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Article

Two new genera of Cyclida (Crustacea: Maxillopoda: Branchiura) from the Cisuralian (Lower Permian) of Southern Urals (Russia)

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With 5 figures

Abstract: *Skuinocyclus juliae* gen. et sp. nov. from Lower Permian limestones of the Shakhtau Reef (Sterlitamak, Republic of Bashkortostan) is the second discovery of a member of the order Cyclida in the Permian of Russia and the oldest member of the family Hemitrochiscidae. Based on the material described by Kramarenko (1961) as *Cyclus miloradovitchi* from the Lower Permian (Asselian) of the Chelyabinsk Region (Southern Urals), we also established *Uralocyclus* gen. nov., which has significant morphological differences with the genus *Cyclus*, to which it was originally assigned.

Key words: Crustacea, Branchiura, Cyclida, Permian, Asselian, Sakmarian, Russia, Shakhtau.

1. Introduction

Cyclids are enigmatic extinct marine crustaceans that existed from the Early Carboniferous to the end of the Cretaceous (Dzik 2008). Due to their rarity, they are a poorly studied group of invertebrates with weakly developed taxonomy.

The first description of a member of the Cyclida was made by J. Phillips (1836), who depicted and described the carapace as the trilobite *Agnostus*? *radialis*. Later, De Koninck (1841) came to the conclusion that this animal is not a trilobite, although he had no clear idea about its taxonomic placement. One year later, De Koninck (1842) described another species, *Cyclus brongniartianus*, but subsequently reported by Woodward (1870) as a trilobite hypostome. Cyclids were later considered to be members of Xiphosura or true crabs (Packard 1872; Oosterink 1978). Schram et al. (1997) classified the cyclids as a sister group of crustaceans within the Maxillopoda, and Dzik (2008) placed them in a subclass Branchiura, which contained only one modern family of fish lice, Argulidae.

Members of the order Cyclida have some resemblance to brachyurans and most likely inhabited a similar ecological niche (Schweigert 2007) and were also outcompeted by them at the end of the Mesozoic. The largest size of a cyclid carapace was reported for *Opolanka decorosa* Dzik, 2008, which exceeds 6 cm (Dzik 2008: 1501). There is a dispute about the relationship of the order Cyclida with other arthropods. Despite the fact that they are considered crustaceans, doubts were expressed about homology and their relationship to chelicerates (Boxshall & Jaume 2009). Nevertheless, considering cyclids as an order within the subclass Branchiura, we herein use the classification proposed by Dzik (2008).

2. Systematics and distribution of Cyclida

The order Cyclida comprises 6 families (Fig. 1). The principles of separation of these families occur both in the features of the morphology of the carapace, and in the different number of pairs of thoracic appendages (5

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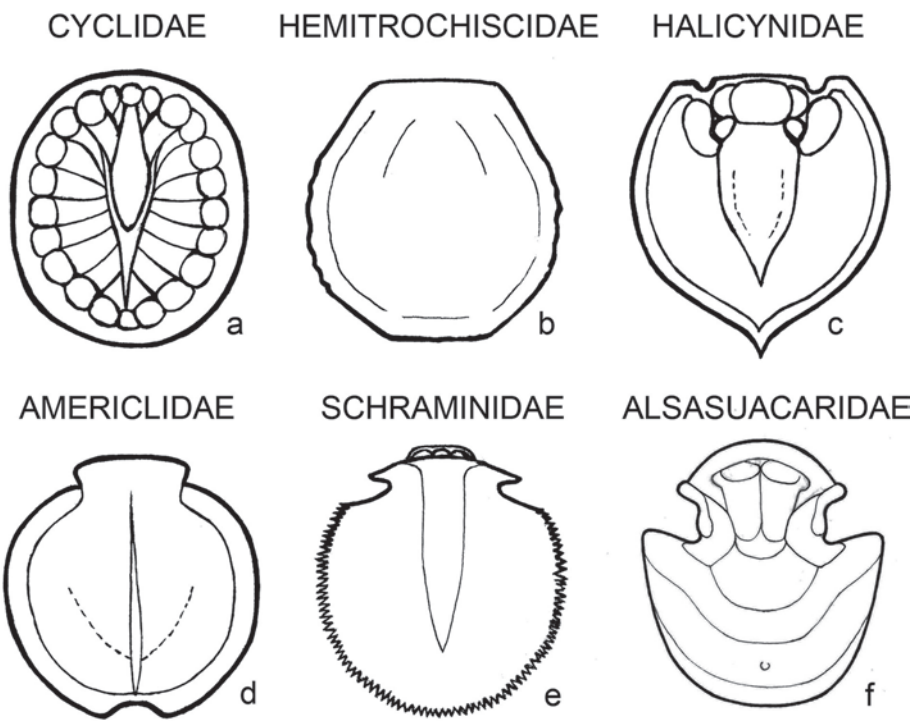

Fig. 1. General carapace morphology of families of the Cyclida. **a** – *Cyclus radialis* (Phillips, 1836); **b** – *Hemitrochiscus paradoxus* Schauroth, 1854; **c** – *Halicyne agnota* (v. Meyer, 1847); **d** – *Americlus americanus* (Packard, 1885); **e** – *Schramine max* (Schram, Vonk & Hof, 1997); **f** – *Alsasuacaris nostradamus* Bakel, Jagt, Fraaije & Artal, 2011 (data from Packard 1885; Stolley 1915; Schram et al. 1997; Dzik 2008; van Bakel et al. 2011).

to 6). Unfortunately, appendages are extremely rare in the fossil record of cyclids. The systematics of cyclids presented here is based on the studies of a number of researchers (Packard 1885; Trauth 1918; Glaessner 1969; Gall & Grauvogel 1967; Dzik 2008; Bakel et al. 2011) and is published as a whole for the first time. Thus, the relationship of the genus *Stagmacaris* Schweigert, 2006 from the Upper Jurassic (Kimmeridgian, *Hybonoticeras beckeri* Zone) of southern Germany to the family Alsasuacaridae is extremely conditional, due to the problematic definition of this form as a cyclid. Some authors (Bakel et al. 2011; Fraaije et al. 2012) consider the carapace of *S. quenstedtii* to be an abdominal somite of a hermit crab of the family Pylochelidae. Species of *Cyclus limbata*, *C. packardi* and C. *peremarginata*, described by Rogers (1902) from the Missourian, Pennsylvanian, of Kansas (Iola Formation) were included in the genus *Halicyne* (Schram et al. 1997: 262), but are assigned here (Fig. 2) to the genus *Americlus*. These forms have a morphology similarity to *A. americanus* (Packard, 1885), the type species of *Americlus*, which was described from the Essex Biota of the famous Mazon Creek conservation Lagerstätte in the Illinois Basin (Packard 1885; Hopwood 1915; Dzik 2008), and the age of which correlates with the Podolskian Substage of the Moscovian. There are 17 genera and 54 species of cyclids (Fig. 2). The greatest species diversity is in the Carboniferous (15 species in the Mississippian and 12 in the Pennsylvanian). In the Permian, there is a decline in the known diversity of cyclids (7 species), but in the Triassic, the number of recorded species is 17. The Permian decline in diversity is probably associated with limited outcrops of Permian fossil-bearing strata. Post-Triassic cyclids are rare and represented by one Jurassic and two Cretaceous species only (Fig. 2). It is important to note that in a recently published study (Hyžný et al. 2016) it is justified that *Mesoprosopon triasinum* Stolley, 1915 is a eumalacostracan larva and not a cyclid.

The geographic distribution of the group is limited to Europe (Austria, Belgium, Bosnia and Herzegovina, England, France, Germany, Ireland, Italy, Netherlands, Poland, Russia, Slovakia), Asia (China, Japan, Russia, Tajikistan), Africa (Madagascar) and North America

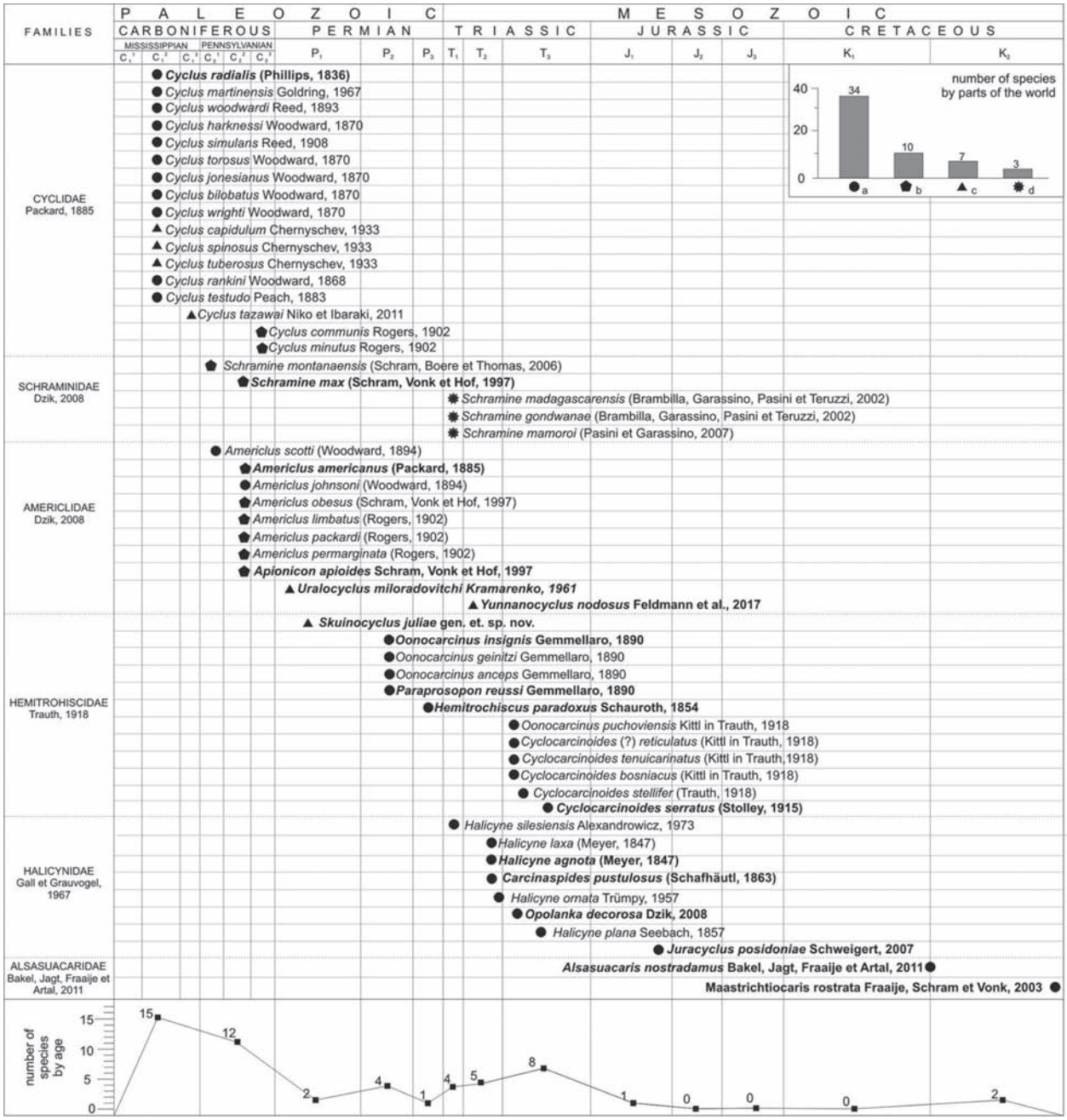

Fig. 2. Stratigraphic and geographical distribution of all known species of the order Cyclida. Type species are in bold. Legend: a – Europe; b – North America; c – Asia; d – Africa (Madagascar).

(U.S.A.) (Phillips 1836; De Koninck 1842; Gemmellaro 1890; Stolley 1915; Trauth 1918; Hopwood 1925; Chernyshev 1933; Trümpy 1957; Kramarenko 1961; Gall & Grauvogel 1967; Schram et al. 1997; Brambilla et al. 2002; Fraaije et al. 2003; Dzik 2008; Niko & Ibaraki 2011; Feldmann et al. 2017). Most species are described from European locations (34), less from North America (10), Asia (7), and Africa (3) (Fig. 2).

Up to the present, 4 genera and 6 species of cyclids from the Permian of European localities have been re-

ported. Three species of *Oonocarcinus* Gemmellaro, 1890 (*O. insignis*, *O. geinitzi*, *O. anceps*) and *Paraprosopon reussi* Gemmellaro, 1890 were described from the Middle Permian (Wordian, Waagenoceras zone; "Pietra di Salomone" Formation) olistostromes of the Sosio Valley in Sicily (Gemmellaro 1890; Trauth 1918; Dzik 2008: 1513). *Hemitrochiscus paradoxus* Schauroth, 1854 was reported from Zechstein dolomites (Lopingian, Wuchiapingian) in the vicinity of Pößneck in Germany (Schauroth 1854; Dzik 2008: 1513), and *Cyclus miloradovitchi* Kramarenko, 1961 was described from the Lower Permian (Asselian) of Russia (Kramarenko 1961).

3. History of the study of cyclids in Russia

The first very brief information about the fossil record of cyclids, referred to the genus *Cyclus* appeared in the report of B.I. Chernyshev, at a meeting of the Russian Paleontological Society on April 25, 1930 (Chernyshev 1935a). According to B.I. Chernyshev, these crustaceans were "primitive crabs". In 1931, he returned to this topic and on April 17, 1931, at a meeting of the Russian Paleontological Society, he told about "his finds" of a number of arthropods, including *Cyclus* from the Lower Carboniferous of the Urals and Turkestan (Chernyshev 1935b). Later, Chernyshev (1933: 20-21) described members of the genus *Cyclus* from Lower Carboniferous limestones of the Alapaevsk District of the Sverdlovsk Region (one specimen of *C. capidulum*) and the Lower Carboniferous locality of Shurab II on the northern slope of the Turkestan Range in Tajikistan (*C. spinosus* and *C. tuberosus*).

The revised edition of the textbook on paleontology by Zittel (1934) in the class Crustacea between Phyllocarida and Syncarida, p. 899, contains a very brief "addition", the author of which should be considered B.I. Chernyshev, who took part in the writing of the section on arthropods. We give it completely in translation from Russian:

"From the Lower Carboniferous, Permian and Triassic, calcareous remains of crustaceans were described in the cup-like form with tubercles in the region of the head and a middle furrow. These fossils cannot yet get a sufficiently clear position in the systematics. They were considered as larvae of Merostomata, then as primitive crabs. Glaessner thinks that this is Phyllocaridae. Currently, they are isolated in a special group Cycloidea Glaessner with the genera *Cyclus* de Kon. – Lower Carboniferous, England, Belgium, the Urals, Turkestan; *Halycine* Meyer – Cretaceous and Triassic, Germany. *Oonocarcinus* Gemmellaro (fig. 1767) – Permian, Sicily; the Upper Carboniferous, the Urals. *Paraprosopon* Gemmellaro – Permian, Sicily" (Weber et al. 1934: 899). In this text, there is great interest in indicating the presence of *Oonocarcinus* in the "Upper Carboniferous" (rather than in the Lower Permian by the current stratigraphy) of the Urals.

Additional information on the cyclids of the USSR is contained in the "Atlas of the Guiding Forms of Fossil Faunas of the USSR", Volume 4, the Lower Series of the Carboniferous System, ready for publication in 1937, but published finally in 1941, it also belongs to B.I. Chernyshev (1941: 154): "Very original forms from the Viséan deposits, which did not yet have a determinate place in the system and were united in the Cycloidea group, which until recently was known almost exclusively from Belgium and England (a small number was found in North America), were first discovered in Fergana on the Shurab River. Later they were found in the Urals and Novaya Zemlya in a significant number in the same Viséan strata. Fergana-forms with spines are closer to what was known from America, but here are the same as in Europe and the Urals. Forms devoid of thorns show similarities with European ones. These forms are so typical and still limited in time that can be good indicators of the age of their embedding deposits."

Explanation in relation to the "Upper Carboniferous" cyclids, B.I. Chernyshev reported in 1939: "For other areas of the USSR we know crustaceans only in the number of two species of the genus *Oonocarcinus* from the Urals (they are found in the Eichwald collection) and from there one member of Triopsidae. These highly interesting forms indicate the age of the strata" (Chernyshev 1939: 141-142). The collection of Eichwald to his "Lethaea rossica" is mostly preserved in St. Petersburg University and the cyclids are possibly still in it.

Thus, B.I. Chernyshev in the 1930s had quite a few specimens of cyclids from the Lower Carboniferous and, possibly, even the Bashkirian (in those years the Viséan could include younger Serpukhovian deposits and others) including from Novaya Zemlya. Unfortunately, Chernyshev had not returned to the study of this group, and the materials he collected may have been lost during the Second World War.

Material relative used for the article of Chernyshev (1933), with a description of the Carboniferous cyclids, is stored in the TsNIGR Museum (St. Petersburg, A.P. Karpinsky Russian Geological Research Institute) under no. 3694 (Kulikov 1985: 138-139).

Later, Librovich (1939: 18) in geological outcrop no. 160 located north of the Murchison Hill (right bank of the Shartymka River, Chelyabinsk Region, eastern slope of Southern Urals) found a cyclid determined by him as *Cyclus* sp. in the Upper Serpukhovian Horizon 4 associated with trilobites.

Kramarenko (1961) described the new species *Cyclus miloradovitchi* based on 7 well-preserved specimens from the Lower Permian (Asselian) location "Kazarmennyy kamen" on the Sim River (Chelyabinsk Region, Southern Urals).

Unfortunately, in the volumes of the Russian "Foundations of Paleontology" dedicated to arthropods, the genus *Cyclus* De Koninck, determined by B.I. Chernyshev, are absent. However, in the section on decapod crustaceans Birshtein (1960: 440) placed a note with the following content: "Permian and Triassic crustaceans described by Schafhäutl (1863), Frech (1900) and Trauth (1918), as Brachyura, according to Glaessner (1928) do not apply to Decapoda and should be isolated in a special group Cycloidea, close to Phyllopoda from one side and Phyllocarida on the other." Thus, this group of fossils was not completely forgotten.

It is important to note that all the described records of cyclids in Russia and the countries of the former USSR are represented exclusively by carapaces without imprints of appendages and soft tissues.

4. Locality

During field work in the Shakhtau Reef in Bashkiria (Southern Urals) (Fig. 3) in June 2016, A.V. Mazaev, M.S. Boyko and the first author found two specimens of the cyclid *Skuinocyclus juliae* gen. et. sp. nov. in gray limestones. Shakhtau is part of a larger reef complex along with Shikhans of Tratau, Yuraktau, and Kushtau. It formed on the slope of the East European Craton in the Early Permian and extruded on the surface as a result of neotectonic uplift of the Cisuralian Foreland Basin (Puchkov 2010). This reef system extends along the eastern frame of the Russian Platform and has a complex structure and history. Now Shakhtau is a quarry (limestone extraction for soda) about 20 meters in depth and 1.5 km by 0.8 km long, stretching in northwest direction. The Shakhtau reef has been studied by many researchers (Rauzer-Chernousova 1950; Shamov 1957, 1984; Kulik 1978; Chuvashov 1983; Korolyuk 1985; Rauzer-Chernousova & Korolyuk 1991). The position of age boundaries (horizons and zones of the upper parts of the Asselian and Sakmarian) in the reef body are very complicated (Rauzer-Chernousova et al. 1977) and to establish the exact age of the cyclids is not possible. No conodonts or other diagnostic microfossils were found in the samples. Moreover, it is important to note that in the limestones where the specimens were found, no associated macrofauna was found. In a sample of limestone from Shakhtau, which contained the pygidium of a trilobite, A.S. Alekseev discovered one specimen of the conodont *Mesogondolella obliquimarginata* (Chernykh in Chernykh et al., 1991). According to Chernykh (2006: 40-41), this species is widespread in the Southern Urals in the *postfusus* (terminal part of Asselian) and *merrilli* (basal part of Sakmarian) conodont zones.

5. Systematic palaeontology

Superclass Crustacea Pennant, 1777
Class Maxillopoda Dahl, 1956
Subclass Branchiura Thorell, 1864
Order Cyclida Schram, Vonk & Hof, 1997
Family Hemitrochiscidae Trauth, 1918

Genus *Skuinocyclus* nov.

Etymology: In honour of the district geologist I.A. Skuin, who collected a unique collection of Lower Permian fossils in the mine of Shakhtau added by *Cyclus*, type genus of Cyclida.

Type species: *Skuinocyclus juliae* sp. nov.

Diagnosis: Carapace bilaterally symmetric, hemispherical, cap-like. Marginal carapace corniceis framed by two half-rings of parallel arranged granular ridges. In the posterior part of the carapace there is a median groove, dividing it into two symmetrical halves. Frontal area steep. On the frontal area there are two large flattened and serrated on the edges lobes. A large medial bulge is located closer to the central rhombic bulge between these lobes. On the lateral sides of the carapace in its anterior half there are two or three rows of large tubercles converging to the central convexities. Number of tubercles in each row is 4 to 5. On the ventral part of the carapace on both sides is a pair of small curved lugs.

Remarks: In form and shape of the carapace the new genus is similar to *Hemitrochiscus* Schauroth, 1854, from the Upper Permian of Germany, but is more flattened at the anterior and posterior margins. As far as it be judged from the reconstructions and description of *Hemitrochiscus* (Schauroth, 1854: 558-559, pl. 22, fig. 1; Dzik 2008: fig. 11), the carapace of the latter was devoid of clear sculptural elements (lobes and bulges) that in large numbers are observed in *Skuinocyclus*. The new genus differs from *Oonocarcinus* Gemmellaro,

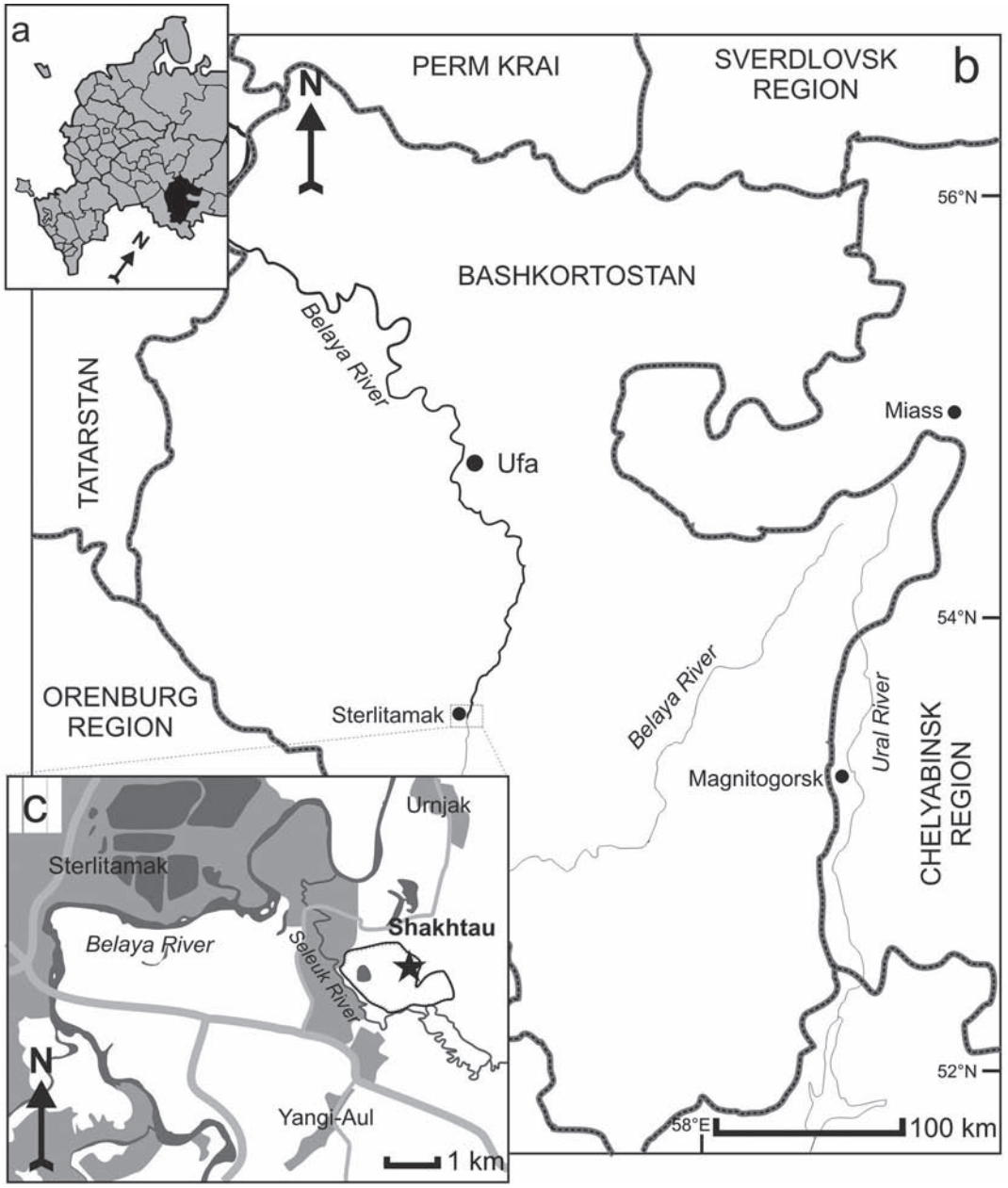

Fig. 3. Geographical map of the location of *Skuinocyclus juliae* gen. et. sp. nov. a – European part of Russia with administrative division; b – republic Bashkortostan and adjacent regions; B – the vicinity of the location of Shakhtau.

1890, whose members are known from the Middle Permian (Wordian) of Italy (Gemmellaro 1890: 24-29; Dzik 2008: 1513) and the Upper Triassic (Norian) of Slovakia (Trauth 1918: 184), in having a less elongated and less convex carapace, having more tubercles on the entire surface, elongated lateral lobes, and the presence of two granular ridges around the subventral part of the carapace. It is similar to the Middle Permian genus *Paraprosopon* Gemmellaro, 1890, having a central rhombic bulge, medial bulge and lateral lobes. *Skuinocyclus* is less elongated than *Paraprosopon* and also has rows of tubercles in the frontal and subventral areas of the carapace. The carapace of *Paraprosoon* does not have lugs. It is close to *Cyclocarcinoides* (Stolley, 1915) from the Upper Triassic of the Carnic Alps, but *Skuinocyclus* differs by a complex ornament of sculptural elements (lobes, bulges and tubercle) and smaller granules on the marginal cornice.

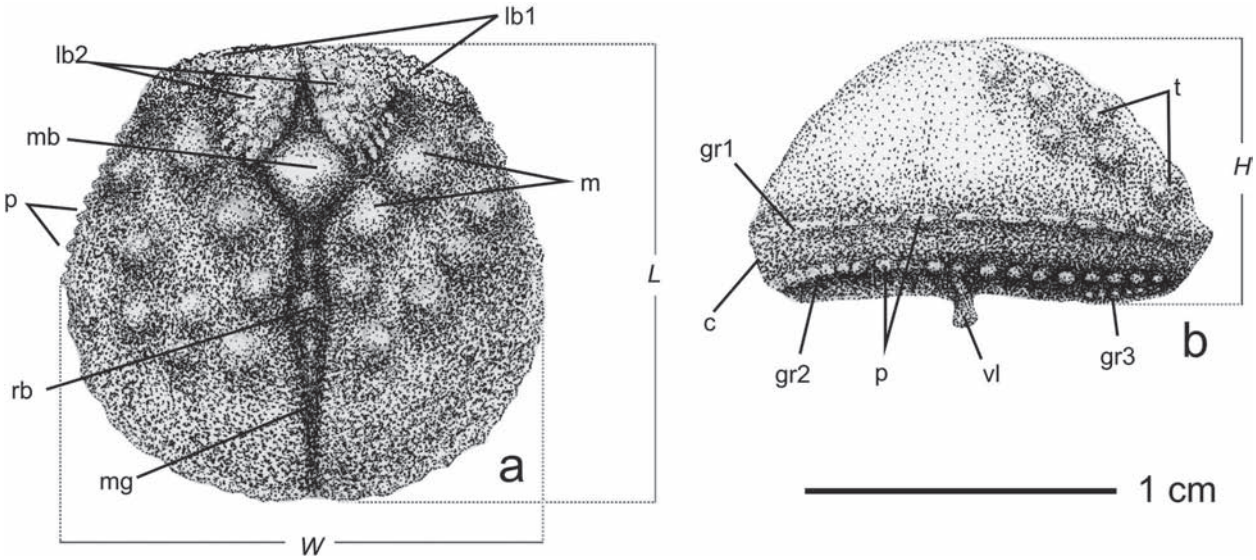

Fig. 4. Drawing of the carapace of *Skuinocyclus juliae* gen. et sp. nov. and its morphology. a – dorsal view; b – lateral view; *W* – width; *L* – length; *H* – height; mg – median groove; rb – rhombic central bulge; mb – medial bulge; lb2 – second pair of lobes; lb1 – first pair of lobes; g – granules; c – marginal carapace cornice; gr1 – first granular ridge; gr2 – second granular ridge; gr3 – third granular ridge; vl – ventral lug; t – tubercles.

An important morphological feature of *Scuinocyclus* is the presence of two symmetrically arranged lugs on the sides in the ventral part of the carapace. A similar structure is not observed in other members of the family Hemitrochiscidae and of the order Cyclida. The function of these lugs is still unclear.

Distribution: Lower Permian, upper part of Asselian to lower part of Sakmarian; Russia, Bashkortostan, Southern Urals.

Skuinocyclus juliae sp. nov.
Figs. 4 a, b, 5a-d

Etymology: In honour of the artist Julia Kosheleva, who made the reconstructions for the joint articles of the authors.

Holotype: An almost complete carapace, PIN, No. 5610/1 (collection of the Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia).

Type locality and horizon: Russia, Bashkortostan, Ishimbay District, neighborhood of Sterlitamak, quarry Shakhtau; Lower Permian, upper part of the Asselian or lower Sakmarian.

Diagnosis: As for genus.

Description: Carapace is semicircular, bilaterally symmetric, relatively large (about 16 mm in diameter), hemispherical cap-like shape. The largest width of the carapace is on posterior half; narrowest at the frontal area. The frontal area is flattened, the posterior area is convex. Laterally the carapace is bent into the marginal cornice (Fig. 4c), which is framed by two ridges of small granules (Fig. 4, gr1-gr2). These ridges encircle the carapace, terminating at the front and running parallel to each other. The granules are closely spaced, elongated in width, flattened. The distance between the ridges is about 2 mm. The bend of the marginal eaves to the ventral side starts from the second ridge and slightly extends below the first one. In the frontal area under the ventral most ridge (Fig. 4, gr2) on both sides there is a small granular ridge (Fig. 4, gr3), consisting of 7 to 8 granules.

The surface of the carapace is ornamented by various elements. On the posterior part there is a median groove (Fig. 4, mg), dividing the carapace into two symmetrical halves. The pronounced median groove starts posteriorly from the ventral most granular ridge and runs towards the anterior medial bulge (Fig. 4, mb). It occupies more than half the length of the carapace. Centrally, within the median groove there is an elongated central, rhombic bulge (Fig. 4, rb), which consists of a large tubercle.

The frontal area of the carapace is less sloping than the posterior area. In the central region of the anterior part there is a large bulge, the most prominent sculptural element of the carapace, here referred to as the medial bulge (Fig. 4, mb). Below this bulge, on both sides, there are large flattened lateral lobes (Fig. 4, lb2). The edges of the lobes are jagged in the form of a series of elongated granules separated by wide furrows. Laterally of the carapace, below the medial bulge, the lateral lobes meet each other.

On the right side of the right lateral lobe, close to the margin, is a semicircular lobe (Fig. 4, lb1), densely wound with small granules. The granules are oval in shape, oriented from the center of the area to its edge. In this area there are just over 30 granules. On the anterior part of the carapace there are 2 to 3 rows of large tubercles (Fig. 4, t), converging at the central rhombic bulge. The first row is located closer to the lobes (Fig. 4, lb1-lb2) and consists of 4 large tubercles of irregular shape.

The first pair of tubercles, located between the first (Fig. 4, lb1) and the second (Fig. 4, lb2) pairs of lobes, appears to be a twin tubercle of two smaller ones. The second row consists of 5 smaller and considerably more distant tubercles than in the first row. On both sides of the second row of tubercles, single tubercles are randomly located in the number of two in the left half and one in the right. The size of the tubercles in both rows decreases as they approach the central rhombic bulge.

On both sides of the carapace there is a pair of small curved lugs in its ventral part (Fig. 4, vl).

Dimensions: The maximum width on the posterior half is 17 mm, the width of the frontal area is 9.5 mm, the maximum length of the carapace is 16 mm; the maximum height is 8 mm.

Material: Two specimens, one well-preserved carapace, the second one is a fragment of the subventral part of the carapace.

Family Americlidae Dzik, 2008
Genus *Uralocyclus* nov.

Etymology: Named after the Urals Mountains in combination with the name of the type genus of the order Cyclida, *Cyclus.*

Type species: *Cyclus miloradovitchi* Kramarenko, 1961 (Fig. 5e-h) from the Lower Permian (Asselian) of Southern Urals (location "Kazarmennyy kamen", Chelyabinsk Region, Russia).

Diagnosis: Carapace bilateral symmetrical, swollen, cap-shaped, laterally bordered by a marginal rim. Shape of the carapace rounded, flattened from anteriorly and posteriorly Marginal rim is a series of elongated tubercles, reaching the half of the width of the limb. Frontal area of carapace is dissected by large, symmetrical lobes. On both sides of the median groove there are two crescent-shaped ridges, consisting of condensed small granules. Between these ridges and the lateral rim there are 7 pairs of large bulges elongated from the center to the marginal rim. Appendages and ventral aspects of the carapace are not preserved.

Remarks: The most similar to *Americlus* Dzik, 2008 and particularly similar to the species *A. johnsoni* and *A. scotti*, described from the Westfalian of England (Woodward 1905; Dzik 2008: 1514). *Uralocyclus* differs by exhibiting more various sculpture carapace: presence of a number of tubercles on the marginal rim, large bulges arranged along the sides of the carapaces and a more dissected frontal area. From the genus *Apionicon* Schram, Vonk & Hof, 1997, from the Pennsylvanian conservation Lagerstätte Mazon Creek, it differs more by a more elongated carapace, the presence of numerous lobes, tubercle and other sculptural elements on it, as well as a distinct and marginal rim. From *Yannanocyclus* Feldmann et al., 2017 known from the Lower Triassic of Southern China as flat prints (Feldmann et al. 2017) of carapace, it differs by a complex and dissected carapace sculpture.

Distribution: Lower Permian, Asselian; location "Kazarmennyy kamen", Chelyabinsk Region, Russia).

5. Discussion

The new genus *Skuinocyclus* is the stratigraphically oldest one in small family Hemitrochiscidae, whose members were known from the Middle and Upper Permian and the Triassic (Fig. 2). *Skuinocyclus* has morphological features that are relatively unusual for the other cyclids, especially the presence of a pair of ventral lugs (Fig. 4, vl) and serrated lobes (Fig. 4, lb2). The presence of the lugs is a new morphological feature for Cyclida. According to Dr. René H.B. Fraaije, if the cyclids were indeed parasites, then the ventral side of the carapace should have been smooth.

The new genus *Uralocyclus* is a taxon close to *Americlus*, known from the Pennsylvanian of Europe and North America and the Triassic of Asia (Fig. 2). The similarity of these genera is suggested by a similar morphology of the carapace, or rather, its shape (Fig. 1d) and the dissected frontal area into a series of symmetrical bulges. Most likely, this genus is phylogenetically derived from *Americlus.*

Fig. 5. a-d – *Skuinocyclus juliae* gen. et sp. nov.; holotype, PIN, №5610/1, full carapace; Russia, Bashkortostan, Ishimbay District, neighborhood of Sterlitamak, quarry on Shakhtau; Lower Permian, upper part of the Asselian or lower Sakmarian; (a) top view, (b) front view, (c) side view, (d) rear view. **e-h** – *Uralocyclus miloradovitchi* (Kramarenko, 1961); Russia, Chelyabinsk region, locality "Kazarmennyy kamen"; Lower Permian, Asselian. e, f: spec. PIN, no. 1792/5, paratype; e: top view; f: rear view. g, h: spec. PIN, no. 1792/3, paratype; g: top view; h: side view. Scale bars = 5 mm. PIN – Borissiak Paleontological Institute, Russian Academy of Sciences (Moscow, Russia).

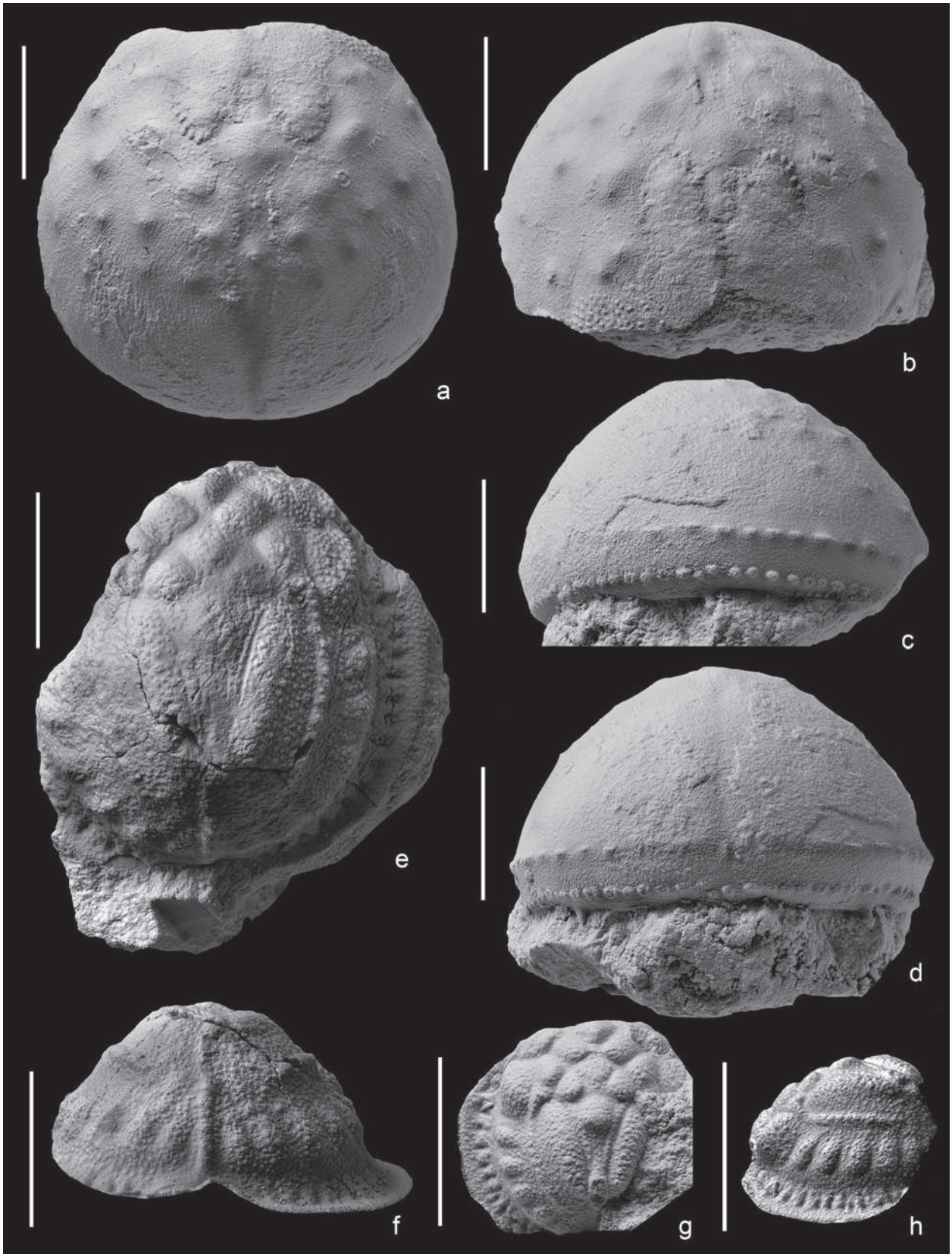

Fig. 5. a-d

Both species, *Scuinocyclus juliae* and *Uralocyclus miloradovitchi*, inhabited almost coeval Early Permian reef environments of the western margin of the ancient sea basin. These are so far the only records of cyclids from Lower Permian deposits worldwide. This fact indicates low diversity of cyclids at this geological time, as well as their relation to reefal habitats.

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