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Article

New genus of Cyclida (Crustacea) from Lower Carboniferous (Mississippian, Viséan) of Russia and England and new species from Viséan of Russia

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With 6 figures

Abstract: Within the crustacean group Cyclida, *Prolatcyclus* gen. nov. includes two species, *Prolatcyclus martinensis* (Goldring, 1967) and *P. kindzadza* sp. nov., described from the Lower Carboniferous (Mississippian, upper Viséan) of England and the Southern Urals of Russia, respectively. Members of the genus have a unique feature for cyclids – large hypertrophied second axial lobes. The species *P. kindzadza* is 2.5 times larger than *P. martinensis*. Both species are exclusively inhabitants of reef environments.

Key words: Crustacea, Cyclidae, Lower Carboniferous, Mississippian, Viséan, Russia, England, Akkermanovka Quarry, Cliff Quarry.

1. Introduction

Cyclids are enigmatic extinct marine crustaceans that existed from the Early Carboniferous to the Early Jurassic (possibly to the end of the Cretaceous considering members of Alsasuacaridae). Due to their rarity, they are a poorly studied group of invertebrates whose systematic placement is uncertain. These small animals (up to 6 cm long) resemble crabs but have a larger number of limbs (10–14 pairs), different morphology of gills, and other specific features. Some researchers (Dzik 2008, and others) included the cyclids in the subclass Branchiura, along with modern parasitic carp lice. However, there are structural features that do not allow assignment of cyclids to Branchiura. For instance, *Skuinocyclus juliae* Mychko & Alekseev, 2018, has small lugs on the ventral side of the carapace that significantly complicate the idea of an ectoparasitic lifestyle.

Occurrences of cyclids in Russia are extremely rare. Five species and forms are known: *Cyclus capidulum* Chernyshev, 1933 (Serpukhovian; the Sverdlovsk Oblast), *Cyclus* sp. (Serpukhovian; Chelyabinsk Oblast), *Uralocyclus miloradovitchi* (Kramarenko, 1961) (Asselian; Chelyabinsk Oblast), *Skuinocyclus juliae* Mychko & Alekseev, 2018 (Upper Asselian; Republic of Bashkortostan), and *Oonocarcinus* (?) sp., from the collection of E.I. Eichwald, who sampled in the Southern Urals (Chernyshev 1939). Therefore, each new discovery is very important for studying the diversity and evolution of the group.

During fieldwork in the summer of 2018 in Akkermanovka Quarry (Russia, Southern Urals, Orenburg Oblast; Fig. 1a–d), one of us (E.M.) made new collections of cyclids in a Lower Carboniferous reef limestone. Upon analyzing their morphology, it turned out that although these cyclids were morphologically very

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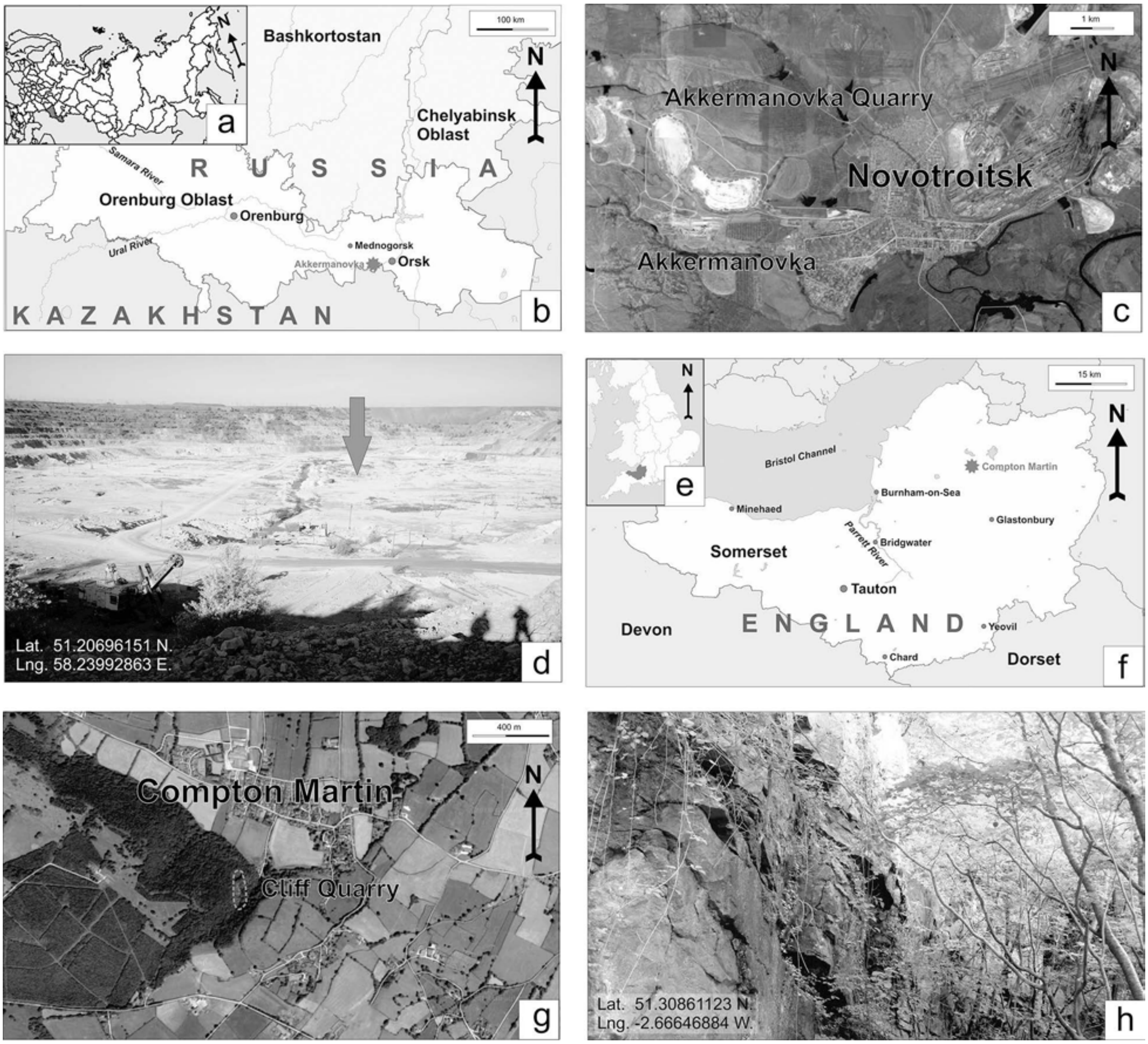


Fig. 1. Localities of *Prolatcyclus kindzadza* sp. nov. (a–d) and *P. martinensis* (Goldring, 1967) (e–h); a – map of Russia; b – map of Orenburg Oblast; (c) satellite image of Novotroitsk District, the red dashed line is the contour of Akkermanovka Quarry; (d) view of the Akkermanovka Quarry, the red arrow indicates the exact locality; (e) map of England, UK; (f) map of Somerset; (g) satellite image of Compton Martin, the red dashed line is the contour of Cliff Quarry; (h) photo of the Cliff Quarry.

similar to *Cyclus martinensis* Goldring, 1967, from the Lower Carboniferous (Mississippian, upper Viséan) of England, they represent a new species. Furthermore, the morphology of the carapace of the new species and that of *C. martinensis* is significantly different from the type species of the genus, *C. radialis* Phillips, 1836. This prompted us to establish a new genus *Prolatcyclus* gen. nov. that includes two species, *P. martinensis* (Goldring, 1967) and *P. kindzadza* sp. nov.

2. Localities

The studied samples of cyclids occur at two Lower Carboniferous localities in England and Russia. Both sites are late Viséan in age on northern margins of the Paleo-Tethys (Fig. 2).

Akkermanovka Quarry, Russia: This site is located on the lower bench of the Akkermanovka Quarry

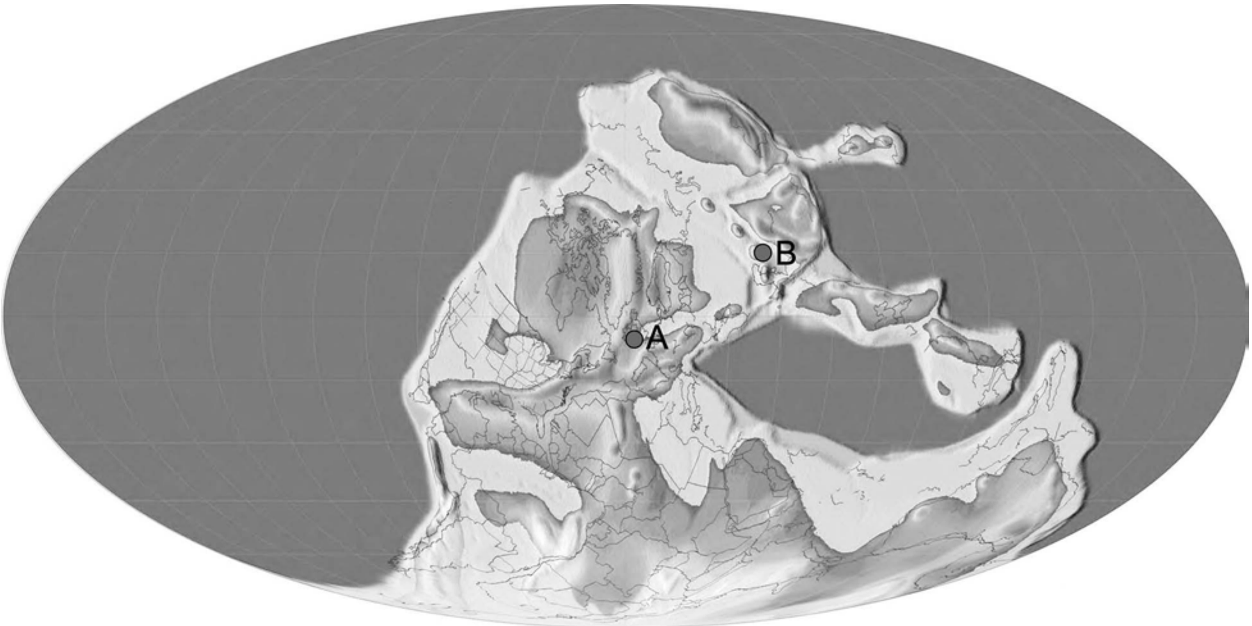


Fig. 2. Paleogeographic map of the Lower Carboniferous (Mississippian, early Viséan) (data of Scotese 2017, map 62): (A) locality of *P. martinensis* (Goldring, 1967); (B) locality of *P. kindzadza* sp. nov.

near Novotroitsk (Fig. 1a–c) in the Southern Urals in Russia. The Lower Carboniferous limestone has been unearthed (Fig. 1d) to a depth of about 100 meters. The presence of a very diverse fossil fauna in this locality was first discovered in 2014. It is considered to be a completely new Konzentrat-Lagerstätte of reef organisms in Russia. Fossils from various groups can be found there, mainly brachiopods, gastropods, bivalves, ammonites, trilobites and less commonly tetracorals, crustaceans, and rostroconchs. Brachiopods (especially *Striatifera striata* Fischer) in this community were reef-forming organisms reaching very large sizes, up to half a meter in height.

Lower Carboniferous rocks in the Khabarnoye – Akkermanovka area on the right bank of the Ural River in the Guberlinsky Mountains downstream from the city of Orsk became known following the work of M. E. Yanishevsky (1910), in which he described the extremely rich and diverse marine fauna of the reef limestone.

It was later found that the section exposed in this area includes deposits from the Devonian (Famennian), Mississippian (Tournaisian, Viséan, and Serpukhovian), and Pennsylvanian (Bashkirian) (Teodorovich 1941; Voinova 1941; Librovich 1964). Detection of a Jurassic weathering crust of iron and manganese ore and bauxite led to the excavation of small pits for their production, which later grew to a pit about 2 km long, which produced Carboniferous limestones as a fluxing raw material. Unfortunately, the section has never been studied biostratigraphically, and there are only old lists of foraminifera that do not provide the necessary accuracy for determining the age.

Carboniferous deposits discovered in the quarry are confined to the Khalilov Suture Zone in the area of the Main Uralian Fault. This geological fault separates the structures of the passive margin of the East European Craton from the tectonically concentrated volcanic arcs of the Ural Ocean. They compose the western flank of a meridionally stretched syncline measuring 12 x 2–3 km, enclosed in a graben with a tattered major fault on the eastern flank (Sharkov 2009; Lisov et al. 2017).

Four formations are exposed in Akkermanovka Quarry: Novotroitsk Formation (intercalated limestone, siltstone, and shales, 200–250 m), Izvestkovy Dol Formation (mainly limestone, 150–200 m), Beloglinka Formation (intercalated limestone, flintstones, spongolite, with manganese ores, 200 m), and Akkermanovka Formation (interbedded marl and dolomitic limestone, 350–400 m). The Novotroitsk and Izvestkovy Dol formations are Viséan. The Beloglinka Formation is Serpukhovian, and the Akkermanovka is Bashkirian (Lisov et al. 2017). The characteristics of these formations and the description of their stratotypes have not been published, and the age is established on the basis of very limited data.

Rocks containing cyclids were exposed in the central part at the bottom of the quarry and most likely belong to the Izvestkovy Dol Formation.

To determine the age of this locality, 20 microsections were made of limestone samples containing cyclids. Nilyufer B. Gibshman and Karina V. Sakhnenko (Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow) discovered foraminifera, calcareous algae and heterocorals in these microsections. Foraminifera are rare, but among them were *Pseudolituotuba enormis* (Brazhnikova & Rostovtseva), *Endothyranopsis crassa* (Brady), *Howchinia bradyana* (Howchin), *Forschia subangulata* Mikhailov, *Bradyina rotula* (Eichwald), *Omphalotis omphalota* (Rauser-Chernousova & Reitlinger), *Mirifica mirifica* (Rauser-Chernousova), *Cribrospira* (?) *rara* Rauser-Chernousova, *Archaediscus* aff. *moelleri* Rauser-Chernousova, *Rugosoarchaediscus* aff. *celsus* Conil & Lys, *Eostaffella* cf. *proikensis* Rauser-Chernousova, *Koskinotextularia bradyi* (Lipina), *Consobrinellopsis consobrina* (Lipina), and *C. lipinae* (Conil & Lys). This complex is undoubtedly upper Viséan, and the presence of *Koskinotextularia bradyi* and *Eostaffella* cf. *E. proikensis*, which appear in the Moscow Basin in the Aleksinian Regional Substage (Kabanov et al. 2016), allows a correlation of the layers with cyclids with the MFZ13-MFZ15 foraminiferal zones of the Warnantian and Asbian substages of the Viséan (Poty et al. 2014).

Calcareous algae include *Shartymophycus fusus* R. Ivanova, *Exvotarisella index* (Eherenberg), and *Fasciella kizilia* R. Ivanova, which are common in the upper Viséan and Serpukhovian of the paleoequatorial region (Gibshman & Alekseev 2017). Together with bacterial overgrowths, they compose the main part of the reefal boundstones.

In association with algae and bacterial overgrowths, there are quite frequent narrow (less than 1 mm in diameter) corallites of the heterocoral *Hexaphyllia prismatica* Stuckenberg, which was described from the upper Viséan (regional substage unknown) of the southern part of the Moscow Basin (Stuckenberg 1904).

Numerous species within the genus *Hexaphyllia* may be synonymous and belong to *H. marginata* (Duncan), which is common in the Viséan; when *Hexaphyllia* spp. are known more precisely, it would correlate with the upper Viséan of various regions of the world (Cossey 1997; Sobhy & Ezaki 2006).

V. A. Konovalova (PIN RAS, Moscow) identified ammonoids, which were found at the Akkermanovka locality. In her opinion, this ammonoid assemblage allows the recognition of the *Hypergoniatites–Ferganoceras* Genozone in the region. This genozone is correlated with the Viséan–Serpukhovian boundary interval on the eastern slope of the Southern Urals Sections (Nikolaeva & Konovalova 2017).

Conodonts could provide more accurate data for the age of this locality. For this, a sample of limestone weighing 3761 g was dissolved. Only a few conodont elements were recovered which were identified as *Kaldognathus* sp. and *Synclydognathus* sp. Both genera have apparatuses consisting only of ramiform elements and are characteristic for very shallow-water settings in the Viséan and Serpukhovian (Rexroad & Varker 1992; Somerville & Somerville 1998).

Cliff Quarry, England: The Mendip Hills in northern Somerset are the southernmost Carboniferous limestone uplands in Britain. The Mendip Hills comprise three major anticlinal structures, each with a core of older Devonian sandstone and Silurian volcanic rocks. These limestones are being actively developed at different quarries, including at Cliff Quarry. Currently there are two parts of the Cliff Quarry; the East Quarry is exposed but the West Quarry is overgrown. The quarry was used to supply hard road stone but was closed in 1956 as the big Eastern Mendip quarries had better transport links to the main markets in southeastern England. The quarry is cut into the Oxwich Head Limestone (previously known as Hotwells Limestone) which was deposited in a shallow shelf sea during the Asbian – Brigantian stage (later Viséan) of the Early Carboniferous. This limestone is included in the Pembroke Limestone Group and was deposited in shallow muddy conditions (Barclay 2011).

Goldring (1967) described well-preserved carapaces of *Cyclus martinensis* from the Oxwich Head Limestone. The specimens of these cyclids were found between the corallites of the phaceloid *Lithostrotion* or *Syringopora*. He noted that the association of the cyclids with the coral was too constant to be fortuitous and that it seemed likely that coral thickets were the habitat of the species (Goldring 1967).

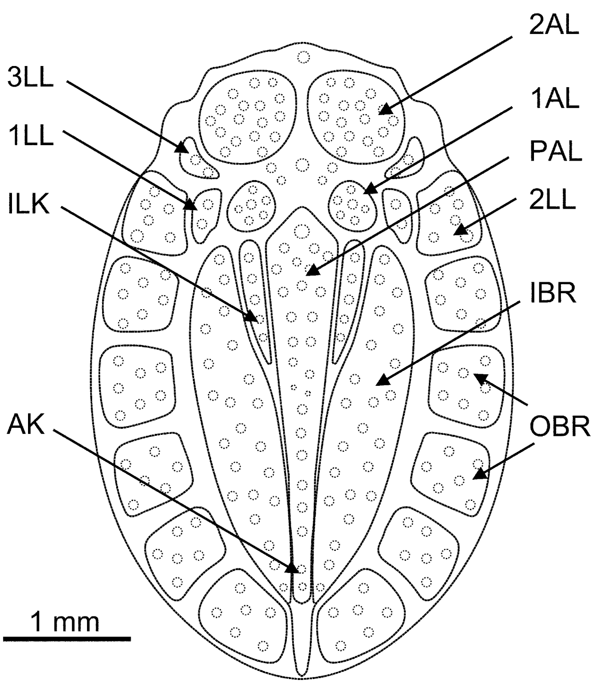


Fig. 3. Carapace morphology of *Prolatcyclus martinensis*; 1AL – first axial lobe; 2AL – second axial lobe; 1LL – first lateral lobe; 2LL – second lateral lobe; 3LL – third lateral lobe; ILK – inner lyrate keel; IBR – inner branchial region; OBR – outer branchial region; AK – axial keel.

3. Systematic paleontology

Superclass Crustacea Pennant, 1777
Order Cyclida Schram, Vonk & Hof, 1997
Family Cyclidae Packard, 1885

Included genera: *Cyclus* de Koninck, 1841; *Prolatcyclus* gen. nov.; *Uralocyclus* Mychko & Alekseev, 2018.

Genus *Prolatcyclus* nov.

Etymology: From the Latin *prolatus* (=elongate) and the genus *Cyclus*, nominative genus of Cyclida. The gender is masculine.

Type species: *Cyclus martinensis* Goldring, 1967, by original designation.

Included species: *Prolatcyclus martinensis* (Goldring, 1967) and *P. kindzadza* sp. nov. (Fig. 3)

Diagnosis: Carapaces small, from elongate-oval to ovoid. Lateral margins composed of a series of small arcs. Posterior axial lobe large, pentagonal or elongate-hexagonal, swollen. First lateral lobe small, circular, and coarsely granular, less inflated than hypertrophied, very large, semi-spherical second axial lobes. Outer branchial region wide, corrugated, separated into five wide, coarsely granular sections on either side, separated from axial keel by relatively deep groove. Overall surface granular.

Occurrences: Lower Carboniferous (Mississippian, upper Viséan); Eurasia (England and Southern Urals).

Discussion: *Prolatcyclus* differs from all other cyclids in its large, hypertrophied, second axial lobes. We do not exactly know the function of this feature; however, it can be assumed that this is an apomorphy, which is associated with lifestyle.

It is important to note that *Prolatcyclus* is an exclusive inhabitant of Carboniferous reefs, on margins of the Palaeo-Tethys Sea. Specimens of *P. martinensis* were found together with corals, and *P. kindzadza* lived in brachiopod reefs, where corals were rare. Many other cyclids are confined to reef deposits. For example, the type species of Cyclidae, *Cyclus radialis* Phillips, 1836, is known to be associated with fenestellid bryozoans from the Viséan Carboniferous in Yorkshire (Goldring 1967: 317). The cyclids *Uralocyclus miloradovitchi* Kramarenko, 1961, and *Skuinocyclus juliae* Mychko & Alekseev, 2018, were found in Early Permian bioherms and reefs in the Southern Urals (Mychko & Alekseev, 2018).

Both *P. martinensis* (Goldring, 1967) and *P. kindzadza* sp. nov. are very similar morphologically but have minor differences. Members of *P. kindzadza* sp. nov. from the Urals are almost 2.5 times larger than *P. martinensis* from England (Fig. 4).

Morphological terminology and abbreviations follow Feldmann & Schweitzer (2019).

Prolatcyclus martinensis (Goldring, 1967)
Fig. 5a–k

1967 *Cyclus martinensis* Goldring, p. 318, pl. 51, figs. 1–8.
1997 *Cyclus martinensis* Goldring. – Schram et al., p. 263.
2008 *Cyclus martinensis* Goldring. – Dzik, p. 1514, fig. 11.
2017 *Cyclus martinensis* Goldring. – Feldmann et al., p. 2.
2018 *Cyclus martinensis* Goldring. – Mychko & Alekseev, p. 25.

Types: An almost complete carapace, holotype GSM 102638 (collection of the Geological Survey Museum, British Geological Survey, Keyworth, England). Paratypes include GSM 102639–102647.

Type locality and horizon: England, Somerset, near Compton Martin village, the Cliff Quarry, around 400 m southwest of Compton Martin church; Lower Carboniferous, Mississippian, upper Viséan (Asbian – Brigantian substages), Oxwich Head Limestone.

Description: Carapace elongate-oval, longer than wide. Frontal margin weakly projected or straight, with a wide transverse rim extending into triangular posteriorly-directed

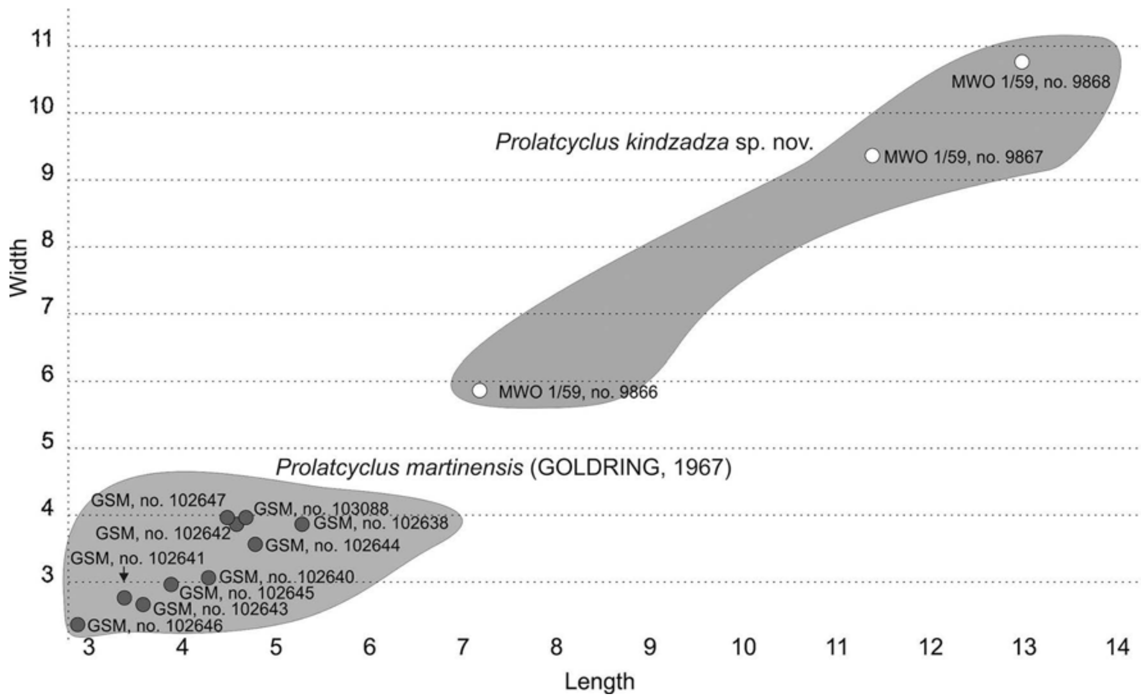


Fig. 4. Length-to-width relationship of carapaces (in mm) between *Prolatcyclus martinensis* (Goldring, 1967) and *P. kindzadza* sp. nov.

projection axially. Lateral margins composed of a series of arcs; first arc extending from frontal margin in weakly convex lobe, diverging posteriorly; followed by bulbous projection of second lateral lobe; then margin arcs moderately convexly to posterior margin, which is rimmed, short, and weakly convex. Posterior axial lobe elongate-hexagonal, coarsely granular; first axial lobe chevron-shaped, directed anteriorly, weakly inflated; second axial lobes paired, very large, semi-spherical. First lateral lobe small, circular, coarsely granular, less inflated than large, swollen second lateral lobe; third lateral lobe small, situated at posterolateral corner of second axial lobe. Posterior axial lobe extends into a widened axial area that reaches the posterior rim, narrowing posteriorly to the hexagonal area, widening again in "cardiac" area, and narrowing posteriorly; hexagonal area bordered by lyrate, longitudinal keels. Inner lyrate keel narrow, longer that posterior axial lobe, terminating posteriorly along axial ridge. Inner branchial region large, swollen, converging posteriorly to terminate adjacent to "cardiac" region. Outer branchial region wide, corrugated, separated into five wide, coarsely granular thoracic ridges on either side, and separated from axial keel by relatively deep groove. Overall surface granular; where cuticle preserved, granules appear to have been sharp tubercles.

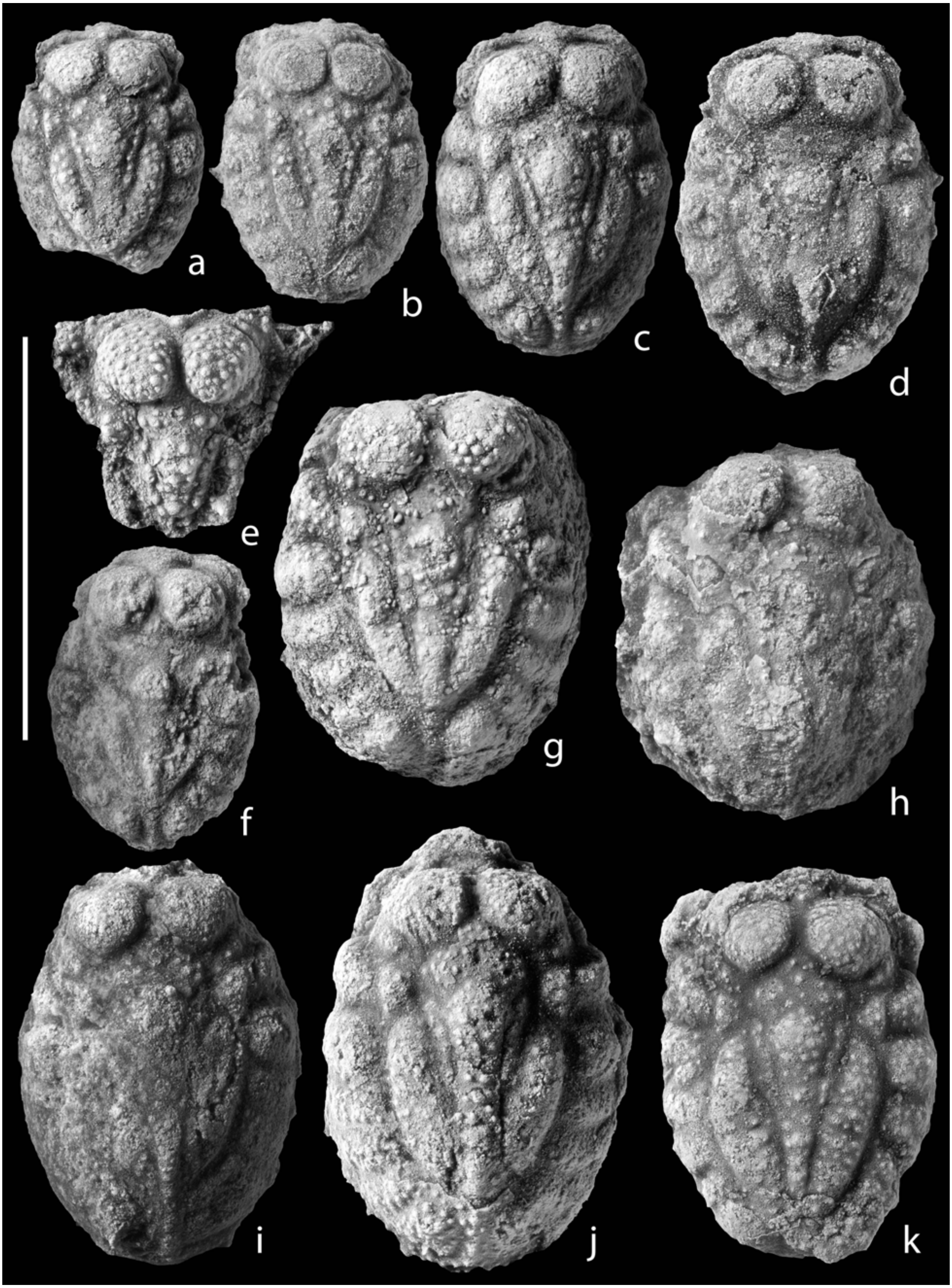
Dimensions (in mm):

Specimen	Length	Width	Width/Length
GSM, no. 102638 (Holotype)	5.4	3.8	0.70
GSM, no. 102639*	–	–	
GSM, no. 102640	4.4	3	0.68
GSM, no. 102641	3.5	2.7	0.77
GSM, no. 102642	4.7	3.80	0.81
GSM, no. 102643	3.7	2.6	0.70
GSM, no. 102644	4.9	3.5	0.71
GSM, no. 102645	4	2.9	0.73
GSM, no. 102646	3	2.3	0.81
GSM, no. 102647	4.8	3.9	0.85
GSM, no. 103088	4.6	3.9	0.74
mean value:	4.3	3.2	0.75

* fragment of carapace.

Material: 11 specimens, 10 well-preserved carapaces and one fragment of central part of carapace.

Fig. 5. *Prolatcyclus martinensis* (Goldring, 1967); England, Somerset, near Compton Martin village, Cliff Quarry, around 400 m south-west of Compton Martin church; Lower Carboniferous, Mississippian, upper Viséan (Asbian – Brigantian substages), Oxwich Head Limestone; (a) GSM 102646, paratype; (b) GSM 102641, paratype; (c) GSM, no. 102645; (d) GSM 102640, paratype; (e) GSM 102639, paratype; (f) GSM 102643, paratype; (g) GSM 102647, paratype; (h) GSM 103088, paratype; (i) GSM 102644, paratype; (j) GSM 102638, holotype; (k) GSM 102642, paratype. Scale bars = 5 mm.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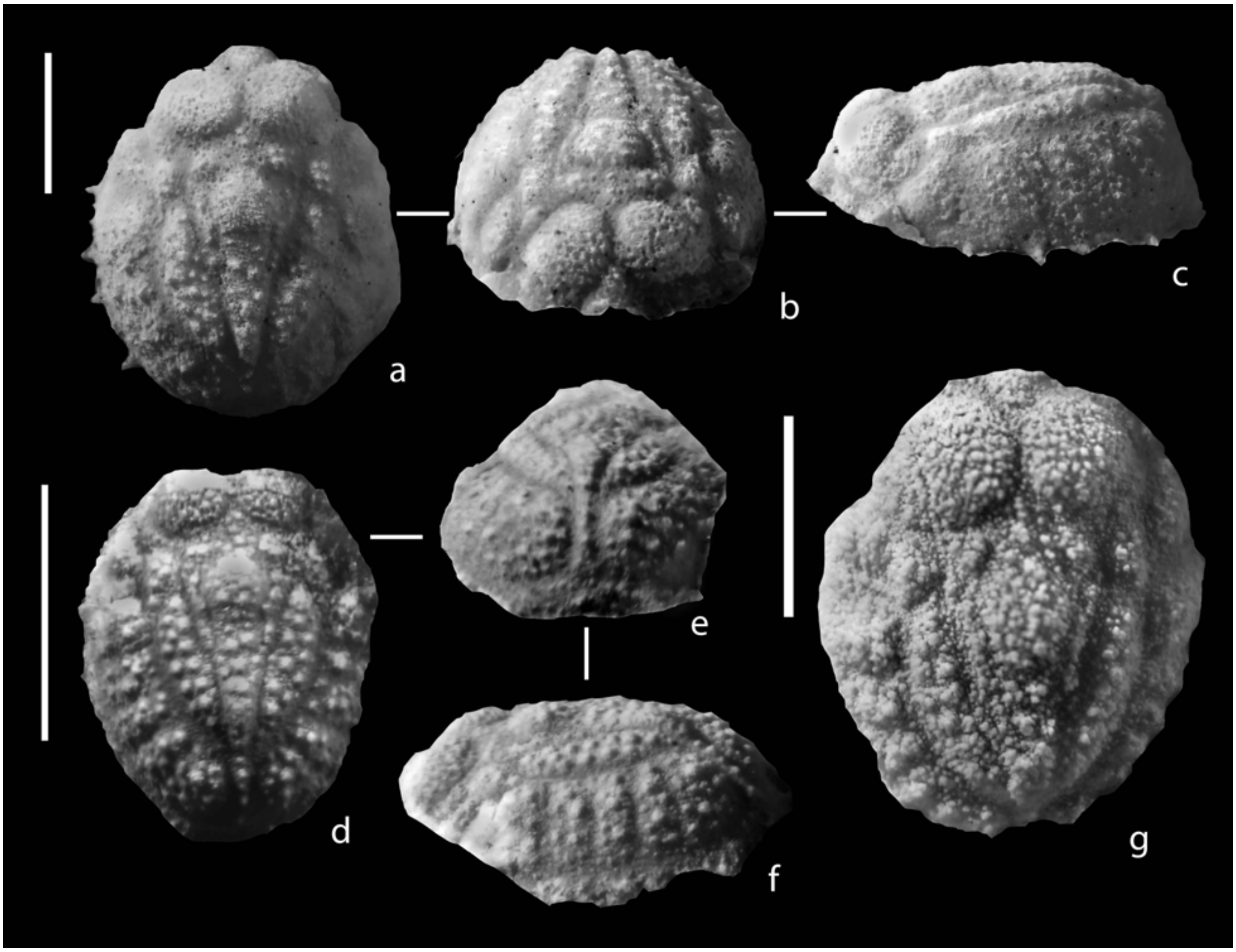

Fig. 6. *Prolatcyclus kindzadza* sp. nov.; Russia, Orenburg Oblast, the Novotroitsk District, the Akkermanovka Quarry; Lower Carboniferous, Mississippian, upper Viséan; (a–c) MWO 1/59, no. 9868, holotype; (a) dorsal view; (b) frontal view; (c) left lateral view; (d–f) MWO 1/59, no. 9866, paratype; (d) dorsal view; (e) frontal view; (f) left lateral view; (g) MWO 1/59, no. 9867, paratype, dorsal view. Scale bars = 5 mm.

Prolatcyclus kindzadza sp. nov.
Fig. 6a–g

Etymology: In honor of the cult sci-fi dystopian tragicomedy Soviet film "Kin-dza-dza!" directed by Georgiy Daneliya in 1986.

Types: An almost complete carapace, MWO 1/59, no. 9868 (collection of the Museum of the World Ocean, Kaliningrad, Russia), and paratypes MWO 1/59, no. 9866–9867.

Type locality and horizon: Russia, Orenburg Oblast, Novotroitsk District, lower bench of Akkermanovka Quarry; Lower Carboniferous, Mississippian, upper Viséan.

Description: Carapace ovoid, length about 1.2 times the maximum width measured at about mid-length. Highly vaulted transversely and longitudinally, highest in posterior 1/3. Frontal margin bilobed, formed by anterior margin of second axial lobes. Lateral margin convex, bearing at least four short, sharply-pointed spines. Posterior margin convex, with a narrow rim. Entire surface of carapace granular. Posterior axial lobe large, pentagonal, swollen. First axial lobe chevron-shaped with weak swelling on distal ends. Second axial lobes extremely large, width of both together ½ maximum width, forming front margin of carapace. First lateral lobe small, circular; second lateral lobe larger, longitudinally elongate; third lateral lobe small, circular, almost continuous with 2nd axial lobe. Axial keel tapers from posterior axial lobe to narrow structure reaching posterior margin. Inner lyrate keel narrow, about as long as posterior axial lobe. Inner branchial region swollen, broad anteriorly, narrowing posteriorly to terminate at axial keel. Outer branchial region bearing about 5 arcuate, wide, corrugated thoracic ridges on larger specimen; thoracic ridges not expressed on smaller specimen. Granulations on small specimen are relatively larger than those on larger specimens.

Dimensions (in mm):

Specimen	Length	Width	Height	Width/ Length
MWO 1/59, no. 9868	13.1	10.7	6.7	0.82
MWO 1/59, no. 9867	11.5	9.3	5	0.81
MWO 1/59, no. 9866	7.3	5.8	4	0.79
mean value:	10.6	8.6	5.2	0.81

Material: Three specimens, well-preserved carapaces.

Discussion: The new species is very similar to *Prolatcyclus martinensis* (Goldring, 1967), but differs in several ways. The ratio of width to length is somewhat higher in *P. kindzadza*, although there is some overlap between the two species. The inner branchial region in *P. kindzadza* does not extend as far posteriorly as that of *P. martinensis*, in which it extends nearly to the posterior border of the carapace. The carapace shape of *P. kindzadza* is more rounded, whereas that of *P. martinensis* is more longitudinally elongate.

The elongate spines on the lateral margins are well enough preserved to describe in *Prolatcyclus kindzadza* but are only preserved as broken bases in some specimens of *P. martinensis*. It is unknown as to whether this is a taphonomic feature or whether the spines were smaller and more delicate in *P. martinensis*. It is also possible that the spines were broken in *P. martinensis* during extraction from the rocks or preparation.

4. Conclusions

The description of a new genus for a species previously referred to *Cyclus*, as well as an additional new species from Russia, indicates that diversity in this group was higher than previously recognized. Study of members of Cyclidae and the larger group Cyclida is ongoing and indicate that diversity within the group was indeed much higher than previously recognized. The group apparently radiated in the late Paleozoic and became a notable part of the crustacean fauna during that time.

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