N. Jb. Geol. Paläont. Abh. 296/3 (2020), 245–303
Stuttgart, June 2020

Article

Revision of Cyclida (Pancrustacea, Multicrustacea), with five new genera

Carrie E. Schweitzer, Eduard V. Mychko, and Rodney M. Feldmann

With 28 figures

Abstract: All cyclidan species represented by existing material are illustrated photographically. New genera within Cyclidae include *Ambocyclus* new genus; *Carabicyclus* new genus; *Chernyshevine* new genus, *Litocyclus* new genus; and *Tazawacyclus* new genus with the following new combinations: *A. capidulum* (Chernyschev, 1933); *A. simulans* (Reed, 1908); *A.*? *minutus* (Rogers, 1902); *Carabicyclus wrighti* (Woodward, 1870); *L. bilobatus* (Woodward, 1870); *L.*? *communis* (Rogers, 1902); *L. jonesianus* (Woodward, 1870); *L.*? *permarginatus* (Rogers, 1902); *L. torosus* (Woodward, 1870); *Chernyshevine spinosus* (Chernyschev, 1933); *T. tazawai* (Niko & Ibaraki, 2011); *U. harknessi* (Woodward, 1870); and *U. woodwardi* (Reed, 1893). New genera within Americlidae include *Brittaniclus* and *Dziklus* with the following new combinations: *B. rankini* (Woodward, 1868); *B. scotti* (Woodward, 1894); *B. testudo* (Peach, 1882); and *D. obesus* (Schram, Vonk & Hof, 1997). A neotype is herein designated for *Halicyne plana*. Each family within Cyclida occupies a distinct morphospace. Two families survived the end-Permian mass extinction event. Most cyclidans occupied marine conditions, but some are known from marginal marine and freshwater environments.

Key words: Crustacea, Paleozoic, Mesozoic, systematics.

1. Introduction

Cyclida embraces an enigmatic group of crustaceans ranging in age from Early Carboniferous (Mississippian) to Late Cretaceous (Maastrichtian). Although individuals within the group can be arrayed into as many as 25 genera, there are sufficient numbers of similarities to support the Order Cyclida Schram, Vonk & Hof, 1997. They are characterized by small, nearly circular carapaces; a pair of antennal structures, of which the first (the antennules) are most prominent; a markedly reduced abdomen; and a horseshoe-shaped array of gill filaments. Because individuals may be preserved in different orientations and different preservational styles, no single taxon necessarily exhibits all of the defining characters to support their inclusion within the group. Recent examination of two species previously thought to be cyclidans have been reassigned. Neither *Mesoprosopon* Stolley, 1915, nor *Stagmacaris* Schweigert, 2006, conform to the definition of the group, and have been assigned to other taxa (van Bakel et al. 2011; Hyžný et al. 2016; Feldmann & Schweitzer 2019). They will not be considered further.

Cyclidans have been recognized since 1836, when Phillips referred *Agnostus*? *radialis* to the Trilobita. Subsequent to that, several additional species, primarily from Carboniferous rocks, were recognized in the 19th Century, documenting centers of diversity in the British Isles and North America. Additional species

DOI: 10.1127/njgpa/2020/0905
www.schweizerbart.de
0077-7749/2020/0905 $ 14.75

were recognized throughout the 20th Century and new taxa continue to be named. The result is that the geographic distribution as well as the stratigraphic distribution has been greatly expanded. Efforts have been made to assign the genera to families, but assignment of Cyclida with confidence has been elusive. Clark et al. (2020) recently suggested that Cyclida was best allied with Multicrustacea within Pancrustacea, which we follow here.

Many species within Cyclida have never been illustrated photographically, so that attempts to interpret the species and to arrange them into generic and family categories has suffered from lack of direct knowledge of the type and associated specimens. Some species were named on the basis of specimens that were lost or destroyed in World War II. Others were retained in private collections or were placed in depositories that cannot be located. Every effort has been made to locate missing specimens, although some remain lost.

Thus, the purpose of this work is to illustrate all cyclidan species for which material is known, to develop diagnoses and descriptions based upon the material evidence rather than non-photographic illustrations, to propose a revised family and generic level classification, and compile up-to-date geographic and stratigraphic data. In the course of this work it became clear that terminology defining cyclidan morphology was not uniform; therefore, it was judged that rectifying that issue was essential prior to reconsidering descriptions and evaluating placement. Thus, Feldmann & Schweitzer (2019) defined and illustrated morphological features in a manner that would permit careful comparison; those terms will be applied herein.

2. Systematic paleontology

For convenience we follow Oakley et al. (2012) for higher level classification of crustacean groups. Multiple other schemes exist (Legg et al. 2013; Edgecombe & Legg 2014; Schwentner et al. 2017). A summary of the classification presented here with all species, genera, and families, is presented in Supplemental Table 1. We use “cyclidan” to refer to members of the Order Cyclida and “cyclid” for members of the Family Cyclidae.

Morphological terminology: Feldmann & Schweitzer (2019) recently codified terminology for cyclidan morphology. We follow that terminology here: a1: antennule; a2: antennae; abd: abdomen; ak: axial keel; al 1 – al 3: axial lobes 1–3; alp: outer orbital tooth; br: branchial region; cd: concentric depression; cm: marginal carapace cornice; cn: crenulate edge of carapace; cr: caudal rami; eb: raised orbital rim; g: gills; gmi: gastric muscle insertion; gon: gonopod; gr2 – gr 4: arcuate, transverse granular ridge; ibr: inner branchial region; ilk: inner lyrate keel; ll 1 – ll 3: lateral lobes 1–3; mck: median concentric keel; mr: marginal rim; mrk: marginal rim keel; mx: maxilla; mxpd: maxilliped; obr: outer branchial region; ocs: ovate central structure of sternum; olk: outer lyrate keel; on: optic notch; op: orbital process; pal: posterior axial lobe; pap: papillae; pc: small circular pit; pn: posterior notch in marginal rim; r: rostral plate; sp: sunken pit; t2 – t6: thoracic appendages; tc: transverse crest; th: thoracic somites (sternal); tr: thoracic ridges (dorsal); x: anterior or post-optic bulge; y: posterior or cardiac bulge.

Institutional abbreviations: GLAHM, Hunterian Museum; University of Glasgow, UK; NHMUK, The Natural History Museum, London, UK; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; CMNH, Cleveland Museum of Natural History, Cleveland, Ohio, USA; FMM, Fossil Magna Museum, Itoigawa, Niigata, Japan; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; FSUJIG, Friedrich Schiller University of Jena, Institute of Geosciences, Jena, Germany; GSM, Geological Survey Museum, British Geological Survey, Keyworth, UK; L, MM, Manchester Museum, University of Manchester, UK; LF, Lauer Foundation for Paleontology, Science, and Education, NFP, Wheaton, Illinois, USA; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology, California, USA; LLG, the local museum of Luoping County, Yunnan Province, China; LPI, Invertebrate Paleontology Collection, Chengdu Institute of Geology and Mineral Resources, Chengdu, Sichuan Province, China; MAB k., Oertijdmuseum, Boxtel, The Netherlands; MCP, Mazon Creek Project, Northeastern Illinois University, Northfield, Illinois, USA; MGSB, Museo Geológico del Seminario de Barcelona, Spain; MSNM, Museo civico di Storia naturale, Milan, Italy; MVO, Museum of the World Ocean, Kaliningrad, Russia; NHMW, Natural History Museum of Vienna, Austria; NMC, Naturkunde-Museum Coburg, Germany; NMS.G, National Museum of Scotland, Edinburgh, UK; PAN, Polish Academy of Sciences, Warsaw, Poland; PWN, Polish Scientific Publishers, Warsaw, Poland; PINRAN, Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow; SM, Sedgwick Museum, Cambridge University, UK; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; TsNINGR, Academician F.N. Chernyshev Central scientific research geological survey museum, St. Petersburg, Russia; UMPC, University of Montana Paleontology Center, Missoula, Montana, USA; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Infraphylum Pancrustacea Zrzavý & Štys, 1997

Discussion: We place the Cyclida within Pancrustacea based upon possession of two pairs of antennae, present in multiple species and traditionally diagnostic for crustaceans. Cyclidans have a carapace covering the thoracic somites and specialized frontal appendages for feeding. Tagmosis is less pronounced in cyclidans than other pancrustaceans, but there does appear to be a head, a thorax, and rarely preserved, a tiny abdomen.

Boxshall & Jaume (2009) suggested that Cyclida were doubtfully crustaceans and more aligned with chelicerates. In part they based this decision on the gill interpretation of Dzik (2008). Our interpretation of the gills is quite different and aligns with that seen in crustaceans. In addition, we interpret the walking legs as arising laterally on a sternal structure, not extending from the "median sternite" as interpreted by Boxshall & Jaume (2009). Our interpretation is congruent with the structures seen in crustaceans, including two pairs of antennae.

Class Multicrustacea Regier et al., 2010
Order Cyclida Schram, Vonk & Hof, 1997

Included families: Alsasuacaridae van Bakel, Jagt, Fraaije & Artal, 2011; Americlidae Dzik, 2008; Cyclidae Packard, 1885; Halicynidae Gall & Grauvogel, 1967; Hemitrochiscidae Trauth, 1918; Schraminidae Dzik, 2008.

Diagnosis: Pancrustaceans with domed or flattened carapace covering cephalic and thoracic regions, carapace oval to subcircular in outline, usually with a marginal rim; eyes stalked; antennules stout and long, antennae much reduced in size; thoracomeres expressed ventrally, usually six or seven visible; sometimes thoracic segmentation expressed as dorsal ridges; at least eight pairs of appendages excluding antennae, anterior-most pseudochelate, posterior appendages with sharp dactyli; gills forming horseshoe-shaped lamellate structure.

Discussion: Cyclida usually has been allied with either Maxillopoda, now interpreted to be a polyphyletic group, or Branchiura. Schram et al. (1997) summarized the convoluted systematic history of cyclidans, noting that they have been classified as anything ranging from horseshoe crab larvae to trilobites to copepods to crustaceans of unknown affinity. Schram et al. (1997) considered the group as a subclass of Maxillopoda, and in a phylogeny of maxillopodans recovered Cycloidea as sister to the Copepoda. Dzik (2008) embraced an older hypothesis, following Hopwood (1925) in placing cycloids within Branchiura, the fish lice. We elect to place the Cyclida within Multicrustacea based upon its apparent similarities with Copepoda and Malacostraca (Clark et al. 2020). Work on placement of Cyclida within Pancrustacea is ongoing.

Family Cyclidae Packard, 1885

Included genera: *Ambocyclus* new genus; *Carabicyclus* new genus; *Chernyshevine* new genus; *Cyclus* de Koninck, 1841 *sensu stricto*; *Litocyclus* new genus; *Prolatcyclus* Mychko, Feldmann, Schweitzer & Alekseev, 2019; *Tazawacyclus* new genus; *Uralocyclus* Mychko & Alekseev, 2018.

Diagnosis: Carapace small, outline circular or oval, generally strongly domed, highest in posterior half; carapace with marginal rim, rim sometimes with narrow or wide posterior notch; carapace surface granular, with clearly or poorly defined regions, always with posterior axial keel; carapace lobes exhibiting varying degree of development, posterior axial lobe always present; branchial regions granular, sometimes with thoracic ridges.

Discussion: Glaessner (1928) provided a useful diagnosis for the family, and his 1969 diagnosis was nearly the same. The diagnoses of both Packard (1885) and Schram et al. (1997) included the morphology of *Cyclus americanus* Packard, 1885, at that time referred to *Cyclus* but now referred to *Americlus* Dzik, 2008, in Americlidae. Packard's diagnosis included description of an abdomen with three segments, whereas Schram et al. (1997), based upon more material than available to Packard (1885), noted two segments. In addition, Packard's (1885) illustration of *Cyclus americanus* may be upside down, as he shows radiating appendages anteriorly on the body. Such radiating structures are the posterior thoracic somites in all specimens of *A. americanus* we have examined. Abdomen and ventral surfaces are not known for Cyclidae sensu stricto.

Recently, a new genus was erected to embrace a Russian species originally referred to *Cyclus*, *Uralocyclus miloradovitchi* (Kramerenko, 1961) (Mychko & Alekseev 2018). That genus was placed within Americlidae, but based upon its highly vaulted and ornamented carapace, we place it within Cyclidae. *Prolatcyclus* was recently erected to embrace *Cyclus martinensis* and a new species from Russia (Mychko et al. 2019).

The diagnosis for *Cyclus* sensu lato up until now has included a broad range of variation in specimens referred to it. It has become a catchall for domed, Carboniferous forms. Thus, we herein arrange the species referred to *Cyclus* by Feldmann & Schweitzer (2019) into a new generic framework. Of the species originally referred to *Cyclus*, type material appears to have been lost for all of the species named by Rogers (1902). *Cyclus tazawai* was well-illustrated. We illustrate with photographs, to our knowledge for the first time, *C. bilobatus*, *C. harknessi*, *C. jonesianus*, *C. radialis*, *C. simulans*, *C. torosus*, *C. woodwardi*, and *C. wrighti*. We provide descriptions of material to augment the photos of these taxa.

Geologic range: Tournaisian (Lower Mississippian) – Asselian (Lower Permian).

Genus *Cyclus* de Koninck, 1841 *sensu stricto*

Type and sole species: *Agnostus? radialis* Phillips, 1836, by original designation.

Diagnosis: Carapace ovate to subcircular, strongly vaulted transversely and longitudinally; with well-developed, smooth marginal rim, posterior notch wide; axial and lateral lobes well-developed; inner and outer lyrate keels present, posterior axial keel strong; about 7 very well-defined thoracic ridges, extending from axial regions to marginal rim, inner and outer branchial regions not differentiated.

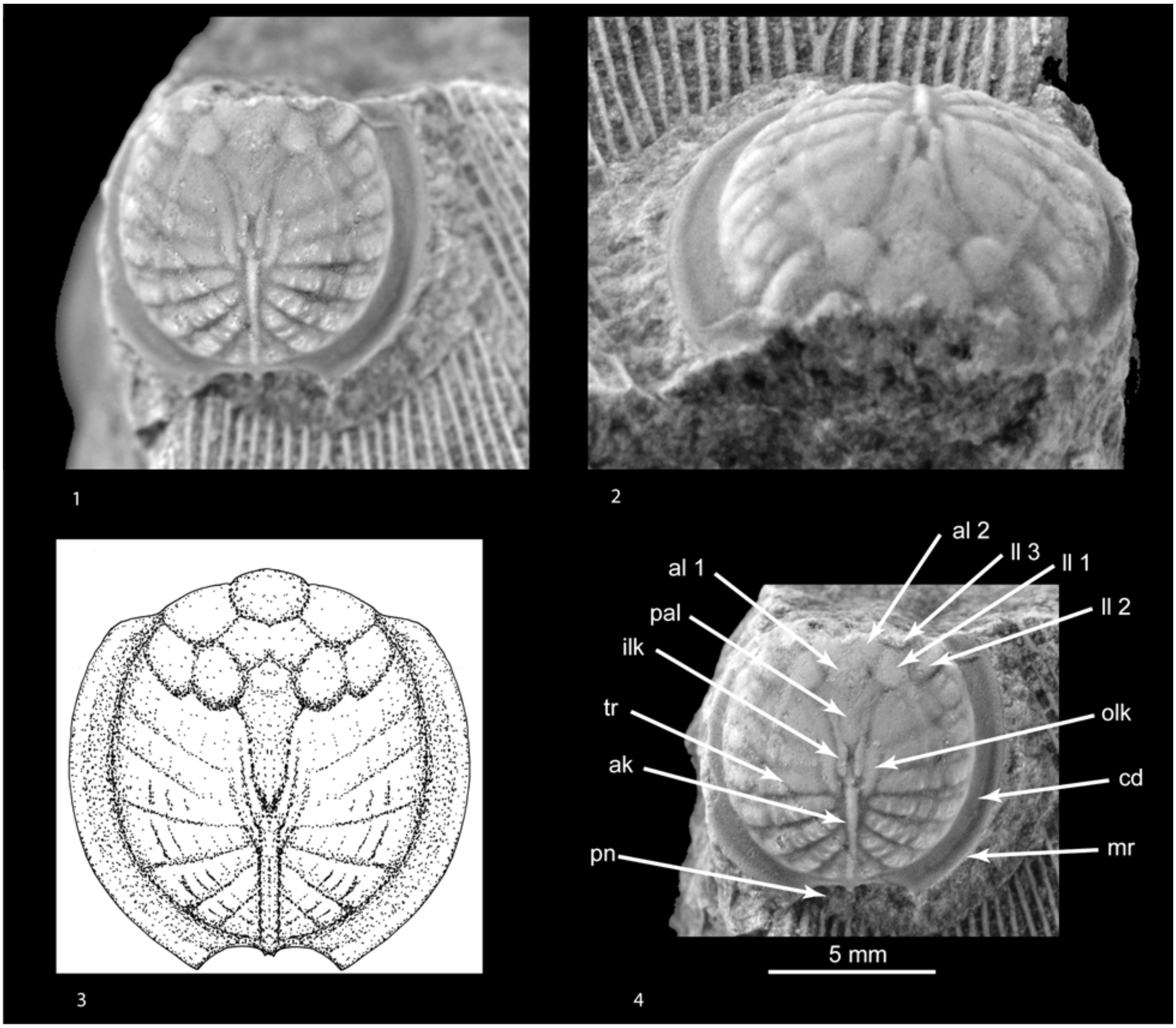


Fig. 1. Cyclidae, *Cyclus radialis* (PHILLIPS, 1836), MM L.11676. **1** – Dorsal view. **2** – Anterior view. **3** – Line drawing with anteriormost regions interpolated. **4** – Labeled regions. Scale bar = 5 mm.

Discussion: *Cyclus radialis* is the only species within Cyclidae with well-defined thoracic ridges on the dorsal carapace extending from the axial region to the lateral margin. *Cyclus radialis* has a very wide, smooth lateral rim with a broad posterior notch, not seen in other taxa. Thus, it is the sole species referred to *Cyclus*. A few other species have thoracic ridges in the outer branchial region only, and these are herein referred to new genera.

Geologic range: Lower to Middle Mississippian (Tournaisian?–Viséan).

Cyclus radialis (PHILLIPS, 1836)
Fig. 1

1836 *Agnostus*? *radialis* PHILLIPS, p. 240, pl. 22, fig. 5.
1841 *Cyclus radialis* (PHILLIPS, 1836). – DE KONINCK, p. 13.
1868 *Cyclus radialis* (PHILLIPS, 1836). – WOODWARD, p. 73.
1870 *Cyclus radialis* (PHILLIPS, 1836). – WOODWARD, p. 557.
1878 *Cyclus radialis* (PHILLIPS, 1836). – WOODWARD, p. 249.
1894 *Cyclus radialis* (PHILLIPS, 1836). – WOODWARD, p. 530.

1885 *Cyclus radialis* (Phillips, 1836). – Packard, p. 144.
1902 *Cyclus radialis* (Phillips, 1836). – Rogers, p. 274.
1925 *Cyclus radialis* (Phillips, 1836). – Hopwood, p. 290.
1928 *Cyclus radialis* (Phillips, 1836). – Glaessner, p. 394.
1957 *Cyclus radialis* (Phillips, 1836). – Trümpy, p. 545.
1967 *Cyclus radialis* (Phillips, 1836). – Goldring, p. 317.
1969 *Cyclus radialis* (Phillips, 1836). – Glaessner, p. R569.
1971 *Cyclus radialis* (Phillips, 1836). – Akagi, p. 80.
1997 *Cyclus radialis* (Phillips, 1836). – Schram et al., p. 262.
2008 *Cyclus radialis* (Phillips, 1836). – Dzik, p. 1512.
2017 *Cyclus radialis* (Phillips, 1836). – Feldmann et al., p. 407.
2018 *Cyclus radialis* (Phillips, 1836). – Mychko & Alekseev, p. 25.
2019 *Cyclus radialis* (Phillips, 1836). – Feldmann & Schweitzer, p. 2.
2019 *Cyclus radialis* (Phillips, 1836). – Mychko et al., p. 85.
2020 *Cyclus radialis* (Phillips, 1836). – Clark et al., p. 1.

Material examined: Syntypes NHMUK 58883a–c; NHMUK I4579; NHMUK In.58881–82; SM E3710-3723; Manchester Museum L.11676a-c; GSM 60815.

Diagnosis: Carapace ovate, slightly longer than wide, strongly vaulted longitudinally and transversely; regions well-defined anteriorly, axial keel and lyrate keels well-developed; dorsal carapace surface exhibiting thoracic segmentation extending from lyrate keels to marginal rim; marginal rim wide, flattened, with wide posterior notch.

Description: Carapace nearly circular; slightly longer than wide, width about 96% length, widest at about midlength; highly vaulted with greatest height posterior to midlength.

Frontal margin not well known. Marginal rim uniformly ca. 1 mm wide laterally, positioned below remainder of carapace surface, smooth; marginal rim with wide posterior notch, notch terminating laterally by acute point and interrupted axially by small spine, notch about 45% carapace width; inner margin of marginal rim, depressed, forming concentric depression.

Posterior axial lobe elongate, tapers posteriorly, bounded laterally by well-defined grooves terminating anterior to axial keel. First axial lobe small, ovate, weakly separated from pair of second axial lobes, which are spherical. First lateral lobe rounded-triangular, widest posteriorly; second lateral lobe oblique, elongate, more or less parallel to apparent somite segments of remainder of carapace; third lateral lobe only posteriorly preserved, apparently rounded. Posterior axial lobe bounded by narrow, inner lyrate keel extending posteriorly beyond it, keels defining an axial groove posterior to posterior median lobe; inner lyrate keels bounded by wider longitudinal outer lyrate keel that is weakly arcuate, terminating on either side of anterior end of axial keel, axial keel narrowing posteriorly, terminating at small axial spine on posterior margin.

Lateral surface of carapace with seven radiating thoracic ridges, ridges ornamented with longitudinal rugae, becoming more rugose posteriorly. Rugae on carapace ridges arrayed in regular pattern to define overall concentric pattern.

Abdomen, venter, and appendages not preserved.

Localities & formation: There are three localities: Little Island, County Cork, Ireland, Cork Beds in Little Island Formation; Viséan Limestone, Belgium; and Cawden Hill, Yorkshire, England, UK, Carboniferous Limestone.

Geologic range: Lower to Middle Mississippian (Tournaisian-Viséan).

Lithology & environment: Little Island Formation: massive pale grey limestone (biomicrite), shallow marine; Cawden Hill and Belgium: limestone; shallow marine.

Prolatcyclus Mychko, Feldmann, Schweitzer & Alekseev, 2019

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

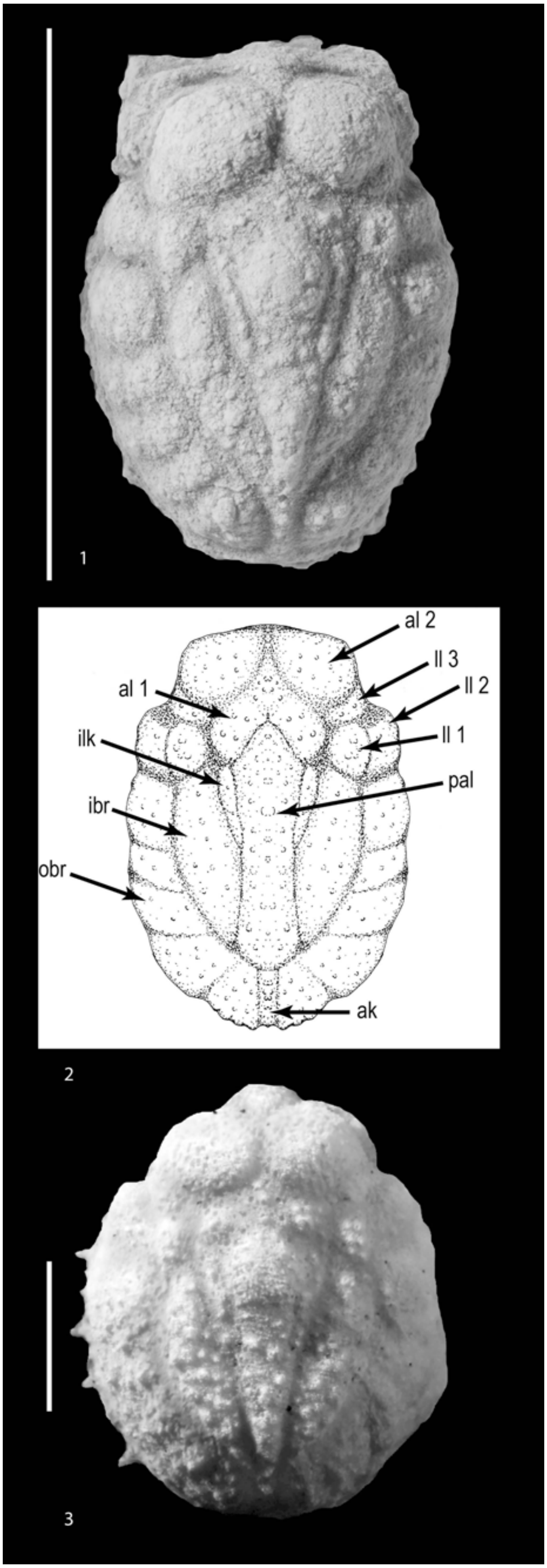
Other species: *Prolatcyclus kindzadza* Mychko, Feldmann, Schweitzer & Alekseev, 2019.

Diagnosis: Carapace elongate ovate, longer than wide; posterior axial lobe strong, confluent with axial keel; first axial lobe chevron-shaped; second axial lobes large; third axial and lateral lobes smaller; inner lyrate keel present; inner branchial and outer branchial regions well-defined, separated by median concentric groove, outer branchial region separated into six thoracic ridges.

Geologic range: Middle Mississippian (Viséan) of England and Russia.

Prolatcyclus martinensis (Goldring, 1967)
Fig. 2.1, 2.2

1967 *Cyclus martinensis* Goldring, 1967, p. 318, pl. 51, figs. 1–12.
1971 *Cyclus martinensis* Goldring, 1967. – Akagi, p. 81.
1997 *Cyclus martinensis* Goldring, 1967. – Schram et al., p. 263.
2008 *Cyclus martinensis* Goldring, 1967. – Dzik, p. 1512.
2017 *Cyclus martinensis* Goldring, 1967. – Feldmann et al., p. 407.
2018 *Cyclus martinensis* Goldring, 1967. – Mychko & Alekseev, p. 25.
2019 *Cyclus martinensis* Goldring, 1967. – Feldmann & Schweitzer, p. 2.
2019 *Prolatcyclus martinensis* (Goldring, 1967). Mychko et al., p. 85.



Material examined: GSM 1026838, holotype; GSM 102639–102647, paratypes.

Diagnosis: As in Mychko et al. (2019).

Description: As in Mychko et al. (2019).

Locality & formation: Cliff Quarry, near Compton Martin, Somerset, England, UK, Oxwich Head Limestone Formation.

Geologic range: Middle Mississippian (Upper Viséan, Asbian–Brigantian substages).

Lithology & environment: Reefal limestones; shallow marine, reef facies.

Prolatcyclus kindzadza Mychko, Feldmann, Schweitzer & Alekseev, 2019
Fig. 2.3

2019 *Prolatcyclus kindzadza* Mychko, Feldmann, Schweitzer & Alekseev, p. 88, fig. 6.

Material examined: Holotype MWO 1/59, no. 9868; paratypes MWO 1/59, no. 9866–9867.

Diagnosis: Carapace rounded-ovoid, wider than long, width about 80 % maximum length; inner branchial region short; elongate spines on lateral margins of rim.

Description: As in Mychko et al. (2019).

Locality & formation: Akkermanovka Quarry, Novotroitsk District, Orenburg Oblast, Russia, Izvestkovy Dol Formation.

Geologic range: Middle Mississippian (Viséan).

Lithology & environment: Reefal limestones; shallow marine, back-reef lagoon.

Genus *Uralocyclus* Mychko & Alekseev, 2018

Type species: *Uralocyclus miloradovitchi* Kramarenko, 1961, by original designation.

Other species: *Uralocyclus harknessi* (Woodward, 1870), *Uralocyclus woodwardi* (Reed, 1908).

Diagnosis: Carapace bilaterally symmetrical, ovate, moderately inflated, cap-shaped, laterally bordered by a marginal rim. Marginal rim ornamented by a series of transversely-elongated tubercles which extend from the circular depression to about half the width of the rim, rim appearing to

Fig. 2. Cyclidae, *Prolatcyclus* spp. **1** – *P. martinensis* (Goldring, 1967), GSM 102640, paratype, dorsal view. **2** – Line drawing of *P. martinensis* with labeled regions. **3** – *P. kindzadza* Mychko et al., 2019, MWO 1/59, no. 9868, holotype. Scale bars = 5 mm.

narrow as it approaches posterior margin. Frontal area of carapace is dissected by large, symmetrical lobes; posterior axial lobe elongate, widest anteriorly, then narrowing, then slightly widened posteriorly, extending into axial keel. First axial lobe diamond-shaped, well defined; second axial lobes and third axial lobe about same size and shape as first axial lobe; first lateral lobes about same size and shape as first axial lobe but less inflated; second lateral lobe longer than first, diamond-shaped; third lateral lobe elongate, with arcuate keel on lateral margin, granular. Inner lyrate keel weak, outer lyrate keel absent, median concentric keel strong, inner branchial region granular, moderately inflated; outer branchial region with at least five ovate, transverse swellings.

Discussion: *Cyclus harknessi* and *Cyclus woodwardi* are very similar to one another and co-occur in England. *Cyclus woodwardi* has a small portion of a marginal rim preserved, whereas there is no evidence of the rim in *Cyclus harknessi*, which may be a preservational artifact. These two species have well-defined axial and lateral lobes, a strong median concentric keel, and thoracic ridges on the outer branchial region. In these features the two species are very similar to *Uralocyclus miloradovitchi*. They differ from the latter species in showing no evidence of a lateral rim with transverse ridges, which as noted above, may be a preservational artifact. Because the carapace ornamentation is so distinctive and similar across all three species, we refer *Cyclus harknessi* and *Cyclus woodwardi* to *Uralocyclus* until specimens with marginal rims can be found. If these three species are all confirmed as *Uralocyclus*, the genus would range from the Lower Mississippian to Lower Permian.

Geologic range: Lower? to middle Mississippian (Tournaisian?–Viséan) of England, UK; Viséan of Ireland; Lower Permian (Cisuralian, Asselian) of Russia.

Uralocyclus miloradovitchi (Kramarenko, 1961)
Fig. 3.1–3.3

1961 *Cyclus miloradovitchi* Kramarenko, p. 87, pl. 12, figs. 1–5.
1967 *Cyclus miloradovitchi* Kramarenko, 1961. – Goldring, p. 320.
1971 *Cyclus miloradovitchi* Kramarenko, 1961. – Akagi, p. 81.
1997 *Cyclus miloradovitchi* Kramarenko, 1961. – Schram et al., p. 263.
2008 *Cyclus miloradovitchi* Kramarenko, 1961. – Dzik, p. 1512.
2017 *Cyclus miloradovitchi* Kramarenko, 1961. – Feldmann et al., p. 407.
2018 *Uralocyclus miloradovitchi* (Kramarenko, 1961). – Mychko & Alekseev, p. 30.
2019 *Uralocyclus miloradovitchi* (Kramarenko, 1961). – Feldmann & Schweitzer, p. 3.
2019 *Uralocyclus miloradovitchi* (Kramarenko, 1961). – Mychko et al., p. 85.

Material examined: PIN no. 1792/5, PIN no. 1792/3, paratypes.

Diagnosis: Mychko & Alekseev, 2018, p. 30.

Description: As in Mychko & Alekseev, 2018, p. 30.

Locality & formation: Locality "Kazarmennyy kamen," Chelyabinsk Oblast, Russia.

Geologic range: Permian (Cisuralian, Asselian) of Russia.

Lithology & environment: Reefal limestones; shallow marine, reef facies, back-reef lagoon.

Uralocyclus harknessi (Woodward, 1870) new combination
Fig. 3.4

1870 *Cyclus harknessi* Woodward, 1870, p. 556, pl. 23, fig. 6.
1878 *Cyclus harknessi* Woodward, 1870. – Woodward, p. 252.
1885 *Cyclus harknessi* Woodward, 1870. – Packard, p. 145.
1894 *Cyclus harknessi* Woodward, 1870. – Woodward, p. 530.
1893 *Cyclus harknessi* Woodward, 1870. – Reed, p. 65.
1902 *Cyclus harknessi* Woodward, 1870. – Rogers, p. 274.
1925 *Cyclus harknessi* Woodward, 1870. – Hopwood, p. 290.
1967 *Cyclus harknessi* Woodward, 1870. – Goldring, p. 320.
1971 *Cyclus harknessi* Woodward, 1870. – Akagi, p. 81.
2008 *Cyclus harknessi* Woodward, 1870. – Dzik, p. 1512.
1997 *Cyclus harknessi* Woodward, 1870. – Schram et al., p. 262.
2017 *Cyclus harknessi* Woodward, 1870. – Feldmann et al., p. 407.
2018 *Cyclus harknessi* Woodward, 1870. – Mychko & Alekseev, p. 25.
2019 *Cyclus harknessi* Woodward, 1870. – Feldmann & Schweitzer, p. 2.

Material examined: SM E3707–3709.

Diagnosis: Carapace ovate, highly vaulted longitudinally and transversely; posterior axial lobe, axial lobe one, axial lobe 2, lateral lobe 1, and lateral lobe 2 all about the same size and diamond-shaped, lateral lobe 3 arcuate; axial keel moderate, bounded by lyrate keel; appearing to have a granular median concentric keel separating inner branchial region from outer branchial region.

Description: Carapace rounded, about as wide as long; highly vaulted longitudinally and transversely; with greatest height posterior to midline.

Frontal margin broken or incompletely preserved. Carapace lobes diamond-shaped and nested with one another, all about the same size; posterior axial lobe somewhat longer than wide, extending into weak axial keel that appears to terminate before reaching posterior margin, bounded lat-

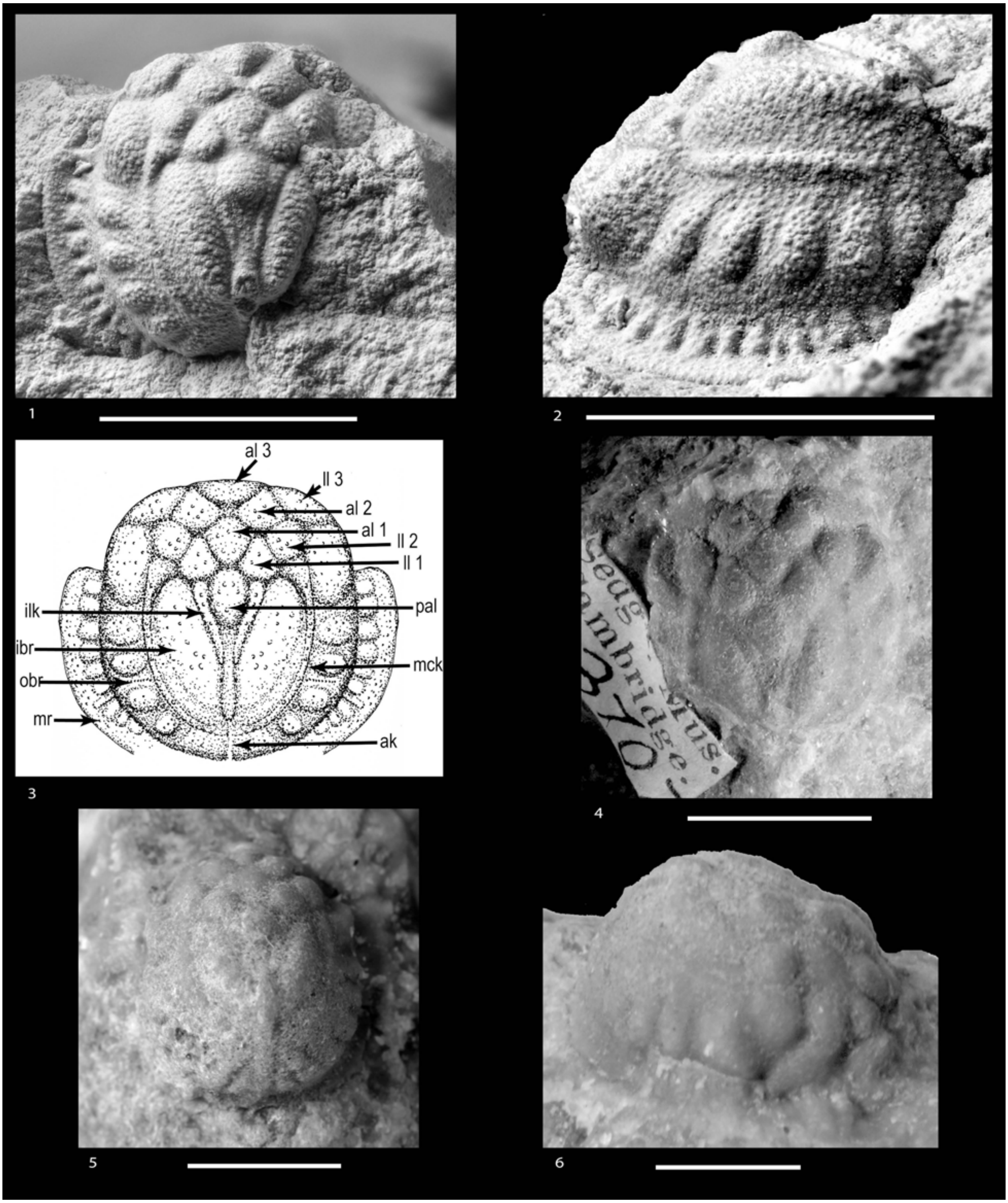


Fig. 3. Cyclidae, *Uralocyclus* spp. **1** – *U. miloradovitchi* (Kramarenko, 1961), PIN no. 1792/3, paratype, dorsal view. **2** – *U. miloradovitchi* (Kramarenko, 1961), PIN no. 1792/3, paratype, left lateral view. **3** – Line drawing of *U. miloradovitchi* with regions labeled; note posterior margin is unknown. **4** – *U. harknessi* (Woodward, 1870) new combination, SM E2707, dorsal view. **5** – *U. woodwardi* (Reed, 1893) new combination, SM E3725, holotype, dorsal view. **6** – *U. woodwardi* (Reed, 1893) new combination, SM E3725, holotype, anterior view. Scale bars = 5 mm.

erally by inner lyrate, narrow keel. First axial lobe about as wide as long, second axial lobes paired, more inflated than first axial lobe, third axial lobe incompletely preserved. First lateral lobes about same size and inflation as paired second axial lobes; second lateral lobes a bit larger than first; third lateral lobes reniform, highest laterally, forming part of lateral margin of carapace. Smooth inner branchial region adjacent to axial regions and lyrate keels, laterally bounded by narrow, granular, median concentric keel, outer branchial region arcuate, formed into band of uniform width paralleling lateral margin, rugose. No evidence of flattened rim on carapace.

Abdomen, venter, and appendages not preserved.

Locality & formation: There are two localities: Little Island, County Cork, Ireland, Cork Beds in Little Island Formation, and Settle, Yorkshire, England, UK, Carboniferous Limestone, possibly Carboniferous Limestone Supergroup.

Geologic range: Middle Mississippian (Viséan) of Ireland; Lower to middle Mississippian (Tournaisian–Viséan) of England(UK).

Lithology & environment: Massive pale grey limestone (biomicrite) for Little Island and limestone for Settle; shallow marine.

Uralocyclus woodwardi (Reed, 1893) new combination
Fig. 3.5, 3.6

1893 *Cyclus woodwardi* Reed, 1893, p. 66.
1894 *Cyclus woodwardi* Reed, 1893. – Woodward, p. 530.
1902 *Cyclus woodwardi* Reed, 1893. – Rogers, p. 275.
1925 *Cyclus woodwardi* Reed, 1893. – Hopwood, p. 290.
1928 *Cyclus woodwardi* Reed, 1893. – Glaessner, p. 392.
1955 *Cyclus woodwardi* Reed, 1893. – Müller, p. 133.
1967 *Cyclus woodwardi* Reed, 1893. – Goldring, p. 320.
1997 *Cyclus woodwardi* Reed, 1893. – Schram et al., p. 262.
2008 *Cyclus woodwardi* Reed, 1893. – Dzik, p. 1512.
2017 *Cyclus woodwardi* Reed, 1893. – Feldmann et al., p. 407.
2018 *Cyclus woodwardi* Reed, 1893. – Mychko & Alekseev, p. 25.
2019 *Cyclus woodwardi* Reed, 1893. – Feldmann & Schweitzer, p. 3.

Material examined: SM E3725, holotype; SM E3727–3728.

Diagnosis: Carapace ovate, highly vaulted longitudinally and transversely; marginal rim smooth; posterior axial lobe, axial lobe 1, axial lobe 2, lateral lobe 1, and lateral lobe 2 all about the same size and diamond-shaped, lateral lobe 3 arcuate; axial keel moderate, bounded by lyrate keel; appearing to have a granular median concentric keel separating inner branchial region from outer branchial region.

Description: Carapace ovate, longer than wide; highly vaulted longitudinally and transversely; with greatest height posterior to midline.

Frontal margin broken or incompletely exposed. Carapace lobes diamond-shaped and nested with one another; posterior axial lobe somewhat longer than wide, extending into weak axial keel that appears to terminate before reaching posterior margin. First axial lobe about as wide as long, second axial lobes paired, third axial lobe about same size as second axial lobe, incompletely preserved at anterior end. First lateral lobes about same size and inflation as paired second axial lobes; second lateral lobes a bit larger than first; third lateral lobes reniform, highest laterally, forming part of lateral margin of carapace, possibly continuous with second axial lobe; fourth lateral lobes situated anterior to third, about same size as first lateral lobes. Inner branchial region smooth, reniform, bounded by narrow median concentric keel; outer branchial regions uniformly wide, paralleling lateral margin, rugose, separated into 6 wide thoracic ridges. Flattened rim preserved on some specimens on posterolateral carapace margin, remainder obscured by sediment.

Abdomen, venter, and appendages not preserved.

Locality & formation: Settle, Yorkshire, England, UK, Carboniferous Limestone, possibly Carboniferous Limestone Supergroup.

Geologic range: Lower? to Middle Mississippian (Tournaisian?–Viséan).

Lithology & environment: Limestone; shallow marine.

Genus *Ambocyclus* nov.

Etymology: The genus name is derived from the Greek word *ambon*, meaning ridge, and *cyclus*, a common stem in the group, in reference to the strong median concentric keel in this genus. The gender is masculine.

Type species: *Cyclus simulans* Reed, 1908, by original designation.

Other species: *Ambocyclus capidulum* (Chernyshev, 1933), questionably *A. minutus* (Rogers, 1902).

Diagnosis: Carapace ovate, strongly vaulted longitudinally and transversely, highest at about midlength; axial and lateral lobes moderately developed; axial area continuous with carapace to either side, forming a large ovate region centrally on the carapace; very strong median concentric keel; carapace surface relatively smooth; sometimes with a small portion of smooth, flattened rim preserved posterolaterally.

Discussion: The genus is diagnosed by moderate development of the axial and lateral lobes, with a very strong median concentric keel. An axial keel may be present or absent. The species named by Rogers (1902) is questionably placed in this genus due to its apparently strong median concentric keels; type material for this species appears to be lost.

Geologic range: Lower Mississippian (Tournaisian) – Upper Pennsylvanian (Kasimovian).

Ambocyclus simulans (Reed, 1908) new combination
Fig. 4.1, 4.2

1908 *Cyclus simulans* Reed, 1908, p. 551.
1971 *Cyclus simulans* Reed, 1908. – Akagi, p. 81.
1997 *Cyclus simulans* Reed, 1908. – Schram et al., p. 262.
2008 *Cyclus simulans* Reed, 1908. – Dzik, p. 1512.
2011 *Cyclus simulans* Reed, 1908. – Niko & Ibaraki, p. 260.
2017 *Cyclus simulans* Reed, 1908. – Feldmann et al., p. 407
2018 *Cyclus simulans* Reed, 1908. – Mychko & Alekseev, p. 25.
2019 *Cyclus simulans* Reed, 1908. – Feldmann & Schweitzer, p. 2.

Diagnosis: Median concentric keel very strong, axial and lateral lobes distinct.

Material examined: SM E3724, holotype.

Description: Carapace ovate, slightly longer than wide, strongly vaulted longitudinally and transversely, highest at about midlength. Posterior axial lobe weak; first axial lobe lobe small, paired; second axial lobes paired, first lateral lobes reniform, just anterior to mid-length; second lateral lobes about same as first lateral; third lateral lobe weakly inflated. Axial area continuous with carapace to either side, forming a large ovate region centrally on the carapace; very strong median concentric keel, keel about three-quarters the distance laterally, keel parallels lateral margins, with an ovate swelling at anterior end; carapace distal to keel apparently somewhat flattened, small portion of smooth, flattened rim preserved posterolaterally, with wide posterior reentrant.

Discussion: The holotype of this species is damaged, so that the specimen appears crushed. Only a small portion of the marginal rim is retained on the right posterior margin.

Locality & formation: St. Doulaghs, County Dublin, Ireland, St. Doulagh's Limestone of Waulsortian Limestone Complex.

Geologic range: Lower Mississippian (Tournaisian) of Ireland.

Lithology & environment: Reefal limestone; shallow marine, reef facies.

Ambocyclus capidulum (Chernyshev, 1933) new combination
Fig. 4.3

1933 *Cyclus capidulum* Chernyshev, p. 21 (Russian), p. 23 (English), pl. 1, fig. 11.
2018 *Cyclus capidulum* Chernyshev, 1933. – Mychko & Alekseev, p. 25.
2019 *Cyclus capidulum* Chernyshev, 1933. – Feldmann & Schweitzer, p. 2.
2019 *Cyclus capidulum* Chernyshev, 1933. – Mychko et al., p. 81.

Description: "Carapace generally cap-like in form. From the most elevated part of the shell there extends backwards a rather broad ridge reaching to its posterior margin. In front of it, two other ridges define a V-shaped area. At a small distance from the just mentioned ridges two other ridges are running parallel to them. The whole of the anterior part of the shell presents a number of swellings, namely: an elongated median swelling constricted towards the anterior border, and six symmetrical lateral swellings, three of which lie on every side of the elongate median swelling. The ridges show faint traces of tubercles. Nothing can be said of the ornamentation of the shell, as it is not preserved" (Chernyshev 1933: 23–24).

Material examined: TsNINGR 15/3694, holotype and sole specimen.

Discussion: The strong median concentric keels and lack of other strong ornamentation place this species in *Ambocyclus*.

Locality & formation: Alapaevsk District, Sverdlovsk Region, Russia, Lower Carboniferous limestones.

Geologic range: Late Mississippian (Serpukhovian).

Lithology & environment: Limestones; shallow marine.

Ambocyclus minutus (Rogers, 1902) new combination
Fig. 4.4

1902 *Cyclus minutus* Rogers, p. 273, pl. 14, fig. 5.
1925 *Cyclus minutus* Rogers, 1902. – Hopwood, p. 290.
1997 *Cyclus minutus* Rogers, 1902. – Schram et al., p. 262.
2017 *Cyclus minutus* Rogers, 1902. – Feldmann et al., p. 407.
2018 *Cyclus minutus* Rogers, 1902. – Mychko & Alekseev, p. 25.
2019 *Cyclus minutus* Rogers, 1902. – Feldmann & Schweitzer, p. 2.

Description: Carapace ovate, longer than wide; axial keel strong; branchial regions separated by a groove; axial and lateral lobes well-defined.

Material examined: Apparently lost.

Discussion: There is only a line drawing of this species. The specimen is very small, less than 2 mm long.

Locality & formation: Kansas City, Missouri, USA, Iola Limestone.

Geologic range: Upper Pennsylvanian (Kasimovian).

Lithology & environment: Wackestone; shallow marine.

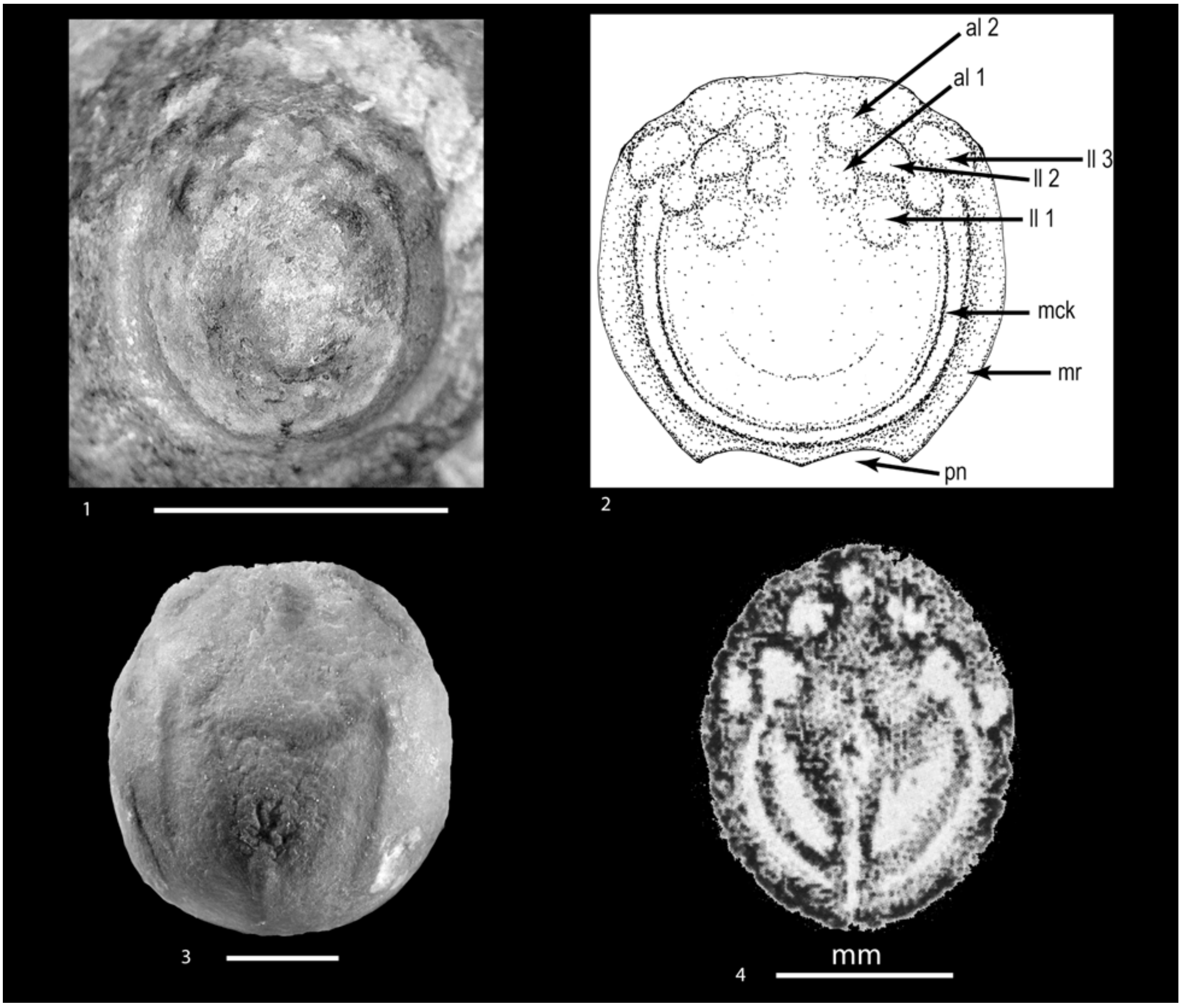


Fig. 4. Cyclidae. *Ambocyclus* spp. **1** – *A. simulans* (Reed, 1908) new combination, SM E3724a, holotype, dorsal view. **2** – Line drawing of *A. simulans* with regions labeled. **3** – *A. capidulum* (Chernyshev, 1933) new combination, TsNINGR 15/3694, holotype. **4** – Illustration of *A. minutus* (Rogers, 1902) new combination (Rogers 1902, pl. 14, fig. 5). Scale bars 1 and 3 = 5 mm; scale bar 4 = 1 mm.

Genus *Carabicyclus* nov.

Etymology: The genus name is derived from the Latin *carabus*, a type of beetle, and *cyclus*, a common ending in the group, in reference to the beetle-like appearance of the carapace. The gender is masculine.

Type and sole species: *Cyclus wrighti* Woodward, 1870, by original designation.

Diagnosis: Carapace longer than wide, ovate, narrowing to a blunt tip posteriorly, anterior margin wide; carapace divided by transverse shallow groove into distinct cephalic and thoracic regions; cephalic region with an axial lobe and pair of first lateral lobes; two median concentric keels, each keel terminating anteriorly in ovate swelling; axial keel developed posteriorly; marginal rim absent or not preserved.

Discussion: The ovate, longer than wide carapace narrowing posteriorly and with a distinct cephalic region differentiated from the thoracic region is unique among species of cyclidan. Thus, a new genus is warranted.

Geologic range: Middle Mississippian (Viséan) of United Kingdom (England) and Ireland.

Carabicyclus wrighti (Woodward, 1870) new combination
Fig. 5

1870 *Cyclus wrighti* Woodward, p. 555, pl. 23, fig. 5.
1878 *Cyclus wrighti* Woodward, 1870. – Woodward, 1878, p. 251.
1894 *Cyclus wrighti* Woodward, 1870. – Woodward, p. 530.
1902 *Cyclus wrighti* Woodward, 1870. – Rogers, p. 275.
1925 *Cyclus wrighti* Woodward, 1870. – Hopwood, p. 290.
1928 *Cyclus wrighti* Woodward, 1870. – Glaessner, p. 392.
1955 *Cyclus wrighti* Woodward, 1870. – Müller, p. 133.
1971 *Cyclus wrighti* Woodward, 1870. – Akagi, p. 81.
1997 *Cyclus wrighti* Woodward, 1870. – Schram et al., p. 262.
2008 *Cyclus wrighti* Woodward, 1870. – Dzik, p. 1512.
2017 *Cyclus wrighti* Woodward, 1870. – Feldmann et al., p. 407.
2018 *Cyclus wrighti* Woodward, 1870. – Mychko & Alekseev, p. 25.
2019 *Cyclus wrighti* Woodward, 1870. – Feldmann & Schweitzer, p. 3.

Material examined: *Carabicyclus wright*, NHMUK I.15513, holotype; GSM KR 8295, referred specimen.

Diagnosis: As for genus.

Description: Carapace longer than wide, ovate, narrowing considerably posteriorly, anterior margin wide, weakly convex; strongly vaulted longitudinally and transversely, highest at posterior two-thirds; carapace surface apparently uneven but not granular.

Carapace divided by weakly sinuous transverse groove about one-fifth the distance posteriorly; area anterior to groove with weakly developed first lateral lobes laterally and wide, smooth first axial lobe axially. Posterior to transverse groove, carapace with two arcuate median concentric keels extending posteriorly, not intersecting posterior margin, one positioned to bisect branchial region, one positioned lateral to bisecting keel, each keel terminating anteriorly in ovate swelling; carapace with axial keel developed posteriorly.

Locality & formation: There are two localities: Little Island, County Cork, Ireland, Cork Beds in Little Island Formation, and Cawden Hill, Yorkshire, England, UK, Carboniferous Limestone.

Geologic range: Middle Mississippian (Viséan).

Lithology & environment: Little Island: massive pale grey limestone (biomicrite), shallow marine; Cawden Hill: limestone; shallow marine.

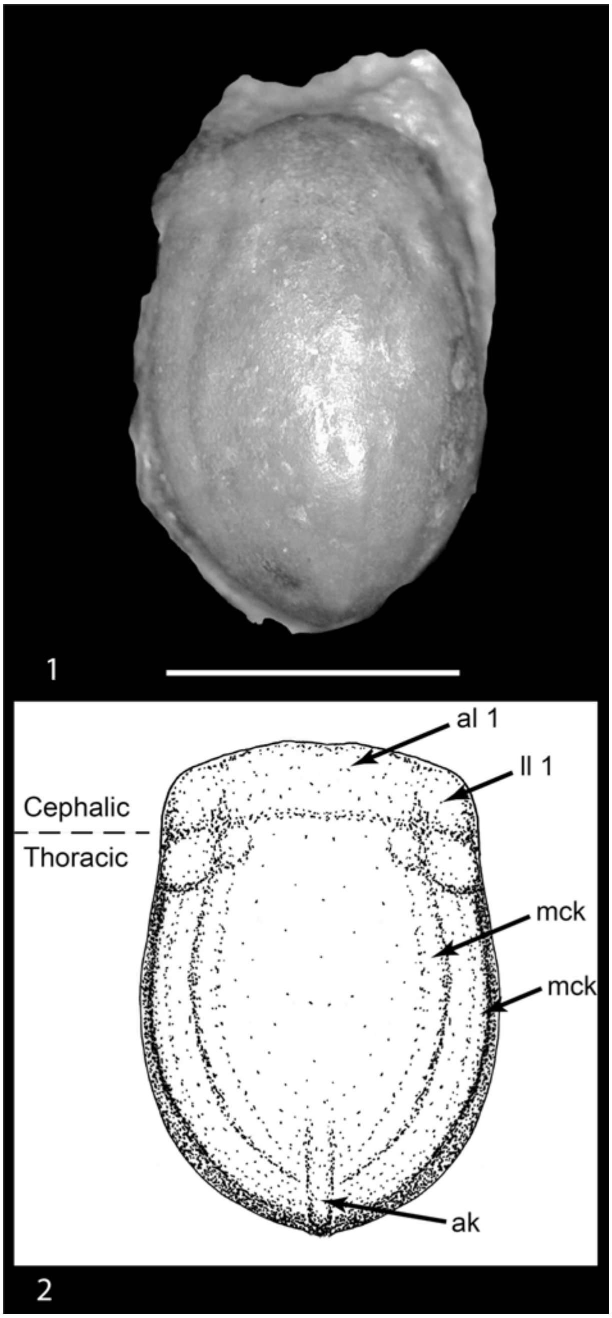


Fig. 5. Cyclidae, *Carabicyclus wright* (Woodward, 1870) new combination. **1** – NHMUK I.15513, holotype, dorsal view. **2** – Line drawing with regions labeled. Scale bar = 5 mm.

Genus *Litocyclus* nov.

Etymology: The genus name is derived from the Greek *litos*, meaning plain, simple, and *cyclus*, a common stem in the group, in reference to the simple ornamentation on members of the genus. The gender is masculine.

Type species: *Cyclus bilobatus* Woodward, 1870, by original designation.

Other species: *Litocyclus jonesianus* (Woodward, 1870); *L. torosus* (Woodward, 1870), questionably *Litocyclus communis* (Rogers, 1902) and *L. permarginatus* (Rogers, 1902).

Diagnosis: Carapace with subdued ornamentation, strongly vaulted; axial keel strong or weak; median concentric keel absent; axial and lateral lobes present but very weakly defined; carapace surface granular; marginal rim smooth, narrow.

Discussion: The genus is diagnosed by simple ornamentation. Axial and lateral lobes are weakly defined, and an axial keel may be present or absent. Where known, the marginal rim is smooth and narrow, and the median concentric keel is absent. The two species named by Rogers (1902) are questionably placed in this genus due to their apparently poorly defined regions and presence of an axial keel. Type material for those two species appears to be lost.

Geologic range: Lower? to middle Mississippian (Tournaisian?–Viséan) of Ireland and England, UK; Upper Pennsylvanian (Kasimovian) of Kansas and Missouri, USA.

Litocyclus bilobatus (Woodward, 1870) new combination
Fig. 6.1, 6.2

1870 *Cyclus bilobatus* Woodward, p. 554, pl. 23, fig. 3.
1878 *Cyclus bilobatus* Woodward, 1870. – Woodward, p. 249.
1894 *Cyclus bilobatus* Woodward, 1870. – Woodward, p. 530.
1902 *Cyclus bilobatus* Woodward, 1870. – Rogers, p. 274.
1925 *Cyclus bilobatus* Woodward, 1870. – Hopwood, p. 290.
2008 *Cyclus bilobatus* Woodward, 1870. – Dzik, p. 1512.
2017 *Cyclus bilobatus* Woodward, 1870. – Feldmann et al., p. 407.
2018 *Cyclus bilobatus* Woodward, 1870. – Mychko & Alekseev, p. 25.
2019 *Cyclus bilobatus* Woodward, 1870. – Feldmann & Schweitzer, p. 2.

Material examined: SM E3706, holotype.

Diagnosis: Carapace round, anterior regions separated from branchial regions by biconvex forward groove; anterior to groove, carapace lobes weakly developed; post-frontal area ornamented with well-developed axial keel; carapace surface densely granular.

Description: Carapace round, about as wide as long, anterior regions separated from branchial regions by biconvex forward groove; anterior to groove, carapace lobes weakly developed; posterior axial lobe absent, first axial lobe extending directly into axial keel, second axial lobes paired, second and third lateral lobes weak; post-frontal area ornamented with well-developed axial keel; carapace surface densely granular; margins unknown.

Locality & formation: Settle, Yorkshire, England, UK, Carboniferous Limestone, possibly Carboniferous Limestone Supergroup.

Geologic range: Lower? to Middle Mississippian (Tournaisian?–Viséan).

Lithology & environment: Limestone; shallow marine.

Litocyclus torosus (Woodward, 1870) new combination
Fig. 6.4

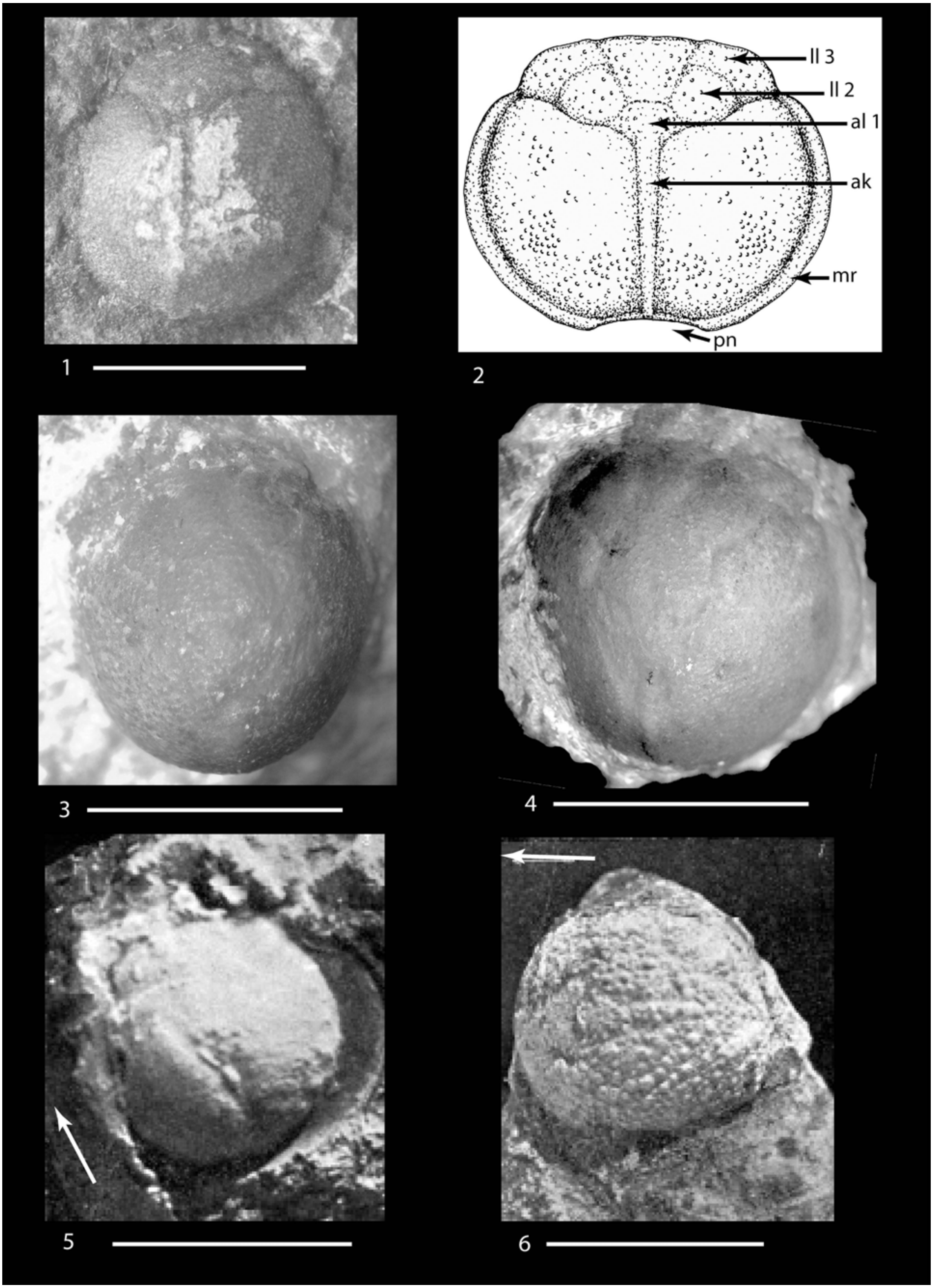
1870 *Cyclus torosus* Woodward, p. 555, pl. 23, fig. 4.
1878 *Cyclus torosus* Woodward, 1870. – Woodward, p. 250.
1894 *Cyclus torosus* Woodward, 1870. – Woodward, p. 530.
1902 *Cyclus torosus* Woodward, 1870. – Rogers, p. 275.
1925 *Cyclus torosus* Woodward, 1870. – Hopwood, p. 290.
1997 *Cyclus torosus* Woodward, 1870. – Schram et al., p. 262.
2008 *Cyclus torosus* Woodward, 1870. – Dzik, p. 1512.
2011 *Cyclus torosus* Woodward, 1870. – Niko & Ibaraki, p. 260.
2017 *Cyclus torosus* Woodward, 1870. – Feldmann et al., p. 407.
2018 *Cyclus torosus* Woodward, 1870. – Mychko and Alekseev, p. 25.
2019 *Cyclus torosus* Woodward, 1870. – Feldmann & Schweitzer, p. 3.

Material examined: NHMUK I.15512, holotype.

Diagnosis: Carapace coarsely granular, strongly vaulted; marginal rim present; anterior carapace lobes weakly defined; axial keel absent.

Description: Carapace round, uniformly coarsely granular, very strongly vaulted transversely and longitudinally.

Frontal margin broken or incompletely preserved. Various carapace lobes situated on anterior one-third of carapace, weakly inflated. Posterior axial region not well-delimited, appearing to be wide, more or less longitudinally ovate extending posteriorly in a narrow axial keel. First axial lobe longitudinally ovate, most inflated posteriorly; second axial lobe paired, weak; third axial lobe weak. First lateral lobes larger than first axial lobe, diamond shaped; second lateral lobes a bit larger than first, situated at posterolateral angle of first lateral lobes, oblique; anterior to first lateral lobe, narrow


ll 3
ll 2
al 1
ak
mr
pn
1
2
3
4
5
6

third lateral lobe apparently parallel to lateral margin; second lateral lobe weakly developed. Lateral rim appears to begin just posterior to third lateral lobe, flattened, smooth.

Reniform region adjacent to axial regions very weakly defined by shallow groove and very weak inner and outer lyrate keels, remainder of carapace not differentiated into regions.

Locality & formation: Little Island, County Cork, Ireland, Cork Beds of Little Island Formation.

Geologic range: Middle Mississippian (Viséan).

Lithology & environment: Massive pale grey limestone (biomicrite); shallow marine.

Litocyclus jonesianus (Woodward, 1870) new combination Fig. 6.3

1870 *Cyclus jonesianus* Woodward, p. 557, text-figs. 1, 2.
1878 *Cyclus jonesianus* Woodward, 1870. – Woodward, p. 254.
1894 *Cyclus jonesianus* Woodward, 1870. – Woodward, p. 530.
1885 *Cyclus jonesianus* Woodward, 1870. – Packard, p. 143.
1902 *Cyclus jonesianus* Woodward, 1870. – Rogers, p. 274.
1925 *Cyclus jonesianus* Woodward, 1870. – Hopwood, p. 290.
1928 *Cyclus jonesianus* Woodward, 1870. – Glaessner, p. 392.
1955 *Cyclus jonesianus* Woodward, 1870. – Müller, p. 133.
1997 *Cyclus jonesianus* Woodward, 1870. – Schram et al., p. 262.
2008 *Cyclus jonesianus* Woodward, 1870. – Dzik, p. 1512.
2011 *Cyclus jonesianus* Woodward, 1870. – Niko & Ibaraki, p. 260.
2017 *Cyclus jonesianus* Woodward, 1870. – Feldmann et al., p. 407.
2018 *Cyclus jonesianus* Woodward, 1870. – Mychko & Alekseev, p. 25.
2019 *Cyclus jonesianus* Woodward, 1870. – Feldmann & Schweitzer, p. 2.

Material examined: NHMUK I.15511, holotype.

Diagnosis: Carapace granular, anterior lobes weakly defined, axial keel present; marginal rim smooth.

Description: Carapace very strongly vaulted longitudinally and transversely, granular overall; rimmed; weak axial keel posteriorly; posterior axial lobe very weakly defined; first axial lobe weak, longitudinally ovate; second axial lobes paired; third axial lobe weak; first lateral lobe larger than first axial lobe; second and third lateral lobes weak. Marginal rim smooth, narrow, appearing to narrow posteriorly.

Localities & formations: There are two localities: Little Island, County Cork, Ireland, Cork Beds of Little Island Formation, and Settle, Yorkshire, England, UK, Carboniferous Limestone, possibly Carboniferous Limestone Supergroup.

Geologic range: Lower? to middle Mississippian (Tournaisian?–Viséan).

Lithology & environment: Massive pale grey limestone (biomicrite) for Little Island and limestone for Settle; shallow marine.

Litocyclus communis (Rogers, 1902) new combination Fig. 6.6

1902 *Cyclus communis* Rogers, p. 270, pl. 14, fig. 1.
1925 *Cyclus communis* Rogers, 1902. – Hopwood, p. 290.
1928 *Cyclus communis* Rogers, 1902. – Glaessner, p. 393.
1997 *Cyclus communis* Rogers, 1902. – Schram et al., p. 262.
2017 *Cyclus communis* Rogers, 1902. – Feldmann et al., p. 407.
2018 *Cyclus communis* Rogers, 1902. – Mychko & Alekseev, p. 25.
2019 *Cyclus communis* Rogers, 1902. – Feldmann & Schweitzer, p. 2.

Material examined: Apparently lost.

Description: Carapace circular strongly domed, maximum height in posterior one-third of carapace; with a marginal rim; axial keel moderately developed; some regional definition in anterior part of carapace; carapace surface densely granular overall; compound eye reported but not illustrated.

Discussion: The diagnosis provided here is a combination of features observed from the illustrations as well as details from the published description. It is notable that the specimens of this species were very small, ranging from 4.5 to 6 mm in length.

Fig. 6. Cyclidae, *Litocyclus* spp. **1** – *L. bilobatus* (Woodward, 1870) new combination, SM E706, holotype, dorsal carapace. **2** – Line drawing of *L. bilobatus* with anterior regions and marginal rim interpolated. **3** – *L. jonesianus* (Woodward, 1870) new combination, NHMUK I.15511, holotype. **4** – *L. torosus* (Woodward, 1870) new combination, NHMUK I.15512, holotype. **5** – *L. permarginatus* (Rogers, 1902) new combination (Rogers, 1902, pl. 14, fig. 3), arrow indicates anterior. **6** – *L. communis* (Rogers, 1902) new combination (Rogers 1902, pl. 14, fig. 1), arrow indicates anterior. Scale bars = 5 mm.

Locality & formation: Kansas City, Missouri, USA, Iola Limestone.

Geologic range: Upper Pennsylvanian (Kasimovian).

Lithology & environment: Wackestone; shallow marine.

Litocyclus permarginatus (Rogers, 1902) new combination
Fig. 6.5

1902 *Cyclus permarginatus* Rogers, p. 272, pl. 14, fig. 3.
1925 *Cyclus permarginatus* Rogers, 1902. – Hopwood, p. 290.
1997 *Cyclus permarginatus* Rogers, 1902. – Schram et al., p. 262.
2017 *Cyclus permarginatus* Rogers, 1902. – Feldmann et al., p. 407.
2019 *Cyclus permarginatus* Rogers, 1902. – Feldmann & Schweitzer, p. 2.
2018 *Americlus permarginatus* (Rogers, 1902). – Mychko & Alekseev, p. 24.

Material examined: Apparently lost.

Description: Carapace weakly vaulted, ovate; marginal rim wide, extending around the posterior margin; posterior axial keel moderately developed, posterior axial lobe weakly bounded by shallow grooves; branchial regions with 6 or 7 very weak transverse ridges; anterior carapace lobes not well-defined.

Discussion: The diagnosis provided here is a combination of features observed from the illustrations as well as details from the published description. The specimen is 8 mm wide.

Locality & formation: Kansas City, Missouri, USA, Iola Limestone.

Geologic range: Upper Pennsylvanian (Kasimovian).

Lithology & environment: Wackestone; shallow marine.

Genus *Chernyshevine* nov.

Etymology: The genus name honors B. I. Chernyshev, who originally described the species here removed to the genus and added to the study of arthropods in Russia. The gender is masculine.

Type species: *Cyclus spinosus* Chernyshev, 1933 (= *Cyclus tuberosus* Chernyshev, 1933), by original designation.

Diagnosis: As for species.

Chernyshevine spinosus (Chernyshev, 1933)
Fig. 7

1933 *Cyclus spinosus* Chernyshev, p. 20 (Russian), p. 23 (English), p. 1, fig. 9.
1961 *Cyclus spinosus* Chernyshev, 1933. – Kramarenko, p. 88.
2018 *Cyclus spinosus* Chernyshev, 1933. – Mychko & Alekseev, p. 25.
2019 *Cyclus spinosus* Chernyshev, 1933. – Feldmann & Schweitzer, p. 3.
1933 *Cyclus tuberosus* Chernyshev, p. 20 (Russian), p. 23 (English), p. 1, fig. 10.
2018 *Cyclus tuberosus* Chernyshev, 1933. – Mychko & Alekseev, p. 25.
2019 *Cyclus tuberosus* Chernyshev, 1933. – Feldmann & Schweitzer, p. 3.

Material examined: TsNINGR 12/3694, holotype of *Cyclus spinosus*; TsNINGR 14/3694, holotype for *Cyclus tuberosus*.

Diagnosis: Carapace longer than wide, ovate; carapace lobes well-defined, inner lyrate keel present, median concentric groove (?); marginal rim well-developed, with long posterolaterally directed spines.

Description: "In the posterior part of the carapace, from about its middle, or its most elevated portion runs a ridge ornamented with a row of rather large tubercles. Directed forwards from that ridge two other ridges are departing, defining a V-shaped area. In front of it lies a small longitudinally extended swelling. Below this latter lies a broad swelling separated by a deep depression from the lower margin of the carapace. In front of it lies a small transverse swelling and higher there seems to lie a large median swelling. Along the border of the carapace runs a narrow limb ornamented with fine depressions and produced marginally into large, backwardly recurved spines. The surface of the carapace is covered with large tubercles arranged in longitudinal rows. Between the large tubercles lie numerous finer ones" (Chernyshev 1933: 23).

Discussion: The new genus can accommodate the very strong posterolateral spines in this taxon. No other member of Cyclidae has such spines. It appears that Chernyshev (1933) based the two species he named on specimens with differing preservation but from the same locality. Thus, we synonymize the species.

Locality & formation: Locality Shurab II, Turkestan Range, Tajikistan.

Geologic range: Middle Mississippian (Viséan).

Lithology & environment: Limestone; shallow marine.

Genus *Tazawacyclus* nov.

Etymology: The genus name combines the specific name of the type species with *cyclus*, a common stem in the group. The gender is masculine.

Type species: *Cyclus tazawai* Niko & Ibaraki, 2011, by original designation.

Diagnosis: As for species.

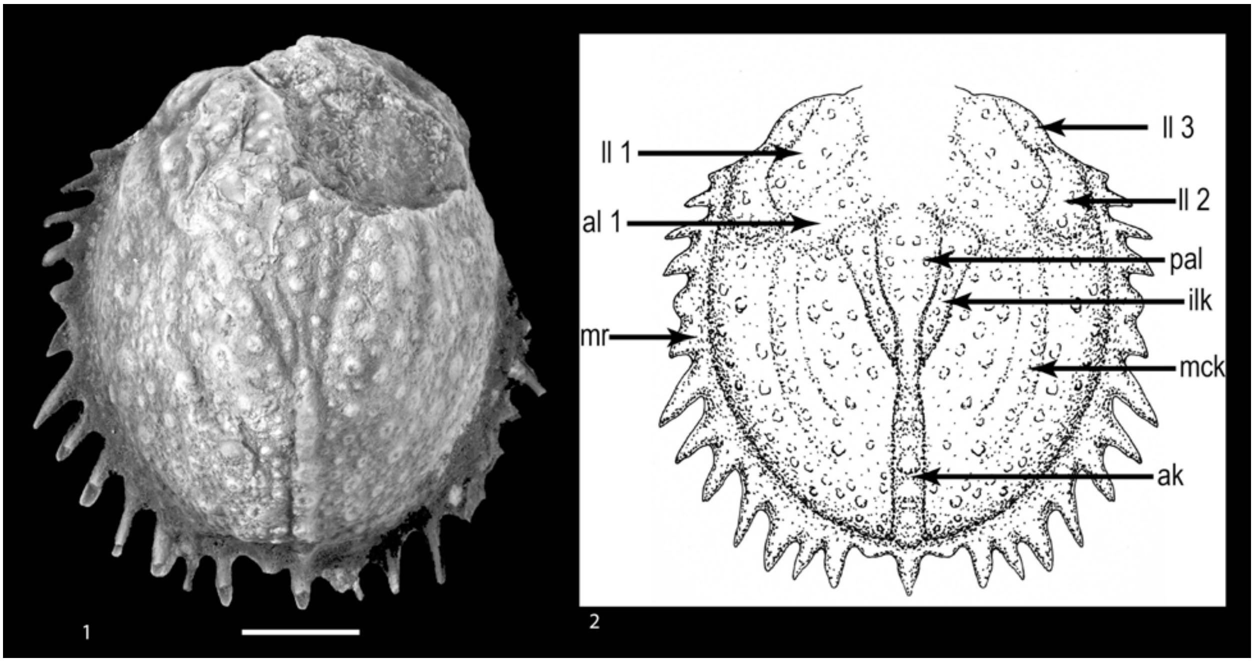


Fig. 7. Cyclidae, *Chernyshevine spinosus* (Chernyshev, 1933) new combination. **1** – TsNINGR 12/3694, holotype. **2** – Line drawing with regions labeled; central anterior regions unknown. Scale bar = 5 mm.

Discussion: The taxon shares many affinities with other cyclidans, but the enormous second axial lobes, transversely ovate carapace, and strong granular marginal rim are unique.

Geologic range: Upper Mississippian (Serpukhovian) of Japan.

Tazawacyclus tazawai (Niko & Ibaraki, 2011) new combination Fig. 8

2011 *Cyclus tazawai* Niko & Ibaraki, p. 259, figs. 1, 2.
2018 *Cyclus tazawai* Niko & Ibaraki, 2011. – Mychko & Alekseev, p. 25.
2019 *Cyclus tazawai* Niko & Ibaraki, 2011. – Feldmann & Schweitzer, p. 3.

Diagnosis: Carapace ovate, wider than long; marginal rim well-developed, ornamented with tubercles, narrowing posteriorly, posterior notch present, wide; axial keel strong, posterior axial lobe absent, first axial lobe small, wider anteriorly; second axial lobes very large, sharing a long, straight axial edge; third axial lobe small; first lateral lobe positioned at posterolateral corner of second axial lobe, longer than wide; second lateral lobe reniform; third lateral lobe transversely ovate, anterior to second axial lobe, not well-visible in dorsal view; branchial regions separated by medial weak groove.

Discussion: The specimen of this species is very small, 4.2 mm wide.

Locality & formation: Tsuchikura-za-wa Valley, Itoigawa, Niigata Prefecture, Japan; a float block, probably of a rock unit within the Hida-Gaien Belt, contained within the Kotaki Formation.

Geologic range: Upper Mississippian (Serpukhovian).

Lithology & environment: Black limestone (bioclastic wackestone); shallow marine.

Family Alsasuacaridae van Bakel, Jagt, Fraaije & Artal, 2011

Included genera: *Alsasuacaris* van Bakel, Jagt, Fraaije & Artal, 2011; *Maastrichtiocaris* Fraaije, Schram & Vonk, 2003.

Diagnosis: Carapace overall ovate; rostrum may extend well beyond orbits or only moderately, rostrum very wide to narrow, always widest distally and narrowing to base; orbits well-defined, may be directed anteriorly or anterolaterally; carapace surface densely or sparsely granular; with rim posteriorly; carapace regions defined anteriorly.

Remarks: This family includes two genera that share the character of distinct orbits and rimmed margins. As each genus and species was well described and illustrated recently,

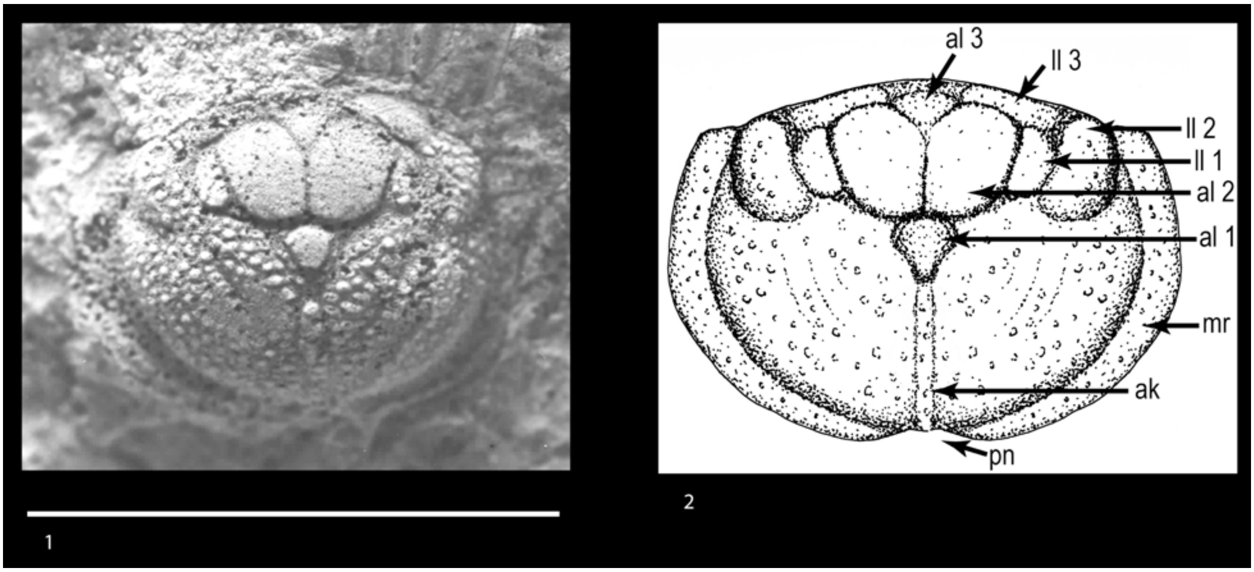


Fig. 8. Cyclidae, *Tazawacyclus tazawai* (Niko & Ibaraki, 2011) new combination, FMM 1998, holotype. Photograph originally published in Niko & Ibaraki (2011, fig. 1A) in Journal of the Geological Society of Japan. **2** – Line drawing with regions labeled. Scale bar = 5 mm.

diagnoses and descriptions may be found in these publications. They seem to differ from other cyclidans in possessing very strong orbits.

Geologic range: Lower Cretaceous (Albian) to Upper Cretaceous (Maastrichtian).

Genus *Alsasuacaris* van Bakel, Jagt, Fraaije & Artal, 2011

Type and sole species: *Alsasuacaris nostradamus* van Bakel, Jagt, Fraaije & Artal, 2011, by original designation.

Diagnosis: As in van Bakel et al. (2011).

Geologic range: Cretaceous (Albian–Cenomanian).

Alsasuacaris nostradama van Bakel, Jagt, Fraaije & Artal, 2011
Fig. 9.3, 9.4

2011 *Alsasuacaris nostradamus* van Bakel, Jagt, Fraaije & Artal, 2011, p. 47.
2017 *Alsasuacaris nostradamus* van Bakel, Jagt, Fraaije & Artal, 2011. – Feldmann et al., p. 2.
2018 *Alsasuacaris nostradamus* van Bakel, Jagt, Fraaije & Artal, 2011. – Mychko & Alekseev, p. 24.
2018 *Alsasuacaris nostradamus* van Bakel, Jagt, Fraaije & Artal, 2011. – Feldmann & Schweitzer, p. 2.

Nomenclatorial note: The Latin word *caris*, meaning crab, is feminine (Brown 1956). The original authors did not designate a gender for *Alsasuacaris*; thus, according to ICZN Article 30.1.1 (ICZN 1999), the gender of the genus name is feminine. We have changed the ending of the trivial name accordingly.

Material examined: MGSB 75.424, holotype.

Description: As in van Bakel et al. (2011).

Locality & formation: Koskobilo quarry, Olazti near Alsasua, Navarra, Spain, Albeniz Unit of Eguino Formation.

Geologic range: Cretaceous (Albian–Cenomanian).

Lithology & environment: Reefal limestones; marine, coral associated.

Genus *Maastrichtiocaris* Fraaije, Schram & Vonk, 2003

Type and sole species: *Maastrichtiocaris rostratus* Fraaije, Schram & Vonk, 2003, by original designation.

Diagnosis: As in Fraaije et al. (2003).

Geologic range: Upper Cretaceous (Maastrichtian).

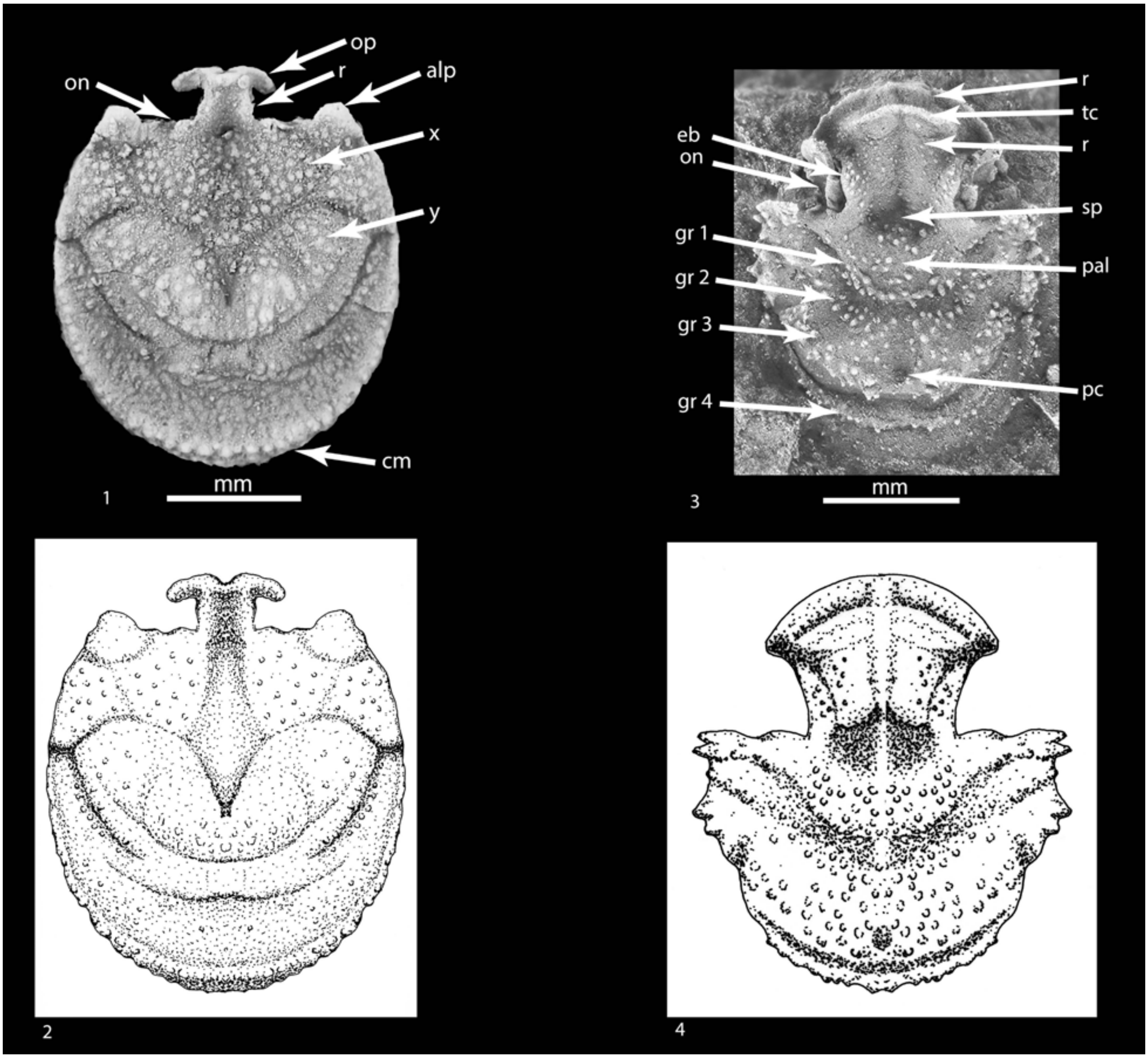


Fig. 9. Alsasuacaridae. **1** – *Maastrichtiocaris rostrata* FRAAIJE et al., 2003, MAB k 1399, holotype, with regions labeled. **2** – Line drawing of *M. rostrata*. **3** – *Alsasuacaris nostradama* VAN BAKEL et al., 2001, MGSB 75.424, holotype, with regions labeled. **2** – Line drawing of *A. nostradama*. Photographs 9.1 and 9.3 by BARRY VAN BAKEL. Scale bars = 1 mm.

Maastrichtiocaris rostrata FRAAIJE, SCHRAM & VONK, 2003
Fig. 9.1, 9.2

2003 *Maastrichtiocaris rostratus* FRAAIJE, SCHRAM & VONK, p. 386.
2007 *Maastrichtiocaris rostratus* FRAAIJE, SCHRAM & VONK, 2003. – SCHWEIGERT, p. 213.
2011 *Maastrichtiocaris rostrata* FRAAIJE, SCHRAM & VONK, 2003. – VAN BAKEL et al., 2011, p. 47.
2008 *Maastrichtiocaris rostrata* FRAAIJE, SCHRAM & VONK, 2003. – DZIK, p. 1511.
2017 *Maastrichtiocaris rostrata* FRAAIJE, SCHRAM & VONK, 2003. – FELDMANN et al., p. 2.
2018 *Maastrichtiocaris rostrata* FRAAIJE, SCHRAM & VONK, 2003. – MYCHKO & ALEKSEEV, p. 25.
2019 *Maastrichtiocaris rostrata* FRAAIJE, SCHRAM & VONK, 2003. – FELDMANN & SCHWEITZER, p. 2.

Nomenclatorial note: The Latin word *caris*, meaning crab, is feminine (BROWN 1956). The original authors did not designate a gender for *Maastrichtiocaris*; thus, according to

ICZN Article 30.1.1 (ICZN 1999), the gender of the genus name is feminine.

Material examined: MAB k 1399, holotype; MAB k 1398 and MAB k 2364, paratypes.

Description: As in Fraaije et al. (2003).

Locality & formation: Nederland BV quarry, near Maastricht, Limburg, The Netherlands, Middle Meerssen Member (IVf4), *Belemnitella junior* Zone.

Geologic range: Upper Cretaceous (Maastrichtian).

Lithology & environment: Sandy limestone; shallow marine.

Family Americlidae Dzik, 2008

Included genera: *Americlus* Dzik, 2008; *Brittaniclus* new genus; *Dziklus* new genus.

Diagnosis: Carapace flattened, about as wide as long (some *Brittaniclus*) to wider than long and bilobed (*Americlus*, some *Brittaniclus*, *Dziklus*); with weak (*Americlus*) to moderate (*Brittaniclus*, *Dziklus*) carapace regional definition; marginal rim well-developed, wide, may be serrate (*Americlus*), with posterior notch (*Americlus*, *Brittaniclus*) or continuous (*Dziklus*); rostral lobe extending beyond carapace, usually with optic notches; gills arranged as tiny parallel filaments in a horse-shoe shaped structure; first antennae strong, thick, with long flagella; second antennae slender, shorter; first pair of visible non-antennal appendages short; 2 pairs of subchelate appendages with sickle-like dactyls; 5 pediform thoracic appendages posterior to subchelate appendages; male gonopod present, interpreted as a modified exopod of last thoracic appendage; caudal rami present; sternal region with 7 visible, well-defined somites, ovate central sternal area; abdomen with 2–4 somites (modified from Feldmann & Schweitzer 2019).

Discussion: The diagnosis here is based upon the three genera referred to the family. It is somewhat broader than the original diagnosis (Dzik 2008: 1517). The family is characterized by flattened, circular to ovate taxa with wide marginal rims and well-defined sternal elements.

Geologic range: Middle Mississippian (Viséan) to Upper Pennsylvanian (Kasimovian).

Genus *Americlus* Dzik, 2008

Type species: *Cyclus americanus* Packard, 1885, by original designation.

Included species: *Americlus americanus*; questionably *A. limbatus* (Rogers, 1902); *A. packardi* (Rogers, 1902).

Diagnosis: Carapace flattened, about as wide as long, weakly bilobed; with weak carapace regional definition; marginal rim well-developed, wide, with posterior notch, with tiny marginal serrations; posterior axial keel present; rostral lobe extending beyond carapace, optic notches not well developed; carapace with strongly, broadly spaced papillae posteriorly and laterally; first antennae strong, thick, with long flagella; second antennae slender, shorter; two pairs of subchelate appendages with sickle-like dactyls extending anteriorly from ventral to rostral lobe; 5 pediform thoracic appendages posterior to subchelate appendages; caudal rami lanceolate, long, slender; sternal region with at least five visible, well-defined somites, ovate central sternal area present; possible abdomen with 2–4 somites (modified from Feldmann & Schweitzer 2019).

Discussion: Dzik (2008) erected *Americlus* to embrace the type species, *Americlus americanus*. In fig. 11, he placed *Cyclus johnsoni*, *C. obesus*, and *C. scotti* in *Americlus*. Later, Mychko & Alekseev (2018) referred these species in addition to *Cyclus limbatus*, *Cyclus packardi*, and *C. permarginatus* to *Americlus*. Feldmann & Schweitzer (2019) referred the species mentioned by Dzik (2008) as well as *Cyclus rankini* and *C. testudo* to *Americlus*.

We remove most species referred previously to *Americlus* to new genera, all within Americlidae. *Americlus* sensu stricto now embraces *A. americanus* and questionably includes *A. limbatus* and *A. packardi*. *Cyclus obesus* is referred to a new genus, and *C. johnsoni* and *C. scotti* are synonymized and placed within a new genus along with *C. testudo*. The two species described by Packard (1902) are questionably placed in *Americlus* based upon their flattened, ovate carapace.

Americlus sensu stricto differs from all other genera within Americlidae in possessing strong papillae on the posterior and lateral margins, a serrate edge on the marginal rim, and a carapace about as wide as long and in lacking lyrate keels and a median concentric keel.

Geologic range: Middle Mississippian (Viséan) to middle Pennsylvanian (Moscovian).

Americlus americanus (Packard, 1885)
Fig. 10.1–10.3

1885 *Cyclus americanus* Packard, p. 143.
1902 *Cyclus americanus* Packard, 1885. – Rogers, p. 269.
1925 *Halicyne americanus* (Packard, 1885). Hopwood, p. 307.
1997 *Cyclus americanus* Packard, 1885. – Schram et al., p. 265.
2006 *Cyclus americanus* Packard, 1885. – Schram et al., p. 7.
2008 “*Cyclus*” *americanus* (Packard, 1885). – Dzik, 2008, p. 1513.
2008 *Americlus americanus* (Packard, 1885). – Dzik, p. 1512.
2018 *Americlus americanus* (Packard, 1885). – Mychko & Alekseev, p. 24.
2017 *Americlus americanus* (Packard, 1885). – Feldmann et al., p. 407.
2019 *Americlus americanus* (Packard, 1885). – Feldmann & Schweitzer, p. 2.
2020 *Americlus americanus* (Packard, 1885). – Clark et al., p. 185.

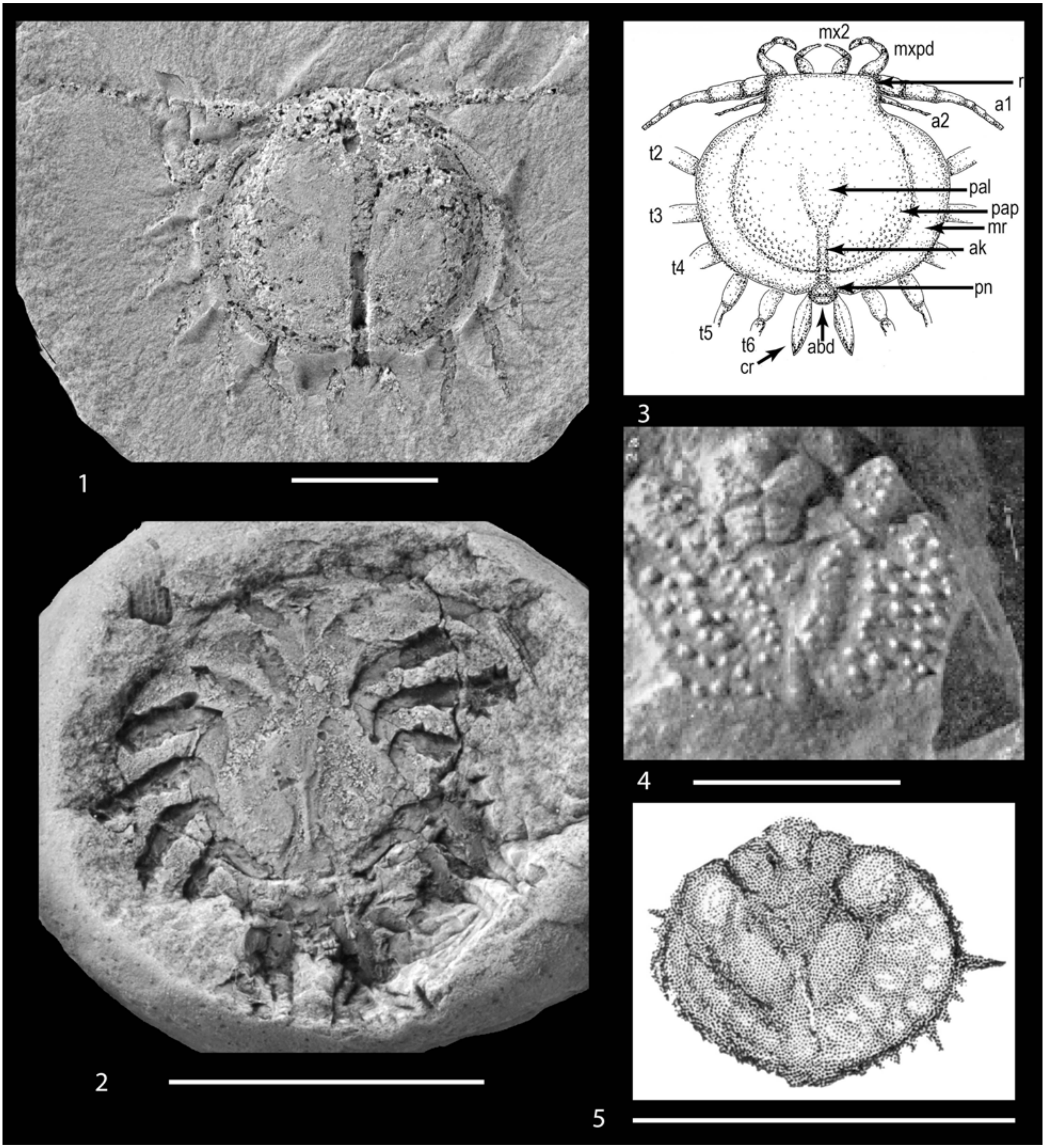


Fig. 10. Americlidae *Americlus* spp. **1** – *A. americanus* (Packard, 1885), MCP 507. **2** – *A. americanus*, FMNH PE21013. **3** – Line drawing of *A. americanus* with morphology labeled. **4** – *A. packardi* (Rogers, 1902) (Rogers 1902, pl. 14, fig. 2). **5** – *A. limbatus* (Rogers, 1902) (Rogers 1902, pl. 14, fig. 4). Scale bars = 5 mm.

Material examined: Holotype USNM 38863; FMNH PE 20601, 20985, 22421, 22462, 22472, 22478, 22498, 24959, 34759, 34763, 34954; LF 2125; CMNH 6909.

Diagnosis: As for genus.

Description: Carapace circular, weakly bilobed, about as long as wide or slightly wider than long, W/L ranging from 0.97–1.13; rostral lobe projected beyond orbits, anterior margin weakly convex, orbital reentrant absent; marginal rim narrow, maintaining width along most of length until narrowing to posterior reentrant, circular depression wide, tiny serrations on margin of rim.

Posterior axial lobe flattened, widest anteriorly, narrowing into well-developed axial keel; weak swellings anteriorly are possibly second lateral lobe, oriented oblique to axis, weakly inflated. Inner lyrate keel weak, merging into axial keel; median concentric keel absent; branchial regions granular posteriorly and laterally.

Basal articles of antennules long, stout. At least two pairs of mouthparts with sickle-shaped dactyls, interpreted here as second maxillae and maxillipeds. Basal elements of five thoracopods preserved. Seven visible thoracic sternites, first two directed anterolaterally, third sternite directed laterally, sternites 4–7 directed posterolaterally; all about same height, sternal sutures terminating well lateral to axis except last suture which terminated at axis. Gut cast well preserved, paired lobate digestive glands at about mid length. Caudal rami long, sharp.

Discussion: We have developed a reconstruction of the dorsal and ventral morphology. One specimen retains what is probably paired digestive glands.

Locality & formation: Peabody Coal Company Pit 11, Will and Kankakee counties, Illinois, USA, Francis Creek Shale Member of Carbondale Formation.

Geologic range: Middle Pennsylvanian (Moscovian).

Lithology & environment: The concretions with fossils occur in localized deposits within silty to sandy mudstones; sediment deposited in a deltaic system.

Americlus? *limbatus* (Rogers, 1902)
Fig. 10.5

1902 *Cyclus limbatus* Rogers, p. 273, pl. 14, fig. 4.
1925 *Cyclus limbatus* Rogers, 1902. – Hopwood, p. 307.
1997 *Cyclus limbatus* Rogers, 1902. – Schram et al., p. 262.
2011 *Cyclus limbatus* Rogers, 1902. – Niko & Ibaraki, p. 260.
2017 *Cyclus limbatus* Rogers, 1902. – Feldmann et al., p. 407.
2019 *Cyclus limbatus* Rogers, 1902. – Feldmann & Schweitzer, p. 2.
2018 *Americlus limbatus* (Rogers, 1902). – Mychko & Alekseev, p. 24.

Material examined: Apparently lost.

Description: Carapace transversely ovate, wider than long; marginal rim with spines, longest at about mid-length and possibly a stout spine at posterior corner; posterior axial lobe narrow posteriorly and widened anteriorly, merging into first axial lobe, second axial lobes paired, about same size as third axial lobe; first lateral lobe large; inner and outer branchial regions separated by a groove.

Discussion: This description is based upon the drawing in Rogers (1902). It is very small, only about 3 mm long. The drawing indicates strong regional development and spines on the marginal rim. The incomplete nature of the material plus the fact that the specimen is apparently lost make placement of this species difficult, which is why we place it with the slightly older species *Americlus americanus*, which is also known from North America.

Locality & formation: Kansas City, Missouri, USA, Iola Limestone.

Geologic range: Upper Pennsylvanian (Kasimovian).

Lithology & environment: Wackestone; shallow marine.

Americlus? *packardi* (Rogers, 1902)
Fig. 10.4

1902 *Cyclus packardi* Rogers, p. 271, pl. 14, fig. 2.
1925 *Cyclus packardi* Rogers, 1902. – Hopwood, p. 307.
1997 *Cyclus packardi* Rogers, 1902. – Schram et al., p. 262.
2017 *Cyclus packardi* Rogers, 1902. – Feldmann et al., p. 407.
2019 *Cyclus packardi* Rogers, 1902. – Feldmann & Schweitzer, p. 2.
2018 *Americlus packardi* (Rogers, 1902). – Mychko & Alekseev, p. 24.

Material examined: Apparently lost.

Description: Carapace flattened, ovate, axial keel strong; posterior axial region flattened, first axial lobes paired, with transverse ridges; second axial lobes paired, diamond shaped, larger than first axial lobes; third axial lobe about as large as second axial lobe; first lateral lobe not well defined; second axial lobe large ovate; third axial lobe diamond shaped. Inner lyrate keel granular; branchial regions with two longitudinal, narrow inflations positioned on axial half of branchial regions; carapace surface coarsely granular.

Discussion: The carapaces of this species are small in size, between 8 and 11 mm wide. The apparently flattened carapace with possible median concentric keels suggests that its affinity may be more strongly with Americlidae rather than Cyclidae. Thus, we follow Mychko & Alekseev (2018) in placing this species within *Americlus* for now. The incomplete nature of the material plus the fact that the specimen is apparently lost make placement of this species difficult; thus, we place it with the slightly older species *Americlus americanus*, which is also known from North America.

Locality & formation: Kansas City, Missouri, USA, Iola Limestone.

Geologic range: Upper Pennsylvanian (Kasimovian).

Lithology & environment: Wackestone; shallow marine.

Genus *Brittaniclus* nov.

Etymology: The genus name is based upon the Latin word *Brittanicus* for the region now known as Britain and from where specimens of all three referred species were collected. The gender is masculine.

Type species: *Cyclus rankini* Woodward, 1868, by original designation.

Included species: *Brittaniclus rankini*; *B. scotti* Woodward, 1893 (= *B. johnsoni* Woodward, 1894); *B. testudo* (Peach, 1882).

Diagnosis: Carapace flattened, wider than long, bilobed; moderate carapace regional definition; marginal rim well-developed, wide, with posterior notch, may have strong keel on margin of rim (*A. scotti*); posterior axial keel strong; lyrate keels may be present (*A. scotti*); median concentric keel strong; rostral lobe extending beyond carapace, with optic notches, with one to three transverse crests; axial and lateral regions moderately defined; first antennae strong, thick, with three stout basal articles and long flagella; second antennae slender, shorter; first pair of visible non-antennal appendages short; followed by 2 pairs of subchelate appendages with sickle-like dactyls; 5 pediform thoracic appendages posterior to subchelate appendages; male gonopod present, interpreted as exopod of last thoracic appendage; caudal rami present; sternal region with seven or eight visible, well-defined somites, ovate central sternal area; abdomen with 2–4 somites (modified from Feldmann & Schweitzer 2019).

Discussion: *Brittaniclus rankini* and *B. scotti* are some of the best-preserved members of Cyclida. *Brittaniclus* nov. differs from other members of Americlidae in possessing a strong median concentric keel, moderately defined carapace regions, a smooth carapace that is wider than long and clearly bilobed, and a rostral lobe with transverse keels. All three referred species are from northern Britain, and interestingly, are each of a different age, suggesting possible anagenesis as a speciation mechanism.

Geologic range: Middle Mississippian (Viséan) – Middle Pennsylvanian (Moscovian).

Brittaniclus rankini (Woodward, 1868) new combination
Fig. 11.3, 11.4

1868 *Cyclus rankini* Woodward, p. 73, pl. 2, fig. 2.
1870 *Cyclus rankini* Woodward, 1868. – Woodward, p. 558, pl. 23, fig. 1.
1878 *Cyclus rankini* Woodward, 1868. – Woodward, p. 254, pl. 32, fig. 42.
1882 *Cyclus rankini* Woodward, 1868. – Peach, p. 526.
1894 *Cyclus rankini* Woodward, 1868. – Woodward, p. 530, pl. 15, fig. 8.
1905 *Cyclus rankini* Woodward, 1868. – Woodward, p. 490.
1902 *Cyclus rankini* Woodward, 1868. – Rogers, p. 275.
1925 *Cyclus rankini* Woodward, 1868. – Hopwood, p. 308.
1989 *Cyclus rankini* Woodward, 1868. – Clark, p. 190.
1997 *Cyclus rankini* Woodward, 1868. – Schram et al., p. 279.
2017 *Cyclus rankini* Woodward, 1868. – Feldmann et al., p. 407.
2018 *Cyclus rankini* Woodward, 1868. – Mychko & Alekseev, p. 25.
2019 *Americlus rankini* (Woodward, 1868). – Feldmann & Schweitzer, p. 2.
2020 *Americlus rankini* (Woodward, 1868). – Clark et al., p. 187.

Material examined: GLAHM A2801–2803, 2806–2815, 2817, 2561, 21498, 21528, 21556, 28541, 163101.

Diagnosis: Carapace ovate, wider than long, appearing clearly bilobate; rostral lobe with transverse crest, optic notches; marginal rim wide, narrowing to small posterior reentrant; median concentric keel present; thoracic somites well-defined ventrally; appendages with sickle-shaped dactyls; caudal rami ovate, spinose.

Discussion: See Clark et al. (2020).

Locality & formation: Near Carluke, South Lanarkshire, Scotland, UK, Shrimp Beds, Limestone Coal Formation.

Geologic range: Upper Mississippian (Serpukhovian).

Lithology & environment: Limestone; marine.

Brittaniclus scotti (Woodward, 1893) new combination
Fig. 11.1, 11.2

1893 *Cyclus scotti* Woodward, p. 28.
1894 *Cyclus scotti* Woodward, 1893. – Woodward, p. 536.
1894 *Cyclus johnsoni* Woodward, p. 537.
1905 *Cyclus johnsoni* Woodward, 1894. – Woodward, p. 490.
1925 *Halicyne scotti* (Woodward, 1893). – Hopwood, p. 308.
1925 *Halicyne johnsoni* (Woodward, 1894). – Hopwood, p. 307.
1928 *Cyclus johnsoni* Woodward, 1894. – Glaessner, p. 394.
1957 "*Cyclus*" *johnsoni* Woodward, 1894. – Trümpy, p. 548.

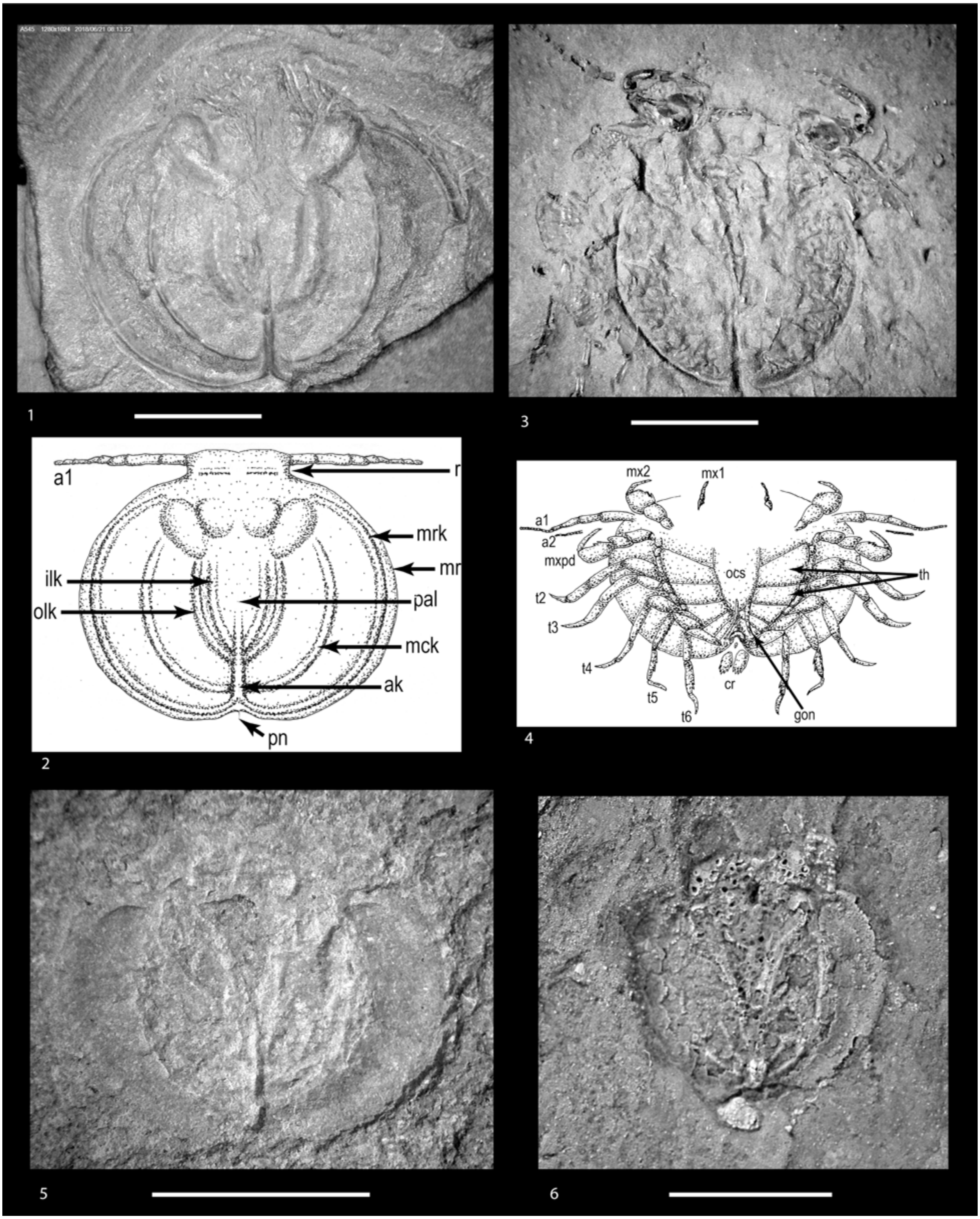


Fig. 11. Americlidae. *Brittaniclus* spp. **1 –** *B. scotti* (Woodward, 1893) new combination, MM I 10220 (=L.926), holotype. **2 –** Line drawing of *B. scotti* with morphology labeled. **3 –** *B. rankini* (Woodward, 1868) new combination, GLAHM A2811. **4 –** Line drawing of ventral morphology of *B. rankini*. **5 –** *B. testudo* (Peach, 1882) new combination, NHMUK 22379. **6 –** *B. testudo*, L9285a, note tiny pelecypod at posterior margin. Scale bars = 5 mm.

1967 *Cyclus johnsoni* WOODWARD, 1894. – GALL & GRAUVOGEL, p. 11.
1997 *Cyclus scotti* WOODWARD, 1893. – SCHRAM et al., p. 262.
2008 "*Cyclus*" *scotti* (WOODWARD, 1893). – DZIK, p. 1514.
2008 *Americlus scotti* (WOODWARD, 1893). – DZIK, p. 1512.
2008 "*Cyclus*" *johnsoni* WOODWARD, 1894. – DZIK, P. 1514.
2008 *Americlus johnsoni* (WOODWARD, 1894). – DZIK, p. 1512.
2017 *Americlus scotti* (WOODWARD, 1893). – FELDMANN et al., p. 407.
2017 *Americlus johnsoni* (WOODWARD, 1894). – FELDMANN et al., p. 407
2018 *Americlus scotti* (WOODWARD, 1893). – MYCHKO & ALEKSEEV, p. 25.
2018 *Americlus johnsoni* (WOODWARD, 1894). – MYCHKO & ALEKSEEV, p. 25
2019 *Americlus scotti* (WOODWARD, 1893). – FELDMANN & SCHWEITZER, p. 2.
2019 *Americlus johnsoni* (WOODWARD, 1894). – FELDMANN & SCHWEITZER, p. 2.
2020 *Americlus scotti* (WOODWARD, 1893). – CLARK et al., p. 185.
2020 *Americlus johnsoni* (WOODWARD, 1894). – CLARK et al., p. 185.

Material examined: *Brittaniclus scotti*: holotype, MM I 10220 (=L.926); MM LL.15941.943a, b; NHMUK I.13903, I.13904, 13945, 18591, 22370; SM E16936; GSE 26710–11, 26716–17; BGS Za 2904–2906, GSM 26061. *Brittaniclus johnsoni*: NHMUK In. 22371–22374, syntypes; NHMUK I.3164, 3167, 13843, 13845, 13873, 13875, 41507, 41508; SM E 16911; MM L. 1175, 7098, 8185, 11753, 11754, 11902; GLAHM A2565; NMS.G.1911.6.12.

Diagnosis: Carapace ovate; rostral lobe with three transverse crests; marginal rim maintaining consistent width until nearing posterior notch, at which point the rim narrows, marginal rim with strong, narrow keel near edge; median concentric keel strong; inner and outer lyrate keels strong; axial regions moderately well defined; thoracic sternum with eight preserved somites.

Description: Carapace overall ovate, wider than long, W/L ranging from 1.13–1.28, flattened, bilobed; rostral lobe projected well beyond carapace, quadrate, with three pairs of transverse crests arranged on either side of an axial keel; optic notches deep. Marginal rim wide, flattened, bounded axially by deep concentric depression, marginal rim narrowed anteriorly, then widening and maintaining consistent width until nearing posterior notch, narrow strong keel paralleling edge of marginal rim. Posterior axial lobe flattened, widest anteriorly and narrowing posteriorly and merging into axial keel; first axial lobe rounded; second and third axial lobes more poorly defined, apparently circular. First lateral lobe small, ovate, obliquely directed posterolaterally; second lateral lobe very strong, large, ovate, directed anterolaterally. Posterior axial lobe bounded by wide inner lyrate keel, arcuate; outer lyrate keel about as wide as inner; branchial region smooth, bisected by strong median concentric keel.

First antennae stout, with four stout basal articles, basal two articles and fourth about same length, third article twice as long as others, at least nine segments of flagella visible; second antennae much smaller and shorter. Ventral surface with foregut and gut casts. Eight thoracomeres visible, first somite narrow, somites 2–4 about same length, widest, somites 5–8 about same length and shorter than 2–4; sutures 1/2 and 2/3 directed anterolaterally, sutures 3/4 and 4/5 directed laterally, sutures 5/6 to 7/8 directed posterolaterally; at lateral-most edge of somites, two ovate structures, one anterior which is the smaller and one posterior which is about twice as large as the anterior ovate structure; thoracic sutures 1/2, 2/3, 3/4, 4/5, 5/6, and 6/7 not appearing to extend to axis, instead terminating short of the axis at an arcuate longitudinal suture which terminates at suture 6/7, suture 7/8 intersects axis. Marginal rim extends well-lateral of sternal elements. Possibly abdominal somites preserved, caudal rami present but incompletely preserved.

Discussion: Both *Brittaniclus johnsoni* and *B. scotti* were described by WOODWARD in the late 19th Century. Material referred to *B. johnsoni* was collected from the "Pennystone Ironstones", "Middle Coal Measures", and "Coal Measures," whereas *B. scotti* was collected from "Lower Coal Measures", "Pennystone Ironstone", "Coal Measures", and "Ten-foot Ironstones" (WOODWARD 1893; WOODWARD 1894; WOODWARD 1905; MORRIS 1980; labels associated with specimens). All but one specimen was collected from Staffordshire or Lancashire, England, UK. The formation most likely to have yielded the specimens is the Pennine Lower Coal Measures Formation (bgslexicon).

The holotype of *Brittaniclus scotti* is a mostly well-preserved dorsal carapace that is missing the rostral lobe and some of the anterior carapace. The syntypes of *Brittaniclus johnsoni* are ventral views of the sternum or dorsal views of the sternum with little remaining carapace. Of specimens of *B. johnsoni* with carapace preserved, they seem to differ from *B. scotti* in lacking a very strong second lateral lobe. Later authors referred some ventral material to *B. scotti*. HOPWOOD (1925) referred NHMUK In.18591 questionably to *B. scotti*; that specimen is nearly identical to those referred to *B. johnsoni*. Because *Brittaniclus scotti* was named for dorsal carapace material, and the syntypes of *B. johnsoni* were largely ventral views, in addition to the fact that the specimens were found in the same region and probably the same formation, we suggest that the two species are synonymous.

Brittaniclus scotti differs from other species of the genus in having wide, well developed inner and outer lyrate keels as well as well marked axial and lateral lobes. Although many specimens have excellent sternal preservation, there is no evidence of appendages beyond the first antennae.

Four specimens originally referred to *Cyclus* sp. and deposited in the collections of the British Geological Survey are here referred to *Brittaniclus scotti*. Specimens Za 2904 and 2905 retain dorsal carapaces that have the strong keels and large second lateral lobe typical of *B. scotti*. GSM 26061 also has these keels and a large second lateral lobe, and it has a well-preserved, quadrate rostral lobe with 3 pairs of transverse keels arranged on either side of an axial keel. Za 2906 retains eight sternites as seen in specimens originally referred to *B. johnsoni*. These specimens expand the geographic range for the species into Derbyshire, Nottinghamshire and Yorkshire; note that these are in the northwestern region of England, similar to previous known occurrences. The geologic range is unchanged by the new occurrences, referred on their labels to the Coal Measures Group.

Locality & formation: Near Dudley, Staffordshire, England, UK, Pennine Middle Coal Measures Formation.

Geologic range: Middle Pennsylvanian (Moscovian).

Lithology & environment: Mudstone or siltstone; marine.

Brittaniclus testudo (Peach, 1882) new combination Fig. 11.5, 11.6

1882 *Cyclus testudo* Peach, p. 527, p. 28, fig. 9.
1885 *Cyclus testudo* Peach, 1882. – Packard, p. 144.
1894 *Cyclus testudo* Peach, 1882. – Woodward, p. 534.
1925 *Cyclus testudo* Peach, 1882. – Hopwood, p. 309.
1983 *Cyclus testudo* Peach, 1882. – Schram, p. 5.
1997 *Cyclus testudo* Peach, 1882. – Schram et al., p. 262.
2017 *Cyclus testudo* Peach, 1882. – Feldmann et al., p. 407.
2018 *Cyclus testudo* Peach, 1882. – Mychko & Alekseev, p. 25.
2019 *Americlus testudo* (Peach, 1882). – Feldmann & Schweitzer, p. 2.
2020 *Americlus testudo* (Peach, 1882). – Clark et al., p. 185.

Material examined: GSE 2056–2058, syntypes; GSE 2048–2054; NHMUK In. 22378, 22379, 22386; L 9285.

Diagnosis: Carapace appearing circular, flattened, dorsal surface not well-known; sternum divided into at least 7 somites; lateral rim wide, flattened; rostral lobe may be axially sulcate, posterior axial keel strong.

Description: Carapace ovate, slightly wider than long. Rostral lobe projected beyond carapace, anterior margin straight. Marginal rim very wide, widest at about midlength, narrowing to posterior notch, may have marginal keel; inner lyrate keel and median concentric keel present; axial keel strong.

Sternum with seven somites preserved, anterior sutures extending nearly to axis, posterior sternal sutures terminating at axis, ovate central structure absent. Basal segments of antennules preserved, few articles of thoracopods preserved.

Discussion: This species is referred to *Brittaniclus* based upon its possession of a flattened carapace with a wide lateral rim and well-developed thoracic sternites. These features are of the same general form as *B. rankini*, the type species. *Brittaniclus testudo* is not well-preserved. Many of the specimens referred to this species are preserved with granular or roseate circular structures (GSE 2048–2054). The origin of the structures is unknown, but they may be a diagenetic product involving the cuticle. It seems that over the decades specimens that appear to be cyclidans that have a strongly granular carapace, even with no other features, and collected from the Eskdale locality, have been referred to this species.

Locality & formation: Glencartholm, Langholm, Dumfriesshire, Scotland, UK, Tyne Limestone Formation.

Geologic range: Middle Mississippian (Viséan).

Lithology & environment: Limestone and sandstone (locally thin coals are developed; local development of volcanic tuffs and basalt lavas); shallow marine.

Genus *Dziklus* nov.

Etymology: The genus name honors Jerzy Dzik, Polish Academy of Sciences, Institute of Paleobiology, Warsaw, Poland, for his contribution to cyclidan paleobiology. The gender is masculine.

Type species: *Cyclus obesus* Schram, Vonk & Hof, 1997, by original designation.

Diagnosis: Carapace much wider than long, rostral lobe wide, with straight anterior margin; marginal rim wide, continuous with no posterior notch, with short transverse keel anteriorly; median concentric keel continuous, forming a semicircular keel extending posteriorly; posterior axial keel absent; proximal elements of first antennae preserved.

Geologic range: Middle Pennsylvanian (Moscovian).

Dziklus obesus (Schram, Vonk & Hof, 1997) new combination Fig. 12

1997 *Cyclus obesus* Schram, Vonk & Hof, p. 271.
2008 *Americlus obesus* (Schram et al., 1997). – Dzik, p. 1512
2017 *Americlus obesus* (Schram et al., 1997). – Feldmann et al., p. 407.
2018 *Americlus obesus* (Schram et al., 1997). – Mychko & Alekseev, p. 24
2019 *Americlus obesus* (Schram et al., 1997). – Feldmann & Schweitzer, p. 2.
2020 *Americlus obesus* (Schram et al., 1997). – Clark et al., p. 185.

Material examined: FMNH PE 30630, holotype; FMNH PE 23041, 24975, 34834, 34880, 39056.

Diagnosis: As for genus.

Description: Carapace wider than long, W/L ranging from 1.16 to 1.31, transversely ovate, not bilobed, flattened, lack-

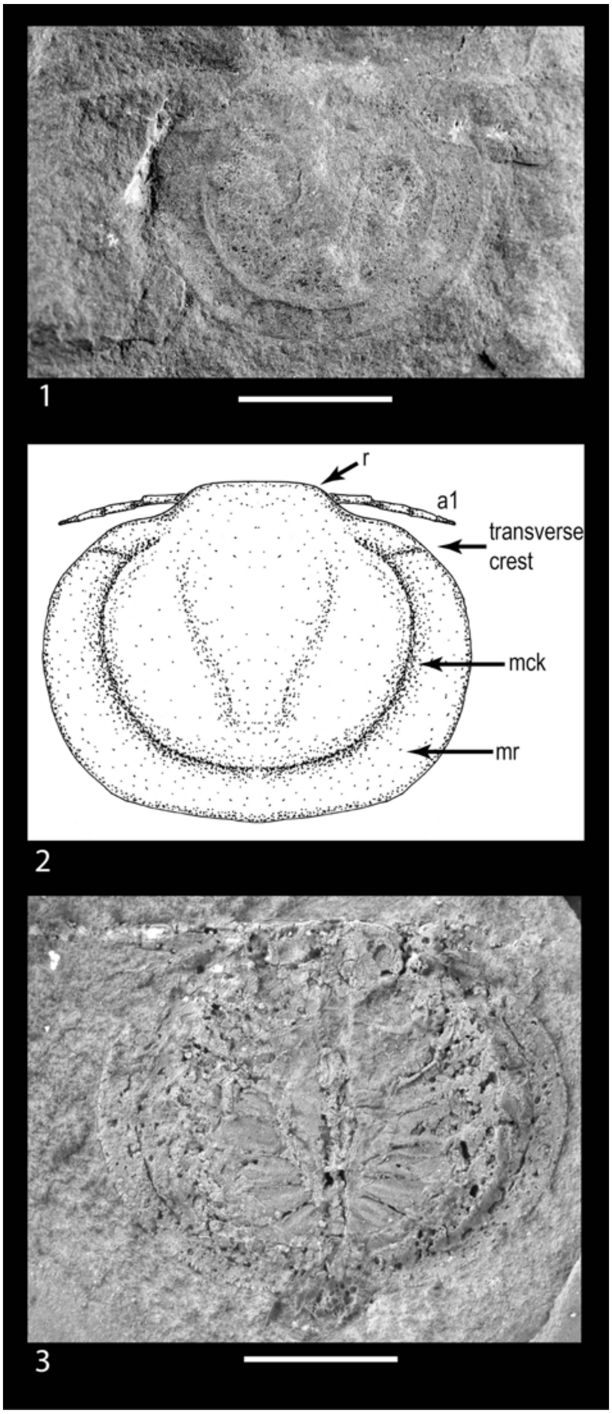


Fig. 12. Americlidae. *Dziklus obesus* (Schram et al., 1997) new combination. **1** – FMNH PE 30630, holotype, dorsal view. **2** – Line drawing of *D. obesus* with morphology labeled. **3** – FMNH PE 34880, ventral view. Scale bars = 5 mm.

ing most ornamentation; rostral lobe not projecting much beyond carapace, with straight anterior margin; optic notches short, deep; marginal rim wide, extending from anterior edge of carapace and extending around entire posterior margin, no posterior notch; median concentric keel entire, semicircular, encircling entire posterior margin; transverse keel located just posterior to optic notch and extending entire width of marginal rim; antennules with stout basal articles, few basal elements of antennule preserved, extending laterally parallel to rostral lobe; gut cast well developed; six thoracic sternites visible, anterior sutures directed anterolaterally; posterior sutures directed posterolaterally, sutures terminating axially well lateral to axis, central ovate structure not well-defined.

Discussion: The holotype and one other specimen of *Dziklus obesus* retain the dorsal carapace, showing the marginal rim clearly extending around the posterior margin of the carapace with no posterior notch. The lack of posterior notch, the continuous median concentric keel and transverse keel on the marginal rim are unique among cyclidans. Thus, we place this species in a separate genus. Two specimens referred to the species have sternal somites and sutures much like other members of Americlidae, but on those two specimens, it is difficult to determine if the marginal rim is continuous as it is poorly preserved. The flattened carapace and strong marginal rim indicate placement within Americlidae.

Locality & formation: Peabody Coal Company Pit 11, Will and Kankakee counties, Illinois, USA, Francis Creek Shale Member of Carbondale Formation.

Geologic range: Middle Pennsylvanian (Moscovian).

Lithology & environment: The concretions with fossils occur in localized deposits within silty to sandy mudstones; sediment deposited in marine environment near a deltaic system.

Family Halicynidae Gall & Grauvogel, 1967 (nom. corr. ex Halicynae Gall & Grauvogel, 1967)

Included genera: *Carcinaspides* Glaessner, 1969; *Halicyne* von Meyer, 1844; *Juracyclus* Schweigert, 2007.

Diagnosis: Carapace ovate, covering the entire cephalothoracic region; pedunculate eyes generally situated in shallow orbital notches on either side of a frontal or rostral area which may be lobate; antennae well-developed; carapace moderately inflated, with regionalization anteriorly and axially, posterior axial region ovate, extending into weak axial keel; lateral rim entire or lobate; at least 5 non-antennal appendages, with sickle-shaped dactyls; gills lamellate (modified after Gall & Grauvogel 1967).

Geologic range: Lower Triassic (Olenekian) to Lower Jurassic (Toarcian).

Genus *Halicyne* von Meyer, 1844

Type species: *Limulus agnotus* von Meyer, 1838, by monotypy.

Included species: *Halicyne agnota* (von Meyer, 1838); *H. laxa* von Meyer, 1847; *H. oosterinkorum* Schweitzer, Feldmann & Schinker, 2019; *H. ornata* Trümpy, 1957; *H. plana* von Seebach, 1857; *H. silesiensis* Alexandrowicz, 1973.

Diagnosis: Carapace ovate, covering the entire cephalothoracic region; pedunculate eyes generally situated in shallow orbital notches on either side of a frontal or rostral area which may be lobate; antennae well-developed; carapace moderately inflated, with regionalization anteriorly and axially, posterior axial lobe ovate, extending into weak axial keel; marginal rim entire; at least 5 non-antennal appendages, with sickle-shaped dactyls; gills lamellate (modified after Gall & Grauvogel 1967).

Geologic range: Lower Triassic (Olenekian) – Middle Triassic (Ladinian).

Remarks: A species originally referred to *Halicyne* has been removed from the genus. Reuss (1867) named *Halicyne elongata* and this species was mentioned by Haack (1923). These specimens are now referred to as cephalopod anaptychi (Trauth 1935).

Halicyne agnota (von Meyer, 1838)
Fig. 13.1

1838 *Limulus agnotus* von Meyer, p. 415.
1847 *Halicyne laxa* (von Meyer, 1838). – Von Meyer, p. 136.
1847 *Halicyne agnota* (von Meyer, 1838). – Von Meyer, p. 134.
1857 *Halicyne laxa* (von Meyer, 1838). – Von Seebach, p. 205.
1857 *Halicyne agnota* (von Meyer, 1838). – Von Seebach, p. 205.
1864 *Halicyne agnota* (von Meyer, 1838). – Von Alberti, p. 190.
1864 *Halicyne laxa* (von Meyer, 1838). – Von Alberti, p. 190.
1867 *Halicyne agnota* (von Meyer, 1838). – Reuss, p. 281.
1867 *Halicyne laxa* (von Meyer, 1838). – Reuss, p. 281.
1868 *Halicyne laxa* (von Meyer, 1838). – Woodward, p. 73.
1868 *Halicyne agnota* (von Meyer, 1838). – Woodward, p. 73.
1870 *Cyclus (Halicyne) agnotus* von Meyer, 1838. – Woodward, p. 559
1870 *Cyclus (Halicyne) laxus* von Meyer, 1838. – Woodward, p. 559.
1878 *Halicyne agnota* (von Meyer, 1838). – Woodward, p. 255.
1878 *Halicyne laxa* (von Meyer, 1838). – Woodward, p. 255.
1893 *Cyclus (Halicyne?) agnotus* von Meyer, 1838. – Woodward, p. 29.
1894 *Halicyne laxa* (von Meyer, 1838). – Woodward, p. 530.
1894 *Cyclus (Halicyne) agnotus* von Meyer, 1838. – Woodward, p. 530.
1923 *Halicyne agnota* (von Meyer, 1838). – Haack, p. 591.
1923 *Halicyne laxa* (von Meyer, 1838). – Haack, p. 591.
1925 *Halicyne agnota* (von Meyer, 1838). – Hopwood, p. 307.
1925 *Halicyne laxa* (von Meyer, 1838). – Hopwood, p. 308.
1954 *Halicyne agnota* (von Meyer, 1838). – Poborski, p. 992.
1954 *Halicyne laxa* (von Meyer, 1838). – Poborski, p. 992.
1955 *Halicyne agnota* (von Meyer, 1838). – Müller, p. 133.
1955 *Halicyne laxa* (von Meyer, 1838). – Müller, p. 131.
1957 *Halicyne agnota* (von Meyer, 1838). – Trümpy, p. 544.
1957 *Halicyne laxa* (von Meyer, 1838). – Trümpy, p. 544.
1961 *Halicyne agnota* (von Meyer, 1838). – Linck, p. 120.
1961 *Halicyne agnota granosa* Linck, 1961, p. 122.
1961 *Halicyne laxa* (von Meyer, 1838). – Linck, p. 120.
1969 *Halicyne agnota* (von Meyer, 1838). – Glaessner, p. R569.
1973 *Halicyne agnota* (von Meyer, 1838). – Alexandrowicz, p. 257.
1973 *Halicyne laxa* (von Meyer, 1838). – Alexandrowicz, p. 257.
1978 *Halicyne agnota* (von Meyer, 1838). – Oosterink, p. 4.
1986 *Halicyne agnota* (von Meyer, 1838). – Oosterink, p. 59.
1991 *Halicyne agnota* (von Meyer, 1838). – Bürgin et al., p. 933.
1997 *Halicyne agnota* (von Meyer, 1838). – Schram et al., p. 262.
1997 *Halicyne laxa* (von Meyer, 1838). – Schram et al., p. 292.
2006 *Halicyne agnota* (von Meyer, 1838). – Schram et al., p. 6.
2007 *Halicyne agnota* (von Meyer, 1838). – Pasini & Garassino, p. 86.
2008 *Halicyne agnota* (von Meyer, 1838). – Dzik, p. 1510.
2008 *Halicyne laxa* (von Meyer, 1838). – Dzik, p. 1511.
2009 *Halicyne agnota* (von Meyer, 1838). – Schweigert et al., p. 17.
2017 *Halicyne agnota* (von Meyer, 1838). – Feldmann et al., p. 407.
2017 *Halicyne laxa* (von Meyer, 1838). – Feldmann et al., p. 407.

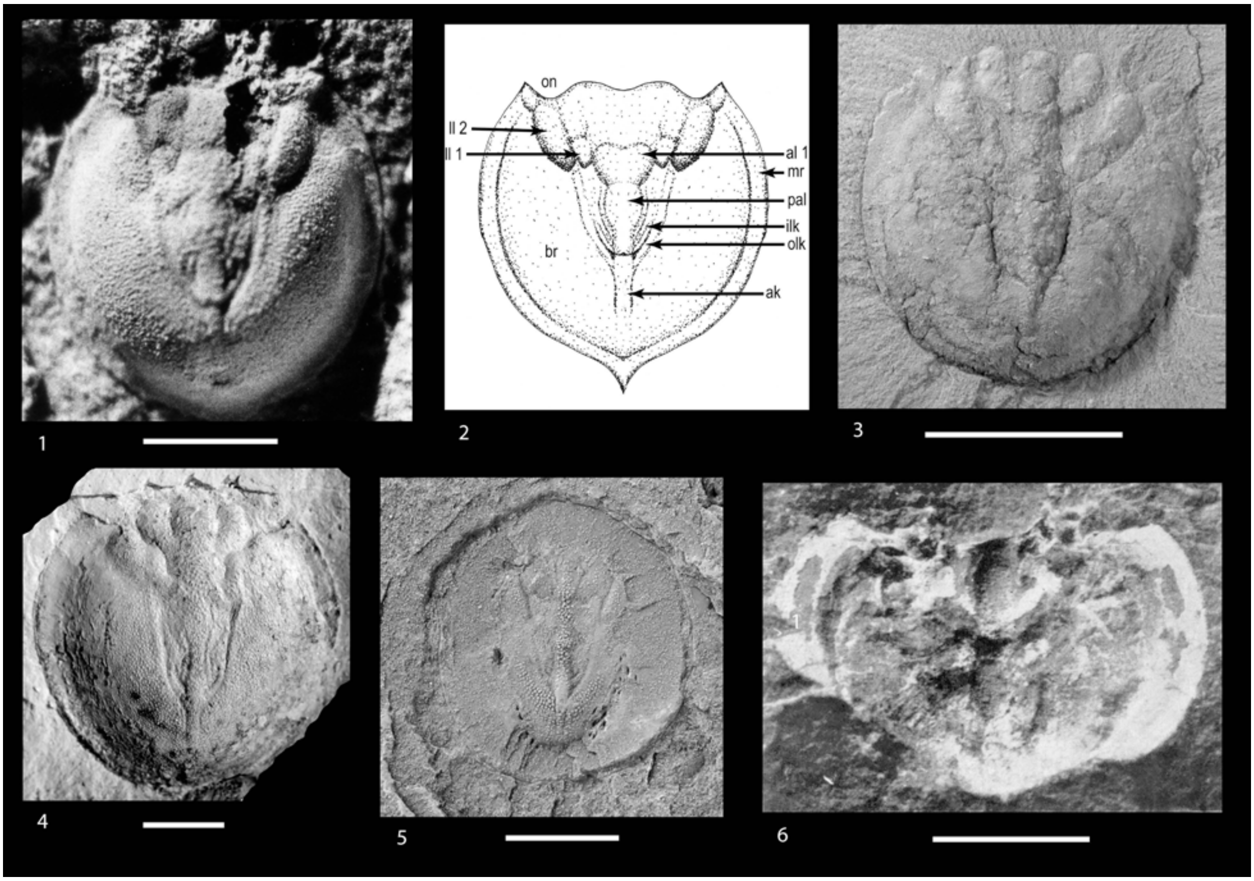


Fig. 13. Halicynidae. *Halicyne* spp. **1** – *H. agnota* (von Meyer, 1838), SMNS 22152, holotype, dorsal view, photograph by G. Schweigert. 2 – Line drawing of *H. ornata* with regions labeled. **3** – *H. oosterinkorum* Schweitzer et al., 2019, MAB k.003756, holotype. 4 – *H. ornata* Trümpy, 1957, SMNS 75571, photograph by J.C. Gall. **5** – *H. plana* (von Seebach, 1857), FSUJIG no. P 263, Müller (1955) specimen. **6** – *H. silesiensis* Alexandrowicz, 1973 (Alexandrowicz, 1973, photo 1 with permission from PAN and PWN). Scale bars = 5 mm except Fig. 13.6 which = 1 cm.

2018 *Halicyne agnota* (von Meyer, 1838). – Mychko & Alekseev, p. 24.
2018 *Halicyne laxa* (von Meyer, 1838). – Mychko & Alekseev, p. 25.
2019 *Halicyne agnota* (von Meyer, 1838). – Schweitzer et al., p. 68.
2019 *Halicyne agnota* (von Meyer, 1838). – Feldmann & Schweitzer, p. 3.
2019 *Halicyne agnota* (von Meyer, 1838). – Furrer, p. 70.
2019 *Halicyne laxa* (von Meyer, 1838). – Schweitzer et al., p. 68.
2019 *Halicyne laxa* (von Meyer, 1838). – Feldmann & Schweitzer, p. 3.

Material examined: Photograph of holotype SMNS 22152 by G. Schweigert.

Diagnosis: Carapace ovate, straight anteriorly, narrowing posteriorly, weakly vaulted, most strongly vaulted in posterior one-third; anterior margin lobate, with shallow orbital notches laterally. Marginal rim flat, narrow, narrowing posteriorly and very narrow at posterior tip, tip sharp, directed posteriorly. Posterior axial lobe elongate, slightly constricted at about mid-length; first axial lobe circular, weakly differentiated from posterior axial lobe, second axial lobe elongate, flattened; first lateral lobes ovate, narrow; second lateral lobes ovate, longitudinally elongate, strongly inflated. Inner lyrate keel very weak, outer lyrate keel separate from inner lyrate keel; branchial region finely granular, not differentiated, axial keel weak, strongest anteriorly and nearly disappearing at posterior.

Description: Carapace ovate, cordate, narrowing posteriorly, uniformly granular. Frontal margin overall straight, with concavities at distal extremes that may be orbital notches. Marginal rim beginning at outer-orbital angle, not uniform in width, widest anteriorly and narrowing posteriorly, apparently extending around posterior margin and terminating in a strong posterior spine, marginal rim positioned below remainder of carapace surface, rim with smooth surface and smooth margin.

Axial region long, narrow, extending 75–85 percent length of carapace; posterior axial lobe elongate, slightly constricted centrally and tapering posteriorly, extending posteriorly into axial keel; first axial lobe rounded, merging into quadrate second axial lobe. First lateral lobe quadrate, longer than wide, lying alongside first axial lobe; second lateral lobe oblique, reniform, elongate, terminating anteriorly just posterior to orbital notch. Inner lyrate keel weak, short, separated from long outer lyrate keel extending from posterior of second lateral lobe, arcing axially crossing axis. Branchial regions undifferentiated.

Discussion: Von Meyer originally described this specimen oriented upside down, i.e., he thought the frontal margin was the posterior margin. Linck (1961) erected a new subspecies, *H. agnota granosa*; the holotype of that subspecies appears to be lost (pers. commun. Ingmar Werneburg, July 2019). Zorn (1971) synonymized *H. agnota* and *H. laxa* based upon their similar morphologies and localities.

Locality & formation: There are two localities: Wutach river, Fluhhalde opposite Degernau, Baden-Württemberg, Germany, Rottweil Formation (Muschelkalk), and outcrops of Prosanto Formation, Ducan-Landwasser area, Silvretta Nappe in Switzerland.

Geologic range: Middle Triassic (Anisian–Ladinian).

Lithology & environment: Dolomite; shallow marine.

Halicyne oosterinkorum Schweitzer, Feldmann & Schinker, 2019
Fig. 13.3

2019 *Halicyne oosterinkorum* Schweitzer, Feldmann & Schinker, p. 68, fig. 1.
2019 *Halicyne oosterinkorum* Schweitzer, Feldmann & Schinker, 2019. – Feldmann & Schweitzer, p. 3.

Material examined: Holotype MAB k.003756.

Diagnosis: As in Schweitzer et al. (2019).

Description: As in Schweitzer et al. (2019).

Locality & formation: Winterswijk quarry complex, Winterswijk, The Netherlands, Vossenveld Formation.

Geologic range: Middle Triassic (Anisian).

Lithology & environment: Calcareous marl; shallow marine.

Halicyne ornata Trümpy, 1957
Fig. 13.2, 13.4

1957 *Halicyne ornata* Trümpy, p. 546.
1961 *Halicyne ornata* Trümpy, 1957. – Linck, p. 120.
1967 *Halicyne ornata* Trümpy, 1957. – Gall & Grauvogel, p. 4, text-figs. 1–3, pl. A.
1971 *Halicyne ornata* Trümpy, 1957. – Gall, p. 55, pls. 14–16.
1973 *Halicyne ornata* Trümpy, 1957. – Alexandrowicz, p. 257.
1978 *Halicyne ornata* Trümpy, 1957. – Busse & Horn, p. 138.
1991 *Halicyne ornata* Trümpy, 1957. – Bürgin et al., p. 933.
1997 *Halicyne ornata* Trümpy, 1957. – Schram et al., p. 262.
2006 *Halicyne ornata* Trümpy, 1957. – Schram et al., p. 6.
2007 *Halicyne ornata* Trümpy, 1957. – Pasini & Garassino, p. 86.
2008 *Halicyne ornata* Trümpy, 1957. – Dzik, p. 1512.
2009 *Halicyne ornata* Trümpy, 1957. – Schweigert et al., p. 17.
2013 *Halicyne ornata* Trümpy, 1957. – Żyła et al., p. 140.
2017 *Halicyne ornata* Trümpy, 1957. – Feldmann et al., p. 407.
2018 *Halicyne ornata* Trümpy, 1957. – Mychko & Alekseev, p. 25.
2019 *Halicyne ornata* Trümpy, 1957. – Schweitzer et al., p. 68.
2019 *Halicyne ornata* Trümpy, 1957. – Feldmann & Schweitzer, p. 3.

Material examined: Photograph of SMNS 75571 by J.-C. Gall.

Diagnosis: Carapace ovate, covering the entire cephalothoracic region; pedunculate eyes generally situated in shallow orbital notches on either side of rostral lobe; antennae well-developed; carapace moderately inflated, highest in posterior one-third, with regionalization anteriorly and axially, posterior axial region ovate, extending into weak axial keel; marginal rim entire, narrowing posteriorly, posterior spine absent; at least 5 non-antennal appendages, with sickle-shaped dactyls; gills lamellate.

Description: Carapace ovate, about as wide as long; pedunculate eyes situated in shallow orbital notches on either side of a lobate rostral lobe; carapace moderately inflated, highest in posterior one-third; posterior axial region narrow, elongate, constricted centrally, extending into very weak axial keel that does not extend to posterior margin. Entire axial region long, narrow, extending 75–85 percent length of carapace; posterior axial lobe elongate, tapers posteriorly, extending posteriorly into axial keel; first axial lobe rounded, with oblique weak swellings at posterolateral corners; merging into quadrate and unpaired third axial lobe; second axial lobes positioned alongside first and third axial lobes, longitudinally elongate. First lateral lobe quadrate, longer than wide; second lateral lobe oblique, elongate, terminating anteriorly just posterior to orbit. Inner lyrate keel narrow, bounding posterior axial lobe; outer lyrate keel separated from inner lyrate keel, longer and wider, merging with axial keel. Branchial regions granular undifferentiated. Marginal rim entire, narrowing posteriorly, posterior spine absent; antennules well-developed; at least 5 non-antennal appendages, with sickle-shaped dactyls; gills lamellate.

Discussion: Trümpy (1957) originally described this species from a dorsal carapace specimen only, found in the Middle Triassic (Anisian) of Germany. His illustration (Trümpy 1957, fig. 1) shows linear structures radiating from the axial regions, and these are weakly expressed in the specimen illustrated by Gall & Grauvogel (1967, pl. A). Their specimens were recovered from the Anisian of France, and those specimens retained appendages and gills. Specimens more recently referred to *Halicyne ornata* were collected from Olenekian rocks of Germany (Busse & Horn 1978; Kozur & Weems 2010).

Locality & formation: There are 3 localities. Two are in Germany: Upper Buntsandstein and Solling Formation (Karlshafen Beds); one is in France (Grès à Voltzia Formation).

Geologic range: Lower–Middle Triassic (Olenekian–Anisian).

Lithology & environment: Upper Buntsandstein – red sandstone, shallow marine; Solling Formation – greenish-grey claystone, shallow marine; Grès à Voltzia Formation – red sandstone, fluvio-delta environment.

Halicyne plana (von Seebach, 1857)
Fig. 13.5

1857 *Halicyne plana* von Seebach, p. 205.
1867 *Halicyne plana* von Seebach, 1857. – Reuss, p. 281.
1923 *Halicyne plana* von Seebach, 1857. – Haack, p. 591.
1955 *Halicyne plana* von Seebach, 1857. – Müller, p. 131.
1957 *Halicyne plana* von Seebach, 1857. – Trümpy, p. 544.
1961 *Halicyne plana* von Seebach, 1857. – Linck, p. 120.
1973 *Halicyne plana* von Seebach, 1857. – Alexandrowicz, p. 257.
1997 *Halicyne plana* von Seebach, 1857. – Schram et al., p. 272.
2006 *Halicyne plana* von Seebach, 1857. – Schram et al., p. 6.
2017 *Halicyne plana* von Seebach, 1857. – Feldmann et al., p. 407.
2018 *Halicyne plana* von Seebach, 1857. – Mychko & Alekseev, p. 25.
2019 *Halicyne plana* von Seebach, 1857. – Schweitzer et al., p. 68.
2019 *Halicyne plana* von Seebach, 1857. – Feldmann & Schweitzer, p. 3.

Material examined: FSUJIG № P 263, Müller (1955) specimen, herein designated as the neotype. The holotype of von Seebach is apparently lost (pers. commun. G. Schweigert, December 2019).

Diagnosis: Carapace ovate, narrowing to a posterior spine; anterior margin poorly preserved, possibly with a concavity forming an orbit; marginal rim wide; axial structures densely granular; appearing to have posterior axial, first axial, second axial, second lateral, and third lateral lobes; inner and outer lyrate keels present; arcuate granular structures on branchial regions.

Description (using von Seebach (1857) description and illustration): Carapace ovate, narrowing to a posterior spine; anterior margin poorly preserved, possibly with a concavity forming an orbit; rostral lobe broken; marginal rim wide, maintaining width to posterior spine, entire; posterior axial lobe elongate, bilobed, constricted centrally, extending into axial keel that appears to terminate at marginal rim; first axial lobe circular; second axial lobe and third axial lobes confluent, longer than wide; first lateral lobe not well defined; second lateral lobe large; region of third lateral lobes appearing to be complex with several small swellings; inner and outer lyrate keels present, apparently parallel to one another; branchial region granular.

Description of Müller (1955) specimen: Preserved area of carapace longer than wide, lateral margins either not preserved or not exposed. Axially, carapace with posterior axial lobe extending anteriorly into first and third axial lobes and posteriorly into axial keel, forming a nearly continuous, densely granular structure. Lateral lobes 2 and 3 elongate, ovate, granular. Anterior margin unknown. Weak indication of inner and outer lyrate keels. At posterior end of posterior axial lobe, arcuate wide band extending anterolaterally onto branchial region, bands widest posteriorly and narrowing anteriorly, densely granular.

Discussion: Von Seebach (1857) described this species from Triassic (Ladinian) rocks of what is now the Erfurt Formation near Weimar. He described the specimen upside down (rotated 180 degrees); thus, what he interpreted as the posterior margin is actually the anterior margin. In von Seebach's description and illustration, this species is quite similar to *H. agnota* but appears to have better defined anterior regions and lyrate keels. The description above is extracted from the original description and the illustration (von Seebach 1857); however, the holotype has apparently been lost. Both *H. agnota* and *H. plana* are from the Ladinian of Germany, although from different formations and environments (Feldmann & Schweitzer 2019).

Müller (1955) reported a specimen of *Halicyne plana* from the Triassic (Ladinian) Erfurt Formation of Germany, from a location near Bedheim, about 100 km from the type locality. The specimen is unusually preserved and no margins are visible. Apparently during preparation, a circular area was inscribed around the specimen, making it appear in the photograph (Müller 1955, pl. 13) that it had a very wide marginal rim. This is only an artifact of preparation.

There are similarities and differences between the description and illustrations of von Seebach's and Müller's material. Von Seebach's reconstruction looks quite similar to those of *Halicyne agnota* and *H. laxa*, whereas the Müller actual specimen bears some similarity to *Halicyne* spp. The axial, elongate keel-like structure, with widened areas delineating the first axial, second axial, and posterior axial lobes, is similar to other species of *Halicyne*. The development of lateral lobes anteriorly is also similar to other species of *Halicyne*. *Halicyne plana* sensu Müller (1955) has arcuate granular structures posteriorly on the branchial regions, not illustrated by von Seebach (1857) but possibly mentioned by him, where he described "crescent-shaped lobes beginning on either side". These arcuate granular structures are not known from other species of *Halicyne*. Comparison of von Seebach's illustration and the Müller specimen is hampered by the incomplete nature of the latter, in which no margins are known. Because the holotype of *H. plana* has not been found, and because the holotype and Müller specimen appear to have been collected from the same formation, within about 100 km of the type locality, we herein designate the Müller specimen, FSUJIG № P 263, as the neotype.

Locality & formation: Near Weimar and Bedheim, Thuringia, Germany, Erfurt Formation.

Geologic range: Middle Triassic (Ladinian).

Lithology & environment: Dolomite, lacustrine limestones, claystone, evaporites, and fluviatile sandstones.

Halicyne silesiensis Alexandrowicz, 1973
Fig. 13.6

1973 *Halicyne silesiensis* Alexandrowicz, p. 260, fig. 2, photos 1–4.
2008 *Halicyne silesiensis* Alexandrowicz, 1973. – Dzik, p. 1513.
2013 *Halicyne silesiensis* Alexandrowicz, 1973. – Żyła et al., p. 143.
2017 *Halicyne silesiensis* Alexandrowicz, 1973. – Feldmann et al., p. 407.
2018 *Halicyne silesiensis* Alexandrowicz, 1973. – Mychko & Alekseev, p. 25.
2019 *Halicyne silesiensis* Alexandrowicz, 1973. – Schweitzer et al., p. 68.
2019 *Halicyne silesiensis* Alexandrowicz, 1973. – Feldmann & Schweitzer, p. 3.

Material examined: Specimen lost (pers. commun. M. Krobicki, 2017).

Diagnosis: Carapace slightly wider than long, transversely ovate, weakly vaulted, highest in posterior 40 %; rostral lobe not preserved; marginal rim very wide, downturned at edges; posterior axial lobe and first axial lobes developed; first and second lateral lobes weakly developed; axial keel well-developed; surface of carapace granular.

Discussion: The specimen referred to *H. silesiensis* is incomplete, with broken anterior margins and left posterolateral margins. It differs from other species of *Halicyne* in being wider than long and exhibiting a very wide marginal rim. Alexandrowicz (1973) noted that the species has a better developed axial keel than other species of the genus.

Locality & formation: Near Siewierz, Silesian Voivodeship, Poland, Röt Formation, with *Lingularia tenuissima*.

Geologic range: Middle Triassic (Anisian).

Lithology & environment: Dolomites; shallow subtidal.

Genus *Carcinaspides* Glaessner, 1969 (non *Carcinaspis* Stimpson, 1858; Crustacea).

Type and sole species: *Carcinaspis pustulosa* Schafhäutl, 1863, by monotypy.

Geologic range: Lower–Upper Triassic (Ladinian–Carnian).

Carcinaspides pustulosus (Schafhäutl, 1863)
Fig. 14

1863 *Carcinaspis pustulosa* Schafhäutl, p. 423, pl. 74, fig. 16.
1928 *Carcinaspis pustulosa* Schafhäutl, 1863. – Glaessner, p. 389.
1969 *Carcinaspides pustulosus* (Schafhäutl, 1863). – Glaessner, p. R569.
1997 *Carcinaspis pustulosa* Schafhäutl, 1863. – Schram et al., p. 292.
2002 *Carcinaspis pustulosa* Schafhäutl, 1863. – Brambilla et al., p. 107.
2007 *Carcinaspis pustulosa* Schafhäutl, 1863. – Schweigert, p. 214.
2008 *Carcinaspides pustulosus* (Schafhäutl, 1863). – Dzik, p. 1512.
2009 *Carcinaspides pustulosus* (Schafhäutl, 1863). – Schweigert et al., p. 18.
2017 *Carcinaspides pustulosus* (Schafhäutl, 1863). – Feldmann et al., p. 407.
2018 *Carcinaspides pustulosus* (Schafhäutl, 1863). – Mychko & Alekseev, p. 25.
2019 *Carcinaspides pustulosus* (Schafhäutl, 1863). – Feldmann & Schweitzer, p. 3.

Material examined: The material was part of a private collection that is now considered lost (pers. commun. G. Schweigert, December, 2019).

Diagnosis: Carapace ovate, front straight, possibly with weak concavities for orbits; axial regions well-defined, with posterior axial, all three axial lobes, and all three pairs of lateral lobes defined; margin rimmed, rim with wide, quadrate teeth; branchial regions ornamented with arcuate, parallel rows of large tubercles.

Description: Carapace ovate, longer than wide, widest about 60 % the distance posteriorly; frontal margin sinuous but overall straight, possibly with weak orbital notches; marginal rim narrower anteriorly and widening posteriorly, extending all the way around posterior margin, cut into wide,

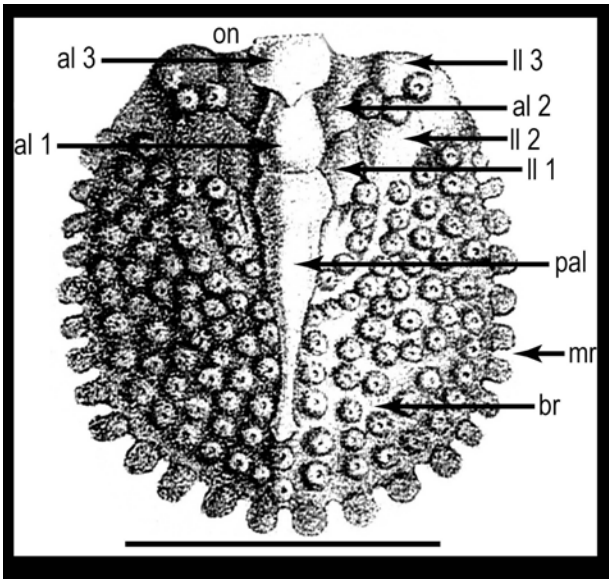


Fig. 14. Halicynidae. *Carcinaspides pustulosus* (Schafhäutl, 1863). Labeled drawing from Schafhäutl (1863, pl. 74, fig. 16b). Scale bar = 10 mm.

quadrate teeth; posterior axial region elongate, narrowing posteriorly; first axial lobe longitudinally ovate, second axial lobes weaker than first and third, third axial lobe transversely ovate; first lateral lobe elongate, narrow; second and third lateral lobes strongly inflated; three large anterior tubercles, one each situated on second axial lobe, second lateral and third lateral lobe; branchial regions ornamented with tubercles arrayed in concentric rows paralleling lateral margins.

Discussion: The current location of the type specimen is unknown. It appears that Schafhäutl (1863) described this species upside down, as he illustrated it. The 3 or 4 lobes he mentioned appear to be the axial and lateral lobes. The tubular lappets described as defining the orbits are actually on the posterior margin of the carapace. When the specimen is considered in the orientation suggested here (rotated 180° from his orientation), the carapace regions are quite similar in arrangement and size to those of *Halicyne*. It differs from *Halicyne* in possessing very strongly ornamented dorsal carapace and lateral margins.

Locality & formation: Isar Valley, Bavaria, Germany; Wetterstein Formation.

Geologic range: Lower–Upper Triassic (Ladinian–Carnian).

Lithology & environment: Reefal limestones and dolomites; shallow marine.

Genus *Juracyclus* Schweigert, 2007

Type and sole species: *Juracyclus posidoniae* Schweigert, 2007, by original designation.

Geologic range: Lower Jurassic (Toarcian).

Juracyclus posidoniae Schweigert, 2007
Fig. 15

2007 *Juracyclus posidoniae* Schweigert, p. 213.
2008 *Juracyclus posidoniae* Schweigert, 2007. – Dzik, p. 1511.
2009 *Juracyclus posidoniae* Schweigert, 2007. – Schweigert et al., p. 20.
2011 *Juracyclus posidoniae* Schweigert, 2007. – Van Bakel et al., p. 47.
2017 *Juracyclus posidoniae* Schweigert, 2007. – Feldmann et al., p. 407.
2018 *Juracyclus posidoniae* Schweigert, 2007. – Mychko & Alekseev, p. 25.
2019 *Juracyclus posidoniae* Schweigert, 2007. – Feldmann & Schweitzer, p. 3.

Material examined: Photograph of SMNS 65488 holotype by G. Schweigert.

Diagnosis: Carapace apparently longer than wide; developed into lobes anteriorly including first axial lobe, first lateral lobe, second lateral lobe, lobes ornamented with large tubercles; posterior axial lobe confluent with axial keel, wide; branchial regions with transverse ridge anteriorly, otherwise undifferentiated, ornamented with widely spaced tubercles.

Description: As in Schweigert (2007).

Discussion: Schweigert (2007) originally compared this species with *Halicyne agnota* but placed the new taxa in Cyclidae. We place *Juracyclus posidoniae* in Halicynidae based upon its flattened carapace, not typical of Cyclidae. The anterior lobes are similar in arrangement to those of *H. agnota*; however, *J. posidoniae* possesses a transverse ridge about one-third the distance posteriorly on the carapace. This feature is not known from any other halicynids or even cyclidans.

Locality & formation: Gomaringen near Tübingen, Baden-Württemberg, Germany, Posidonienschiefer Formation (Posidonia Shale).

Geologic range: Lower Jurassic (Toarcian); *Harpoceras falciferum* Ammonite Zone.

Lithology & environment: Shale; deep marine.

Family Hemitrochiscidae Trauth, 1918

Included genera: *Cyclocarcinides* Glaessner, 1969; *Hemitrochiscus* Schauroth, 1854; *Oonocarcinus* Gemmellaro, 1890; *Paraprosopon* Gemmellaro, 1890; *Skuinocyclus* Mychko & Alekseev, 2018.

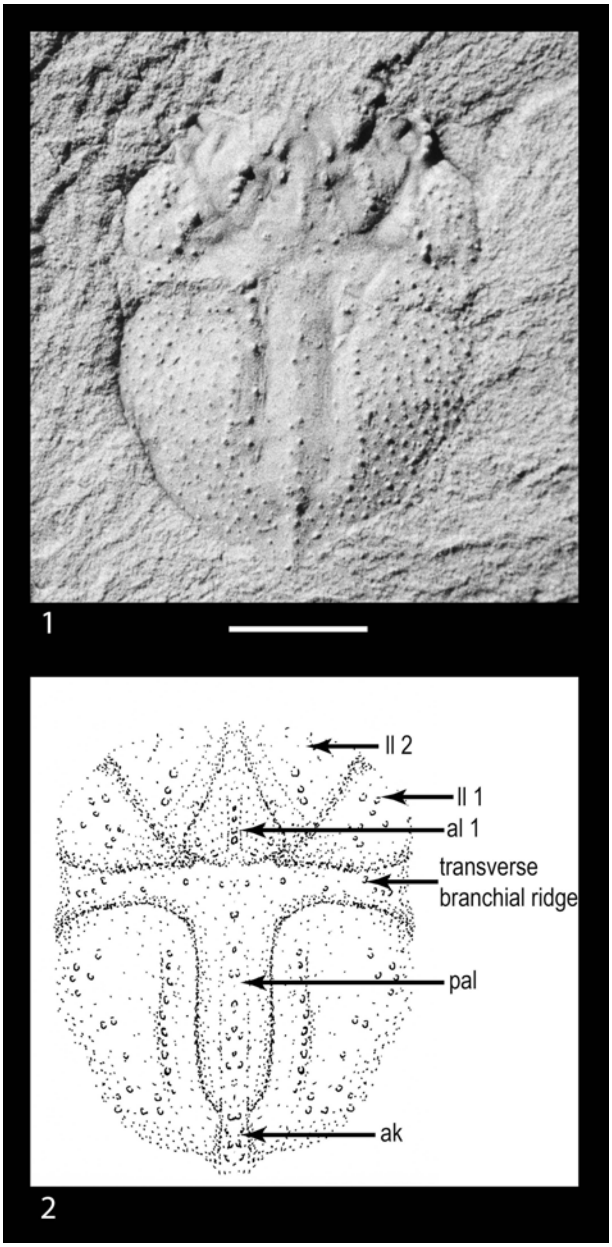


Fig. 15. Halicynidae. *Juracyclus posidoniae* Schweigert, 2007, SMNS 65488, holotype. **1** – dorsal carapace, photograph by G. Schweigert. **2** – Line drawing with morphology labeled; note margins are unknown. Scale bar = 5 mm.

Diagnosis: Carapace ovate, strongly vaulted, usually with an overall straight front and rounded posterior; orbital notches set laterally, rounded, eyes apparently protruding from orbit; carapace margins usually ornamented, either with spines or strong tubercles; carapace surface with regularly spaced granules, tubercles or ridges; carapace regions weakly defined. Ventral surface of carapace with evidence of thoracic segmentation, sometimes with broad serrations; inner surface of lateral margins with thoracic segmentation. No appendages are known.

Discussion: Trauth (1918) recognized the family as embracing taxa with very convex dorsal carapaces with simple ornamentation, with well-developed orbits and lateral margins with spines or nodes. Glaessner (1928) later reiterated the presence of well-developed orbits and a rostral lobe as well as marginal ornamentation. The very strongly convex carapace of taxa referred to this family differentiate them clearly from other cyclidans. This vaulting and the granular ornamentation of most members is rather different from other cyclidans as well. One specimen of one taxon retains evidence of thoracic segmentation that is rather like that of other cyclidans.

Geologic range: Middle Pennsylvanian (Moscovian) to Late Triassic (Carnian).

Genus *Hemitrochiscus* Schauroth, 1854

Type and sole species: *Hemitrochiscus paradoxus* Schauroth, 1854, by monotypy.

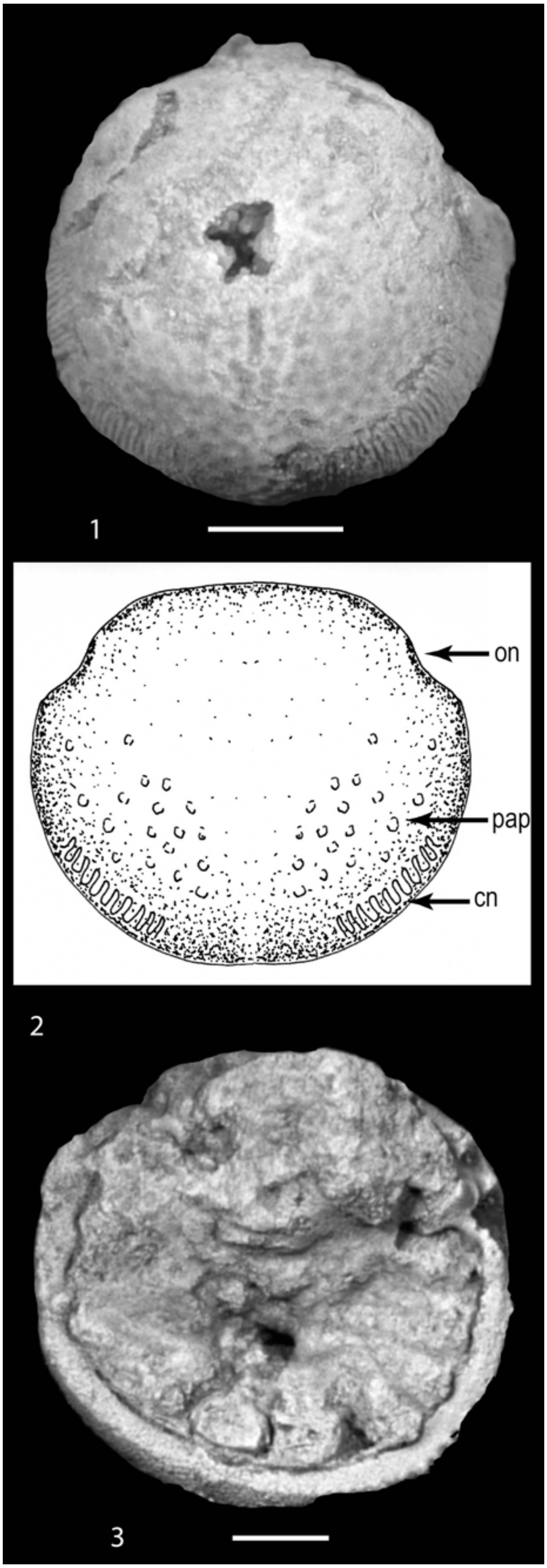
Diagnosis: Carapace semi-circular, strongly domed, optic notches deep; vermiform lines on posterolateral margins of carapace; thoracic somites visible ventrally and laterally where carapace is broken.

Geologic range: Permian (Lopingian).

Hemitrochiscus paradoxus Schauroth, 1854
Fig. 16

1854 *Hemitrochiscus paradoxus* Schauroth, p. 558, pl. 22, fig. 1.
1890 *Hemitrochiscus paradoxus* Schauroth, 1854. – Gemmellaro, p. 25.
1915 *Hemitrochiscus paradoxus* Schauroth, 1854. – Stolley, p. 675.
1918 *Hemitrochiscus paradoxus* Schauroth, 1854. – Trauth, p. 181.
1969 *Hemitrochiscus paradoxus* Schauroth, 1854. – Glaessner, p. R569.
1997 *Hemitrochiscus paradoxus* Schauroth, 1854. – Schram et al., p. 262.
2002 *Hemitrochiscus paradoxus* Schauroth, 1854. – Brambilla et al., p. 107.
2008 *Hemitrochiscus paradoxus* Schauroth, 1854. – Dzik, p. 1512.
2017 *Hemitrochiscus paradoxus* Schauroth, 1854. – Feldmann et al., p. 407.
2018 *Hemitrochiscus paradoxus* Schauroth, 1854. – Mychko & Alekseev, p. 24.
2018 *Hemitrochiscus paradoxus* Schauroth, 1854. – Feldmann & Schweitzer, p. 3.

Material examined: Three syntypes NMC 1648.



Measurements: Measurements (in mm) taken specimens of *Hemitrochiscus paradoxus*: specimen with crenulations: maximum width, 3.9; maximum length 3.8; length from front to posterior edge of orbit, 1.2; carapace thickness, 0.5. Specimen with eye: maximum width, 3.7; maximum length, 3.7, length from front to posterior edge of orbit, 0.9; carapace thickness, 0.3. Smallest specimen, maximum width, 2.3; maximum length, 2.5; length from front to posterior edge of orbit, 0.5.

Diagnosis: As for genus.

Description: Carapace semi-spherical, about as wide as long, highly domed, most strongly domed in posterior one-third; about as long as wide; optic notches positioned on lateral margins about one-third the distance posteriorly, circular, directed forward, moderately deep; labrum or rostral lobe between optic notches weakly convex, apparently with some tiny spines; eye apparently extending beyond notch; marginal rim absent; carapace with papillae, vermiform lines on lateral branchial regions; ventral surface and lateral margin where carapace removed with evidence of thoracomeres; at least five somites visible ventrally; six somites visible laterally, first three visible sutures between somites directed anterolaterally, last two sutures directed laterally.

Discussion: Schauroth (1854) illustrated several views of the specimens referred to the species, including the ventral and lateral thoracic segmentation (Schauroth, fig. 22.1c, f). His illustration fig. 22.1b shows an anterior, spherical extension axially, which is actually an eye. The orbits on this species are well-developed and deep. Visible on the specimens is a unique area of crenulate grooves along the lateral margins of the carapace. Such structures are unknown in any other cyclidans. Unique in this family is the presence of preserved thoracic segmentation.

The sole species is similar to *Oonocarcinus* in having optic notches positioned laterally on the carapace and in having a strongly domed carapace. The specimens of *Hemitrochiscus paradoxus* are notable in their tiny size. They are some of the smallest cyclidans with which we are familiar.

Locality & formation: Pößneck, Thuringia, Germany; Zechstein.

Geologic range: Permian (Lopingian).

Lithology & environment: Limestone; warm, shallow and very salty conditions.

Fig. 16. Hemitrochiscidae. *Hemitrochiscus paradoxus* Schauroth, 1854. **1** – Syntype NMC 1648, dorsal carapace. **2** – Line drawing with morphology labeled. **3** – Syntype NMC 1648, ventral surface showing thoracic segmentation. Scale bars = 1 mm.

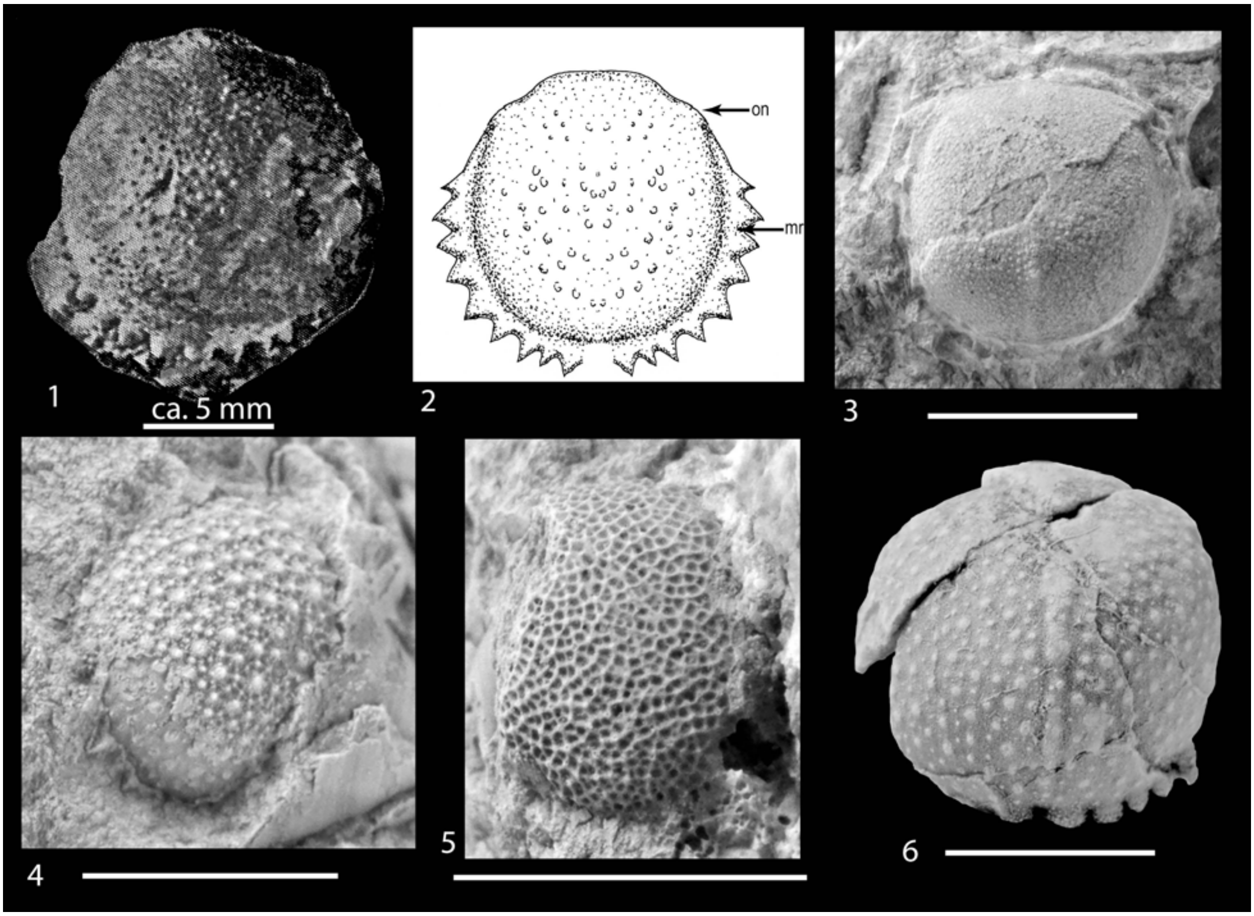


Fig. 17. Hemitrochiscidae. *Cyclocarcinides* spp. **1** – *Cyclocarcinides serratus* (Stolley, 1915), original illustration (Stolley 1915, pl. 40, fig. 1); note that the specimen seems to be rotated about 45 degrees counterclockwise. **2** – Line drawing of *C. serratus*; note that posterior most margin is unknown. **3** – *C. bosniacus* (Kittl *in* Trauth, 1918), NHMW 2018/0192/0003, holotype. **4** – *C. stellifer* (Trauth, 1918), NHMW 2018/0192/0001, holotype. **5** – *C. reticulatus* (Trauth, 1918), NHMW 2018/0192/0002, holotype. **6** – *C. tenuicarinatus* (Kittl *in* Trauth, 1918), NHMW 1859/00050/0229b, holotype. Scale bars = 5 mm.

Genus *Cyclocarcinides* Glaessner, 1969 (non *Cyclocarcinus* Guérin-Méneville *in* Duperry, 1838)

Type species: *Cyclocarcinus serratus* Stolley, 1815, by monotypy.

Included species: *Cyclocarcinides bosniacus* (Kittl in Trauth, 1918); *C. reticulatus* (Kittl in Trauth, 1918); *C. serratus*; *C. stellifer* (Kittl in Trauth, 1918); *C. tenuicarinatus* (Kittl in Trauth, 1918).

Diagnosis: Carapace circular or ovate, strongly domed; orbits positioned 20–33 % the distance posteriorly on carapace; surface uniformly granular or with reticulate or linear ornamentation; carapace lobes or other regions not defined; marginal rim strong, divided into sharp triangular spines.

Discussion: The material referred to each species within *Cyclocarcinides* exhibits varying degrees of preservation. Some species were named based upon unorientable fragments. The genus seems to be best characterized by the triangular spines on the lateral margins and placement of orbits well posterior to the frontal margin.

Geologic range: Upper Triassic (Carnian).

Cyclocarcinides serratus (Stolley, 1915) Fig. 17.1, 17.2

1915 *Cyclocarcinus serratus* Stolley, p. 676, pl. 40, figs. 1, 2.

1918 *Cyclocarcinus serratus* Stolley, 1915. – Trauth, p. 186.
1969 *Cyclocarcinides serratus* (Stolley, 1915). – Glaessner, p. R569.
1997 *Cyclocarcinus serratus* Stolley, 1915. – Schram et al., p. 262.
2002 *Cyclocarcinus serratus* Stolley, 1915. – Brambilla et al., p. 107.
2008 *Cyclocarcinides serratus* (Stolley, 1915). – Dzik, p. 1512.
2017 *Cyclocarcinoides serratus* (Stolley, 1915). – Feldmann et al., p. 407.
2018 *Cyclocarcinoides serratus* (Stolley, 1915). – Mychko & Alekseev, p. 25.
2019 *Cyclocarcinides serratus* (Stolley, 1915). – Feldmann & Schweitzer, p. 3.

Material: The holotype was destroyed during World War II (pers. commun. G. Schweigert, M. Reich, E. Seibertz, November, 2019).

Diagnosis: Carapace small, circular, granular, regions undifferentiated; anterior margin wide, with shallow orbits; lateral margins with strong triangular spines which become smaller posteriorly.

Description: Carapace small, ranging from 9–12 mm wide, circular, granular, regions undifferentiated; strongly domed, highest just posterior to midlength; anterior margin wide, with shallow orbits; lateral margin with flattened rim that is ornamented with strong triangular spines, spines beginning just posterior to orbit, becoming smaller posteriorly.

Discussion: The diagnosis and description are a combination of Stolley's original observations plus examination of the illustration.

Locality & formation: Near Siriuskogel, Bad Ischl, Salzkammergut, Austria; deposits of "Hallstätter Kalk" (Hallstatt Formation).

Geologic range: Upper Triassic (Carnian).

Lithology & environment: Beds containing micritic limestones with predominantly pelagic fauna and low clay content; possibly deep sea.

Cyclocarcinides bosniacus (Kittl in Trauth, 1918)
Fig. 17.3

1918 *Cyclocarcinus bosniacus* Kittl in Trauth, p. 190.
2019 *Cyclocarcinides bosniacus* (Kittl in Trauth, 1918). – Feldmann & Schweitzer, p. 3.
2018 *Cyclocarcinoides bosniacus* (Kittl in Trauth, 1918). – Mychko & Alekseev, p. 25.

Material examined: Holotype NHMW 2018/0192/0003.

Measurements: Measurements (in mm) taken on the holotype: carapace width, 7.2; carapace length, 7.3; frontal width, 6.6; length from front to posterior edge of orbit, 2.5.

Diagnosis: Carapace rounded quadrate, very strongly domed, front wide, axial keel developed posteriorly.

Description: Carapace rounded-quadrate, about as long as wide, very strongly domed, highest in posterior one-quarter. Frontal margin wide, over 90 % maximum carapace width, weakly convex; orbits situated about one-third the distance posteriorly on lateral margins, appearing to be circular, rimmed, directed laterally; lateral margins posterior to orbits straight, arcing into broadly convex posterior margin; actual lateral margins not known; carapace surface densely rugose; axial keel beginning about two-thirds the distance posteriorly, weakening posteriorly.

Discussion: This species differs from others referred to *Cyclocarcinides* in having a more rectangular overall outline and a very wide front.

Locality & formation: Dragoradi near Čveljanović (just north of Sarajevo), Bosnia and Herzegovina; deposits of "Hallstätter Kalk" (Hallstatt Formation).

Geologic range: Upper Triassic (Carnian).

Lithology & environment: Beds containing micritic limestones with predominantly pelagic fauna and low clay content; possibly deep sea.

Cyclocarcinides reticulatus (Trauth, 1918)
Fig. 17.5

1918 *Cyclocarcinus* (?) *reticulatus* Trauth, p. 188.
2019 *Cyclocarcinides reticulatus* (Trauth, 1918). – Feldmann & Schweitzer, p. 3.
2018 *Cyclocarcinoides (?) reticulatus* (Trauth, 1918). – Mychko & Alekseev, p. 25.

Material examined: Holotype NHMW 2018/0192/0002.

Measurements: Maximum width of carapace fragment: 4.5 mm.

Diagnosis: Apparent carapace fragment ornamented with a dense network of ridges.

Description: Carapace preserved as a fragment, not possible to determine orientation; fragment vaulted, ornamented with a series of interconnecting ridges forming a network and defining polygons of usually four sides and different shapes and sizes; no margins appear to be preserved.

Discussion: It is really not possible to know what this is. The ornamentation is unique among species referred to Cyclida.

Locality & formation: Naturpark Hohe Wand, Lower Austria, Austria; deposits of "Hallstätter Kalk" (Hallstatt Formation).

Geologic range: Upper Triassic (Carnian).

Lithology & environment: Beds containing micritic limestones with predominantly pelagic fauna and low clay content; possibly deep sea.

Cyclocarcinides stellifer (Trauth, 1918)
Fig. 17.4

1918 *Cyclocarcinus stellifer* Trauth, p. 188.
2018 *Cyclocarcinoides stellifer* (Trauth, 1918). – Mychko & Alekseev, p. 25.
2019 *Cyclocarcinides stellifer* (Trauth, 1918). – Feldmann & Schweitzer, p. 3.

Material examined: Holotype NHMW 2018/0192/0001.

Measurements: Maximum width of carapace fragment: 5.8 mm.

Diagnosis: Carapace with triangular marginal spines and tubercular stellate ornamentation.

Description: Orientation not possible to determine. Moderately domed, marginal triangular spines increase in size posteriorly (?). Ornamentation composed of regularly spaced large tubercles with smaller tubercles interspersed, all connected by sinuous weak ridges yielding a stellar pattern; where cuticle is broken exposing mold of interior, only larger tubercles visible.

Discussion: Placement within *Cyclocarcinides* seems justified based upon the triangular marginal spines. The ornamentation is unique in the family and order.

Locality & formation: Near Bad Aussee, Upper Styria, Austria; deposits of "Hallstätter Kalk" (Hallstatt Formation).

Geologic range: Upper Triassic (Carnian).

Lithology & environment: Beds containing micritic limestones with predominantly pelagic fauna and low clay content; possibly deep sea.

Cyclocarcinides tenuicarinatus (Kittl in Trauth, 1918)
Fig. 17.6

1918 *Cyclocarcinus tenuicarinatus* Kittl in Trauth, p. 189.
2018 *Cyclocarcinoides tenuicarinatus* (Kittl in Trauth, 1918). – Mychko & Alekseev, p. 25.
2019 *Cyclocarcinides tenuicarinatus* (Kittl in Trauth, 1918). – Feldmann & Schweitzer, p. 3.

Material examined: Holotype NHMW 1859/0050/0229b.

Measurements: Measurements (in mm) taken on the holotype: carapace width, 8.3; carapace length, 8.7; thickness of carapace on posterior margin, 1.3.

Diagnosis: Carapace ovate, with orbits situated well above ventral margin; ventral margin of inner surface of carapace with axially directed spines.

Description: Carapace ovate, very strongly domed, highest about 60 % the distance posteriorly; anterior margin nearly straight, possibly with some small spines; orbits apparently ovate, situated well above ventral margin; carapace surface weakly granular anteriorly and strongly granular on posterior two-thirds; axial keel beginning about half the distance posteriorly, narrowing posteriorly; ventral margin under orbits with sharp axially directed spines; marginal rim composed of short projections posterior to orbits, then becoming triangular spines increasing in size posteriorly; carapace thick, thickness about 16 % length, posteriorly with small sharp spines on inner surface directed axially.

Discussion: The marginal spines confirm placement with *Cyclocarcinides*. This species is unusual in possessing an orbit situated quite high above the ventral surface and a thick carapace with sharp spines on the inner ventral surface.

Locality & formation: Limestone cliffs by Kotskote, east of Púchov, Slovakia; deposits with brachiopods *Amphiclina amoena*.

Geologic range: Upper Triassic (Carnian).

Lithology & environment: Lithified, black, gray wackestone and lithified gray grainstone; deep subtidal.

Genus *Oonocarcinus* Gemmellaro, 1890

Type species: *Oonocarcinus insignis* Gemmellaro, 1890, by subsequent designation (Glaessner, 1969).

Included species: *Oonocarcinus insignis*; *O. puchoviensis* Kittl in Trauth, 1918.

Diagnosis (translated from Italian, Gemmellaro 1890): "These cephalothoraxes are with oval contours, longer than wide, and strongly swollen in their upper part, whose greater swelling is near the posterior third, whence it gradually decreases toward the frontal region and more or less rapidly toward the posterior one. Their upper part is distinct from the lower part by a longitudinal series of granules or tubercles, and in some species there are some larger and more spiny ones. The orbital cavities are circular, complete, directed from the inside out and situated behind the latero-frontal corner, so that they are very far from each other and placed at the sides of the cephalothorax. The eyes are globular, slightly depressed in the center and pedunculate; when they are held by a short peduncle they are actually embedded in the orbit. The orbit-frontal margin is truncated, wide and provided with an edge, which extends from the front corner (inner) to the one of the other orbit. In the anterior part of this edge the front is strongly lowered, and in the center it extends in the shape of a rostral lamina directed obliquely forward; this lamina is provided on its front side with three tubercles, one of which is located at its center and the others, oval and divergent, on its ends. On each side of this lamina is a large sinuosity, which is limited outside by a very prominent, simple, or tubercular apophysis, at the base. These two sinuosities, or incisions, gave probable passage to the internal antennas; while the external antennas passed between the apophyses and the orbital cavities, below which there is a small groove. From the posterior (external) of the orbits starts a small rim, now simple and now grainy, which runs through the ventral region of the cephalothorax dividing it into two parts, of which the interior has on the edge incisions for the passage of the legs. The branchiostegites are more or less convex. The posterior margin of the cephalothorax is arched and lacks incision.

The upper surface of these cephalothoraxes is adorned with numerous granules, among which many large tubercles arise. The latter, however, ordinarily are absent in a large triangular area, which starts from the anterolateral angles and extends to the center of the anteroposterior diameter of these cephalothoraxes. Mainly in this area, which I call an anterior triangular area, as well as in the anterior portion of these cephalothoraxes, we can note some obscure swellings and depressions, which limit the various regions, which are observed more or less clearly in brachyurans. Depressions or swellings are not equally distinct in the different species, but in those only that have large dimensions. In these species the gastric region is very distinct and extensive. The genital region is generally oval in shape, slightly swollen and not well circumscribed, while the cardiac region is distinct for several tubercles arranged in a longitudinal series, which extends more or less backwards from the rear corner of this area. The hepatic regions are always clear, mainly due to the swelling of their upper portion and to the furrow which, although slight, delimits them behind. The branchial regions are large. The limbs and the sternal shield of these crustaceans are not known."

Diagnosis: Carapace longitudinally ovate, very strongly domed; optic notches placed laterally; labrum extending anteriorly from frontal margin; carapace regions poorly defined, surface granular and with large spinose tubercles.

Geologic range: Permian (Guadalupian, Wordian) to Upper Triassic (Carnian).

Oonocarcinus insignis Gemmellaro, 1890
Fig. 18.1–18.3

1890 *Oonocarcinus insignis* Gemmellaro, p. 26, pl. 3, figs. 3–13.
1890 *Oonocarcinus geinitzi* Gemmellaro, p. 27, pl. 3, figs. 14–17.
1890 *Oonocarcinus anceps* Gemmellaro, p. 28, pl. 3, figs. 18–21.
1915 *Oonocarcinus insignis* Gemmellaro, 1890. – Stolley, p. 675.
1915 *Oonocarcinus geinitzi* Gemmellaro, 1890. – Stolley, p. 675.
1915 *Oonocarcinus anceps* Gemmellaro, 1890. – Stolley, p. 675.
1918 *Oonocarcinus insignis* Gemmellaro, 1890. – Trauth, p. 182.
1918 *Oonocarcinus geinitzi* Gemmellaro, 1890. – Trauth, p. 182.
1918 *Oonocarcinus anceps* Gemmellaro, 1890. – Trauth, p. 181.
1928 *Oonocarcinus insignis* Gemmellaro, 1890. – Glaessner, p. 390.
1969 *Oonocarcinus insignis* Gemmellaro, 1890. – Glaessner, p. R569.
1997 *Oonocarcinus insignis* Gemmellaro, 1890. – Schram et al., p. 262.
2002 *Oonocarcinus insignis* Gemmellaro, 1890. – Brambilla et al., p. 107.
2008 *Oonocarcinus insignis* Gemmellaro, 1890. – Dzik, p. 1512.
2008 *Oonocarcinus geinitzi* Gemmellaro, 1890. – Dzik, p. 1513.
2008 *Oonocarcinus anceps* Gemmellaro, 1890. – Dzik, p. 1513.
2017 *Oonocarcinus insignis* Gemmellaro, 1890. – Feldmann et al., p. 407.
2017 *Oonocarcinus geinitzi* Gemmellaro, 1890. – Feldmann et al., p. 407.
2017 *Oonocarcinus anceps* Gemmellaro, 1890. – Feldmann et al., p. 407.
2018 *Oonocarcinus insignis* Gemmellaro, 1890. – Mychko & Alekseev, p. 25.
2018 *Oonocarcinus geinitzi* Gemmellaro, 1890. – Mychko & Alekseev, p. 25.
2018 *Oonocarcinus anceps* Gemmellaro, 1890. – Mychko & Alekseev, p. 25.
2019 *Oonocarcinus insignis* Gemmellaro, 1890. – Feldmann & Schweitzer, p. 4.
2019 *Oonocarcinus geinitzi* Gemmellaro, 1890. – Feldmann & Schweitzer, p. 4.
2019 *Oonocarcinus anceps* Gemmellaro, 1890. – Feldmann & Schweitzer, p. 4.

Material examined: Specimens from the Gemmellaro collection in the Museo Geologico of the Università di Palermo, Palermo, Italy; USNM PAL 633985–633987.

Diagnosis: Specimens large, with strong tubercles on posterior half, frontal margin (rostral lobe?) rimmed.

Description: Carapace longer than wide, ovate, widest just posterior to midlength, very strongly domed, finely granular overall and with large, sharp tubercles posteriorly and laterally. Rostral lobe not extending beyond frontal margin of carapace, with a narrow marginal rim; labrum a smooth extension from the lower margin of the rostral lobe, spatulate, directed ventrally at anterior end; optic notches lateral margin, rimmed. Posterior axial lobe very weakly defined longitudinally elongate, merging into axial keel which is most strongly developed posteriorly. Carapace anterior regions very weak, first axial lobe a granular field; second axial lobe wider than long, granular; third lateral lobe weakly spherical, other axial and lateral lobes not differentiated. Branchial regions not differentiated, strongly ornamented. Lateral margins of carapace wrapping ventrally, edges of ventral extension of lateral margins with large, spine-like projections extending axially.

Discussion: Specimens referred to *Oonocarcinus insignis* have very clearly developed optic notches. The spine-like extensions on the ventral edges were interpreted by Gemmellaro (1890) as bounding the thoracic appendages, for which there is no evidence. Specimens of this species also appear to exhibit a very thick cuticle, especially posteriorly. Work on this is ongoing.

As originally described, Gemmellaro (1890) recognized three species of *Oonocarcinus*. The three were distinguished

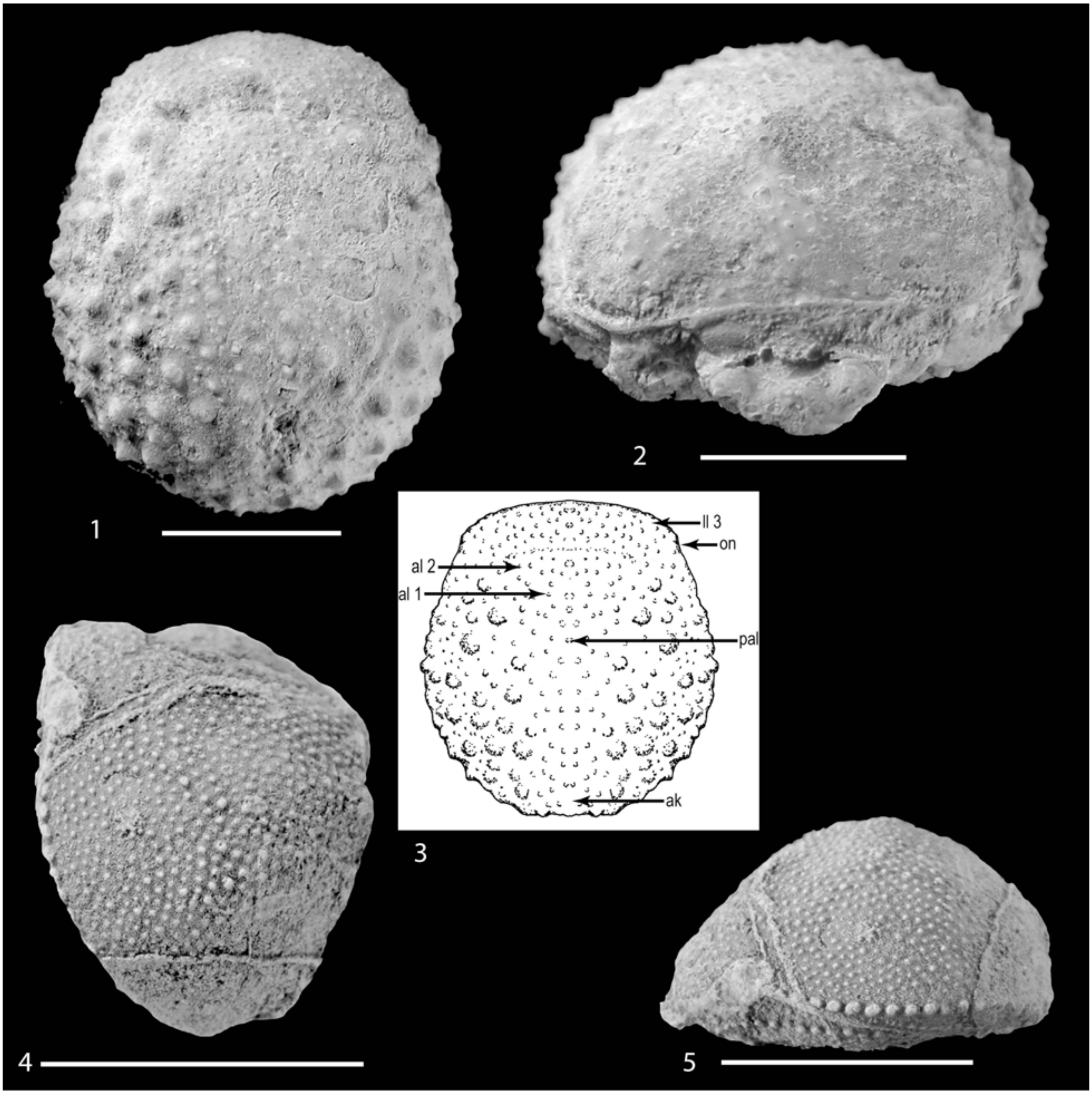


Fig. 18. Hemitrochiscidae. *Oonocarcinus* spp. **1** – *Oonocarcinus insignis* Gemmellaro, 1890, specimen illustrated as pl. 3, fig. 6 (Gemmellaro 1890), dorsal view. **2** – *Oonocarcinus insignis* Gemmellaro, 1890, specimen illustrated as pl. 3, fig. 6 (Gemmellaro 1890), anterior view with labrum. **3** – Line drawing of *O. insignis* with morphology labeled. **4** – *O. puchoviensis* Kittl *in* Trauth, 1918, NHMW 1859/0050/0229a, holotype, dorsal view. **5** – *O. puchoviensis* Kittl *in* Trauth, 1918, NHMW 1859/0050/0229a, holotype, lateral view. Scale bars = 1 cm.

from one another on the basis of their size and the degree of development of ornamentation exhibited on the branchial regions. The smallest individuals, assigned to *O. anceps* by Gemmellaro, have a fine granular surface, judging by his illustrations on pl. 3, figs. 19–21. Larger specimens, illustrated on pl. 3, figs. 14–17, were assigned to *O. geinitzi* and exhibited granular branchial regions. The largest specimens, figured on pl. 3, figs. 3–13, illustrate *O. insignis*. The branchial region on these specimens bear coarser granules than those on the specimens of *O. anceps* or *O. geinitzi*. In fact, the gradient in size and the development of progressively coarser granular surfaces supports the interpretation that the three are size variants of a single species. In other regards, the three are quite similar. The overall highly vaulted, ovoid carapace bearing small, circular orbits situated in the anterolateral corner are characteristics of all the specimens illustrated. In addition, all three species are from the same locality and formation. *Oonocarcinus insignis* is the senior name, based upon page priority, making *O. geinitzi* and *O. anceps* junior synonyms.

A careful search of the Gemmellaro collection in the Museo Geologico G. G. Gemmellaro, of the Università degli Studi Di Palermo by Dott.ssa Carolina D'Arpa, has not yielded any specimens of *Oonocarcinus geinitzi* or *O. anceps*. Specimens of *O. insignis* from that museum supplemented by specimens from United States National Museum, Washington, D. C. confirm the fidelity of Gemmellaro's drawings.

Locality & formation: Sosio Valley, Sicily, Italy; Pietra di Salomone Formation.

Geologic range: Permian (Guadalupian, Wordian); *Waagenoceras* ammonite Zone.

Lithology & environment: Limestones (olistostromes); shallow marine, back-reef lagoon.

Oonocarcinus puchoviensis Kittl in Trauth, 1918
Fig. 18.4, 18.5

1918 *Oonocarcinus puchoviensis* Kittl in Trauth, p. 184.
2018 *Oonocarcinus puchoviensis* Kittl in Trauth, 1918. – Mychko & Alekseev, p. 25.
2019 *Oonocarcinus puchoviensis* Kittl in Trauth, 1918. – Feldmann & Schweitzer, p. 4.

Material examined: Holotype NHMW 1859/0050/0229a.

Measurements: Maximum width of carapace fragment: 13.4 mm.

Diagnosis: Carapace with marginal row of short spines, with two rows of tubercles and a keel ventral to the marginal spines.

Description: Carapace fragment unorientable; moderately vaulted, densely and evenly granular; marginal rim with short, small spines; ventral to the marginal row of spines are 2 rows of smaller tubercles more or less parallel to the marginal spines, one dorsal and one ventral, dorsal row terminating at about position ventral one begins, a keel lies between these two rows of tubercles.

Discussion: This fragment is difficult to identify. It seems to have been associated with *Oonocarcinus* based upon the marginal rows of spines and tubercles.

Locality & formation: Limestone cliffs by Kotskote, east of Púchov, Slovakia; deposits with brachiopods *Amphiclina amoena*.

Geologic range: Upper Triassic (Carnian).

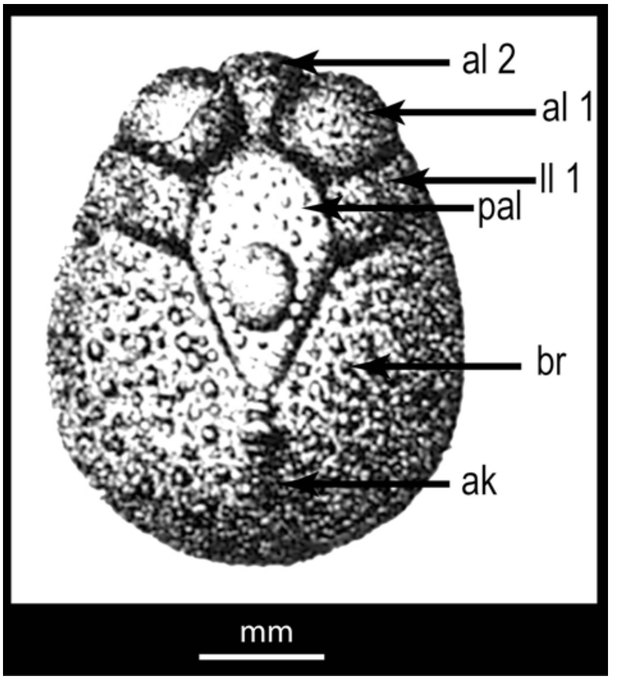


Fig. 19. Hemitrochiscidae. *Paraprosopon reussi* Gemmellaro, 1890. Labeled image from Gemmellaro (1890, pl. 3, fig. 22).

Lithology & environment: Lithified, black, gray wackestone and lithified gray grainstone; deep subtidal.

Genus *Paraprosopon* Gemmellaro, 1890

Type species: *Paraprosopon reussi* Gemmellaro, 1890, by monotypy.

Diagnosis: As for species.

Geologic range: Permian (Guadalupian, Wordian).

Paraprosopon reussi Gemmellaro, 1890
Fig. 19

1890 *Paraprosopon reussi* Gemmellaro, p. 23, pl. 3, fig. 22, pl. 5, fig. 2.
1915 *Paraprosopon reussi* Gemmellaro, 1890. – Stolley, p. 675.
1918 *Paraprosopon reussi* Gemmellaro, 1890. – Trauth, p. 178.
1928 *Cyclus reussi* (Gemmellaro, 1890). – Glaessner, p. 392.
1957 *Cyclus reussi* (Gemmellaro, 1890). – Trümpy, p. 545.

1969 *Cyclus reussi* (Gemmellaro, 1890). – Glaessner, p. R569.
1997 *Paraprosopon reussi* Gemmellaro, 1890. – Schram et al., p. 262.
2008 *Paraprosopon reussi* Gemmellaro, 1890. – Dzik, p. 1512.
2017 *Paraprosopon reussi* Gemmellaro, 1890. – Feldmann et al., p. 407.
2018 *Paraprosopon reussi* Gemmellaro, 1890. – Mychko & Alekseev, p. 25.
2019 *Paraprosopon reussi* Gemmellaro, 1890. – Feldmann & Schweitzer, p. 4.

Diagnosis: Carapace ovate, wider posteriorly; posterior axial, lateral lobes apparently well defined; branchial regions separated by axial keel.

Description: Carapace small, ovate, about 4 mm long and 3 mm wide (Gemmellaro 1890: 23), widest posteriorly; posterior axial lobe elongate ovate, with large axial swelling; first axial lobes paired, spherical; second axial lobe narrowest posteriorly; first lateral lobes extending to lateral margins, rectangular; branchial regions undivided; separated by axial keel; entire carapace surface coarsely granular.

Locality & formation: Sosio Valley, Sicily, Italy; Pietra di Salomone Formation.

Geologic range: Permian (Guadalupian, Wordian); *Waagenoceras* ammonite Zone.

Lithology & environment: Reefal limestones (olistostromes); shallow marine, back-reef lagoon.

Genus *Skuinocyclus* Mychko & Alekseev, 2018

Type and sole species: *Skuinocyclus juliae* Mychko & Alekseev, 2018, by original designation.

Diagnosis: As in Mychko & Alekseev (2018).

Geologic range: Permian (Cisuralian, Asselian).

Skuinocyclus juliae Mychko & Alekseev, 2018
Fig. 20

2018 *Skuinocyclus juliae* Mychko & Alekseev, p. 29, figs. 4, 5.
2019 *Skuinocyclus juliae* Mychko & Alekseev, 2018. – Mychko et al., p. 81.
2019 *Skuinocyclus juliae* Mychko & Alekseev, 2018. – Feldmann & Schweitzer, p. 4.

Material examined: PINRAN 5610/1, holotype.

Diagnosis: As in Mychko & Alekseev (2018).

Description: As in Mychko & Alekseev (2018).

Discussion: One feature not discussed by Mychko & Alekseev (2018) that we label herein is the gastric muscle insertion (gmi). This is clearly expressed on the anterior part of the carapace and resembles muscle scars seen in some brachyurans.

Locality & formation: Shakhtau Quarry, Ishimbay district, Bashkortostan, Russia.

Geologic range: Permian (Cisuralian, Asselian).

Lithology & environment: Reefal limestone; shallow marine, back-reef lagoon.

Family Schraminidae Dzik, 2008

Included genera: *Apionicon* Schram, Vonk & Hof, 1997; *Schramine* Dzik, 2008; *Opolanka* Dzik, 2008; *Yunnanocyclus* Feldmann, Schweitzer & Hu in Feldmann, Schweitzer, Hu, Huang, Zhang, Zhou, Wen, Xie & Maguire, 2017.

Diagnosis: Carapace overall circular, usually with rostral lobe well produced anteriorly and with optic notches at bases; carapace regional development only axial, axial keel may extend nearly entire length of carapace; carapace margins entire or serrate; carapace ornamentation strongly or densely granular either marginally or overall; at least six appendages, anterior-most with sickle-shaped dactyls; caudal furcae extending posteriorly; at least 6 thoracomeres expressed ventrally; gills lamellate, arranged in a horseshoe shaped array.

Geologic range: Lower Pennsylvanian (Bashkirian) to Upper Triassic (Carnian).

Genus *Schramine* Dzik, 2008

Type species: *Halicyne max* Schram, Vonk & Hof, 1997, by original designation.

Included species: *Schramine gondwanae* (Brambilla, Garassino, Pasini & Teruzzi, 2002); *S. madagascariensis* (Brambilla, Garassino, Pasini & Teruzzi, 2002), *S. mamoroi* (Pasini & Garassino, 2007); *S. max*; *S. montanaensis* (Schram, Boere & Thomas, 2006).

Diagnosis: Carapace almost circular in outline, slightly vaulted in cross section, bearing distinct strong papillose ornamentation; marginal rim narrow, with tiny marginal quadrate projections; axial regions well-defined; rostral lobe extending strongly anteriorly; anterior-most appendages with sickle-shaped dactyls, dactyls directed forward.

Discussion: *Schramine* is distinctive in its continuous marginal rim and papillose ornamentation. Dzik (2008) suggested that *Schramine gondwanae*, *S. mamoroi*, and *S. montanaensis* were referable to his new genus *Schramine* by referring them to "*Halicyne*" in the text and *Schramine* in the figure captions. Mychko & Alekseev (2018) referred these three species mentioned here to *Schramine* in addition to *Schramine madagascariensis*. We follow Mychko & Alekseev (2018) in this placement. The five species now referred to *Schramine* differ from Halicynidae in their strong,

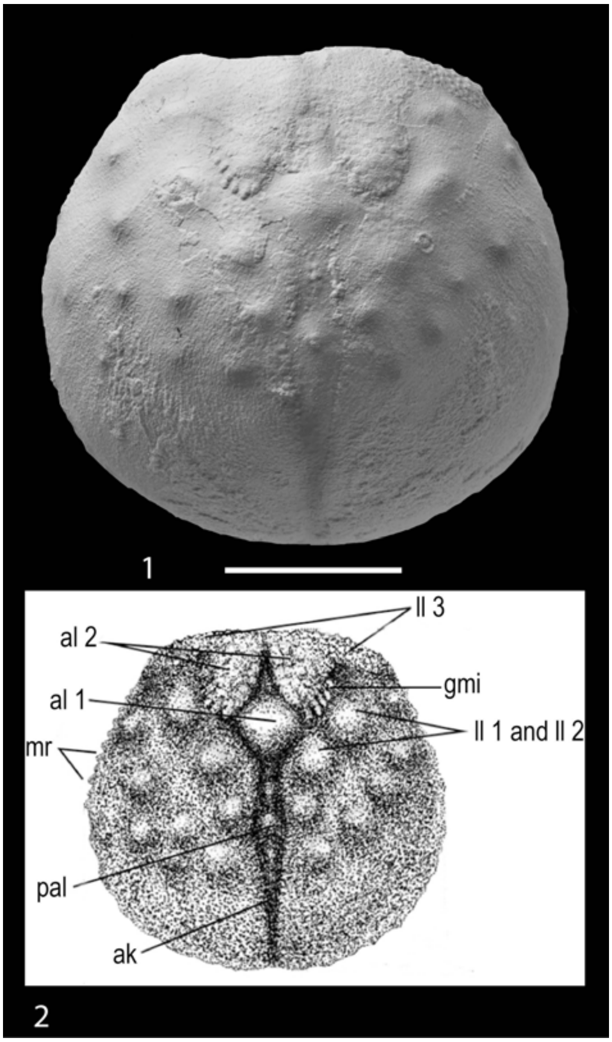


Fig. 20. Hemitrochiscidae. *Skuinocyclus juliae* Mychko & Alekseev, 2018. **1** – PIN 5610/1, holotype, dorsal view. **2** – Line drawing with morphology labeled. Scale bar = 1 cm.

granular ornamentation, rounded carapace, and less-well developed lyrate keels and median concentric keels.

It is quite possible that the three species from Madagascar are synonymous. They all appear to have been collected from the same unit, apparently the Middle Sakamena Formation (Feldmann & Schweitzer 2019), at localities within about 70 kilometers of one another (Brambilla et al. 2002; Pasini & Garassino 2003; Pasini & Garassino 2007). *Schramine madagascariensis* is quite poorly known as is *S. mamoroi*. It is possible that they are less completely preserved specimens of *S. gondwanae*.

Geologic range: Lower Pennsylvanian (Bashkirian) – Lower Triassic (Induan).

Schramine max (Schram, Vonk & Hof, 1997)
Fig. 21.1–21.3

1997 *Halicyne max* Schram, Vonk & Hof, p. 273.
2006 *Halicyne max* Schram et al., 1997. – Schram et al., p. 6.
2007 *Halicyne max* Schram et al., 1997. – Pasini & Garassino, p. 86.
2008 *Schramine max* (Schram et al., 1997). – Dzik, p. 1512.
2017 *Schramine max* (Schram et al., 1997). – Feldmann et al., p. 407.
2018 *Schramine max* (Schram et al., 1997). – Mychko & Alekseev, p. 24.
2019 *Schramine max* (Schram et al., 1997). – Feldmann & Schweitzer, p. 4.

Material examined: FMNH PE 34772, holotype; FMNH PE 11451, 13445, 15233, 18148, 20812, 22453, 24061, 24954, 25662, 28958, 34772.

Diagnosis: Carapace almost circular in outline, slightly vaulted in cross section, bearing distinct strong papillose ornamentation; marginal rim narrow, with tiny marginal quadrate projections; axial regions well-defined; rostral lobe extending strongly anteriorly, with two circular inflations; anterior-most appendages with sickle-shaped dactyls, dactyls directed forward.

Description: Carapace about as long as wide, W/L 0.85–1.05; ornamented overall with large, regularly spaced tubercles (papillae); axial regions well defined, confluent, narrowing posteriorly into axial keel; second and third lateral lobes large, quadrate; rostral lobe extending well-beyond carapace, downturned, frontal margin very weakly convex, lateral margins diverging slightly, with two large circular swellings dorsally; marginal rim narrow, entire, no posterior notch, with tiny, widely spaced peglike projections yielding an overall serrate appearance; gills lamellate, arranged in horseshoe shaped pattern; at least five pairs of appendages, most known only from basal or middle articles; three appendages terminating in long, sickle-like dactyls; first pair short, second pair much longer, third pair shorter than second pair but longer than first pair.

Discussion: *Schramine max* is distinctive in its continuous marginal rim and broadly dispersed tubercles on the carapace. None of the specimens referred to this species retain sternal structures, but gills are preserved in several specimens.

Locality & formation: Peabody Coal Company Pit 11, Will and Kankakee counties, Illinois, USA; Francis Creek Shale Member of Carbondale Formation.

Geologic range: Middle Pennsylvanian (Moscovian).

Lithology & environment: The concretions with fossils occur in localized deposits within silty to sandy mudstones; sediment deposited in marine environment near a deltaic system.

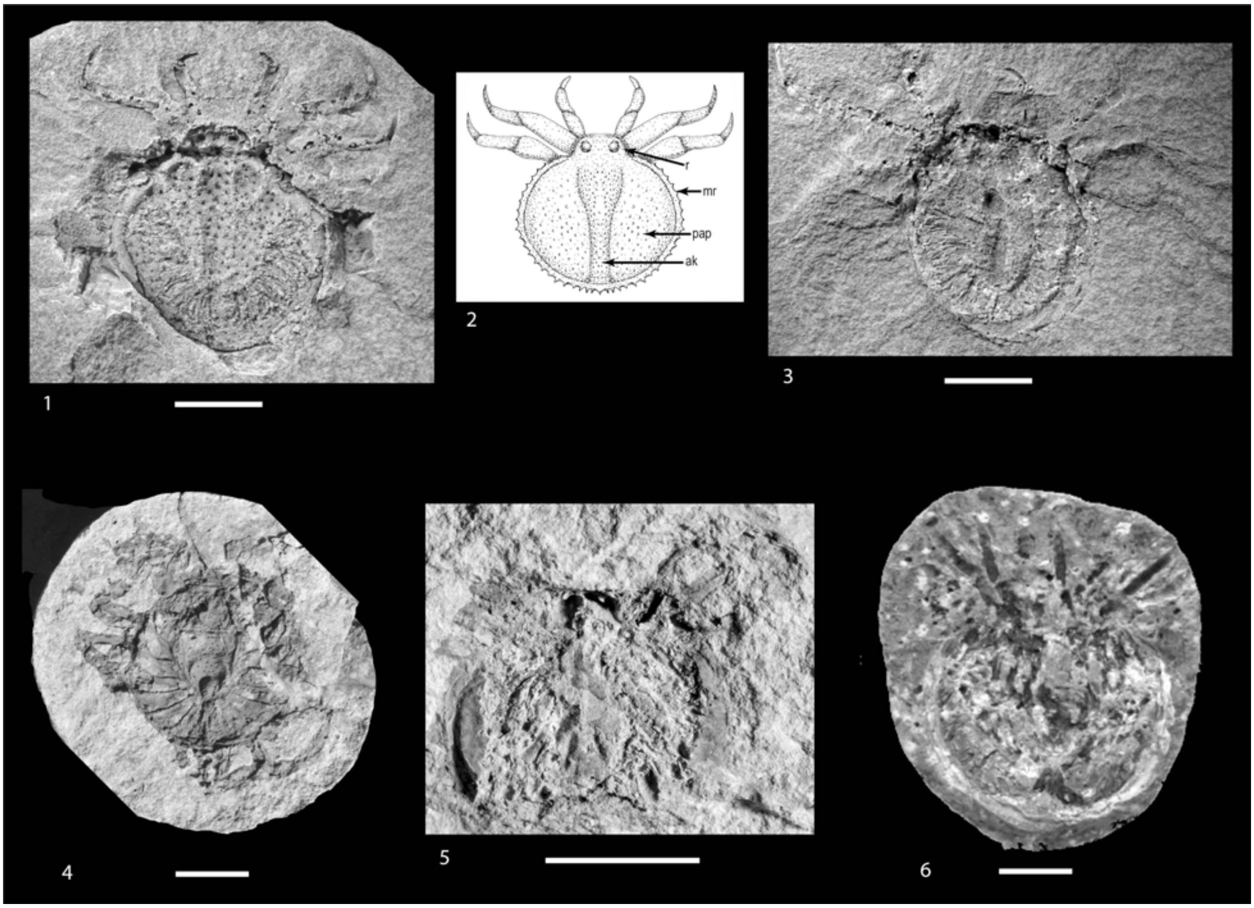


Fig. 21. Schraminidae. *Schramine* spp. **1** – *Schramine max* (Schram, Vonk & Hof, 1997), FMNH PE 34772, holotype. **2** – Line drawing of *S. max* with morphology labeled. **3** – *S. max*, FMNH PE 25662, showing gills. **4** – *S. gondwanae* (Brambilla et al., 2002), MSNM i13280, holotype. **5** – *S. madagascariensis* (Brambilla et al., 2002), MSNM i25462, holotype. **6** – *S. mamoroi* (Pasini & Garassino, 2007), MSNM i26555, holotype. Scale bars = 5 mm. Figures 21.4–21.6 courtesy of A. Garassino.

Schramine gondwanae (Brambilla, Garassino, Pasini & Teruzzi, 2002)
Fig. 21.4

2002 *Halicyne gondwanae* Brambilla, Garassino, Pasini & Teruzzi, p. 111, figs. 3, 4.
2003 *Halicyne gondwanae* Brambilla et al., 2002. – Pasini & Garassino, p. 6.
2006 *Halicyne gondwanae* Brambilla et al., 2002. – Schram et al., p. 6.
2007 *Halicyne gondwanae* Brambilla et al., 2002. – Pasini & Garassino, p. 86.
2008 *Halicyne gondwanae* Brambilla et al., 2002. – Dzik, p. 1508.
2008 "*Halicyne*" *gondwanae* Brambilla et al., 20022. – Dzik, p. 1510.
2017 *Halicyne gondwanae* Brambilla et al., 2002. – Feldmann et al., p. 407.
2008 *Schramine gondwanae* (Brambilla et al., 2002). – Dzik, figs. 7–8, 10 captions.
2018 *Schramine gondwanae* (Brambilla et al., 2002). – Mychko & Alekseev, p. 25.
2019 *Schramine gondwanae* (Brambilla et al., 2002). – Feldmann & Schweitzer, p. 4.

Material examined: MSNM i13280, holotype; MSNM i22868 and i25461, paratypes.

Diagnosis: Carapace circular, about as long as wide, apparently with scattered granules; possibly some regional definition including posterior axial lobe and inner lyrate keel; at least seven thoracic somites preserved, first six sutures terminating at ovate central structure; basal elements of at least six appendages preserved, some may be pseudochelate.

Discussion: This is by far the best preserved species of the Madagascar cyclidans. It retains some features of other cyclidans, such as sternal thoracic segmentation, some regional definition, and appendages, some of which are pseudochelate. It shares with *Schramine max* the papillose ornamentation and circular carapace but differs in having some of the sternal elements preserved.

Locality & formation: Area south of Mahatsara, Ifasy River, Vatovavy-Fitovinany, Madagascar; Middle Karoo Supergroup (Middle Sakamena Group).

Geologic range: Lower Triassic (Induan).

Lithology & environment: Lithified and nodular shale; very shallow conditions, littoral.

Schramine madagascariensis (Brambilla, Garassino, Pasini & Teruzzi, 2002) Fig. 21.5

2002 *Cyclus madagascariensis* Brambilla, Garassino, Pasini & Teruzzi, p. 110, fig. 2.
2017 *Cyclus madagascariensis* Brambilla et al., 2002. – Feldmann et al., p. 407.
2019 *Cyclus madagascariensis* Brambilla et al., 2002. – Feldmann & Schweitzer, p. 4.
2018 *Schramine madagascariensis* (Brambilla et al., 2002). – Mychko & Alekseev, p. 25.

Material examined: MSNM i25462, holotype; MSNM i25460, paratype.

Diagnosis: Carapace ovate, slightly wider than long, marginal rim moderately wide; basal elements of at least three appendages preserved; sternal segmentation indicating at least 5 sternites.

Discussion: Not much detail is known for this species. It appears to retain evidence of sternal segmentation, as well as a marginal rim and appendages, placing it with other cyclidans.

Locality & formation: Area south of Mahatsara, Ifasy River, Vatovavy-Fitovinany, Madagascar; Middle Karoo Supergroup (Middle Sakamena Group).

Geologic range: Lower Triassic (Induan).

Lithology & environment: Lithified and nodular shale; very shallow conditions, littoral.

Schramine mamoroi (Pasini & Garassino, 2007) Fig. 21.6

2007 *Halicyne mamoroi* Pasini & Garassino, p. 86.
2017 *Halicyne mamoroi* Pasini & Garassino, 2007. – Feldmann et al., p. 407.
2008 "*Halicyne*" *mamoroi* Pasini & Garassino, 2007. – Dzik, p. 1509.
2008 *Schramine mamoroi* (Pasini & Garassino, 2007). – Dzik, fig. 9 caption.
2018 *Schramine mamoroi* (Pasini & Garassino, 2007). – Mychko & Alekseev, p. 25.
2019 *Schramine mamoroi* (Pasini & Garassino, 2007). – Feldmann & Schweitzer, p. 4.

Material examined: MSNM i26555, holotype.

Diagnosis: Carapace circular, rimmed entirely around posterior margin; basal elements of at least three appendages preserved.

Discussion: Pasini & Garassino (2007) reported the presence of an eye as well as mandibles and maxillae. Of these, the maxillae appear to be anterior appendages with pseudochelate terminations (Fig. 21.6). The other structures cannot be verified, as the preservation seems to be quite incomplete.

Locality & formation: Mamoro River, Vatovavy-Fitovinany, Madagascar; Middle Karoo Supergroup (Middle Sakamena Group).

Geologic range: Lower Triassic (Induan).

Lithology & environment: Lithified and nodular shale; very shallow conditions, littoral.

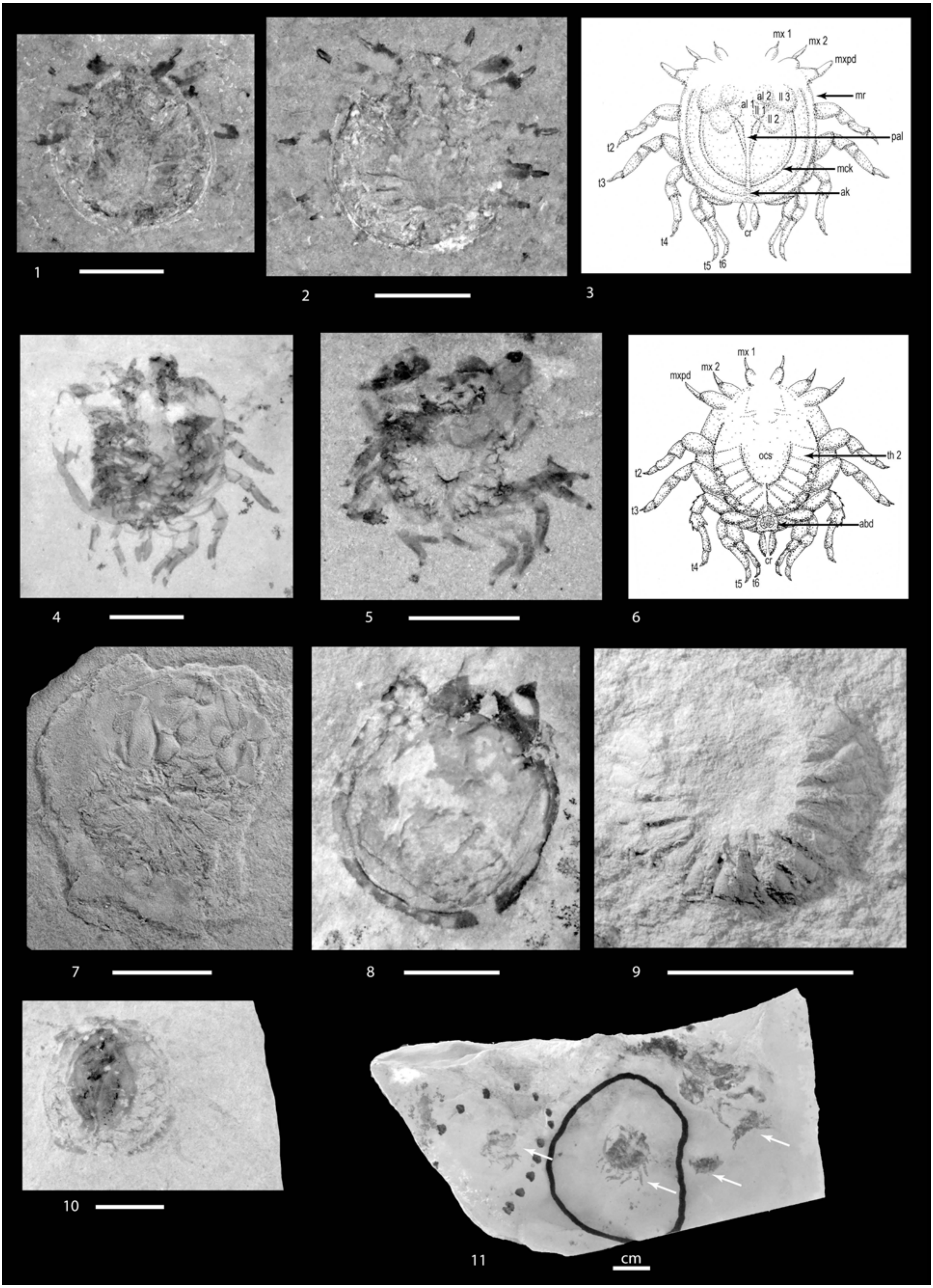
Schramine montanaensis (Schram et al., 2006) Fig. 22

2006 *Halicyne montanaensis* Schram, Boere & Thomas, p. 3.
2007 *Halicyne montanaensis* Schram et al., 2006. – Pasini & Garassino, p. 86.
2008 "*Halicyne" montanaensis* Schram et al., 2006. – Dzik, p. 1510.
2008 *Schramine montanaensis* (Schram et al., 2006). – Dzik, p. 1512.
2017 *Schramine montanaensis* (Schram et al., 2006). – Feldmann et al., p. 407.
2018 *Schramine montanaensis* (Schram et al., 2006). – Mychko & Alekseev, p. 25.
2019 *Schramine montanaensis* (Schram et al., 2006). – Feldmann & Schweitzer, p. 4.

Material examined: LACMIP 7310, holotype; LACMIP 7311–7314, paratypes; CM 53133–53144; UMPC 106033, UMPC 206106 (at least 4 specimens on one slab).

Diagnosis: Carapace circular, about as wide as long, appearing to have been ornamented with widely spaced tubercles; marginal rim narrow, maintaining width continuously around the posterior end of carapace; posterior axial lobe widening anteriorly; first axial lobe widening anteriorly; first lateral lobes circular, second lateral lobes quadrate, inner lyrate keel weak, narrow; at least 7 sternites known; eyes large, multifaceted; thoracic appendages composed of six articles, at least five thoracic appendages known; caudal rami elongate, with lateral setae.

Description: Carapace circular, about as wide as long; anterior end not well preserved; marginal rim narrow, maintaining width for entire extent, smooth. Posterior axial lobe widest anteriorly, narrowing posteriorly into axial keel, merging into first axial lobe; paired second axial lobes small, placed on either side of axis; first lateral lobes small, circular; sec-


1
2
mx 1
mx 2
mxpd
mr
al 2
ll 3
al 1
ll 1
ll 2
pal
t2
mck
t3
ak
cr
t4
t5
t6
3
4
5
mx 1
mx 2
mxpd
th 2
ocs
t2
t3
abd
cr
t4
t5
t6
6
7
8
9
10
11
cm

ond lateral and third lateral lobes much larger, ovate; inner lyrate keel weak; median concentric keel strong; carapace surface ornamented with regularly spaced small tubercles.

Eyes large, multifaceted. Eight pairs of appendages preserved, excluding antennules and antennae (numbering and interpretation of preserved appendages follows SCHRAM et al. 1997: figs. 3.4, 4.1). First 3 pairs of non-antennal appendages appear to be modified as mouthparts, each retaining two distal elements, dactyls sharp, appendages not extending much beyond marginal rim; first pair interpreted as first maxillae, shorter than second and third pairs of appendages, second pair of appendages interpreted as second maxillae, about same size as third pair of appendages, third pair of appendages interpreted as maxillipeds, of same general form as second maxillae.

Five pairs of pediform thoracic appendages, with six visible articles; basal article longer than high, ovate, upper and lower margins convex; second and third articles about as long as high, distal margin of third article with two or three forward-directed spines; fourth article longer than high, lower margin convex, upper margin straight; fifth article short, about as long as high; sixth article appearing to be small, hooked tips.

Ventral surface incompletely preserved; anteriorly with linear structures possibly delineating buccal frame or mandibles; seven thoracic sternites visible, ovate central structure well-developed; sternites becoming shorter posteriorly, with at least one ovate opening at lateral ends; posteriorly with a circular structure with two vertical structures cutting through it which may be part of caudal rami or an abdomen; caudal rami may be composed of two or three segments, terminal segment ovate, with stiff setae on lateral margins.

Discussion: SCHRAM et al. (2006) provided extensive illustrations in his description of *S. montanaensis*. Previously undescribed specimens deposited in the University of Montana Paleontological Collection have added considerably to the description of the species. Whereas the holotype indicates anteriorly placed appendages here interpreted as maxillae 1 and 2 and a maxilliped (Fig. 22.1, 22.2), the new specimens clearly indicate thoracic appendages situated posteriorly (Fig. 22.4, 22.5). In addition, the caudal rami (Fig. 22.4) are clear and may be composed of more than one article. The dorsal carapace presents a median concentric keel not visible in other specimens (Fig. 22.10). Thus, the reconstructions in Figs. 22.3 and 22.6 are composites of multiple specimens. While the carapace regional development is more similar to that seen in Americlidae, the continuous marginal rim suggests placement in Schraminidae is more appropriate.

Notable among the specimens from the University of Montana, UMPC 206106 has at least four individuals preserved proximal to one another (Fig. 22.11). No other examples of multiple specimens preserved in this way are known. This may in part be due to preservational biases, as many cyclidan specimens are found in concretions which seem to preferentially form around one individual. The Montana specimens are flattened and compressed on bedding planes.

Locality & formation: Near Beckett, Montana, USA; Bear Gulch Limestone.

Geologic range: Lower Pennsylvanian (Bashkirian).

Lithology & environment: Limestone; shallow marine or estuarine lagoon.

Genus *Apionicon* SCHRAM, VONK & HOF, 1997

Type and sole species: *Apionicon apioides* SCHRAM, HOF & VONK, 1997, by original designation.

Diagnosis: Carapace longer than wide, W/L 0.73–0.92, longitudinally ovate; with axial keel running entire length of carapace; coarse tubercles ornamenting lateral-most branchial regions and posterior one-quarter of carapace; marginal rim wide, narrowing anteriorly, edge with tiny corrugations.

Discussion: This monotypic genus was originally placed within Cyclidae (SCHRAM et al. 1997). Later FELDMANN & SCHWEITZER (2019) placed it within Hemitrochiscidae, based upon its vaulted carapace and weak regional development. Examination of the holotype and other referred specimens suggests that the genus is best allied with the co-occurring *Schramine* in Schraminidae. It lacks the very strongly vaulted carapace of Hemitrochiscidae, and members of that family appear to have neither a produced rostral lobe anteriorly or a well-developed, flattened marginal rim. Schraminidae can accommodate all of these features. *Apionicon* is not referable to Halicynidae because it lacks the well-developed axial and lateral lobes seen in that family, and it lacks the sinuous frontal margin with optic notches seen in that family. Cyclidae are strongly domed but are characterized by varying levels of ornamentation as well as a marginal rim. The relatively flattened carapace of *Apionicon* suggests better placement in Schraminidae.

Geologic range: Middle Pennsylvanian (Moscovian).

Fig. 22. Schraminidae. *Schramine montanaensis* (SCHRAM et al., 2006). **1** – LACMIP 7310b, holotype, part. **2** – LACMIP 7310a, holotype, counterpart. **3** – composite line drawing of dorsal view with morphology labeled. **4** – UMPC 206106a, ventral view. **5** – UMPC 206106b, ventral view. **6** – Composite line drawing of ventral view with morphology labeled. **7** – CM 55134, molting specimen, dorsal carapace at upper right. **8** – CM 53136, continuous marginal rim. **9** – CM 53144, internal view of thoracic somites. **10** – UMPC 106033, dorsal view, note antennal fragment at upper left and faint silhouettes of appendages on right. **11** – UMPC 206106, slab with four specimens, “b” circled in dashed line, “a” circled in solid line. Scale bars = 5 mm.

Apionicon apioides Schram, Vonk & Hof, 1997
Fig. 23

1997 *Apionicon apioides* Schram, Vonk & Hof, p. 277, figs. 15.4, 17, 18.
2008 *Apionicon apioides* Schram et al., 1997. – Dzik, p. 1512.
2017 *Apionicon apioides* Schram et al., 1997. – Feldmann et al., p. 407.
2018 *Apionicon apioides* Schram et al., 1997. – Mychko & Alekseev, p. 25.
2019 *Apionicon apioides* Schram et al., 1997. – Feldmann & Schweitzer, p. 3.

Material examined: Holotype FMNH PE 22464; paratypes FMNH PE 20613, 22471, 34764.

Diagnosis: As for genus.

Description: Carapace longer than wide, longitudinally ovate; rostral lobe with weakly convex anterior margin, optic notches not well-preserved; axial and lateral lobes not developed; axial keel extending entire length of carapace, appearing to be oblique outer lyrate keels; coarse tubercles ornamenting lateral-most branchial regions and posterior one-quarter of carapace, axial keel with similar tubercles posteriorly; marginal rim wide, flattened, narrowing anteriorly, edge with tiny corrugations; antennules stout, extending laterally; one specimen with hints of caudal rami (Schram et al. 1997, fig. 17.2).

Discussion: This species is not particularly well preserved, although the carapace shape and described ornamentation are visible on multiple specimens. This ornamentation is distinctive and differentiates *Apionicon apioides* from species of *Schramine*, which is granular overall and also is more circular in shape.

Locality & formation: Peabody Coal Company Pit 11, Will and Kankakee counties, Illinois, USA; Francis Creek Shale Member of Carbondale Formation.

Geologic range: Middle Pennsylvanian (Moscovian).

Lithology & environment: The concretions with fossils occur in localized deposits within silty to sandy mudstones; sediment deposited in marine environment near a deltaic system.

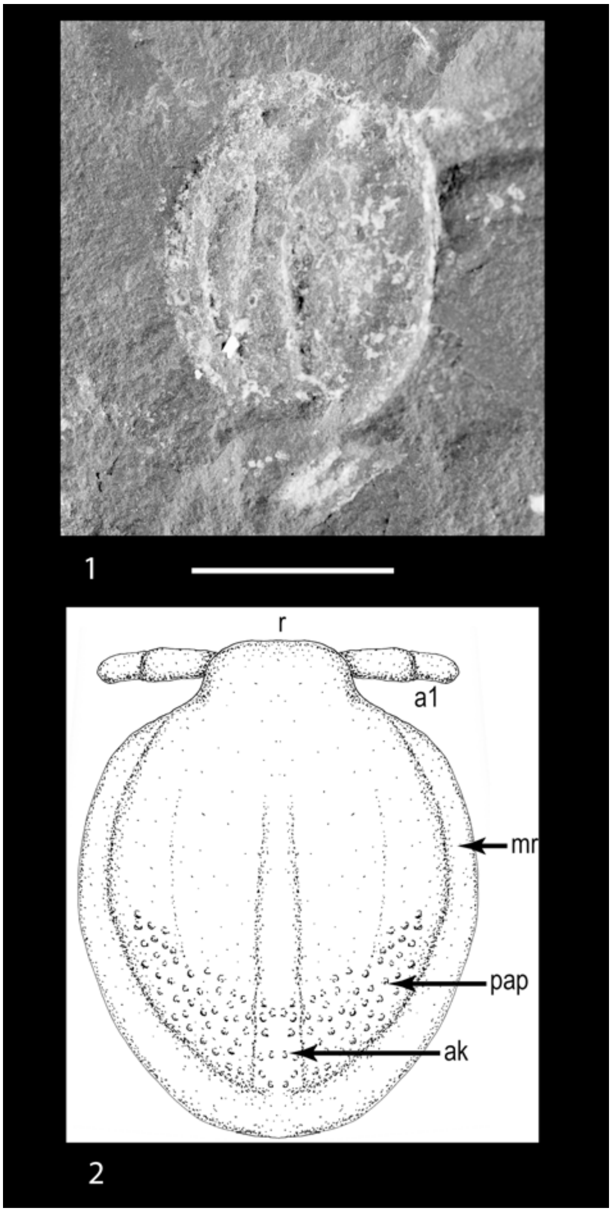


Fig. 23. Schraminidae. *Apionicon apioides* Schram, Vonk & Hof, 1997. **1** – FMNH PE 22464, holotype. **2** – Line drawing with morphology labeled. Scale bar = 5 mm.

Genus *Opolanka* Dzik, 2008

Type species: *Opolanka decorosa* Dzik, 2008, by original designation.

Diagnosis: Carapace ovate, with coarse, widely dispersed papillae; marginal rim wide, flattened, crenulated posteriorly, cut into 6 or so lobes; circular depression appearing to be located at about one-third the distance laterally on the marginal rim; branchial regions appearing to be undifferentiated; gill lamellae well developed on some specimens.

Discussion: Dzik (2008) described this taxon for specimens with weak carapace regional development and a crenulate posterior portion of the rim and placed the genus within Halicynidae. Herein we place *Opolanka* within Schraminidae, based upon its possession of a rostral lobe, absent in Halicynidae, and its entire marginal rim, seen in Schraminidae. *Opolanka* lacks the anteriorly directed optic notches positioned on the frontal margin of the carapace as seen in Halicynidae.

Geologic range: Upper Triassic (Carnian).

Opolanka decorosa Dzik, 2008
Fig. 24

2008 *Opolanka decorosa* Dzik, p. 1517, figs. 1, 2, 4–6.
2013 *Opolanka decorosa* Dzik, 2008. – Żyła et al., p. 140.
2017 *Opolanka decorosa* Dzik, 2008. – Feldmann et al., p. 407.
2018 *Opolanka decorosa* Dzik, 2008. – Mychko & Alekseev, p. 23.
2019 *Opolanka decorosa* Dzik, 2008. – Feldmann & Schweitzer, p. 3.

Material examined: Photograph of ZPAL Ab III/1363, holotype, by J. Dzik.

Diagnosis: As for genus.

Description: As in Dzik (2008).

Locality & formation: Krasiejow, Opole Silesia, Poland, Wesser Formation.

Geologic range: Upper Triassic (Carnian).

Lithology & environment: Claystone; lacustrine deposits.

Genus *Yunnanocyclus* Feldmann, Schweitzer & Hu *in* Feldmann, Schweitzer, Hu, Huang, Zhang, Zhou, Wen, Xie & Maguire, 2017

Type and sole species: *Yunnanocyclus nodosus* Feldmann, Schweitzer & Hu *in* Feldmann, Schweitzer, Hu, Huang, Zhang, Zhou, Wen, Xie & Maguire, 2017, by original designation.

Diagnosis: As in Feldmann et al. (2017).

Discussion: Feldmann et al. (2017) and Feldmann & Schweitzer (2019) considered *Yunnanocyclus* to be a member of Americlidae, based upon its flattened carapace with a strong marginal rim and weak ornamentation. The continuous marginal rim and circular carapace of *Yunnanocyclus*, in addition to the horseshoe array of filamentous gills, suggest placement in Schraminidae might be more appropriate. Among Americlidae, only a trace of the gill area is preserved in *Brittaniclus rankini* (Clark et al. 2020). *Schramine* retains a horseshoe shaped gill array as seen in *Yunnanocyclus*. Most Americlidae possess a bilobate carapace with a posterior notch, which *Yunnanocyclus* lacks. Thus, we place *Yunnanocyclus* within Schraminidae.

Geologic range: Middle Triassic (Anisian).

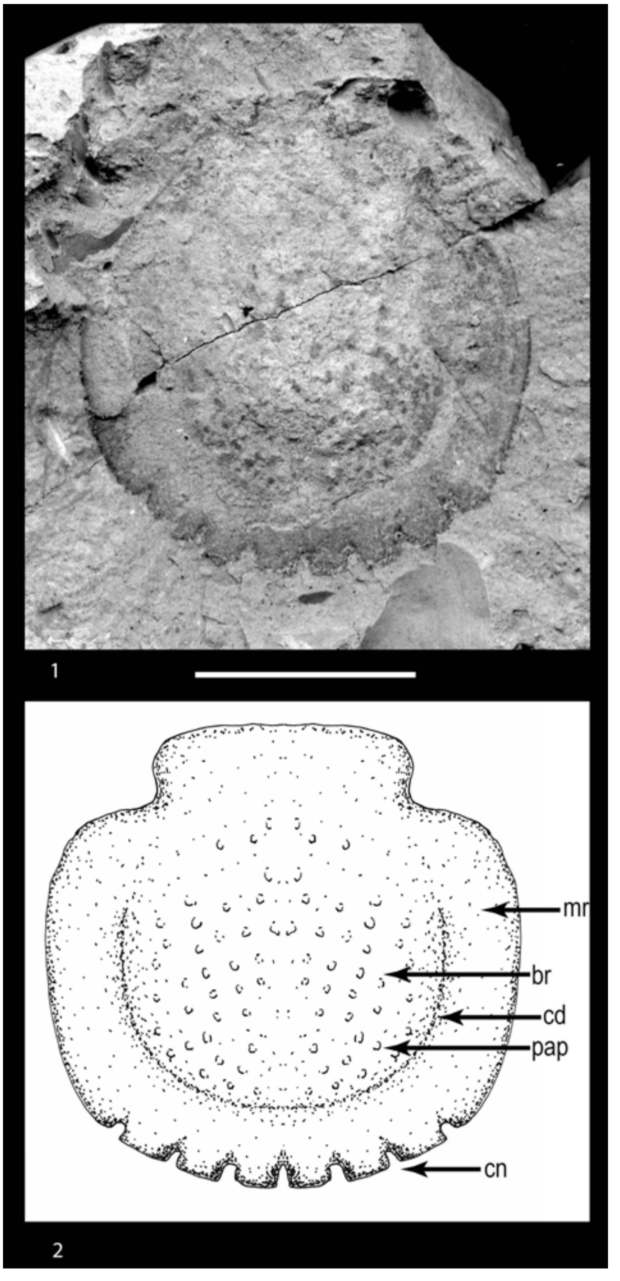


Fig. 24. Schraminidae. *Opolanka decorosa* Dzik, 20008, ZPAL Ab III/1363, holotype. **1** – Dorsal surface, photograph by J. Dzik. **2** – Line drawing with morphology labeled. Scale bar = 1 cm.

Yunnanocyclus nodosus Feldmann, Schweitzer & Hu *in* Feldmann, Schweitzer, Hu, Huang, Zhang, Zhou, Wen, Xie & Maguire, 2017
Fig. 25

2017 *Yunnanocyclus nodosus* Feldmann, Schweitzer & Hu *in* Feldmann, Schweitzer, Hu, Huang, Zhang, Zhou, Wen, Xie & Maguire, p. 408, figs. 2–4.
2018 *Yunnanocyclus nodosus* Feldmann, Schweitzer & Hu *in* Feldmann et al., 2017. – Mychko & Alekseev, p. 25.
2019 *Yunnanocyclus nodosus* Feldmann, Schweitzer & Hu *in* Feldmann et al., 2017. – Feldmann & Schweitzer, p. 2.

Material examined: LPI 33886, holotype; LPI D2239, 32318, 32337, 32347, 32640, 33035, 60315, 60375, 60566, 61172, 61412, 61834, and LLG 1114, paratypes.

Diagnosis: As in Feldmann et al. (2017).

Description: As in Feldmann et al. (2017).

Locality & formation: Dawazi Village, near Luoping, Yunnan Province, China; middle Member of the Guanling Formation.

Geologic range: Middle Triassic (Anisian).

Lithology & environment: Limestone; shallow marine.

Family incertae sedis
Genus *Anhelkocephalon* Bill, 1914
Anhelkocephalon handlirschi Bill, 1914

1914 *Anhelkocephalon handlirschi* Bill, p. 338.
1983 *Anhelkocephalon handlirschi* Bill, 1914. – Schwebel, Gall & Grauvogel, p. 307.
2020 *Anhelkocephalon handlirschi* Bill, 1914. – Schädel & Haug, in press.

Material: As in Schädel & Haug (2020).

Diagnosis: As in Schädel & Haug (2020).

Description: As in Schädel & Haug (2020).

Discussion: We leave the discussion of this taxon and its paleoecology, paleobiogeography, and biostratigraphy to Schädel & Haug (2020).

Locality & formation: Grès à Volzia Formation (Voltziensandstein), France.

Geologic range: Middle Triassic (Anisian).

Lithology & environment: Claystone lenses (Schädel & Haug 2020); freshwater.

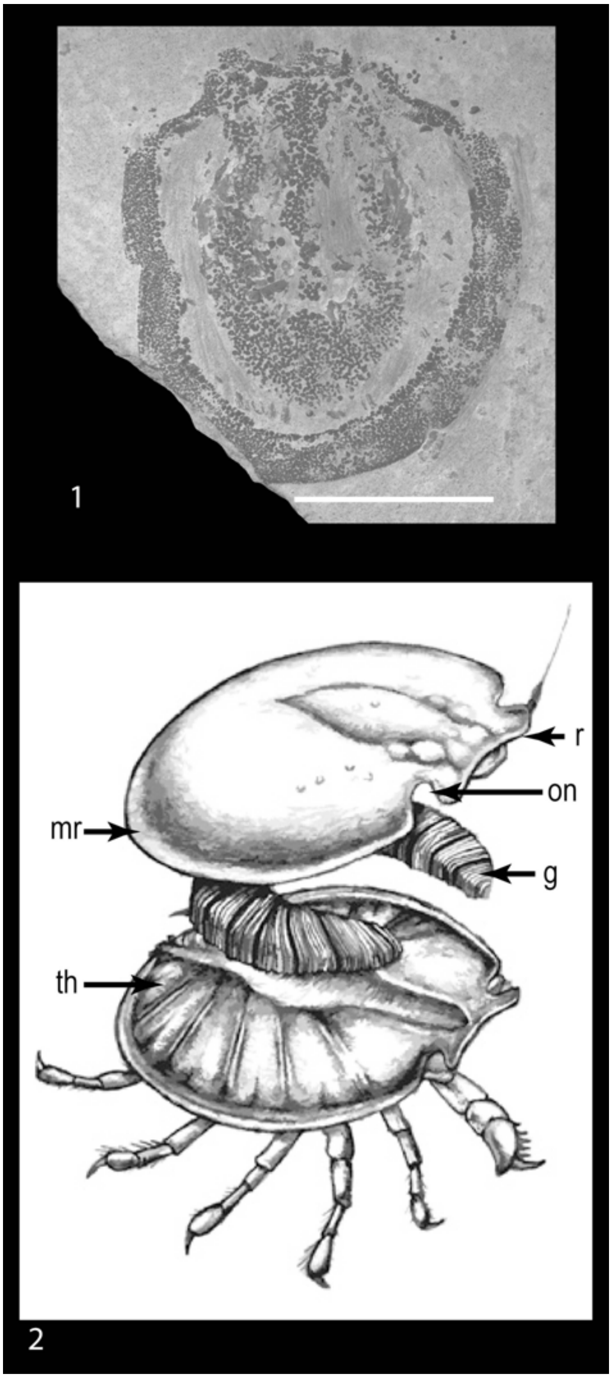


Fig. 25. Schraminidae. *Yunnanocyclus nodosus* Feldmann, Schweitzer & Hu in Feldmann et al. (2017). **1** – LPI 33886, holotype. **2** – Line drawing with morphology labeled; drawing by E. Maguire. Scale bar = 1 cm.

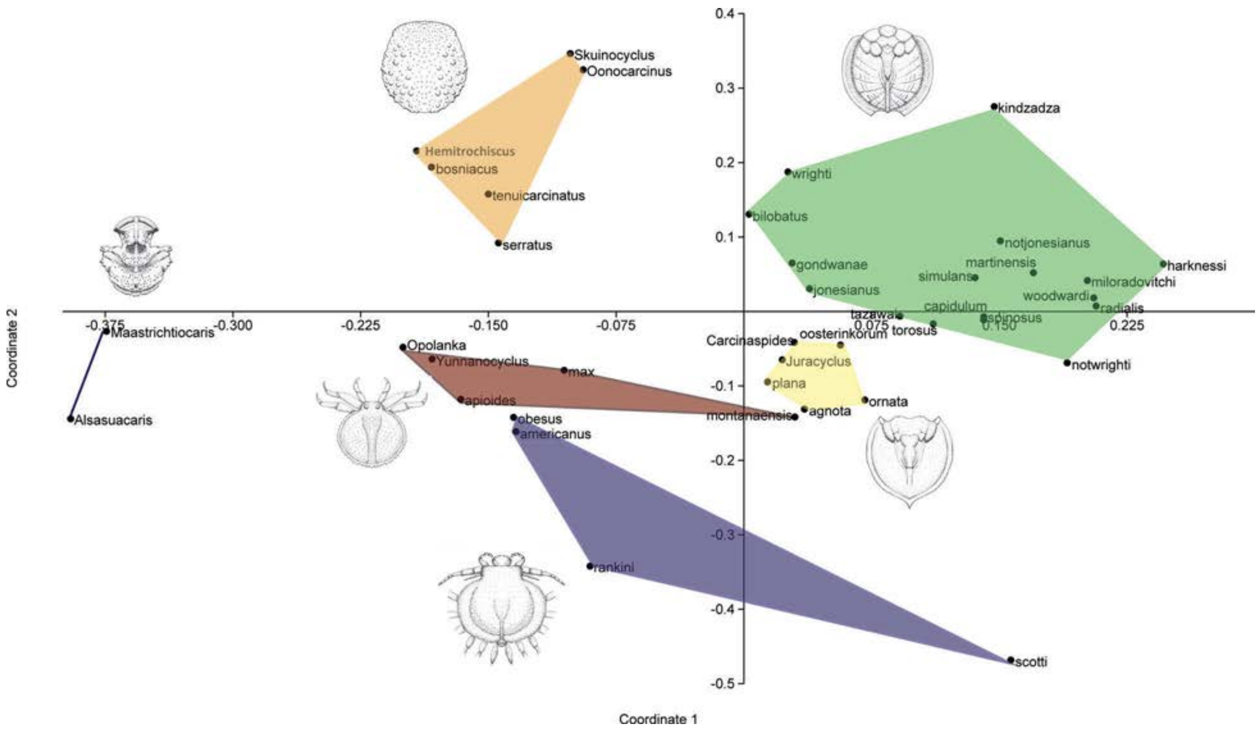


Fig. 26. PCO morphospace analysis (PAST 3.25; Hammer et al. 2001), using Gower Similarity Index, of nearly all cyclidan species, excluding those with very poor preservation. Characters and states in Supplemental Table 2. Statistics in Supplemental Table 3.

3. Discussion

3.1. Morphospace analysis

Morphological characters of the dorsal carapace, appendages, and ventral region, as defined by Feldmann & Schweitzer (2019), were used in the analysis. Unknown character states were scored with a "?" (Supplemental Table 2). Morphospace analysis was conducted using PCO (Gower Similarity index) in PAST version 3.25 (Supplemental Table 3). Families grouped in distinct morphospaces, although Schraminidae and Americlidae nearly overlap and lie close to Halicynidae (Fig. 26). This is probably related to the fact that these three families all have well preserved appendages and ventral surfaces, whereas the other families lack these features. Alsasuacaridae is an outlier, which is not unexpected due to the major differences in carapace ornamentation between this family and the others. Note that this analysis only compares those taxa currently referred to Cyclida and does not include any crustaceans outside of the group. Thus, placement of Cyclida within Crustacea remains untested statistically and we accept the current hypothesis that the group occupies a unique morphospace within Multicrustacea (Clark et al. 2020).

Family groups in this monograph are based upon this morphospace analysis as well as previous placements and discussions (Dzik 2008; Mychko & Alekseev 2018; Feldmann & Schweitzer 2019; Clark et al. 2020). All those genera placed within Cyclidae by these authors grouped together, including only one non-member, *Schramine gondwanae*. This is probably due to the very poor preservation of that species and lack of scorable characters. Indeed, the other species of *Schramine* from Madagascar were not include due to this problem. Species referred to Hemitrochiscidae also grouped together very distinctively. Our analysis suggests that *Apionicon*, *Opolanka*, and *Yunnanocyclus* are better placed within Schraminidae as compared to previously family placements. This appears to be due to the continuous marginal rim with no posterior notch as well as the lack of median concentric keels and other ornamentation.

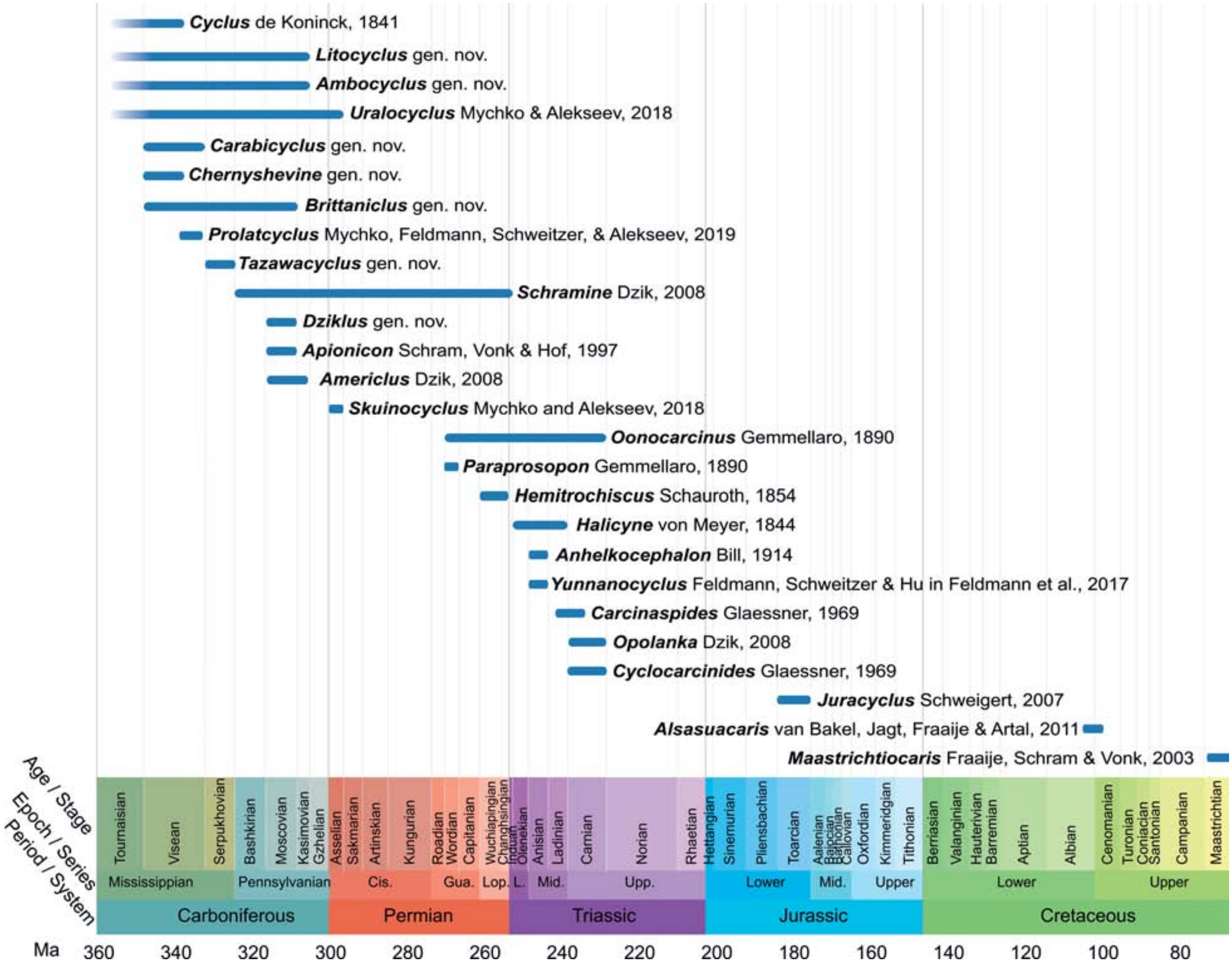


Fig. 27. Biostratigraphic range of all genera within Cyclida.

3.2. Biostratigraphy

Cycloida ranges from the Early Mississippian to the Late Cretaceous (Fig. 27). Note that the group survived the end-Permian mass extinction, being reduced in numbers in the Early Permian and recovering former diversity by the Middle Triassic. The earliest occurrences are those of Cyclidae in the Mississippian and Pennsylvanian, followed closely by Americlidae and Schraminidae. Cyclidae and Americlidae did not survive past the Early Permian. Schraminidae survived into the early Triassic. Hemitrochiscidae appeared in the Early Permian and peaked in the Middle Triassic. Halicynidae appeared in the Early Triassic, peaked in diversity in the Middle Triassic, and became extinct during the Jurassic. Alsasuacaridae are only known from the Late Cretaceous.

3.3. Paleobiogeography

Cyclida was primarily dispersed in coastal Laurussia during the Carboniferous with the exception of one species in northeastern Gondwana (now Japan) (Fig. 28). Permian occurrences are more or less Tethyan, and all Mesozoic occurrences are European except those in what is now Madagascar. North America lacks marine Triassic and Jurassic rocks in large quantities so this could help explain the absence of the group there.

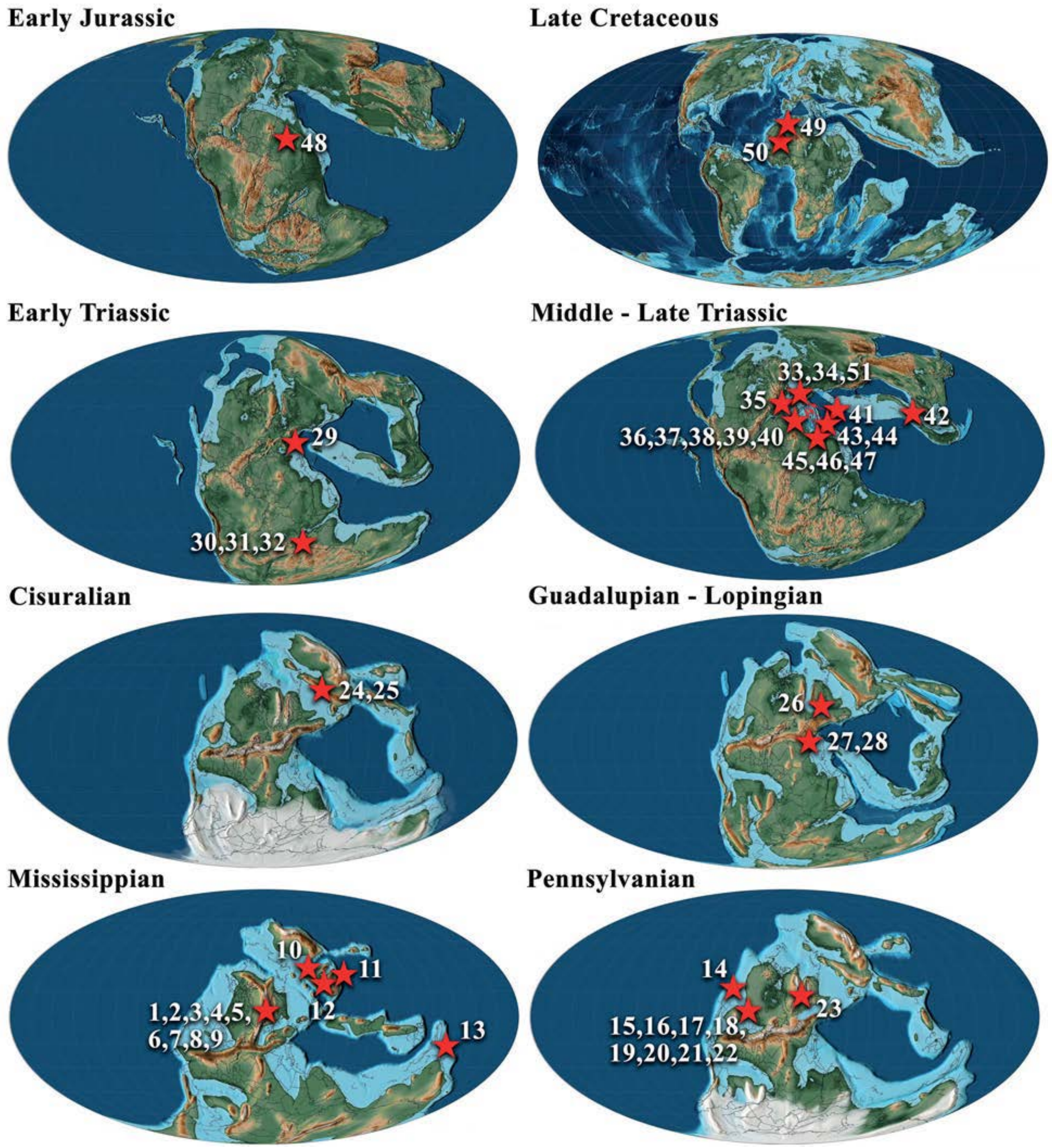


Fig. 28. Paleobiogeographic distribution of all known species of Cyclida. Stars mark localities; numbers – species: **1** – *Brittaniclus rankini*; **2** – *Brittaniclus testudo*; **3** – *Carabicyclus wright*; **4** – *Cyclus radialis*; **5** – *Litocyclus bilobatus*; **6** – *Litocyclus torosus*; **7** – *Litocyclus jonesianus*; **8** – *Prolatcyclus martinensis*; **9** – *Uralocyclus woodwardi*; **10** – *Ambocyclus capidulum*; **11** – *Chernyshevine spinosus*; **12** – *Prolatcyclus kindzadza*; **13** – *Tazawacyclus tazawai*; **14** – *Schramine montanaensis*; **15** – *Ambocyclus minutus*; **16** – *Americlus? limbatus*; **17** – *Americlus? packardi*; **18** – *Apionicon apioides*; **19** – *Dziklus obesus*; **20** – *Litocyclus communis*; **21** – *Litocyclus permarginatus*; **22** – *Schramine max*; **23** – *Brittaniclus scotti*; **24** – *Skuinocyclus juliae*; **25** – *Uralocyclus miloradovitchi*; **26** – *Hemitrochiscus paradoxus*; **27** – *Paraprosopon reussi*; **28** – *Oonocarcinus insignis*; **29** – *Halicyne ornata*; **30** – *Schramine gondwanae;* **31** – *Schramine madagascariensis*; **32** – *Schramine mamoroi*; **33** – *Opolanka decorosa*; **34** – *Halicyne silesiensis*; **35** – *Halicyne oosterinkorum*; **36** – *Carcinaspides pustulosus*; **37** – *Halicyne plana*; **38** – *Halicyne laxa*; **39** – *Halicyne agnota*; **40** – *Halicyne ornata*; **41** – *Cyclocarcinides bosniacus*; **42** – *Yunnanocyclus nodosus*; **43** – *Cyclocarcinides tenuicarinatus*; **44** – *Oonocarcinus puchoviensis*; **45** – *Cyclocarcinides serratus*; **46** – *Cyclocarcinides reticulatus*; **47** – *Cyclocarcinides stellifer*; **48** – *Juracyclus posidoniae*; **49** – *Alsasuacaris nostradama*; **50** – *Maastrichtiocaris rostrata*; **51** – *Anhelkocephalon handlirschi*. Maps from Scotese (2014a; 2014b; 2014c; 2014d).

3.4. Paleoecology

Most likely, we greatly underestimate the true taxonomic diversity of cyclidans, as well as their adaptations. Apparently, cyclidans, like crabs, occupied a variety of ecological niches and habitats. Our review has helped us appreciate this diversity. Many Carboniferous and Permian members of Cyclida are confined to reef and near reef facies (e.g., deposits of backreef lagoon). For example, the Viséan genus *Prolatcyclus* occurs in the reefs of England and the South Urals (Russia). Another cyclid, *Ambocyclus simulans*, was discovered from the Lower Carboniferous reef limestone of Ireland. *Uralocyclus miloradovitchi* and *Skuinocyclus juliae* are known from the Lower Permian reefal limestones in the Urals (Russia) exclusively. Cyclidans from the Wordian olistostromes of Sosio Valley (Italy), namely *Paraprosopon reussi* and *Oonocarcinus insignis*, are confined to reefal facies also. One of the youngest cyclidans, *Alsasuacaris nostradamus*, was found in Cretaceous reef limestones with corals in Spain.

Despite belonging to different families, all cyclidans that inhabited reefs are small in size and had strongly convex carapaces with various levels of ornamentation. Unfortunately, we do not have any evidence of appendages of reef cyclidans, so we cannot fully discuss their morphological-environmental characteristics. Most likely, by analogy with modern crab-dwellers of reefs, these cyclidans fed on organic debris in ancient reefs, crawling between various reef-forming structures.

Some cyclidans were found in deep-water deposits. For example, *Juracyclus posidoniae* comes from the famous Early Jurassic "Posidonia Shale," which was formed in an oxygen-depleted, off-shore shelf environment. Other older members of the genus *Cyclocarcinides* are described from the Upper Triassic (Carnian) Alps. They were discovered in red micritic limestones with a predominantly pelagic fauna and low clay content, which were possibly formed in deep sea environments. *Oonocarcinus puchoviensis* from the Upper Triassic (Carnian) of Slovakia comes from black and gray wackestone and lithified gray grainstones, which formed in deep offshore environments.

In most cases, cyclidan specimens are found in limestones, rarely in sandstones and shales. Thus, most of the known cyclidans were found in marine deposits. However, these seas had different salinities. For example, the species *Hemitrochiscus paradoxus* is described from Zechstein deposits. The Zechstein Sea was a very warm and very salty epicontinental sea that existed in the Guadalupian and Lopingian. The Zechstein Sea occupied the region of what is now the North Sea, plus lowland areas of Britain and the north European plain through Germany and Poland.

There are several cyclidan species known from transitional marine to lake conditions. For example, *Halicyne plana* originates from the Ladinian Erfurt Formation in Thuringia. The Erfurt Formation is known for its vertebrate fossils. Different kinds of fish, amphibians and archosauriforms have been found, suggesting a lake or brackish environment. The taxa from the Mazon Creek localities of the Carbondale Formation are also probably marginal marine, as the environment is interpreted as marine near a deltaic system (Clements et al., 2019). One freshwater cyclidan is known for certain: *Opolanka decorosa* comes from the lake deposits of Krasiejow in the Polish Opole Silesia. It should be noted that *O. decorosa* is the largest cyclidan, up to 6 cm in size. For freshwater and transitional brackish water to freshwater, relatively large sizes and a flattened carapace are observed.

Only a few cyclidan localities have yielded more than one species (Supplemental Table 4). The Mississippian Yorkshire and Irish localities have species of several different genera; thus, it is likely that most of the species at each location are distinct. Those species from the Mazon Creek locations are all referred to different genera as well. The species of Rogers (1902) from the Iola Limestone are lost; however, his illustrations suggest that each is unique. Thus, it appears that assemblages of cyclidans existed, at least in the Paleozoic, wherein multiple taxa shared an environment similar to the situation for crabs and lobsters today.

Acknowledgements

Numerous individuals provided us with access to the collections at their institutions for our study: Claire Mellish (NHMUK); Alessandro Garassino (MSNM); Matthew Riley & Sarah Hammond (SM); David Gelsthorpe (MM); Paul Shepherd, British Geological Survey, Nottingham, England, UK; Andrew Ross (NMS.G); Neil Clark (GLAHM); Kathy Hollis & Mark Florence (USNM Paleobiology); Shixue Hu, Chengdu Institute of Geology and Mineral Resources and China Geological Survey, Chengdu, China. Numerous individuals implemented loans of specimens for this study: Kathy Hollis & Mark Florence (USNM Paleobiology); David Gelsthorpe (MM); Paul Shepherd (GSM); Austin Hendy (LACMIP); Albert Kollar (CM); Joe Hannibal (CMNH); Bruce Lauer (LF); Scott Lidgard (FMNH); Eckhard Mönnig (NMC); Andreas Kroh (NHMW); Carolina D'Arpa, Museo Geologico G.G. Gemmellaro, Palermo, Italy; Rolf Beutel (FSUJIG); Kallie Moore (UMPC); and Charles Shabica (MCP). Mellish and photographer (NHMUK) provided virtual loans of cyclidans. Numerous individuals provided photographs for this study: Alessandro Garassino (MSNM), Jerzy Dzik, Instytut Paleobiologii, Polska Akademia Nauk, Warsaw, Poland; Barry W.M. van Bakel, Oertijdmuseum, Boxtel, The Netherlands; Günter Schweigert (SMNS); Simon Harris, British Geological Survey, Nottingham, England, UK; Jean-Claude Gall, Université de Strasbourg, France; Heinz Furrer, Palaeontological Museum of Zurich University, Switzerland; Nina Kadlec & Daria Pinachina, Academician F.N. Chernyshev Central scientific research geological survey museum of St. Petersburg, Russia. Editor Toshiko Sawaki granted permission to use an image from the Journal of the Geological Society of Japan. The Communications and Science Promotion Department of PAN and PWN granted permission to use an image from the Bulletin of the Polish Academy of Sciences, Sciences of the Earth. Several individuals provided or confirmed our interpretation of stratigraphic information for various species occurrences in their respective countries: Günter Schweigert; Louise Neep, British Geological Survey, Nottingham, England, UK; Neil Clark (GLAHM); Patrick Wyse Jackson, Trinity College, Dublin, Ireland; Sylvain Charbonnier, Muséum nationale d'Histoire naturelle, Paris, France; René H.B. Fraaije, Oertijdmuseum, Boxtel, The Netherlands; Adiel Klompmaker, University of Alabama, USA; Michał Krobicki, Polish Geological Institute, Krakow, Poland; and Carolina D'Arpa. Krobicki, Mike Reich (Bayerische Staatssammlung für Paläontologie und Geologie München), Schweigert, Eckbert Seibertz (Technische Universität Braunschweig); and Ingmar Werneburg (Universität Tübingen) helped determine the fate of many lost specimens. Frederick Schram provided numerous helpful discussions about this group of animals as did Neil Clark. Evin Maguire made the line drawing of *Yunnanocyclus nodosus*. Cynthia Trocchio assisted with translations from original German descriptions. Samm Schinker compiled data, labeled photographs, and described species.

References

Akagi, S. (1971): Lower Permian arthropods from the Taishaku Limestone, southwest Japan. – Journal of the Faculty of Science of Tottori University, Natural Science, **22**: 79–86.

Alberti, F. von (1864): Ueberblick über die Trias, mit Berücksichtigung ihres Vorkommens in den Alpen. – 353 pp.; Stuttgart (Cotta). doi: 10.5962/bhl.title.14903

Alexandrowicz, S.W. (1973): *Halicyne* (Crustacea *incertae sedis*) aus den Rötdolomiten des Oberschlesischen Beckens. – Bulletin of the Polish Academy of Sciences, Sciences of the Earth, **20**: 257–263.

Bill, P.C. (1914): Ueber Crustaceen aus dem Voltziensandstein des Elsasses. – Mitteilungen der Geologischen Landesanstalt von Elsass-Lotharingen, **8**: 289–338.

Boxshall, G.A. & Jaume, D. (2009): Exopodites, epipodites and gills in crustaceans. – Arthropod Systematics & Phylogeny, **67**: 229–254.

Brambilla, S., Garassino, A., Pasini, G. & Teruzzi, G. (2002): Studies of Permo-Trias of Madagascar. 6. First record of Cycloidea from the Lower Triassic (Olenekian) of Ambilobé region (NW Madagascar). – Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano, **143**: 105–115.

British Geological Survey (2020): The BGS Lexicon of Named Rock Units. [bgs.ac.uk/Lexicon].

Brown, R.W. (1956): Composition of Scientific Words. – 882 pp.; Baltimore (Reese Press).

Bürgin, T., Eichenberger, U., Furrer, H. & Tschanz, K. (1991): Die Prosanto-Formation – eine fischreiche Fossil-Lagerstätte in der Mitteltrias der Silvretta Decke (Kanton Graubünden, Schweiz). – Eclogae geologicae Helveticae, **84** (3): 921–990.

Busse, E. & Horn, M. (1978): Neue Fossilfunde im Mittleren Buntsandstein NW-Hessens und ihre Bedeutung für die Paläogeographie. – Geologisches Jahrbuch Hessen, **106**: 131–142.

Chernyshev, B.I. (1933): Arthropoda s Urala i drugikh mest SSSR. VII. Predstaviteli roda *Cyclus* iz nizhnego karbona Urala i Turkestana. Materialy Tsentralnogo Nauchno-issledovatelskogo geologo-razvedochnogo instituta, sbornik 1. Paleontologia i stratigrafia: 20–21 (in Russian with English summary).

Clark, N.D.L. (1989): A study of a Namurian crustacean-bearing shale from the Western Midland Valley of Scotland. – Unpublished Ph.D. thesis, University of Glasgow, Scotland.

Clark, N.D.L., Feldmann, R.M., Schram, F.R. & Schweitzer, C.E. (2020): Redescription of *Americlus rankini* (Pancrustacea: Cyclida: Americlidae) and interpretation of its systematic placement, morphology, and paleoecology. – Journal of Crustacean Biology, doi: 10.1093/jcbiol/ruaa001.

Clements, T., Purnell, M. & Gabbott, S. (2019): The Mazon Creek Lagerstätte: a diverse late Paleozoic ecosystem entombed within siderite concretions. – Journal of the Geological Society, **176**: 1–11. doi: 10.1144/jgs2018-088

Coates, M.I. & Sequeira, S.E.K. (2001): A new stethacanthid chondrichthyan from the Lower Carboniferous of Bearsden, Scotland. – Journal of Vertebrate Paleontology, **21**: 438–459. doi: 10.1671/0272-4634(2001)021[0438:ANSCFT]2.0.CO;2

Dzik, J. (2008): Gill structure and relationships of the Triassic cycloid crustaceans. – Journal of Morphology, **269**: 1501–1519. doi: 10.1002/jmor.10663 PMID: 18690662

Dzik, J. & Sulej, T. (2007): A review of the early Late Triassic Krasiejów biota from Silesia, Poland. – Palaeontologica Polonica, **64**: 3–27.
Edgecombe, G.D. & Legg, D.A. (2014): Origins and early evolution of arthropods. – Palaeontology, **57** (3): 457–468. doi: 10.1111/pala.12105
Falconnet, J., Andriamihaja, M., Läng, E. & Steyer, J.-S. (2012): First procolophonid (Reptilia, Parareptilia) from the Lower Triassic of Madagascar. – Comptes Rendus Palevol., **11**: 357–369. doi: 10.1016/j.crpv.2012.04.001
Feist-Burkhardt, S., Götz, A.E., Szulc, J. et al. (2008): Triassic. – In: McCann, T. (ed.): The Geology of Central Europe. Volume **2**: Mesozoic and Cenozoic. – The Geological Society of London: 749–822.
Feldmann, R.M. & Schweitzer, C.E. (2019): The enigmatic Cyclida (Pancrustacea): morphological terminology and family-level classification. – Journal of Crustacean Biology, **39**: 617–633. doi: 10.1093/jcbiol/ruz053
Feldmann, R.M., Schweitzer, C.E., Hu, S., Huang, J., Zhang, Q., Zhou, C., Wen, W., Xie, T. & Maguire, E.P. (2017): A new Middle Triassic (Anisian) cyclidan crustacean from the Luoping Biota, Yunnan Province, China: morphologic and phylogenetic insights. – Journal of Crustacean Biology, **37**: 406–412. doi: 10.1093/jcbiol/rux052
Fraaije, R.H.B., Schram, F.R. & Vonk, R. (2003): *Maastrichtiocaris rostratus* new genus and species, the first Cretaceous cycloid. – Journal of Paleontology, **77**: 386–388. doi: 10.1017/S0022336000043729
Furrer, H. (2019): Fische und Saurier aus dem Hochgebirge: Fossilien aus der mittleren Trias bei Davos. – Neujahrsblatt der Naturforschenden Gesellschaft in Zürich, NGZH, **221**.
Gall, J.-C. (1971): Faunes et paysages du Grès à Voltzia du Nord des Vosges. – Essai paléoécologique sur le Buntsandstein supérieur. – Mémoires du Service de la Carte Géologique d'Alsace et de Lorraine, **34**: 318 pp.
Gall, J.-C. & Grauvogel, G. (1967): Faune du Buntsandstein II. Les Halicynés. – Annales de Paléontologie, **53**: 3–14.
Garassino, A. & Pasini, G. (2002): Studies on Permo-Trias of Madagascar. 5. *Ambilobeia karojoi* n. gen., n. sp. (Crustacea, Decapoda) from the Lower Triassic (Olenekian) of Ambilobè region (NW Madagascar). – Atti della Società italiana di Scienze Naturali e del Museo civico di Storia naturale in Milano, **143** (1): 95–104.
Gawlick, H.-J., Missoni, S., Sudar, M.N, Goričan, Š., Lein, R., Stanzel, A.I. & Jovanić, D. (2017): Open-marine Hallstatt Limestones reworked in the Jurassic Zlatar Mélange (SW Serbia): a contribution to understanding the orogenic evolution of the Inner Dinarides. – Facies, **63**: 29 doi: 10.1007/s10347-017-0510-3).
Gemmellaro, G.G. (1890): I crostacei dei clacari con *Fusulina* della Valle del Fiume Sosio nella Provincia di Palermo in Sicily. – Memorie della Società Italiana delle Scienze, **8**: 1–29.
Glaessner, M.F. (1928): Zur Frage der ältesten fossilen Krabben. – Centralblatt für Mineralogie, Geologie und Paläontologie, Abteilung B, **6**: 388–398.
Glaessner, M.F. (1969): Cycloidea. – In: Moore, R.C. (ed.): Treatise on Invertebrate Paleontology, Part R, Arthropoda 4, Volume 2: R567–R570; Lawrence (Geological Society of America & University of Kansas Press).
Goldring, R. (1967): *Cyclus martinensis* sp. nov. (Crustacea) from the Upper Viséan of the Mendip Hills, England. – Palaeontology, **10**: 317–321.
Gruber, B. (1975): Unternorische Halobien (Bivalvia) aus Bosnien, Jugoslawien. – Österreichische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Abteilung I, **183** (4–7): 119–130.
Guérin Méneville, F.E. (1838): Première Division. Crustacés, Arachnides et Insects. – In: Voyage autour du monde, éxecuté par ordre du Roi, sur la corvette de la Majesté, La Coquille, pendant les années 1822, 1823, 1824 et 1825, pp. 9-319, pls. 1–21 (Atlas). Paris (Arthus Bertrand).
Haack, W. (1923): Zur Stratigraphie und Fossilführung des Mittleren Buntsandsteins in Norddeutschland. – Jahrbuch der Preußischen Geologischen Landesanstalt zu Berlin, **42**: 589–594.
Hagdorn, H. (2015): Wirbellose des Lettenkeupers. – In: Hagdorn, H., Schoch, R. & Schweigert, G. (eds.): Der Lettenkeuper – ein Fenster in die Zeit vor den Dinosauriern. – Palaeodiversity, Special Issue: 107–140.
Hammer, Ø., Hammer, D.A.T. & Ryan, P.D. (2001): PAST: Paleontological Statistics software package for education and data analysis. – Palaeontologia Electronica, **4** (1): 9 pp.
Histon, K. (1997): Nautiloid species from the Carboniferous of Ireland. – Irish Journal of Earth Sciences, **16**: 45–60.
Hopwood, A.T. (1925): On the family Cyclidae Packard. – The Geological Magazine, **62** (7): 289–309. doi: 10.1017/S0016756800105606
Hyžný, M., Haug, C. & Haug, J.T. (2016): *Mesoprosopon triasinum* from the Triassic of Austria revisited: the oldest eumalacostracan larva known to date and its significance for interpreting fossil cycloids. – Gondwana Research, **37**: 86–97. doi: 10.1016/j.gr.2016.05.010
International Code of Zoological Nomenclature (1999): International Commission on Zoological Nomenclature, Fourth Edition: 306 pp.
Jones, W.T., Feldmann, R.M., Schweitzer, C.E., Reitano, A. & Insacco, G. (2015): New pygocephalomorph (Peracarida) from the Permian of the Sosio Valley (Sicily, Italy). – Journal of Crustacean Biology, **35**: 627–632. doi: 10.1163/1937240X-00002367
Klompmaker, A.A., Artal, P., van Bakel, B.W.M., Fraaije, R.H.B. & Jagt, R.H.B. (2011): Etyid crabs (Crustacea, Decapoda) from mid-Cretaceous reefal strata of Navarra, Northern Spain. – Palaeontology, **54**: 1199–1212. doi: 10.1111/j.1475-4983.2011.01072.x
Koninck, L.G. de (1842): B. Cycloides. – In: Koninck, L.G. de (ed.): Description des animaux fossiles qui se trouvent dan le terraine Carbonifère de Belgique, Liége.
Kozur, H.W. & Weems, R.E. (2010): The biostratigraphic importance of conchostracans in the continental Triassic of the northern Hemisphere. – In: Lucas, S.G. (ed.): The Triassic Timescale. – Geological Society of London, Special Publications **334** : 315–417. doi: 10.1144/SP334.13

Kramarenko, N.N. (1961): Predstavitel' Cyclidae (Crustacea) iz nizhnepermskikh otlozheniy Priuralia. – Paleontologicheskiy Zhurnal, **2**: 86–89 (In Russian).

Legg, D.A., Sutton, M.D. & Edgecombe, G.D. (2013): Arthropod fossil data increase congruence of morphological and molecular phylogenies. – Nature Communications, **4**: 2485 . doi: 10.1038/ncomms3485 PMID: 24077329

Linck, O. (1961): Ein weiterer Fund von *Halicyne* (*H. agnota granosa* n.ssp.) aus dem württembergischen *Trigonodus*-Dolomit. – Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg, **116**: 120–123.

Matthews, S.C. & Naylor, D. (1973): Lower Carboniferous conodont faunas from South-West Ireland. – Palaeontology, **16**: 335–380.

McLean, W.S. (2018): Scottish coal seam names and correlations. – British Geological Survey Open Report **OR/18/027**: 19 pp.

Meischner, K.-D. (1962): Neue Funde von *Psammolimulus gottingensis* (Merostomata, Xiphosura) aus dem Mittleren Buntsandstein von Göttingen. – Paläontologische Zeitschrift, H. Schmidt Festband: 185–193.

Meyer, H. von (1838): Mittheilungen, an Professor Bronn gerichtet. – Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, **1838**: 413–418.

Meyer, H. von (1844): Briefliche Mittheilungen. – Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, **1844**: 564–567.

Meyer, H. von (1847): *Halicyne* und *Litogaster*, zwei Crustaceen-Genera aus dem Muschelkalke Würtembergs. – Palaeontographica, **1**: 134–140.

Morris, S.F. (1980): Catalogue of the type and figured specimens of fossil Crustacea (excl. Ostracoda), Chelicerata, Myriapoda and Pycnogonida in the British Museum (Natural History. – 53 pp.; London (Trustees of the British Museum, Natural History).

Mychko, E.V. & Alekseev, A.S. (2018): Two new genera of Cyclida (Crustacea: Maxillopoda: Branchiura) from the Cisuralian (Lower Permian) of Southern Urals. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **289**: 23–34. doi: 10.1127/njgpa/2018/0747

Mychko, E.V., Feldmann, R.M., Schweitzer, C.E. & Alekseev, A.S. (2019): New genus of Cyclida (Crustacea) from Lower Carboniferous (Mississippian, Viséan) of Russia and England and new species of Viséan of Russia. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **294**: 81–90. doi: 10.1127/njgpa/2019/0847

Müller, A.H. (1955): Über einen Neufund von *Halicyne plana* und die systematische Stellung von *Halicyne* (Crustacea?). – Paläontologische Zeitschrift, **29** (3/4): 131–135. doi: 10.1007/BF03041795

Niko, S. & Ibaraki, Y. (2011): First cyclid crustacean from East Asia. – Journal of the Geological Society of Japan, **117** (4): 259–262. doi: 10.5575/geosoc.117.259

Oakley, T.H., Wolfe, J.M., Lindgren, A.R. & Zaharoff, A.K. (2012): Phylotranscriptomics to bring the understudied into the fold: monophyletic Ostracoda, fossil placement, and pancrustacean phylogeny. – Molecular Biology and Evolution, **30**: 215–233. doi: 10.1093/molbev/mss216 PMID: 22977117

Olszewski, T. (1996): Sequence stratigraphy of an Upper Pennsylvanian, midcontinent syclothem from North America (Iola Limestone, Kansas and Missouri, USA). – Facies, **35**: 81–103. doi: 10.1007/BF02536958

Oosterink, H.W. (1978): Arthropoda (Geleedpotigen) uit de Onder-Muschelkalk van Winterswijk. – Grondboor en Hamer, **1**: 2–8.

Oosterink, H.W. (1986): Winterswijk, Geologie Deel II. De Trias-periode (geologie, mineralen en fossilien). – Wetenschappelijke Mededelingen van de Koninklijke Nederlandse Natuurhistorische Vereniging, **178**: 1–120.

Packard, A.S. (1885): Types of Carboniferous Xiphosura new to North America. – American Naturalist, **19**: 291–294.

Pasini, G. & Garassino, A. (2003): Studies on Permo-Trias of Madagascar. 7. New record of *Halicyne gondwanae* Brambilla et al., 2002 (Crustacea, Cycloidea from the Lower Triassic (Olenekian) of Ambilobè Region (NW Madagascar). – Atti della Societa italiana di Scienze naturali e del Museo civico di Storia naturale in Milano, **144**: 3–9.

Pasini, G. & Garassino, A. (2007): Studies on Permo-Trias of Madagascar. 9. *Halicyne mamoroi* n. sp. (Crustacea, Cycloidea) from the Lower Triassic (Olenekian) of Ambilobe Region (NW Madagascar). – Atti della Societa italiana di Scienze naturali e del Museo civico di Storia naturale in Milano, **148**: 85–95.

Peach, B.N. (1883): Further researches among the Crustacea and Arachnida of the Carboniferous rocks of the Scottish border. – Transactions of the Royal Society, Edinburgh, **30**: 511–529. doi: 10.1017/S0080456800026569

Phillips, J. (1836): Illustrations of the Geology of Yorkshire. II. – The Mountain Limestone District, London (John Murray).

Poborski, S.J. (1964): Virgin Formation (Triassic) of the St. George, Utah, area. – Bulletin of the Geological Society of America, **65**: 971–1006. doi: 10.1130/0016-7606(1954)65[971:VFTOTS]2.0.CO;2

Reed, F.R.C. (1893): Woodwardian Museum notes. – Geological Magazine (Decade 3), **10**: 64–66.

Reed, F.R.C. (1908): A new species of *Cyclus* from the Carboniferous Limestone of Ireland. – Geological Magazine (Decade 5), **5**: 551–552.

Regier, J.C., Shultz, J.W., Zwick, A., Hussey, A., Ball, B., Wetzer, R., Martin, J.W. & Cunningham, C.W. (2010): Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. – Nature, **463**: 1079–1083. doi: 10.1038/nature08742 PMID: 20147900

Reuss, A.E. (1867): Über einige Crustaceenreste aus der alpinen Trias Österreichs. – Sitzungsberichte der kaiserlichen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Classe, **55** (1): 277–284.

Rogers, A.F. (1902): Some new American species of *Cyclus* from the Coal Measures. – Kansas University Science Bulletin, **1**: 269–274.

Röhl, H.-J. & Schmid-Röhl, A. (2005): Lower Toarcian (Upper Liassic) black shales of the Central European Basin: a sequence stratigraphic case study from the SW German Posidonia Shale. – SEPM, Special Publications, **82**: 165–189.

Schädel, M. & Haug, J.T. (2020): A new interpretation of the enigmatic fossil arthropod *Anhelkocephalon handlirschi* Bill, 1914 – important insights in the morphology of Cyclida. – Palaeodiversity, in press.

Schafhäutl, K.E. (1863): Süd-Bayerns lethea geognostica. Der Kressenberg und die südlich von ihm gelegenen Hochalpen. – Leipzig (Leopold Voss).

Schauroth, C. von (1854): Ein Beitrag zur Paläontologie des deutschen Zechsteingebirges. – Zeitschrift der Deutschen Geologischen Gesellschaft, **6**: 539–577.

Schram, F.R. (1983): Lower Carboniferous biota of Glencartholm, Eskdale, Dumfriesshire. – Scottish Journal of Geology, **19**: 1–15. doi: 10.1144/sjg19010001

Schram, F.R., Boere, A.C. & Thomas, N. (2006): Cycloidea of the Mississippian Bear Gulch Limestone of central Montana. – Natural History Museum of Los Angeles County Contribution to Science, **504**: 1–8.

Schram, F.R., Vonk, R. & Hof, C.H.J. (1997): Mazon Creek Cycloidea. – Journal of Paleontology, **71**: 261–284. doi: 10.1017/S0022336000039172

Schwebel, L., Gall, J.-C. & Grauvogel, L. (1983): Faune du Buntsandstein. V. – Description du neotype *d'Anhelkocephalon handlirschi* Bill (1914), crustacé isopode du Trias inférieur des Vosges (France). – Annales de Paléontologie (Vert.-Invert.), **69**: 307–316.

Schweigert, G. (2006): The first cycloid arthropod from the Late Jurassic. – Zitteliana, (A), **46**: 85–89.

Schweigert, G. (2007): *Juracyclus posidoniae* n. gen. and sp., the first cycloid arthropod from the Jurassic. – Journal of Paleontology, **81**: 213–215. doi: 10.1666/0022-3360(2007)81[213:JPNGAS]2.0.CO;2

Schweigert, G., Fraaije, R. & Wulf, M. (2009): Die Cycliden – eine rätselhafte Krebsgruppe. – Fossilien, **2009** (1): 17–22.

Schweitzer, C.E., Feldmann, R.M. & Schincker, M.M. (2019): A new species of Cyclida (Multicrustacea; Halicynidae) from the Triassic of the Netherlands. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **293**: 67–71. doi: 10.1127/njgpa/2019/0831

Schwentner, M., Combosch, D.J., Nelson, J.P. & Giribet, G. (2017): A phylogenetic solution to the origin of insects by resolving Crustacean - Hexapod relationships. – Current Biology, **27**: 1818–1824.E5. doi: 10.1016/j.cub.2017.05.040 PMID: 28602656

Scotese, C.R. (2014a): Atlas of Permo-Carboniferous Paleogeographic Maps (Mollweide Projection), Maps 53–64, Volume **4**, the Late Paleozoic, PALEOMAP Atlas for ArcGIS (PALEOMAP Project, Evanston, IL).

Scotese, C.R. (2014b): Atlas of Permo-Triassic Paleogeographic Maps (Mollweide Projection), Maps 43–52, Volumes **3, 4**, PALEOMAP Atlas for ArcGIS (PALEOMAP Project, Evanston, IL).

Scotese, C.R. (2014c): Atlas of Jurassic Paleogeographic Maps, (Mollweide Projection), Volume **3**, The Jurassic and Triassic, Maps 32–42, PALEOMAP Atlas for ArcGIS (PALEOMAP Project, Evanston, IL).

Scotese, C.R. (2014d): Atlas of Late Cretaceous Paleogeographic Maps (Mollweide Projection), Volume **2**, The Cretaceous, Maps 16–22, PALEOMAP Atlas for ArcGIS (PALEOMAP Project, Evanston, IL).

Seebach, K. von (1857): Entomostraceen aus der Trias Thüringens. – Zeitschrift der Deutschen Geologischen Gesellschaft, **9**: 198–206.

Sevastopolu, G.D. & Wyse Jackson, P.N. (2009): Carboniferous: Mississippian (Tournaisian and Viséan). – In: Holland, C.H. & Sanders, I.S. (eds.): The Geology of Ireland (2nd edition): 215–268; Edinburgh (Dunedin Academic Press).

Shen, Y., Garassino, A. & Teruzzi, G. (2002): Studies on Permo-Triassic of Madagascar. 4. Early Triassic conchostracans from Madagascar. – Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano, **143**: 3–11.

Stimpson, W. (1858): Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers ducibus, observavit et descripsit W. Stimpson. Pars. VI. Crustacea Oxystomata. – Proceedings of the Academy of Natural Sciences, Philadelphia, **10**: 57–61.

Stolley, E. (1915): Über einige Brachyuren aus der Trias und dem Dogger der Alpen. – Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt, **64**: 675–682.

Trauth, F. (1918): Über einige Krustazeenreste aus der alpin-mediterranean Trias. – Annalen des Naturhistorischen Hofmuseums, **32**: 172–192.

Trauth, F. (1935): Die Aptychen der Trias. – Sitzungsberichte der Akademie der Wissenschaften in Wien, mathematisch-naturwissenschaftliche Klasse, **144**: 455–482.

Trümpy, R. (1957): Ein Fund von *Halicyne* (Crustacea incertae sedis) im Mittleren Muschelkalk des Wutachtales. – Eclogae geologicae Helvetiae, **50**: 544–553.

Van Bakel, B.W.M., Jagt, J.W.M., Fraaije, R.H.B. & Artal, P. (2011): A new family, genus and species of cyclid (Crustacea, Branchiura, Cyclida) from mid Cretaceous reefal deposits in northern Spain. – Bulletin of the Mizunami Fossil Museum, **37**: 47–49.

Wilson, H.M. (2005): A new genus of Archipolypodan millipede from the Coseley Lagerstätte, Upper Carboniferous, UK. – Palaeontology, **48**: 1097–1100. doi: 10.1111/j.1475-4983.2005.00496.x

Wolfenden, E.B. (1959): New sponges from Lower Carboniferous reefs of Derbyshire and Yorkshire, England. – Journal of Paleontology, **33**: 566–568.

Woodward, H. (1868): Fourth report on fossil Crustacea. – British Association Reports, Norwich Meeting, **1868**: 72–75.

Woodward, H. (1870): Contributions to British fossil Crustacea. – Geological Magazine, **7**: 554–560. doi: 10.1017/S0016756800003009

Woodward, H. (1878): A Monograph of the British Fossil Crustacea belonging to the Order Merostomata. – Memoirs of the Palaeontographical Society, 263 pp.

Woodward, H. (1893): Note on a new British species of *Cyclus* from the Coal-Measures of Bacup, Lancashire. – Geological Magazine, new series, **10**: 28–29.

Woodward, H. (1894): Contributions to our knowledge of the genus *Cyclus* from the carboniferous formation of various British localities. – Geological Magazine, Series 4, **1**: 530–539. doi: 10.1017/S0016756800145273

Woodward, H. (1905): Further note on *Cyclus johnsoni*, from the Coal-Measures near Dudley. – Geological Magazine, new series, **2**: 489–492.

Zrzavý, J. & Štys, P. (1997): The basic body plan of arthropods: insights from evolutionary morphology and developmental biology. – Journal of Evolutionary Biology, **10**: 353–367. doi: 10.1007/s000360050029

Żyła, D., Wegierek, P., Owocki, K. & Niedźwiedzki, G. (2013): Insects and crustaceans from the latest Early-early Middle Triassic of Poland. – Palaeogeography, Palaeoclimatology, Palaeoecology, **371**: 136–144. doi: 10.1016/j.palaeo.2013.01.002

Manuscript received: March 8th, 2020.
Revised version accepted by the Stuttgart editor: March 20th, 2020.

Addresses of the authors:

Carrie E. Schweitzer, Department of Geology, Kent State University at Stark, North Canton, Ohio 44720, USA;
e-mail: cschweit@kent.edu

Rodney M. Feldmann, Department of Geology, Kent State University, Kent, Ohio 44242, USA;
e-mail: rfeldman@kent.edu

Eduard V. Mychko, Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow, Russia & Museum of the World Ocean, Kaliningrad, Russia & Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia;
e-mail: eduard.mychko@gmail.com

The pdf version of this paper includes an electronic supplement

Please save the electronic supplement contained in this pdf-file by clicking the blue frame above. After saving rename the file extension to .zip (for security reasons Adobe does not allow to embed .exe, .zip, .rar etc. files).

Table of contents – Electronic Supplementary Material (ESM)

Supplemental Table 1. A classification of the Cyclida (Pancrustacea). Age, occurrence, and rock formation from which species were collected is taken from the reference from which the species was originally or subsequently described. Other references used to determine occurrence information are cited. (Word)
Supplemental Table 2. Species, characters, and character states for all taxa analyzed in the PCO analysis (PAST 3.20). "?" indicates that a feature is not preserved or insufficiently preserved to score. (In Excel).
Supplemental Table 3. Correspondence Analysis results from data matrix in Supplemental Table 2 in PAST 3.20. (In Excel).
Supplemental Table 4. Localities with two or more species of cyclidan. (In Word).