collected in them are extremely low. Insect fossils are especially scant and uniform among materials collected in the Induan and Olenekian of European Russia; in the Lower Triassic of Western Europe, no insect fossils have been found. Almost all these fossils are isolated elytra of the formal genus *Pseudochrysomelites*; they most probably belonged to aquatic Adephaga. A single whole beetle, very poorly preserved, is known from the Induan Entala locality. It has eyes on sides of the head and has no visible ring-shaped apodemes of the eyes; therefore, this fossil has no characters signifying that it belonged to Coptoclavidae; thus, Anisian coptoclavids are the earliest known to date. Rather scant but diverse fossil insects have been recorded in the localities Kockatea (Haig et al., 2014) and Arcadia (Northwood, 2005); there are no beetles among them. 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 could serve as a refugium to pre-crisis insects during the Early Triassic. But at the end of the Olenekian diversity begins to increase also in Europe, and in the basal Anisian (Buntsandstein; Bashkuev et al., 2012) diversity is no lower than in terminal Permian localities, and most beetles are similar, but somewhat larger. Subsequently, diversity grows, and the average size of beetles increases. As early as the basal Anisian, xyophilous cupedoid archostematans re-appear. Much of this diversity obviously existed also in the Early Triassic, but the abundance was so low that the beetles are not found in oryctocenoses. We agree with Wignall and Benton (1999) that the low diversity of oryctocenoses in crisis localities was the main reason for the "Lazarus effect," although the possibility of refugia cannot be discarded.

Triassic insect localities remain few to this day, and insects from them are still quite insufficiently known. Fossil beetles are especially poorly known, mainly because these fossils are mostly represented by isolated elytra, which cannot be classified in the natural system. However, even classified in a formal system, deficient as it is, isolated elytra can provide useful information on diversity and stratigraphic distribution of beetles; it is therefore expedient to describe them. Triassic insect localities have been found on all continents, both modern and ancient (Laurentia, Angaraland, Katasia, and Gondwanaland). However, the presence of the water beetle family Coptoclavidae has been proved in only one Triassic locality, the Middle Triassic Monte San Giorgio on the border between Switzerland and Italy (Strada et al., 2014).

Unexpectedly many coptoclavids have been found among insect fossils from the Middle Triassic (Anisian) and Upper Triassic (Keuper) collected in Franconia, Germany. Very small (about 3 mm long) beetles with longitudinal dark stripes on the elytra, similar in coloration pattern to beetles of the genus *Holcoptera* Handlirsch, 1906 from the terminal Triassic and Lower Jurassic of England (Whalley, 1985) and Lower Jurassic of the United States (Huber et al., 2003), have been found in Anisian deposits. Several of these fossils belong to the same species; some of them are whole beetles with clearly visible round ocular apodemes on the head. Because of their small size, the beetles are poorly preserved, and their morphological details are almost indiscernible. Similar but larger beetles (about 5 mm long) have been found in Keuper (Carnian) deposits. Morphological details of some of them could be discerned using a scanning electron microscope. As is often the case with fossil remains of water beetles, thoracic tergites were preserved better than sternites. Unfolded or fragmentary hindwings that also belong to beetles of the same species and match the elytra in size have also been found. They were described as wings of Coptoclavidae based on the basal position of the anal arculus (anarc) and the common base of the apical branches of CuP and AA_{1+2} and the long and straight vein cu2 (Fedorenko, 2014). A small incomplete larva matching these beetles in size has also been found. The beetles are described here as representatives of two new species of a new genus of the subfamily Coptoclaviscinae. It is possible that they should be assigned to the genus *Holcoptera,* but it has to remain formal until the type series of the only species of this genus, stored in the Natural History Museum, London, is re-examined.

In addition to new coptoclavids, the larva of the rather large coptoclavid *Protonectes* Prokin et Ponomarenko, 2013 was described earlier from Keuper deposits (Prokin et al., 2013); it is assigned below to the subfamily Timarchopsinae. Only two elytra with many fine grooves without punctures match this larva in the available collection. Similar elytra were described earlier as *Dinoharpalus* Handlirsch, 1906 from the Jurassic of Europe and Siberia. Coptoclavids described from the Lower Cretaceous of Spain as *Hispaniclavina* (Soriano et al., 2007) also had similar elytra. The presence of such advanced beetles as Coptoclavidae as early as the Lower Anisian shows that the famous Permian–Triassic crisis was not as deep as usually believed and many beetles survived it remaining in the Early Triassic outside the fossil record (Lazarus taxa).

MATERIAL AND METHODS

This study is based on material from the remarkable collection of Triassic Fossils from the Lower Franconia "Sammlung Mainfränkische Trias" (SMTE), collected by four enthusiasts, Jürgen Sell, Horst Mahler, Bernd Neubig, and Michael Henz, and located at Markt Euerdorf, Lower Franconia. A.S. Bashkuev participated in amassing this collection. The examined coleopteran fossils originate from two Triassic horizons:

1. The bed of yellow-grey to straw-yellow dolomitic marls and mudstones, called "Strohgelbe Kalke," that cropped out at Hammelburg, coll. 5825/2, and Gambach am Main, coll. 6024/4 (for details, see: Ansorge and Brauckmann, 2008; Bashkuev et al., 2012). This bed represents the uppermost unit of the Myophorienschichten (Röt Formation, Upper Buntsandstein), and is dated to the Lower Anisian, Middle Triassic.

2. Coburger Sandstein, Hassberge Formation, Middle Keuper, Upper Carnian, accessible in outcrops in a series of quarries in the environs of the towns of Eltmann and Ebelsbach, Lower Franconia. The insect fossils found are confined to thin lenticular interbeds of fine-grained siltstone and mudstone of lake origin. Coptoclavid fossils have been found in the localities Schönbachsmühle (collection no. 5930/1), Gleussner/Passmühle (5930/2), Hermannsberg/Schönbrunn (5930/4), and Eltmann (6030/1). It has to be noted that these localities are quite heterogeneous lithologically and in entomofauna composition and probably belong to different waterbodies or different parts of waterbodies. The coptoclavid finds in the Eltmann quarry are confined to interbeds of the thinnest rocks and often make up as much as 100% of insect fossils; they include isolated elytra and wings, mostly poorly preserved and often lying abundantly on the same surface. At the same time, in adjacent, somewhat more coarse-grained facies, other beetles (mostly Tricoleidae) are equally abundant, and coptoclavids have not been recorded at all. Because of the abundance of material, only several plates from Eltmann present in the collection were selected for study; these plates contain a total of about 50 fossil elytra and about 20 wings.

The most representative locality is Schönbachsmühle. In addition to isolated elytra and hindwings, splendidly preserved, it provided a whole adult beetle and two larvae. The insect assemblage in this locality is much richer than in other localities; among other things, it includes a considerable proportion of larvae of both aquatic and terrestrial insects.

Unfortunately, data on the distribution of insect fossils in the Coburg sandstone are scattered; the material was collected in different years by different researchers and is stored in different private collection and mostly remains unexamined. General description of the entomofauna will be provided in a separate study.

Photographs were taken using a Tescan Vega XMU scanning electron microscope and Leica M165C stereomicroscope attached to a Leica DFC 425 digital camera. Line drawings were prepared with CorelDRAW software (Corel Co., Ottawa, Canada).

SYSTEMATIC PALEONTOLOGY

Order Coleoptera

Suborder Adephaga

Superfamily Dytiscoidea Leach, 1815

Family Coptoclavidae Ponomarenko, 1961

Subfamily Timarchopsinae Wang, Ponomarenko et Zhang, 2010

Genus *Protonectes* Prokin et Ponomarenko, 2013

The genus was described from a single incomplete fossil representing an adult larva (Fig. 1, Prokin et al., 2013) from the Coburg sandstone (Hassberge Formation, Middle Keuper, Upper Carnian) of Schönbachsmühle near Ebelsbach, Lower Franconia. No matching adult beetles have been found among subsequently collected materials either. Judging by the size of the larva, the body length of the beetle should have been about 15–18 mm, and the elytron length should have been 10–13 mm. Only three isolated elytra of such size have been found in the examined collection; two of them, which in spite of the considerable difference in size almost certainly belonged to beetles of the same species, are described below as representatives of a new species of the formal genus *Dinoharpalus* Handlirsch, 1906. Representatives of this genus had 12–18 fine grooves on the disc, whereas other known Early Mesozoic beetles had at most ten such grooves. Elytron with many grooves is known in one genus of Coptoclavidae (*Hispanoclavina* Soriano et al., 2007).

In the original description, this genus was not placed in any subfamily. It should be assigned to Timarchopsinae Wang, Ponomarenko et Zhang, 2010, which also includes the most closely related larvae, *Stygeonectes jurassicus* Ponomarenko, 1977 and *Daohugounectes primitivus* Wang, Ponomarenko et Zhang, 2009. Characters typical of larvae of this subfamily include weakly dilated mid- and hindlegs and Y-shaped epicranial suture with short stem. The larvae cannot belong to a beetle of the second subfamily recorded in this locality, Ñoptoclaviscinae Soriano

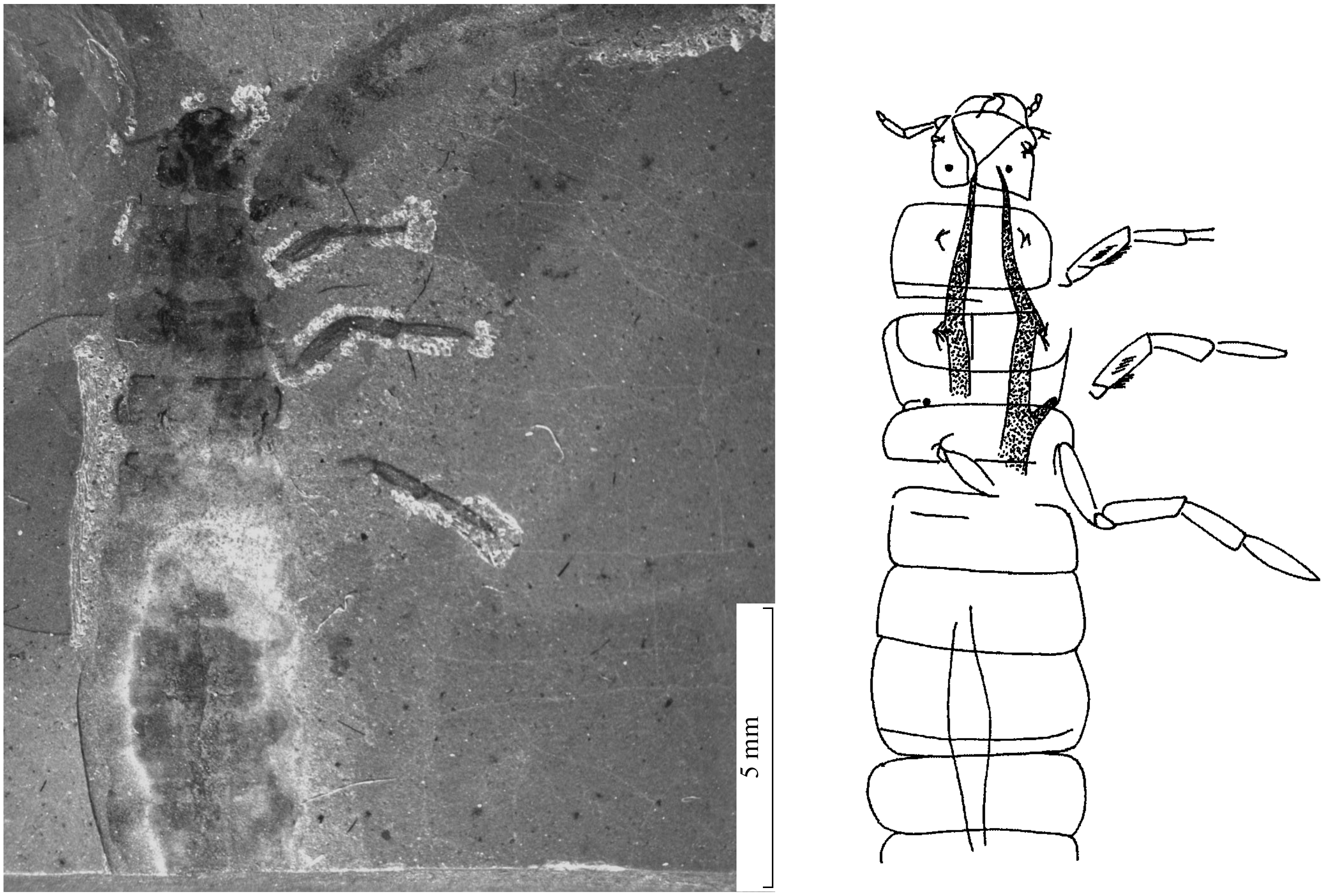

Fig. 1. *Protonectes germanicus* Prokin et Ponomarenko, 2013; holotype SMTE, no. 5930/1-65A.

et al., 2007, since it is much larger than any representative of this subfamily.

Subfamily Coptoclaviscinae Soriano, Ponomarenko et Delclos, 2007

Genus *Stargelytron* Ponomarenko, gen. nov.

E t y m o l o g y. From the Latinized Greek starganon (band) and *elytron* (sheath).

T y p e s p e c i e s. *Stargelytron larissae* Ponomarenko, sp. nov.; Coburger Sandstein (Hassberge Formation, Middle Keuper, Upper Carnian), Lower Franconia.

D i a g n o s i s. Small beetles. Head much larger than pronotum. Metanotum more strongly sclerotized than other parts of body and clearly distinguished in impressions. Metascutum smaller than metascutellum. Elytron weakly convex, not wide, without longitudinal grooves, with four dark longitudinal bands, two of them along margins of elytron and two middle bands shifted towards suture. Boundaries of bands indistinct; band width smaller than distance between bands. Wind short and wide; basal part and folded part almost equal in width; oblongum cell oval, transverse, with three independent veins diverging from its external part: MP1, MP_{3+4}, and CuA_1 (Fedorenko, 2014).

S p e c i e s c o m p o s i t i o n. Type species and new species from the Lower Anisian of Franconia.

C o m p a r i s o n. The new genus is distinguished from all other representatives of the subfamily in the smaller size and in elytra without grooves and with pattern of four narrow dark bands.

R e m a r k s. The genus is assigned to this subfamily based on the wing venation character it shares with *Coptoclavella purbekensis* Ponomarenko et al., 2005, the shape and size of the second anal cell. The maximum width of this cell is situated proximal to its midlength, which is typical of the other Dytiscoidea, in contrast to *Coptoclava* and thus also to the subfamily Coptoclavinae (Fedorenko, 2014). Since in the other subfamilies of Coptoclavidae, except Coptoclavinae and Coptoclaviscinae, wing venation is unknown, this genus is only provisionally assigned to the subfamily Coptoclaviscinae.

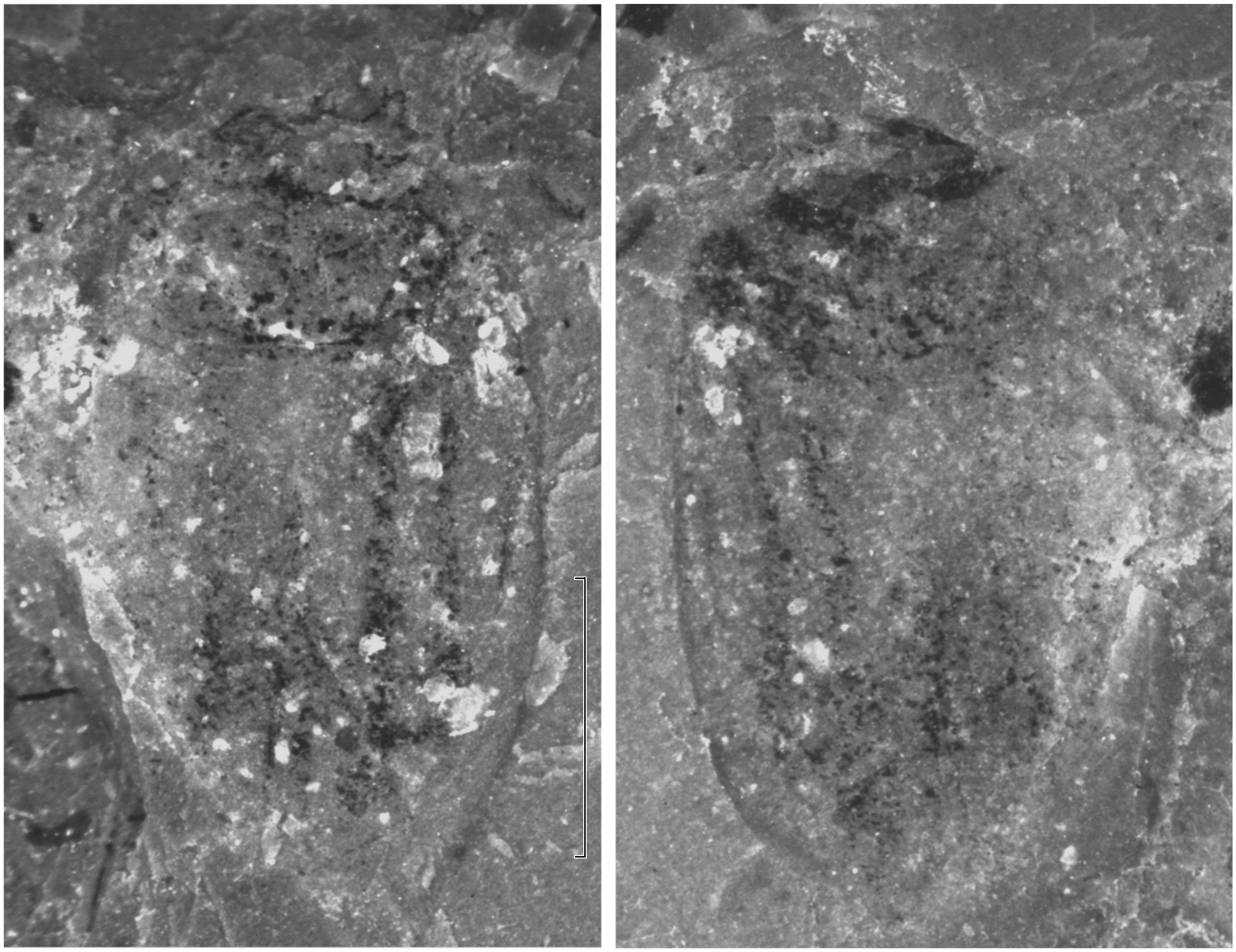

Fig. 2. *Stargelytron larissae* sp. nov.; holotype SMTE, no. 5930/1-159, SEM at different positions of detector; Eltmann Quarry, Franconia, Germany; Middle Keuper.

Stargelytron larissae **Ponomarenko, sp. nov.**

Etymology. In honor of Larissa Henz.

Holotype. SMTE, no. 5930/1-159, part and counterpart of beetle without most legs; Eltmann Quarry, Franconia, Germany; Middle Keuper.

Description (Figs. 2–4). The beetle is 2.5 times as long as wide. The head is rounded anteriorly, not narrowed behind the eyes, slightly wider than long. The lower eyes are large; each eye occupies about one third of the head width. The ocular apodemes are wide. The upper eyes are situated almost laterally, slightly smaller than the lower eyes. The pronotum is wider than long; the head is 2.3 times as long as the pronotum. The prosternum is very short; the procoxae are large, subtriangular. The prosternal process is not narrowed anteriad, not reaching behind the procoxae. The mesonotum is short, much wider than long; the sclerotized part of the scutum forms ovals that are much wider than long. The mesoscutellum is almost as long as wide, slightly narrowed posteriad. The mesocoxae are large, rounded, widely set. The metanotum is three times as long as the mesonotum; the sclerotized part of the metanotum is wide anteriorly and strongly narrowed posteriad; the scutum is smaller than the scutellum in area. The posterolateral and posterior notal processes are strongly developed. The central part of the metanotum is occupied by the rather narrow parallel-sided desclerotized area. The postnotum is narrow; its lateral part bears a protrusion. The metaventrite is much longer than the mesoventrite, strongly narrowed anteriad, and has straight lateral margins. The elytron is rather weakly convex, 2.5–3 times as long as wide, narrowed in the apical one-third, and has the apex shifted towards the suture. The epipleural rim is narrow. The margins of the elytra and two bands on the disc are darkened. The morphology of the wings was described in detail by Fedorenko (2014); in the opinion of Fedorenko (pers. comm.), the abundant new material does not add anything substantial to that description. The protibia is dilated and flattened and bears short triangular spines over its entire surface.

Fig. 3. *Stargelytron larissae,* holotype, drawings based on SEM images: (a) dorsal view; (b) ventral view; (c) ventral view at different position of detector; (d) wing under elytron; (3) meso- and metanotum.

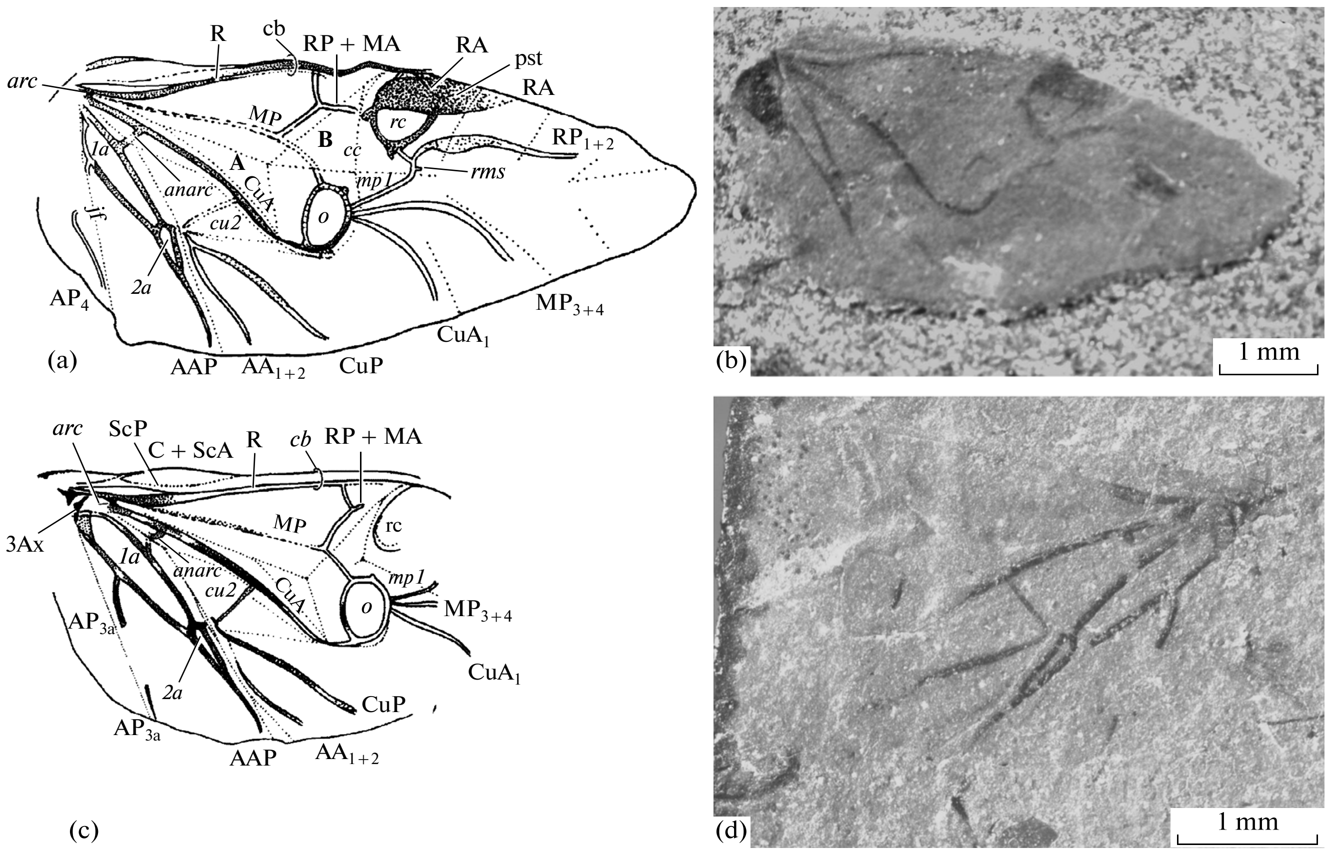

Fig. 4. *Stargelytron larissae,* wings, specimen SMTE, no. 5930/86 (a, b), specimen SMTE, no. 5930-1/112 (c, d).

M e a s u r e m e n t s, mm. Holotype: body length, 4.52; body width, 1.98; head length, 0.72; head width, 0.87; prothorax length, 0.32; elytron length, 3.48; elytron width, 1.10. Other measured specimens: elytron width, 4.10–6.40.

M a t e r i a l. In addition to the holotype, two incomplete remains of the body, isolated abdomen, 52 isolated elytra, and 21 isolated wings, three of them (SMTE, nos. 5930/86, 5930-1/112, and 5930-1/113) almost completely unfolded, from quarries Schöünbachsmühle near Ebelsbach and Eltmann, Lower Franconia, Coburger Sandstein (Hassberge Formation, Middle Keuper, Upper Carnian).

R e m a r k s. The specimen containing the wing of *Stargelytron larissae* (SMTE, no. 5930/1-112) contains also an impression of a holometabolous insect larva about 4 mm long, with a large head, mandible with retinaculum, eyes that consist of five ommatidia of subequal size arranged in a circle, three thoracic segments longer than abdominal segments, and rather long legs (Fig. 5). This larva may also belong to *Stargelytron larissae*, but since it is incompletely preserved, it cannot be proved to belong to Coptoclavidae.

Stargelytron altus Ponomarenko, sp. nov.

E t y m o l o g y. From the Latin *altus* (ancient).

H o l o t y p e. SMTE, no. 5825/2-571; Hammelburg, Franconia, Germany; Middle Triassic, Lower Anisian.

D e s c r i p t i o n (Figs. 6, 7). The beetle is slightly more than twice as long as wide. The head anteriorly is pointed, not narrowed behind the eyes, slightly wider than long. The lower eyes are rather small; each of them occupies about one quarter of the head width. The ocular apodemes are not wide. The upper eyes are situated almost laterally, slightly smaller than the lower eyes. The pronotum is wider than long; the head is 1.5 times as long as the pronotum. The mesocoxae are rather small, rounded, widely set. The metaventrite is much longer than the mesoventrite, r circularly narrowed anteriad. The elytron is not strongly convex, 2.5–3 times as long as wide, narrowed in the apical one-third; its apex is shifted towards the suture. The epipleural rim is narrow. The margins of the elytra and two bands on the disc are darkened.

M e a s u r e m e n t s, mm. Holotype: body length, 3.3; elytron length, 2.0; elytron width, 0.8. Other mea-

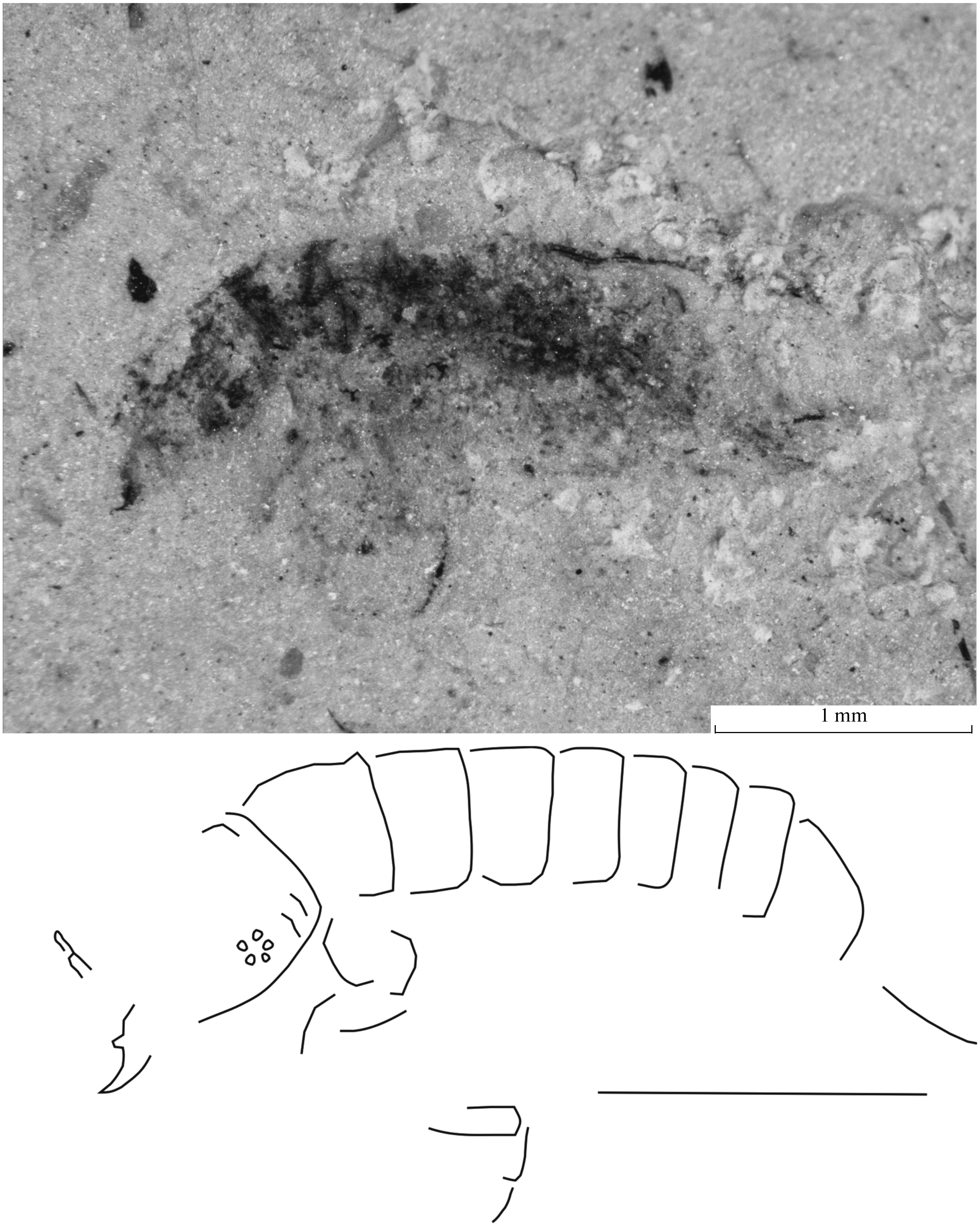

Fig. 5. Possible larva of *Stargelytron larissae,* specimen SMTE, no. 5930/1-112a, photo and drawing.

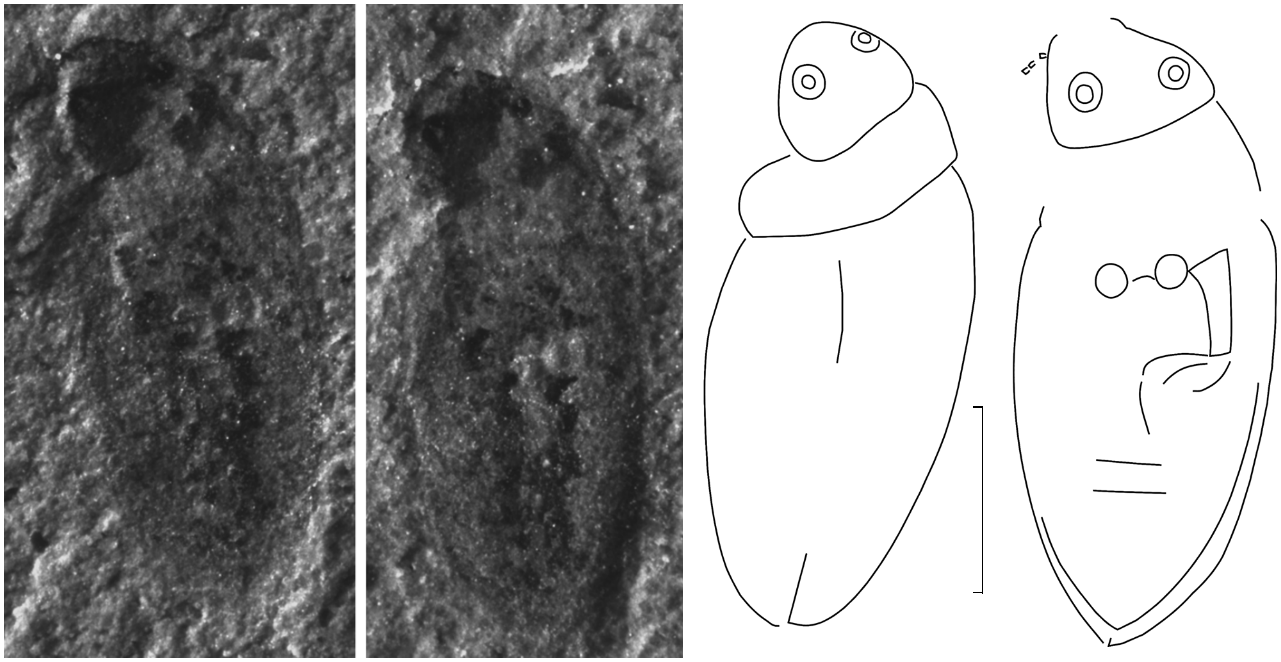

Fig. 6. *Stargelytron altus* sp. nov.; holotype SMTE, no. 5825/2-571; Hammelburg, Franconia, Germany; Middle Triassic, Lower Anisian.

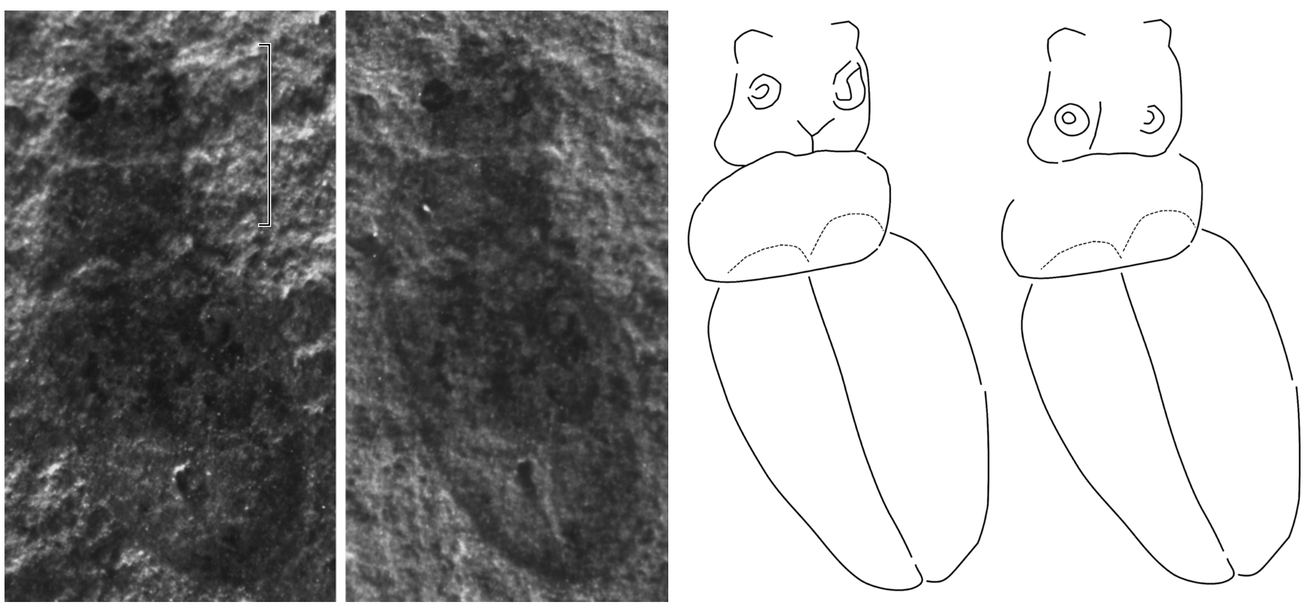

Fig. 7. *Stargelytron altus,* specimen SMTE, no. 6024/4-47; Gambach, Franconia, Germany; Middle Triassic, Lower Anisian.

sured specimens: body length, 3.30–3.46; elytron length, 1.80–2.20.

C o m p a r i s o n. The new species is distinguished from the type species in the smaller size and relatively smaller head pointed anteriad.

M a t e r i a l. In addition to the holotype, two incomplete remains of the body, one from the same locality. The other from the Gambach locality: isolated abdomen, and five isolated elytra.

Family Permosynidae Tillyard, 1924

The family was proposed for isolated elytra from the Late Permian of Australia. It is used as a formal taxon comprising Permian and Mesozoic isolated elytra that have longitudinal grooves on the disc. Using this name is preferable to using the name Ademosynidae, since the holotype of the type species of the genus *Ademosyne* is the body of a beetle, rather than an isolated elytron, and the family name derived from

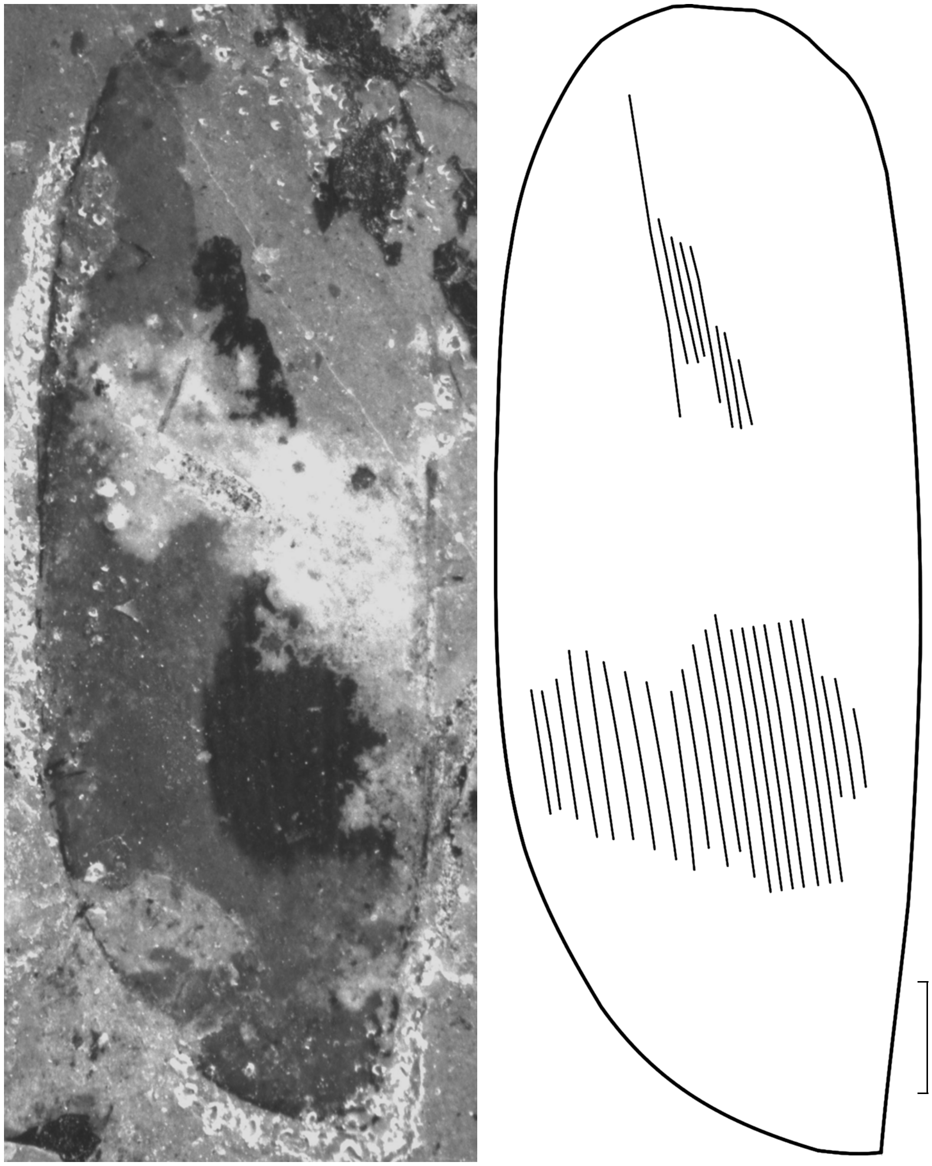

Fig. 8. *Dinoharpalus coptoclavoides* sp. nov., specimen SMTE, no. 5930/1-159, elytron; Eltmann Quarry, Franconia, Germany; Middle Keuper, Upper Carnian.

that genus should be used for more or less complete beetle fossils rather than for isolated elytra.

Genus *Dinoharpalus* Handlirsch, 1906

The genus is used for classifying isolated elytra with 12 or more fine grooves without punctures on the disc. Such elytra are rather rarely found in the Jurassic and even more rarely in the Lower Cretaceous. Mesozoic representatives of the genus are rather large; their elytra are about 1 cm long, whereas such an elytron from the terminal Permian of Nedubrovo, European Russia, is only 3 mm long. The only Mesozoic beetle with elytra of this type is *Hispanoclavina diazromerali* Soriano et al., 2007 from the Las Hoyas locality, Barremian of Spain, of the family Coptoclavidae.

Dinoharpalus coptoclavoides Ponomarenko, sp. nov.

E t y m o l o g y. From the family name Coptoclavidae.

H o l o t y p e. SMTE, no. 5930/1-160, elytron; Eltmann Quarry, Franconia, Germany; Middle Keuper, Upper Carnian.

D e s c r i p t i o n (Figs. 8, 9). The elytron is rather flat, three times as long as wide, narrowed in the apical one-fifth, and has the apex shifted towards the suture. The epipleural rim and rim of the suture are narrow. Large darkened spots are present on the disc. Numer-

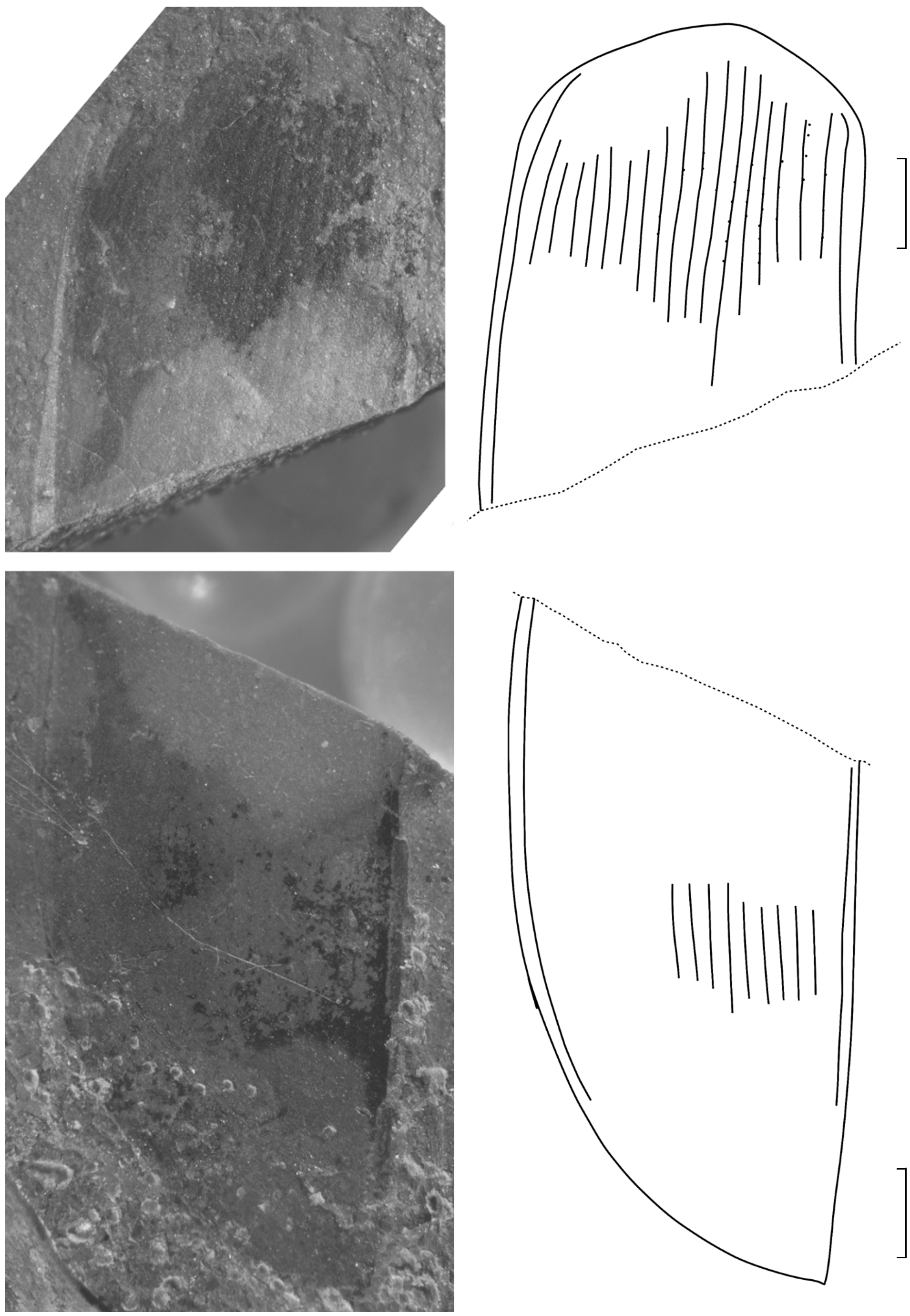

Fig. 9. *Dinoharpalus coptoclavoides*, specimen SMTE, no. 5930/1-110, elytron; Eltmann Quarry, Franconia, Germany; Middle Keuper, Upper Carnian.

ous (up to 20) fine grooves without pronounced punctures are visible only in the dark areas of the elytra.

M e a s u r e m e n t s, mm. Elytron length, 12 (holotype) to 10; elytron width, 4.

M a t e r i a l. In addition to the holotype, incomplete elytron SMTE, no. 5930/1-110, part and counterpart, from the same locality.

ACKNOWLEDGMENTS

We are grateful to R.A. Rakitov (Borissiak Paleontological Institute, Russian Academy of Sciences) for his help in working with the electron microscope.

This study was supported by the program "Origin of the Biosphere and Evolution of Geo-Biological Systems" of the Presidium, Russian Academy of Sciences (A.G. Ponomarenko) and by the Russian Foundation for Basic Research, project no. 15-04-02971 (A.A. Prokin).

REFERENCES

Ansorge, J. and Brauckmann, C., Chaulioditidae from Germany, with description of a new specimen from early Middle Triassic of Gambach/Main, Bavaria (Insecta, Grylloblattida), *Entomol. Gen.,* 2008, vol. 31, no. 3, pp. 251–260.

Bashkuev, A., Sell, J., Aristov, D., Ponomarenko, A., Sinitshenkova, N., and Mahler, H., Insects from the Buntsandstein of Lower Franconia and Thuringia, *Paläontol. Z.,* 2012, vol. 86, no. 2, pp. 175–185.

Fedorenko, D.N., Wings of Coptoclavidae (Coleoptera, Adephaga) from the Keuper of Frankonia, Germany, *Paleontol. J.,* 2014, vol. 48, no. 6, pp. 605–609.

Haig, D.W., Martin, S.K., Mory, A.J., McLoughlin, S., Backhouse, J., Berrell, R.W., Kear, B.P., Hall, R., Foster, C.B., Shi, G.R., and Bevan, J. C., Early Triassic (Early Olenekian) life in the interior of East Gondwana: mixed marine-terrestrial biota from the Kockatea Shale, Western Australia, *Palaeogeogr., Palaeoclimatol., Palaeoecol.,* 2015, vol. 417, no. 1, pp. 511–533.

Huber, Ph. and McDonald, N.G., 13. Early Jurassic insects from the Newark Supergroup, northeastern United States, in *The Great Rift Valleys of Pangea in Eastern North America,* vol. 2: *Sedimentology, Stratigraphy, and Paleontology,* Le Tourneau, P.M. and Olsen, P.E., Eds., New York: Columbia Univ. Press, 2003.

Northwood, C., Early Triassic coprolites from Australia and their palaeobiological significance, *Palaeontology,* 2005, vol. 48, no. 1, pp. 49–68.

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

Soriano, C., Ponomarenko, A.G., and Delclòs, X., Coptoclavid beetles (Coleoptera, Adephaga) from the Lower Cretaceous of Spain: A new feeding strategy in beetles, *Palaeontology,* 2007, vol. 50, no. 2, pp. 525–536.

Strada, L., Montagne, M., and Tintori, A., A new genus and species of the family Trachypachidae (Coleoptera, Adephaga) from the Upper Ladinian (Middle Triassic) of Monte San Giorgio, *Riv. Ital. Paleontol. Stratigr.,* 2014, vol. 120, no. 2, pp. 183–190.

Whalley, P.E.S., The systematics and palaeogeography of the Lower Jurassic insects of Dorset, England, *Bull. British Mus. Nat. Hist. (Geol.),* 1985, vol. 39, no. 3, pp. 107–189.

Wignall, B. and Benton, M.J., Lazarus taxa and fossil abundance at times of biotic crisis, *J. Geol. Soc. Lond.,* 1999, vol. 156, pp. 453–456.

Translated by P. Petrov