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Redescription of *Americlus rankini* (Cyclida, Americlidae) and interpretation of its systematic placement, morphology, and paleoecology

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ABSTRACT

The best-preserved Scottish species of cyclidan is reinterpreted, based upon recent advances in cyclidan paleobiology. *Americlus rankini* (Woodward, 1868) is one of the best preserved members of this crustacean group, and its morphology suggests that it and related forms occupied a unique morphospace within Multicrustacea. Paleoecological evidence suggests that the animal was most likely free living, possibly as a scavenger, in a marginal marine environment. *Americlus* was distributed in Laurentia during the Middle Mississippian (Visean) to Middle Pennsylvanian (Moscovian).

Key Words: Multicrustacea, Paleozoic, Carboniferous, Scotland, United Kingdom

INTRODUCTION

Woodward (1868) first described *Cyclus rankini*, and he republished this description in a longer contribution on cyclid crustaceans (Woodward, 1870). In his original description, he described a ventral surface of *C. rankini*, interpreting it as the dorsal surface, and he compared it to the dorsal carapace of *Cyclus radialis*, which has thoracic ridges that may be a dorsal expression of segmentation. He noted the flattened shape of *C. rankini* and compared it with parasitic crustaceans, including both Branchiura and Isopoda. Peach (1882) reinterpreted *Cyclus rankini* as a ventral surface exhibiting sternites and as being originally illustrated upside down. Peach (1882) was correct in the sternal interpretation, but Woodward (1868) was correct in the orientation of the specimen (Woodward, 1894). Both Peach (1882) and Woodward (1868, 1894) noted that *C. rankini* lacked a well-preserved dorsal carapace. The species received little systematic attention until it was mentioned in an unpublished thesis (Clark, 1989). Subsequently, Feldmann & Schweitzer (2019) placed the species within *Americlus*, with which we concur. Thus, the purpose of this contribution is to redescribe and interpret *Americlus rankini* and evaluate its systematic placement in light of recent advances in the paleobiology of Cyclida, following the most recently published morphological definitions and classification (Feldmann & Schweitzer, 2019).

GEOLOGIC AND PALEOENVIRONMENTAL SETTING

Americlus rankini (Woodward, 1868) was collected from the Shrimp Member of the Limestone Coal Formation at the Bearsden, Scotland, locality near Glasgow (Wood, 1982; Clark, 1989) (Fig. 1). This unit is well known for its fish and crustacean fauna (Wood, 1982; Coates, 1993; 1998; Coates & Sequeira 2001) and consists of marine and non-marine layers (Wood, 1982) (Fig. 2).

The sediments in which *Americlus rankini* is found comprise finely laminated shales in a layer identified as 'Bed A' by Wood (1982) ('Shrimp Member' of Clark, 1989) of the Lower Carboniferous (Serpukhovian) Limestone Coal Formation. Wood indicated that he had also found cyclidans in a layer immediately above 'Bed B' ('Posidonia Member' of Clark, 1989) of the Limestone Coal Formation, although this could not be substantiated from the notes and collections of '*Cyclus*' that were retained in the Hunterian museum. The laminations in 'Bed A' reflect variations in the organic content that has been greatly compressed (Clark, 1989) (Fig. 3). The laminations show signs of bioturbation in early-formed concretions that developed around coprolitic masses, and these shales have abundant nuculid bivalve spat, mostly less than 1 mm in maximum diameter, that represent several growth stages (Clark, 1989). One can infer from this that the bottom waters and a thin layer of the sediment interface may have been periodically oxygenated.

It is notoriously difficult to infer palaeosalinity based on the associated fauna, but it appears that the Posidonia Member is more marine in character than the Shrimp Member due to the abundance of pyrite-coated individuals of the mollusc *Posidonia* associated with large sharks and other faunal elements that are considered to be tolerant of at least brackish to marine salinities (Table 1). The fish exhibit a distinct faunal difference between the two horizons, with only *Woodichthys* being found in both levels. The palaeosalinity tolerances of Carboniferous fish are poorly constrained, and it may be that habitat preference has more to do with the fish faunal differences than salinity (Carpenter *et al.*, 2015). Some of the other more marine elements of the faunas of the Shrimp and Posidonia members could have entered as epifauna attached to floating algae, plant material, or nautiloids. Other more mobile fauna, such as the fish and crustaceans, may have entered the environment of their own accord or have been resident in the body of water

for an extended period. It is likely that deposition of the Shrimp Member occurred over a period of many millennia, suggesting that the environment was relatively stable for an extended period of time. The shape of the basin in which this sedimentation took place suggests it was a land-locked body of water with a restricted connection to the open marine environment to the southeast and occasional incursions from the southwest transgressing the Dusk Water-Inchgotrick fault block barrier (Clark, 1989), perhaps a continuation of the low-lying coastal plain subject to episodic and restricted marine influence seen in the Tournaisian Ballagan Formation (Read *et al.*, 2002; Carpenter *et al.*, 2015). The Posidonia Member represents a temporary transgressive period in the development of the basin where more marine water entered bringing faunal change (Clark, 1989).

In terms of the crustaceans, it is also difficult to be certain of their salinity tolerances. The cyclidans have been found elsewhere in sediments that have been variously interpreted as near shore marine, brackish, off-shore marine, or lagoonal (Schram, 1981; Briggs & Clarkson, 1989; Schweigert, 2007). Clark (1989) suggested that the Shrimp Member was likely to have been a relatively low-oxygen, brackish water environment when compared to the more oxygen-rich marine deposits of the Posidonia Member based on trace element analysis. In thin section, the Shrimp Member exhibits bioturbation in the less organic-rich laminae, suggesting a very shallow, periodically oxygenated top surface to the sediment (Clark, 1989). The bivalve spat, which are ubiquitous throughout the Shrimp Member, indicate that the environmental conditions prevented the bivalves from reaching maturity (Clark, 1989). Although there are no marked seasons in equatorial regions, the rivers flowing into the Midland Valley of Scotland at this time may have been affected by seasonal rainfall within the monsoon belt in their catchment areas, which would affect the clastic, organic, nutrient, and freshwater input into the basin. The

succession of sediments in the basin is indicative of a rapid widespread transgression represented by the Top Hosie Limestone followed by a slow regression into the Shrimp Member of the Limestone Coal Formation, punctuated by several minor transgressions such as the Posidonia Member and some smaller accumulations of shells in younger members (Clark, 1989; Carpenter *et al.*, 2015).

Several of the crustaceans found at Bearsden also co-occur at other localities such as at Muirhouse (Granton Shrimp Bed, West Lothian Oil-Shale Formation, Viséan) (*Crangopsis*, *Palaemysis*, *Tealliocaris*, *Bairdops* and *Minicaris*), Glencartholm (Glencartholm Volcanic Member, Tyne Limestone Formation, Viséan) (*Crangopsis*, *Tealliocaris*, *Bairdops*, and *Americlus*) and Bear Gulch Limestone Member (Heath Formation, Montana, Bashkirian) (*Crangopsis*, *Tealliocaris*, *Schramine*, and *Bairdops*) (Briggs *et al.*, 1991; Clark, 1989; 2013; Schram, 1983; Schram & Horner, 1978; Schram *et al.*, 2006) (Tables 1, 2). If some of the crustacean genera are absent, there are often others with a similar *Bauplan* within the same lithologies.

The crustacean assemblage of the Shrimp Member at Bearsden, however, may not represent a community as it is found over a large area within a nearly 3 m thickness of very finely laminated shales (Clark, 1989). Although the crustaceans found with *Americlus* might not constitute a crustacean palaeocommunity, they are mostly found in close association within the Shrimp Member and many show signs of having undergone similar taphonomic pathways. The preservation of most of the associated crustaceans is very similar to that of *Americlus*, being of a dark phosphatic material (Clark, 1989).

It is often very difficult to determine if a fossil crustacean represents a molt, but in the Shrimp Member, at least a few of the shrimps represent mortalities and have soft-part

preservation including muscles and blood vessels (Clark, 1989; 1991; 2013). It is unclear whether the specimens of *Americlus* are mortalities or not, as we are uncertain as to how this particular crustacean molted, and there is little evidence of soft-tissue preservation, despite some specimens (GLAHM A2563 and GLAHM A2802) appearing to retain gill beneath the carapace. The association of dorsal and ventral surfaces as well as appendages, apparently in place (GLAHM A2808 and others), suggests that they could be corpses.

Of the other crustaceans of the Limestone Coal Formation, the syncarid *Minicaris* is not as widely distributed within the shale horizons as the other taxa including *Americlus*, as it appears to be restricted to the *Lingula* Member (Bed E of Wood, 1982). *Minicaris* also occurs only in the north and northeastern localities at Bearsden and the Red Cleugh Burn (Limestone Coal Formation, Serpukhovian). *Minicaris* is preserved as a light-coloured phosphate cuticle, different from the other arthropods, and tends to be greatly pyritized, supporting the hypothesis that it was derived from a different environment than the associated *Americlus* and the aeschronectidan hoplocarid *Crangopsis* (Clark, 1989). As the morphology of *Minicaris* is similar to that of extant syncarid crustaceans, it is possible that it lived in a similar manner in freshwater streams and lakes (Schram & Schram, 1974; Clark, 1990). Streams entering into the depositional area within the Midland Valley of Scotland may have transported *Minicaris* into a marine or brackish environment.

Thus, the available evidence suggests that *Americlus rankini* inhabited a marginal marine environment, in a restricted basin connected to the open ocean. It was at least periodically oxygenated but generally disoxic and brackish, with freshwater input from streams. The specimens are likely to include both molts and corpses.

SYSTEMATIC PALEONTOLOGY

Institutional abbreviations: GLAHM, The Hunterian; University of Glasgow, Scotland, UK; BMNH, The Natural History Museum, London, England, UK; CMNH, Cleveland Museum of Natural History, Cleveland, OH, USA; FMNH, Field Museum of Natural History, Chicago, IL, USA; GSM, GSE, Geological Survey Museum, British Geological Survey, Keyworth, England, UK; MM, Manchester Museum, University of Manchester, England, UK; LF, Lauer Collection, Lauer Foundation for Paleontology, Science, and Education, NFP, Wheaton, IL, USA; NMS.G, National Museum of Scotland, Edinburgh, Scotland, UK; SM, Sedgwick Museum, Cambridge University, England UK; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Morphological terminology and classification: We follow the terminology, morphology abbreviations, and classification of Feldmann & Schweitzer (2019).

Infraphylum Pancrustacea Zrzavý and Štys, 1997

Class Multicrustacea Regier *et al.*, 2010

Infraclass Halicyna Gall & Grauvogel, 1967

Order Cyclida Schram, Vonk, and Hof, 1997

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

Family Americlidae Dzik, 2008

Included genera: *Americlus* Dzik, 2008; *Yunnanocyclus* Feldmann, Schweitzer & Hu *in* Feldmann, Schweitzer, Hu, Huang, Zhang, Zhou, Wen, Xie & Maguire, 2017.

Diagnosis: Carapace flattened, about as wide as long (*Yunnanocyclus*) to wider than long and bilobed (*Americlus*); lacking (*Yunannocyclus*) or with weak to moderate (*Americlus*) carapace regional definition; marginal rim well-developed, wide, may be ornamented with granular structures (*Yunnanocyclus*); rostral lobe extending beyond carapace, 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).

Remarks: Taxonomy within the group of organisms historically referred to Cyclida is under revision. Dzik (2008) summarized work on the group to date and erected some new families. Americlidae was diagnosed as being flattened, with six thoracic appendages (Dzik, 2008), based upon material that was not as complete as that discussed here. Later, Feldmann *et al.* (2017) added *Yunnanocyclus* to the family, and Feldmann and Schweitzer (2019) diagnosed the family, defined morphological terms, and provided a complete list of species and genera within each family of Cyclida. *Cyclus rankini* possesses all of the diagnostic features of Americlidae.

Genus *Americlus* Dzik, 2008

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

Included species: *Americlus americanus*; *A. johnsoni* (Woodward, 1894); *A. obesus* (Schram, Vonk & Hof, 1997); *A. rankini* (Woodward, 1868); *A. scotti* (Woodward, 1894); *A. testudo* (Peach, 1882).

Diagnosis: Carapace flattened, wider than long, bilobed; with weak to moderate carapace regional definition; marginal rim well-developed, wide; posterior axial keel, lyrate keels, and median concentric keels present; rostral lobe extending beyond carapace, with optic notches; first antennae strong, thick, with 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 7 visible, well-defined somites, ovate central sternal area; abdomen with 2-4 somites (modified from Feldmann & Schweitzer, 2019).

Material examined: *Americlus americanus*, FMNH PE 20601, 20985, 22421, 22462, 22472, 22478, 22498, 24959, 34759, 34763, 34954; LF 2125; USNM 38863; CMNH 6909. *Americlus johnsoni*, (BMNH) In. 22371-22374, MM L 1175, 7098, 8185, 11753, 11754, 11902; GLAHM A2565; NMS.G.1911.6.12. *Americlus obesus*, FMNH PE 23041, 24975, 30630, 34834, 34880, 39056. *Americlus scotti*: MM I 10220 (=L.926), holotype; (BMNH) I.13903, I.13904, 13945, 18591, 22370; SM E16936; GSE 26710-11, 26716-17. *Americlus testudo*, GSM 2056-2058, syntypes; GSM 2048, 2049 m2210, 2050 m1424; (BMNH) In. 22378, 22379, 22386; MM L 9285.

Remarks: Feldmann & Schweitzer (2019) transferred *Cyclus rankini* to *Americlus* based upon its similarity to *Americlus americanus*, the type species of the genus. Herein we elaborate on that placement. *Americlus rankini* shares several morphological features with *A. americanus*: a short,

ventrally placed first maxilla; at least two subchelate appendages with sickle-shaped dactyli interpreted in both species as second maxillae and a maxilliped; strong first and slender second antennae; a flattened carapace with weak ornamentation; a wide marginal rim; at least 7 sternites, the anterior pairs of which terminate in longitudinal arcuate grooves defining an ovate central structure; five pediform thoracopods posterior to the pseudochelate appendages; and caudal rami. *Americlus americanus* is interpreted as possessing mandibles; these structures are not visible in *A. rankini*. *Americlus rankini* differs from *A. americanus* in possessing a more bilobate carapace that is overall wider than long, whereas that of *A. americanus* is more circular and less obviously bilobed. *Americlus americanus* and *A. rankini* each possess a short abdomen (Schram *et al.*, 1997, fig. 6.3), but interpretation of this structure is difficult due to incomplete preservation.

Other species of *Americlus* differ from both *A. americanus* and *A. rankini* in having very distinct, strong, median concentric keels. Both *A. johnsoni* and *A. scotti* have such keels, and they also exhibit somewhat stronger anterior carapace lobe development. *Americlus obesus* is quite distinct in being much wider than long and very weakly ornamented. *Americlus testudo* is the least completely preserved species but has the same overall carapace shape and a few specimens with thoracic sternites preserved so that its placement in *Americlus* is secure.

Americlus exhibits an equatorial tropical distribution associated with Laurussia, primarily Laurentia. The earliest occurrences are in the Middle Mississippian (Visean) to Upper Mississippian (Serpukhovian) of Scotland. Lower to Middle Pennsylvanian (Bashkirian to Moscovian) occurrences are known from England, and North American occurrences are in the Middle Pennsylvanian (Moscovian) of Illinois.

Americlus rankini (Woodward, 1868)

(Figs. 4-8)

Cyclus rankini Woodward, 1868, p.73, pl. 2, fig. 2. Woodward, 1870, p. 558, pl. 23, fig. 1; Woodward, 1878, p. 254, pl. 32, fig. 42; Peach, 1882, p. 526; Woodward, 1894, p. 530, pl. 15, fig. 8; Woodward, 1905, p. 490; Rogers, 1902, p. 275; Hopwood, 1925, p. 308; Schram *et al.*, 1997, p. 279; Feldmann *et al.*, 2017, p. 407; Mychko & Alekseev, 2018.

Americlus rankini (Woodward, 1868). Feldmann & Schweitzer, 2019, p. 2.

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

Description: Carapace (c) ovate, apparently wider than long, bilobate; surface apparently pitted or possibly with widely spaced tubercles (A2806, A2811, A2814) (Fig. 4A, B, E).

Rostral lobe (r) with weakly convex anterior margin, with a transverse crest (tc) (A2814) (Fig. 4E). Marginal rim (mr) wide (A2811, A2806, A2814) (Fig. 4A, B, E), about 20% of carapace width measured at widest point, about 10% width of carapace measured posteriorly, narrowing to a small posterior notch (pn) posteriorly and axially (A2806, Fig. 4B); separated from remainder of carapace by median concentric keel (mck); surface pitted. Surface of carapace not well known, appearing to have elongate posterior axial lobe (pal) extending into axial keel (ak) to posterior edge of carapace; apparently some swellings anteriorly but shape and position not discernible due to distortion (A2806) (Fig. 4B).

At least 7 thoracic somites (th1-7) visible ventrally, interpreted here as sternites, sternites numbered with the first visible sternite as number 1 but it is possible that other unpreserved

sternite lie anterior to our numbered sternite 1; sternites 1-3 (th1-3) directed anterolaterally, wider than long; sternites 4 and 5 (th4, 5) directed laterally, wider than long but less wide than first 3; sternites 6 and 7 (th6, 7) directed posteriorly (A2560, A2802) (Fig. 4C, D). At lateral-most edge 4 of sternites, two ovate structures, one anterior which is the smaller and one posterior which is about twice as large as the anterior ovate structure (A2560) (Fig. 4C). Sternal sutures 1/2, 2/3, 3/4, 4/5, and 5/6 not extending to axis, instead terminating short of the axis at an ovate central structure which terminates at suture 6/7, suture 6/7 intersects axis (A2802, A2560) (Fig. 4C, D); ovate central structure apparently flattened. Marginal rim (mr) extends well lateral of sternal elements (A2806, A2814) (Fig. 4B, E).

Antennule (a1) well preserved (A2814, A2807) (Fig. 4E, 6D), basal articles longer than high, at least three basal articles visible; with long flagellum (A2806) (Fig. 6A). One specimen with weak indication of much smaller, more slender pair of antennae (a2), barely visible long basal articles and a few segments of the flagella (A2807) (Fig. 6D). Gills only preserved in a small area, appearing to be filamentous (A2802) (Fig. 7).

Eight pairs of appendages preserved, excluding antennules, antennae, and male gonopods (numbering and interpretation of preserved appendages follows Schram *et al.* [1997, figs. 3.4, 4.1]). First three pairs of non-antennal appendages appear to be modified as mouth parts, with surfaces pitted (A2806) (Fig. 6C). First pair interpreted as first maxillae (mx1), smallest, much smaller than second and third pairs of appendages, five segments visible, articles becoming shorter and more slender distally, third segment with large pore, possibly with a seta. Second pair of appendages interpreted as second maxillae (mx2), slightly smaller than third pair of appendages, with 5 articles visible, basal article poorly known, second article triangular, widening distally; third article about as long as wide, with pores on outer surface; fourth article

ovate, with pores on outer surface, with pores on outer surface, upper surface serrate; with fifth article sharp, serrations on inner margin, subchelate. Third pair of appendages interpreted as maxillipeds (mxpd), of same general form as second maxillae and slightly larger, first article small, triangular, widening distally, second article longer than wide, third article slightly higher than long, outer surface with pores; fourth article ovate, with serrate upper surface, outer surface with pores, with sharp spines on inner surface (A2806), fifth article much longer than high, sharp, scythe-shaped (A2806); subchelate. A2807 indicates that there may be a sixth article, short, sharp (Fig. 6A, C).

Five pairs of pediform thoracic appendages (t2-6) (A2808) posterior to maxilliped, slender, with articles much longer than high, terminating in scythe-like dactyl (Fig. 5A); interpreted as thoracic appendages 2 through 6. First pair thoracic appendages (t2) poorly known, only a few basal articles preserved. Second pair of thoracic appendages (t3) shorter than pairs three and four, with three distal articles visible. Third and fourth pairs of thoracic appendages (t4, 5) each with four distal articles visible, fifth pair of thoracic appendages (t6) with a short fifth article preserved basally. Male gonopods (A2808) (G1) arcuate, long, slender, directed anteriorly, positioned along either side of axis (Fig. 5B), interpreted as exopod of t6.

A2812 with what appears to be segments of cuticle extending posteriorly from posterior-axial region, may be part of abdomen or a molted carapace (Fig. 6B). Abdomen appearing to be composed of three or four segments (GLAHM A2812) with a ventral tubercle on the penultimate somite. A triangular telson or anal somite at the distal end of the abdomen has two ovate and spinose caudal rami (A2808) (Fig. 5B).

Material examined: GLAHM A2560-2862, A2801, A2802, A2806-2814, A2817, A21498, A21528.

Remarks: All of the specimens of *Americlus rankini* are incompletely preserved; thus, our interpretation of the appendages and other morphology must be considered as an hypothesis following Schram *et al.* (1997). We interpret the carapace as possessing a transversely keeled rostral lobe with optic notches, although the optic notches are not well-preserved. No evidence of eyes can be seen in this species. There is a stout first antenna and a much more slender, smaller, second antenna. The dorsal carapace is poorly preserved, but there is evidence of axial lobes and possibly lateral lobes. The surface appears pitted, and the marginal rim is quite wide, extending well lateral to the bases of the thoracic appendages.

Seven thoracic somites are preserved on what we interpret as a sternum; it is possible that there are more thoracic somites but they are not preserved in these specimens. Only the last suture 6/7 is complete in *Americlus rankini*. Sutures 1/2 through 5/6 terminate along the boundary of an ovate central structure unlike anything seen in other crustaceans to our knowledge. The distal margins of each sternite bear two ovate openings arranged longitudinally, the anterior-most being about one-third the length of the posterior one. The function of these openings is unknown, although they may be for the thoracic appendages. It must be indicated that there is no evidence of an appendage segment actually articulated with any of these openings; however, the thoracic appendages arise from this approximate position on the sternum, interpreted similarly for the appendages of *A. americanus* (Schram *et al.*, 1997). The sternal form is reminiscent of that seen in brachyuran crabs and may be an example of convergence.

Gills are only preserved in a small area in one specimen of *Americlus rankini* (Fig. 7) and appear to be similar in structure to those preserved in *Yunnanocyclus* as well as cyclid genera in other families (Halicynidae and Schraminidae). In all of those taxa, the gills form a horse-shoe shaped structure of thin, subparallel filaments (Feldmann *et al.*, 2017, fig. 2C, D, F).

Anteriorly, *Americlus rankini* possesses three non-antennal appendages which have been interpreted as two pairs of maxillae and one pair of maxillipeds by previous authors (Schram *et al.*, 1997), an interpretation which we follow here. The first maxilla is much shorter than the second maxilla and maxilliped. The second maxilla is shorter than the maxilliped but of the same general form. Both the second maxilla and maxilliped terminate in a subchelae composed of a broad, ovate, spinose propodus with a long dactyl. Posterior to the maxilliped are 5 pairs of thoracopods. All retain at least four appendage articles, and they all terminate in a long, slender dactylus. Thus, we interpret the organism as possessing at least 8 pairs of non-antennal appendages, two of which are cephalic (mx 1 and 2) and 6 of which are thoracic (mxpd and th2-6) (Fig. 8). Mandibles are unknown in *A. rankini* but are present in *A. americanus*, suggesting that they simply are not preserved in *A. rankini*.

The male gonopod is hard to interpret. In brachyurans, a superficially similar structure is the first appendage of the male pleon. Here, we interpret the gonopod as the exopod of the sixth thoracic appendage, not unlike the condition in copepods and thecostracans. Another possibility is that it is the seventh thoracic appendage, as seen in anostracans (fairy shrimp). The gonopod does not appear to be associated with the abdomen, which consists of three or four somites and a pair of caudal rami.

We are aware that the number of preserved thoracic appendages does not correspond to the number of preserved thoracic sternites. Seven sternites are visible, whereas there are six thoracic appendages in our interpretation (mxpd + t2 through t6). Possibilities for reconciliation include interpretation of the gonopod as thoracic appendage 7; alternatively, what we interpret as the second maxillae could be the first maxilliped. Another possibility is that the last sternite, as it is very small, lacked an appendage entirely. None of these interpretations is testable based upon

the material at hand, so reconciling these discrepancies will necessitate more material with appendages preserved.

LIFE HABIT OF *AMERICLUS RANKINI*

It is very difficult to interpret the life habit of this animal, although there are some hints as to what this might be. The posterior-most five thoracopods of this animal, excluding the gonopods, appear to curve forward to a sharp pointed dactylus. The two anterior limbs interpreted here as the second maxilla and the maxilliped exhibit the propodus and dactylus folded over an enlarged carpus, forming a subchelate appendage. These appendages are characteristic of an animal that uses its limbs for grasping. Attached to the carapace of several specimens is a marine epifaunal bivalve (?*Septimyalina*) (GLAHM A2813, GLAHM A2814, Clark, 1989; Okan & Hoşgör, 2007) (Fig. 9A-D). This bivalve has not been found anywhere else in the aforementioned members of the Limestone Coal Formation succession, suggesting that it was brought into the basin from the marine environment with *Americlus rankini*. There is no clear association between *A. rankini* and any other element of the fauna or flora, so it not possible to assign *A. rankini* to any particular feeding habit or lifestyle. Association with larval pelecypods and also larval gastropods was noted for the schraminid cyclid *Schramine gondwanae* (Brambilla *et al.*, 2002) (Dzik, 2008). Previous authors (Dzik, 2008) have suggested affinity with Branchiura and a parasitic life habit. This could be supported by interpreting *A. rankini* as a parasite or epizoan on large fish, on which the larvae of the bivalve may have developed and then attached to the carapace of *A. rankini* at a later stage in their development, much as *Mytilus* is an epibiont on the isopod fish parasite *Mothyocya epemerica* (Oktener *et al.*, 2014). Schram *et al.* (1997) considered a parasitic habit as unlikely for the congeneric *A. americanus* given the size of specimens and claw-like appendages. *Americlus rankini* may have entered the basin attached to floating fronds of algae,

supported by the association of *A. americanus* with plant material (Schram *et al.*, 1997), and algae may also have acted as an area for attachment by the bivalve. Thus, we favour a free-living lifestyle at this time. The only corroborative indication of possible feeding habits of *A. rankini* is one specimen associated with the distended remains of a partially deconstructed coprolite situated near the pseudochelate appendages (GLAHM A21528, Clark, 1989) (Fig. 9E).

SIGNIFICANCE OF *AMERICLUS RANKINI* AND AMERICLIDAE

Cyclida has been interpreted as a member of Crustacea *sensu lato* almost since its inception, supported by presence of two pairs of antennae. Most recently Cyclida has been allied with either Maxillipoda, now held to be a polyphyletic group; Copepoda; or Branchiura (summarized by Schram *et al.*, 1997; Feldmann & Schweitzer, 2019). We follow Feldmann & Schweitzer (2019) in placing the group within Multicrustacea.

Americlus rankini is one of the best and most completely preserved members of Cyclida as currently defined (Feldmann & Schweitzer, 2019). In general, species within Americlidae display better preservation than species in other cyclidan families, making the group of prime importance in determining the best systematic placement for Cyclida. In addition to the dorsal carapace, *A. americanus* and *A. rankini* retain well-preserved appendages and sternal elements, and other species of *Americlus* preserve sternal elements. Among Cyclida, this is uncommon. Whereas all 55 species have reasonably well-preserved dorsal carapaces, only fifteen species in the entire group retain sternal elements and/or appendages (Table 3). In taxa in which sternal features and appendages are known, they are very similar across species placed in four of the six families of Cyclida (Americlidae, Halicynidae, Hemitrochiscidae, Schraminidae). Notably, both

A. americanus and *A. rankini* have one more appendage preserved than other taxa; this is probably the very small first maxillae that are preserved in these two species.

Gill filaments are known from species of Americlidae, Halicynidae, and Schraminidae. Cyclidae is known only from the dorsal carapace as are most Hemitrochiscidae. In all cases where gills are known, they are similar in overall morphology across families and genera. Cyclidae share many carapace features with the four families that are known from ventral surfaces. Alasuucaridae is not similar to any other cyclid families. The similarities in sternum, appendages, and gills across taxa suggests that Cyclida may be monophyletic excluding Alasuucaridae, but that remains to be tested.

If the structures on the specimens of *Americlus rankini* are in fact as we have interpreted them here, the taxon, and by extension, Cyclida as currently construed, can be eliminated from many groups within Pancrustacea. Branchiopoda, reported as a monophyletic group (Meusseman *et al.*, 2010; Oakley *et al.*, 2012; Legg *et al.*, 2013; Edgecombe & Legg, 2014; Schwentner *et al.*, 2017), are characterized by phyllopodous appendages. None of the *A. rankini* specimens shows any evidence of such appendages. Members of Branchiopoda almost all have many more thoracic somites than seen in *Americlus rankini*, generally ranging between 10 and 32 (Schram, 2013). There is no evidence of this number of segments in *A. rankini*. Branchiopoda is part of a larger clade, Allotriocarida, including Branchiopoda, Cephalocarida, Remipedia, and Hexapoda (Oakley *et al.*, 2012). It seems clear that *A. rankini* and related forms can be excluded from Allotriocarida, as they share few characters with insects, remipedes, or cephalocarids, other than basal symplesiomorphies of Arthropoda and Pancrustacea.

Oligostraca includes Mystacocarida, Branchiura, Pentastomida, and Ostracoda (Oakley *et al.*, 2012). Branchiura, the so-called fish lice, possess a carapace, one maxilliped, and four pairs

of thoracic appendages modified for swimming. The sternal area is narrow and longitudinally elongate. *Americlus rankini* has many more appendages than seen in Branchiura, and the sternal architecture is very different in *A. rankini*. Ostracods have much reduced segmentation and appendages as well as a bivalved carapace (Schram, 2013), not seen in *A. rankini*. Mystacocarids possess four pairs of thoracic appendages and a multi-segmented abdomen (Schram, 2013). Pentastomids are worm-like and highly specialized for a parasitic lifestyle. Thus, *A. rankini* and other cyclidans are unlikely to be members of Oligostraca.

This leaves a large grouping, the Multicrustacea, which embraces Malacostraca and Hexanauplia (Oakley *et al.*, 2012) to which *Americlus rankini* might be referred. *Americlus rankini* shares affinities with several taxa within Multicrustacea, which is defined on molecular characteristics and “was not anticipated by morphology” (Regier *et al.*, 2010, p. 1082). Body plan segmentation in Multicrustacea generally conform to two basic plans (cephalic-thoracic-pleonal or abdominal): 1) 5-7-4(0 in Cirripedia only) (Hexanauplia) and 2) 5-8-6(7) for Malacostraca (Schram, 2013). In our interpretation here, if mandibles are assumed as present as they are in *A. americanus*, cyclids would have 5 cephalic appendages, as in both body plans. The maxilliped plus five additional thoracic appendages yield 6 thoracic appendages, but addition of the gonopod would make seven. The abdomen does not appear to conform to Multicrustacea as currently understood.

Cyclidans seem to be most similar to Copepoda or Malacostraca within Multicrustacea. Hexanauplia includes copepods and thecostracans (barnacles and allies). *Americlus rankini* lacks specializations of Thecostraca, which include mineralized shell plates and sessile adult lifestyle (Pérez-Losada *et al.*, 2012). Clark (1989) and Schram *et al* (1997) allied *A. rankini* with the Copepoda, which are characterized by 6 or 7 thoracopods, of which the first is generally

developed as a maxilliped. *Americlus rankini* appears to possess a similar number and arrangement of thoracopods. Copepods are characterized by possession of mandibles, two pairs of maxillae, and one pair of maxillipeds, which seems consistent with *A. rankini*. The maxillae are usually foliaceous, not pediform, and only one group exhibits a subchelate maxilla (Huys & Boxshall, 1991). In addition, maxillae are usually different in form from the maxillipeds (Huys & Boxshall, 1991), whereas in *A. rankini*, the second maxilla and the maxilliped each are interpreted as subchelate. We note that the fossil record for Copepoda is sparse and thus early forms could differ in significant ways from modern forms.

Copepods display clear dorsally expressed segmentation of the anterior-most tagma, which includes the fused segments of the head and three or four thoracic segments. *Americlus rankini* exhibits no evidence of segmentation dorsally, and rather has a non-segmented carapace covering the entire cephalothorax. Members of Cyclidae currently referred to the genus *Cyclus* exhibit clear evidence of thoracomeres dorsally, but they are exhibited as ridges, not as articulating segments as in copepods. Expression of segmentation in *Americlus* is expressed only ventrally as compared to the clear articulating segments of copepods.

Malacostraca contains several groups, including Phyllocarida, Eumalacostraca, and possibly the extinct Thylacocephala (Regier *et al.*, 2010; Oakley *et al.*, 2012; Schwentner *et al.*, 2017). *Americlus rankini* shares some characteristics with Malacostraca, including a dorsal carapace fused to thoracic somites and covering the head (Davie, 2002). Diagnostic features for Malacostraca includes possession of mandibles, maxillae, and maxillipeds, of which specimens of *A. rankini* preserve the latter two and *A. americanus* possesses mandibles (Schram *et al.*, 1997). *Americlus americanus* and *A. rankini* are interpreted to possess an abdomen, whereas malacostracans possess a pleon with appendages, diagnostic for that group.

Thus, we suggest that although cyclidans share characteristics with Copepoda and with some Malacostraca, they most likely form a distinct group within Multicrustacea. Although they are similar in some regards to Copepoda, the lack of dorsal, articulating segmentation seems to exclude them from this group. A key feature differentiating *Amerclus rankini* and other well-preserved cyclids from eumalacostracans is the presence of caudal rami attached to either a telson or an anal somite and lack of a pleon, which argue against placement within Eumalacostraca. It is probable that Cyclida occupies a unique morphospace within Multicrustacea.

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REFERENCES

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

- Ambilobe region (NW Madagascar). *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano*, **143**: 105 – 115.
- Briggs, D. E. G., Clark, N. D. L. & Clarkson, E. N. K. 1991. The Granton “shrimp-bed”, Edinburgh – A Lower Carboniferous Konservat-Lagerstätte. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **82**: 65–85.
- Briggs, D. E. G. & Clarkson, E. N. K. 1989. Environmental controls on the taphonomy and distribution of Carboniferous malacostracan crustaceans. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **80**: 293–301.
- Carpenter, D. K., Falcon-Lang, H. J., Benton, M. J. & Henderson, E. 2015. Carboniferous (Tournaisian) fish assemblages from the Isle of Bute, Scotland: systematics and palaeoecology. *Palaeontology*, **57**: 1215-1240.
- Clark, N. D. L. 1989. *A study of Namurian crustacean-bearing shale from the western Midland Valley of Scotland*. Unpublished Ph.D. dissertation, University of Glasgow, 341 p.
- Clark, N. D. L. 1990. *Minicaris brandi* Schram 1979, a syncarid crustacean from the Western Midland Valley of Scotland. *Scottish Journal of Geology*, **11**: 125–130.
- Clark, N. D. L. 1991. *Palaemysis dunlopi* Peach 1908 (Eocarida, Crustacea) from the Namurian (Carboniferous) of the Midland Valley of Scotland. *Scottish Journal of Geology*, **27**: 1–10.
- Clark, N. D. L. 2013. *Tealliocaris*: a decapod crustacean from the Carboniferous of Scotland. *Palaeodiversity*, **6**: 107–33.
- 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.

- Coates, M. I. 1993. New actinopterygian fish from the Namurian Manse Burn Formation of Bearsden, Scotland. *Palaeontology*, **36**: 123–146.
- Coates, M. I. 1998. Actinopterygians from the Namurian of Bearsden, Scotland, with comments on early actinopterygian neurocrania. *Zoological Journal of the Linnean Society*, **122**: 27–59.
- 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.
- Davie, P. J. F. 2002. Crustacea: Malacostraca: Phyllocarida, Hoplocarida, Eucarida (Part 1). In: Wells, A. & Houston, W. W. K. (eds.), *Zoological Catalogue of Australia*, **19.3A**. CSIRO Publishing, Melbourne, Australia, 551 p.
- Dzik, J. 2008. Gill structure and relationships of the Triassic cycloid crustaceans. *Journal of Morphology*, **269**: 1501–1519.
- Edgecombe, G. D., & Legg, D. A. 2014. Origins and early evolution of arthropods. *Palaeontology*, **357**: 457–468.
- Feldmann, R. M. & Schweitzer, C. E. 2019. The enigmatic Cyclida (Pancrustacea): morphological terminology and family level classification. *Journal of Crustacean Biology*, **39**: 617–633.
- 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.
- Gall, J.-C. & Grauvogel, G. 1967. Faune du Buntsandstein II. Les Halicynés. *Annales de Paléontologie*, **53**: 3–14.

- Grogan, E. D., Lund, R. & Fath, M. 2014. A new petalodont chondrichthyan from the Bear Gulch Limestone of Montana, USA, with reassessment of *Netsepoye hawesi* and comments on the morphology of holomorphic petalodonts. *Paleontological Journal*, **48**(9): 1003-1014.
- Huys, R., & Boxshall, G. A. 1991. *Copepod evolution*. Unwin Brothers, Ltd., Old Woking, Surrey, UK. 468 pp.
- Legg, D. A., Sutton, M. D., & Edgecombe, G. D. 2013. Arthropod fossil data increase congruence of morphological and molecular phylogenies. *Nature Communications*, **4**:2485.
- Lund, R., Greenfest-Allen, E. & Grogan, E. D. 2012. Habitat and diversity of the Bear Gulch fish: Life in a 318 million year old marine Mississippian bay. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **342-343**:1-16.
- Meusemann, K., Von Reumont, B. M., Simon, S., Roeding, F., Strauss, S., Kück, P., Ebersberger, I., Walz, M., Pass, G., Breuers, S., Achter, V., Von Haeseler, A., Burmester, T., Hadrys, H., Wägele, J. W., & Misof, B. 2010. A phylogenomic approach to resolve the arthropod tree of life. *Molecular Biology and Evolution*, **27**:2451-2464.
- 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.
- 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.

- Okan, Y. & Hoşgör, I. 2007. Late Viséan-Early Namurian bivalves from the Zonguldak Coal Basin, Northwestern Turkey. *Turkish Journal of Earth Sciences*, **16**: 225-240.
- Oktener, A., Iliver, G. & Turker, C. D. 2014. *Mytilus* (Mollusca: Bivalvia) epibiontic on the fish parasite *Mothyocya epimerica* (Crustacea: Isopoda) in the Sea of Marmara. *Journal of Conchology*, **41**: 759-764.
- Packard, A.S. 1885. Types of Carboniferous Xiphosura new to North America. *American Naturalist*, **19**: 291–294.
- Peach, B.N. 1882. Further researches among the Crustacea and Arachnida of the Carboniferous rocks of the Scottish border. *Transactions of the Royal Society, Edinburgh*, **30**: 511–528.
- Pérez-Losada, M., Høeg, J. T. & Crandall, K. A. 2012. Deep phylogeny and character evolution in Thecostraca (Crustacea: Maxillopoda). *Integrative and Comparative Biology*, **52**: 430-442.
- Read, W. A., Browne, M. A. E., Stephenson, D. and Upton, B. G. J. 2002. Carboniferous. 251–299. In Trewin, N. H. (ed.). *The Geology of Scotland*. Fourth edition. The Geological Society of London. The Geological Society, London, 576 pp.
- Regier, J. C., J. W. Shultz, A. Zwick, A. Hussey, B. Ball, R. Wetzner, J. W. Martin, and C. W. Cunningham. 2010. Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. *Nature*, **463**: 1079-1083.
- Rogers, A.F. 1902. Some new American species of *Cyclus* from the Coal Measures. *Kansas University Science Bulletin*, **1**: 269–274.
- Schram, F. R. 1981. Late Paleozoic crustacean communities. *Journal of Paleontology*, **55**: 126-137.

- Schram, F. R. 1983. Lower Carboniferous biota of Glencartholm, Eskdale, Dumfriesshire. *Scottish Journal of Geology*, **19**: 1-15.
- Schram, F. R. 2013. Comments on Crustacean biodiversity and disparity of body plans, pp. 1-33. In L. Watling and M. Thiel, eds., *Functional Morphology and Diversity, The Natural History of Crustacea*, Vol. **1**. Oxford University Press.
- Schram, F. R. and Horner, J. 1978. Crustacea of the Mississippian Bear Gulch Limestone of Central Montana. *Journal of Paleontology*, **52**: 394-406.
- 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.
- Schram, J. M. and Schram, F. R. 1974. *Squillites spinosus* Scott 1938 (Syncarida, Malacostraca) from the Mississippian Heath Shale of central Montana. *Journal of Paleontology*, **48**: 95-104.
- Schweigert G., 2007. *Juracyclus posidoniae* n. gen. and sp., the first cycloid arthropod from the Jurassic. *Journal of Paleontology*, **81**: 213 – 215.
- 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**:181-1824.
- Trauth, F. 1918. Über einige Krustazeenreste aus der alpin-mediterranean Trias. *Annalen des Naturhistorischen Hofmuseums*, **32**: 172–192, pl. 1.

- 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.
- Wood, S. P. 1982. New basal Namurian (Upper Carboniferous) fishes and crustaceans found near Glasgow. *Nature*, **297**: 574-577.
- 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.
- Woodward, H. 1878. A Monograph of the British Fossil Crustacea belonging to the Order Merostomata. *Palaeontographical Society Memoir*, 263 p., 36 plates.
- Woodward, H. 1894. Contributions to our knowledge of the genus *Cyclus*. *Geological Magazine*, n.s., **1** (12): 530-539.
- 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.

Table 1. Fossil biota associated with the Shrimp (Bed A), *Posidonia* (Bed B) and *Lingula* (Bed E) members of the Limestone Coal Formation based on the collections of the Hunterian (University of Glasgow) and Wood (1982), Clark (1989, 1990, 1991, 2013), Coates (1993, 1998), and Coates & Sequeira (2001). Gray shading indicates presence of faunal element. (published version)

| Taxon | Bed A | Bed B | Bed E |
|-----------------------|--------------|--------------|--------------|
| <i>Mesopoma</i> | | | |
| <i>Watsonichthys</i> | | | |
| <i>Melanecta</i> | | | |
| <i>Palaeophoxinus</i> | | | |
| <i>Acanthodes</i> | | | |
| Rhizodont | | | |
| Coelacanth | | | |
| <i>Tristychius</i> | | | |
| <i>Woodichthys</i> | | | |
| <i>Akmoniston</i> | | | |
| Orestiacanthid | | | |
| Bradyodont | | | |
| <i>Falcatus</i> | | | |
| <i>Denae</i> | | | |
| <i>Amphicentrum</i> | | | |
| <i>Megalichthys</i> | | | |
| <i>Deltoptichus</i> | | | |

| | | | |
|------------------------|--|--|--|
| <i>Rhizodopsis</i> | | | |
| <i>Helodus</i> | | | |
| <i>Frederichthys</i> | | | |
| Guilayichthyform | | | |
| Iniopterygian | | | |
| Conodonts | | | |
| <i>Lingula</i> | | | |
| <i>Crurithyris</i> | | | |
| Nuculid spat | | | |
| <i>Septimyalina</i> | | | |
| <i>Posidonia</i> | | | |
| <i>Myalina</i> | | | |
| <i>Streblochondria</i> | | | |
| Gastropod indet. | | | |
| Orthocone | | | |
| Nautiloid | | | |
| <i>Tyrannophontes</i> | | | |
| <i>Dithyrocaris</i> | | | |
| <i>Palaemysis</i> | | | |
| <i>Tealliocaris</i> | | | |
| <i>Americlus</i> | | | |
| <i>Crangopsis</i> | | | |

Table 2. Scottish Carboniferous crustacean localities yielding Cyclida and related North American localities. Ma = millions of years ago.

| Locality | Chronostratigraphy | Lithostratigraphy | Notes on Lithostratigraphy | Notes |
|---|--|---|--|--|
| Mazon Creek, Illinois, USA | Moscovian (Clements <i>et al.</i> , 2019) | Francis Creek Shale Member; Carbondale Formation | | Cyclidans are part of the Essex Biota |
| Bear Gulch, Montana, USA | Bashkirian (318 ma, Lund <i>et al.</i> , 2012) or Serpukhovian (323 ma, Grogan <i>et al.</i> , 2014) | Bear Gulch Beds; Heath Formation; Big Snowy Group | Some reports suggest it is in the Tyler Formation (Schram & Horner, 1978) | Age not constrained well? |
| Carluke, Scotland | Arnsbergian, Serpukhovian | Calmy Limestone; Upper Limestone Formation | | Cyclidans in concretions with cuticular preservation |
| Bearsden, Burniebrae Burn, Redcleugh Burn, Lochermill, Corrie Burn, Spouthead and Peel Glen, Scotland, UK | Serpukhovian | Limestone Coal Formation; Clackmannan Group | Base of this formation is the top of the Top Hosie Limestone and the top is the base of the Index Limestone. | There are many localities around the Midland Valley of Scotland that are equivalent in lithostratigraphic level. |
| Carluke, Scotland | Brigantian, Viséan | Charlestown Main Limestone; Lower Limestone Formation; Clackmannan Group | Equivalent to the Blackhall Limestone | Single specimen of cyclidan circular central structure in relief composed of carbonate. |
| Glencartholm, Scotland | Holkerian-Asbian; Viséan | Glencartholm Volcanic Member (=Glencartholm Volcanic Beds of old literature); Tyne Limestone Formation; Yordale Group | | |
| Muirhouse, Scotland | Holkerian-Asbian; Viséan | Granton Shrimp Bed; West Lothian Oil-Shale Formation; Strathclyde Group | | Possibly contemporaneous with the Glencartholm fauna. |
| Broomhouse, Whiteadder Water, Scotland | Courceyan - Chadian | Ballagan Formation; Inverclyde Group | | One possible specimen of a cyclidan |

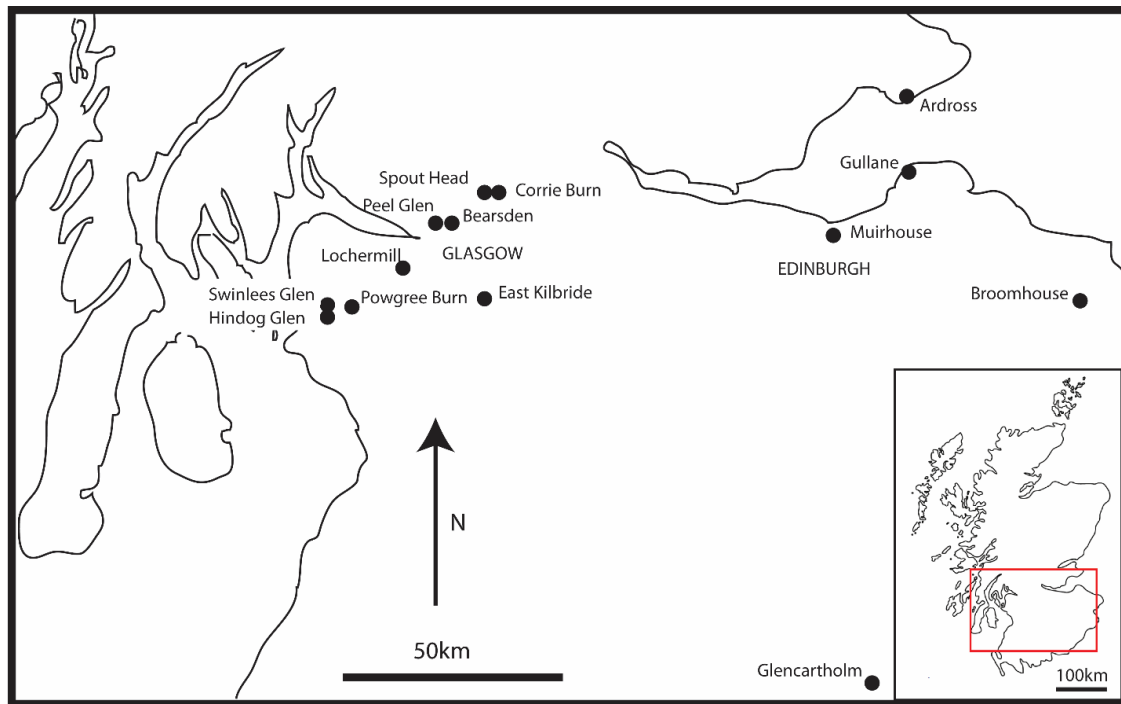
Supplementary Material:

Cyclid species with ventral and/or appendage characters preserved. See Feldmann & Schweitzer (2019) for complete listing of species and generic names and authorships.

| Characters | Americidae: <i>Americus</i> & <i>Yunnanocyclus</i> | | | | | | | Schraminiidae: <i>Schramine</i> | | | | | Halicynidae: <i>Halicyne</i> & <i>Opolanka</i> | | | Hemitrochiscidae |
|--|--|----------------------|-------------------|------------------|-------------------|-------------------|---------------------|---------------------------------|-------------------|------------------------|---------------|------------------|--|--------------------|-----------------------|------------------|
| | <i>A. johnsoni</i> | <i>A. americanus</i> | <i>A. rankini</i> | <i>A. obesus</i> | <i>A. scottii</i> | <i>Y. nodosus</i> | <i>S. gondwanae</i> | <i>S. madagascariensis</i> | <i>S. mamoroi</i> | <i>S. montanaensis</i> | <i>S. max</i> | <i>H. ornata</i> | <i>H. agnota</i> | <i>O. decorosa</i> | <i>Hemitrochiscus</i> | |
| Abdomen or pleon: absent (0), present (1) | 1 | 1 | 1 | ? | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | | |
| Caudal rami: absent (0), present (1) | 1 | 1 | 1 | ? | 1 | ? | ? | ? | ? | 1 | 1 | ? | ? | ? | | |
| number of thoracomeres (ventral): number observed | 7 | 7 | 7 | 7 | 7 | 7 | 7 | ? | ? | 6 | ? | ? | 7 | ? | | |
| thoracic appendages ornamented with spines: absent (0), present (1) | ? | 1 | 1 | ? | ? | 1 | 0 | ? | ? | ? | ? | ? | ? | ? | | |
| appendages placement: anterior to posterior (0), concentrated anteriorly (1) | ? | 0 | 0 | ? | ? | 0 | 0 | ? | ? | 0 | 0 | 1 | ? | ? | | |
| propodus of mouthparts: as long as high (0), much longer than high (1) | ? | 0 | 0 | ? | ? | 0 | ? | ? | ? | ? | 1 | 1 | ? | ? | | |
| thoracomeres terminating in ovate central structure: absent (0), present (1) | 1 | 1 | 1 | ? | 1 | 1 | 1 | ? | ? | 1 | ? | ? | 1 | ? | | |
| thoracomeres straight: absent (0), present (1), concave forward (2) | 1 | 1 | 1 | ? | 1 | 2 | 2 | ? | ? | 1 | ? | ? | 1 | ? | | |
| thoracomeres with two ovate structures distally: absent (0), present (1) | 1 | 1 | 1 | ? | 1 | ? | 1 | ? | ? | ? | ? | ? | ? | ? | | |
| maximum number of non-antennal appendages observed: number observed | ? | 8 | 8 | ? | ? | 6 or 7 | 5 | 3 | 5 | 5 | 7 | 5 | ? | 2 | | |
| horseshoe gill array: absent (0), present (1) | ? | ? | 1 | ? | ? | 1 | ? | ? | ? | ? | 1 | 1 | ? | 1 | | |

Figure Captions

A.



B.



Figure 1. Map of localities for Scottish cyclidans. Generalized map of central Scotland (A); Detail map of Bearsden localities (B). HBF = Highland Boundary Fault; OF = Ochil Fault; DWF = Dusk Water Fault; IF = Inchgotrick Fault; PF = Pentland Fault; SUF = Southern Upland Fault.

| Stratigraphy of the Manse Burn Formation | | Bed thickness in cm | Wood 1982, beds |
|--|--|---------------------|-----------------|
| Lingula Member | | 100 | Bed E |
| Betwixt Member | | 80 | unfossiliferous |
| Platey Shale Member | | 28 | Bed D |
| Nodular Shale Member | | 187 | Bed C |
| Posidonia Member | | 48 | Bed B |
| Shrimp Member | | 280 | Bed A |
| Top Hosie Limestone | | | |

Figure 2. Succession of sediments of the Limestone Coal Formation as defined in Clark (1989) and equivalent beds identified from Wood (1982).

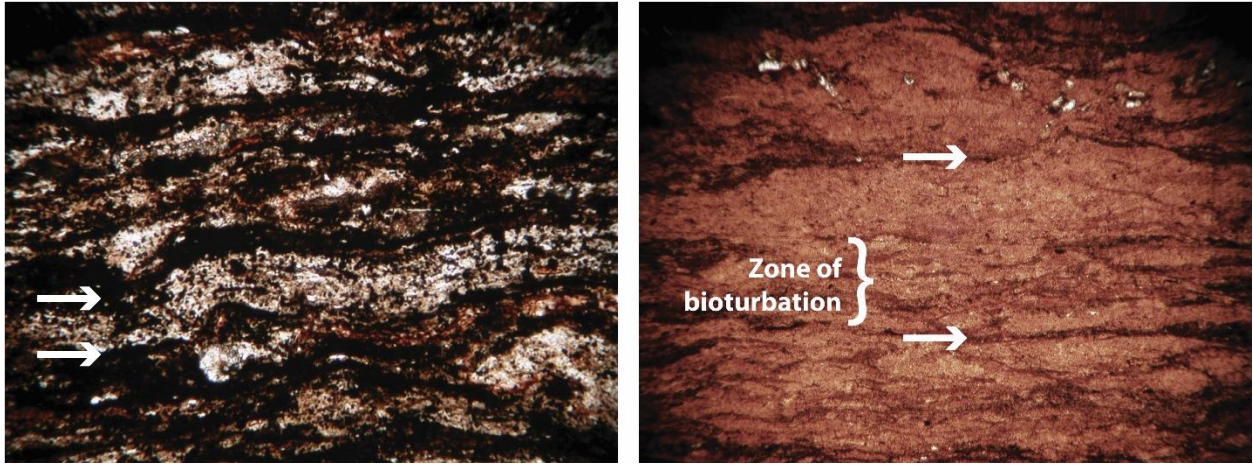


Figure 3. Organic material in the Limestone Coal Formation (**A**, **B**, arrows) and zone of bioturbation (**B**).

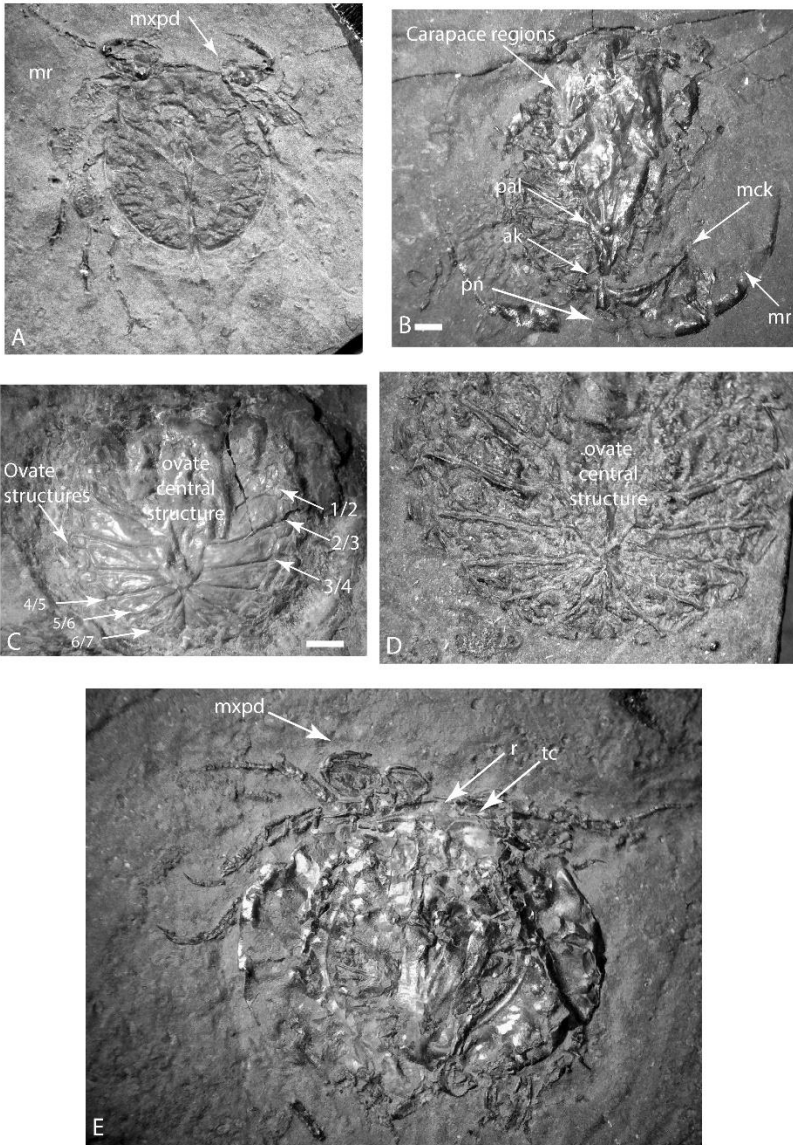


Figure 4. *Americlus rankini*. GLAHM A2811, overview of animal with wide marginal rim (mr) and maxilliped (mxpd) indicated (A). GLAHM A2806, carapace regions (axial keel, ak, and posterior axial lobe, pal) as well as median concentric keel (MCK) and wide marginal rim (mr) (B). GLAHM A2560, sternum, ovate structures and central ovate structure indicated as well as sternal sutures (C). GLAHM A2802, sternum (D). GLAHM 2814, carapace and anterior appendages: second maxilla (mx2), maxilliped (mxpd), and antennules (a1) (E). Scale bars = 1 mm.

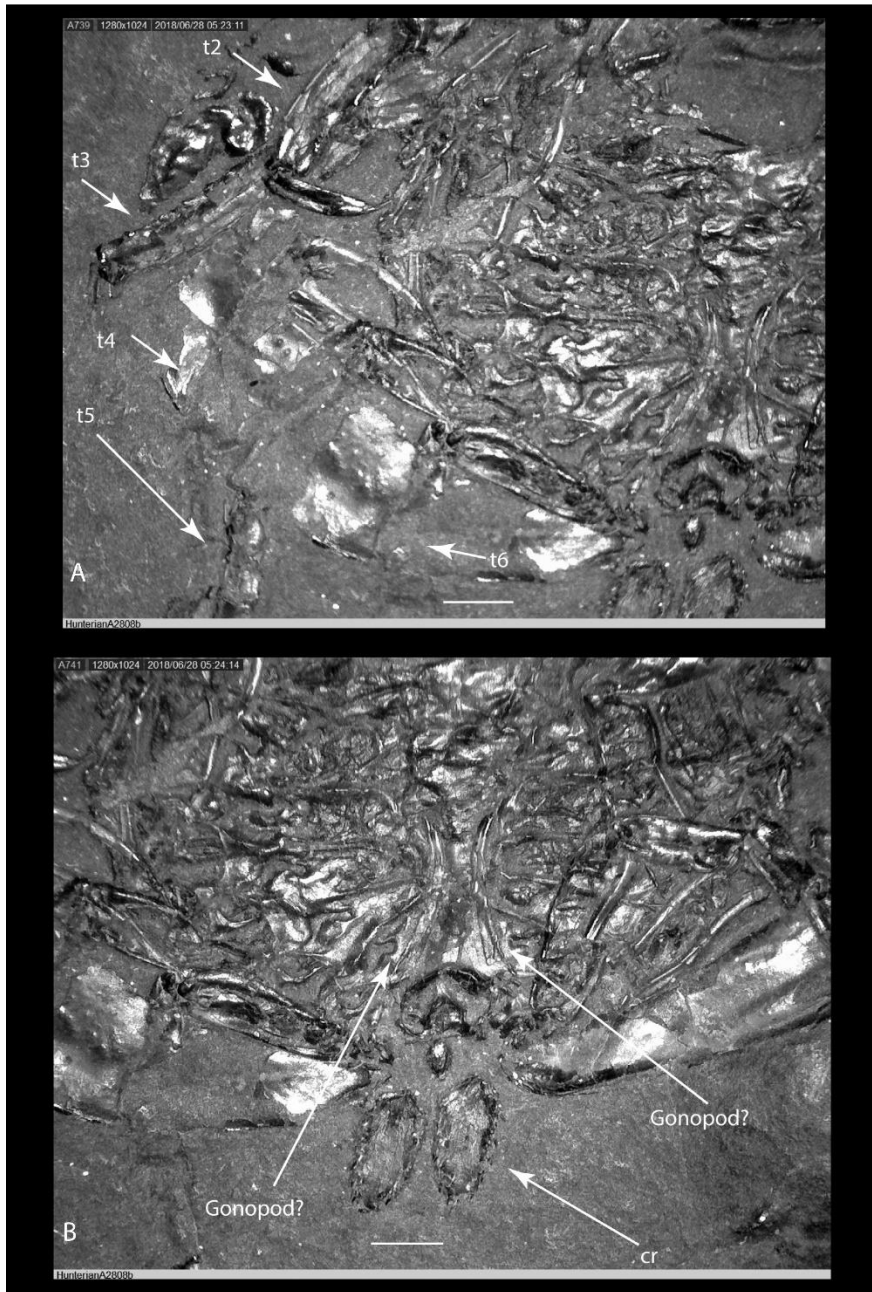


Figure 5. *Americlus rankini*, GLAHM A2808, ventral surface; thoracic appendages t2-t6 (A) and posterior anatomy including possible gonopods and caudal rami (cr) (B). Note ovate structures anterior to cr, which are possible abdominal somites. Scale bars = 1 mm.

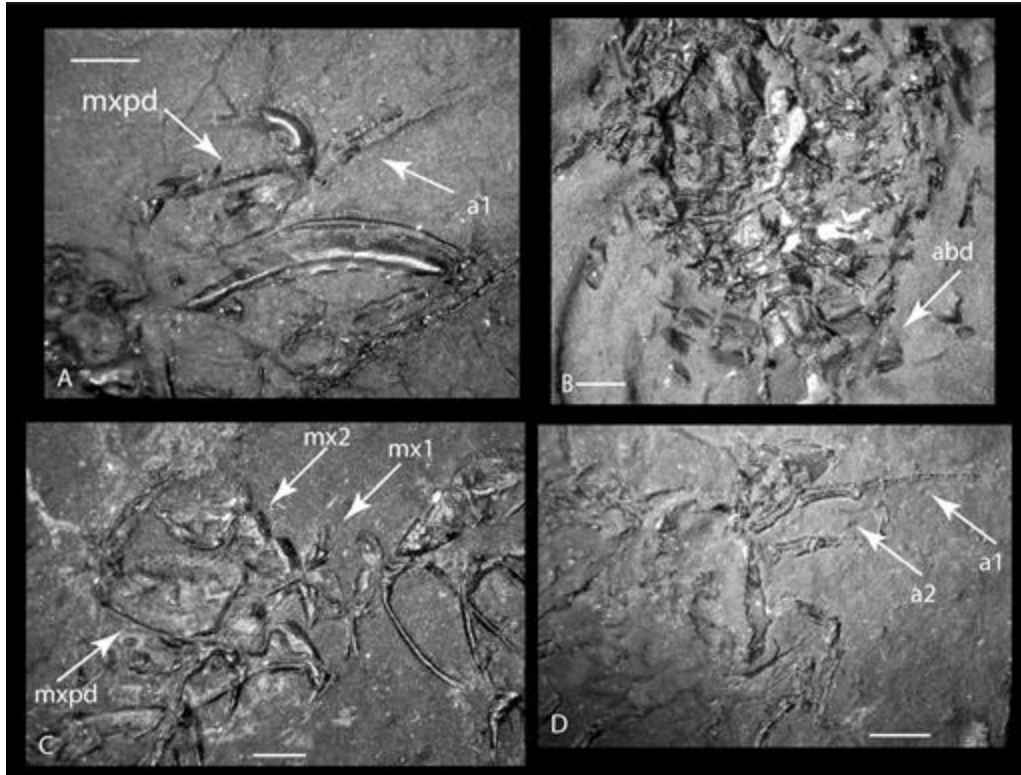


Figure 6. *Americlus rankini*. GLAHM A2806, antennule (a1) and maxilliped (mxpd) (A). GLAHM A2812, ventral view with possible abdomen extending posteriorly (B). GLAHM A2806, well-preserved mouth parts, including first and second maxillae (mx1, mx2) and maxilliped (mxpd) (C). GLAHM A2807, antennules (a1) and antenna (a2) (D). Scale bars = 1 mm.

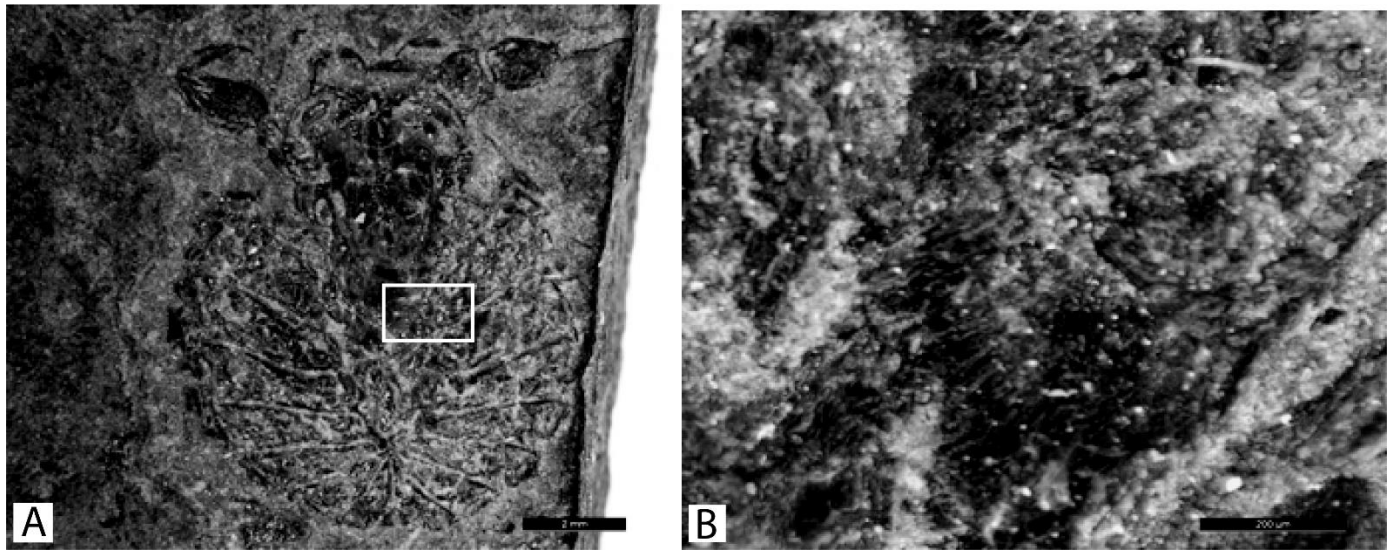


Figure 7. GLAHM A2802 showing preservation of possible gill structures dorsal to the central disk structure, white rectangle is area enlarged (**A**); enlarged close up showing lamellar structure of possible gills (**B**). Scale bar A = 2mm; B = 200μm.

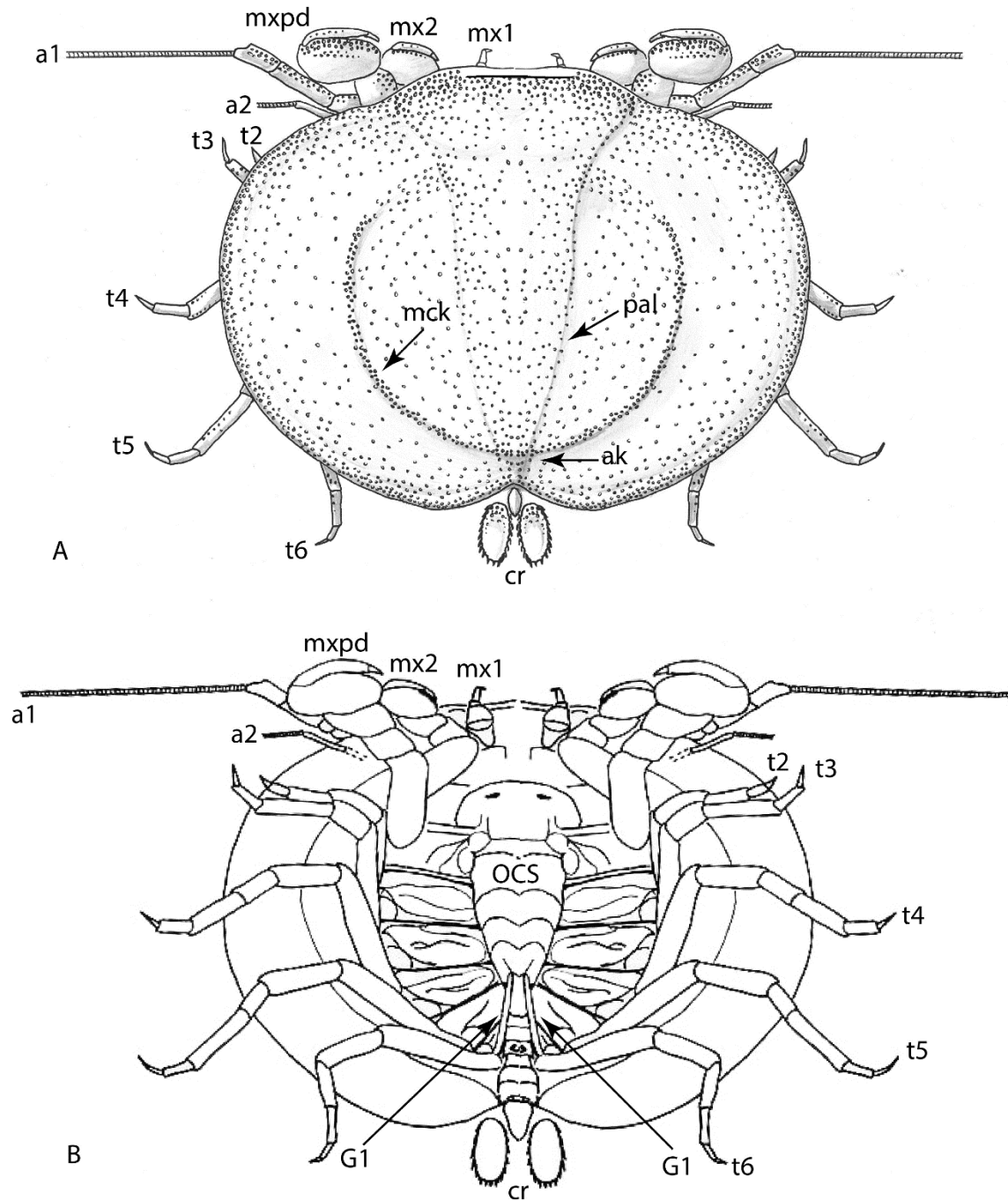


Figure 8. Dorsal (A) and ventral (B) reconstruction of *Americlus rankini* based upon specimens illustrated here. Abbreviations as in other figures; G1 = gonopod, OCS = ovate central structure.

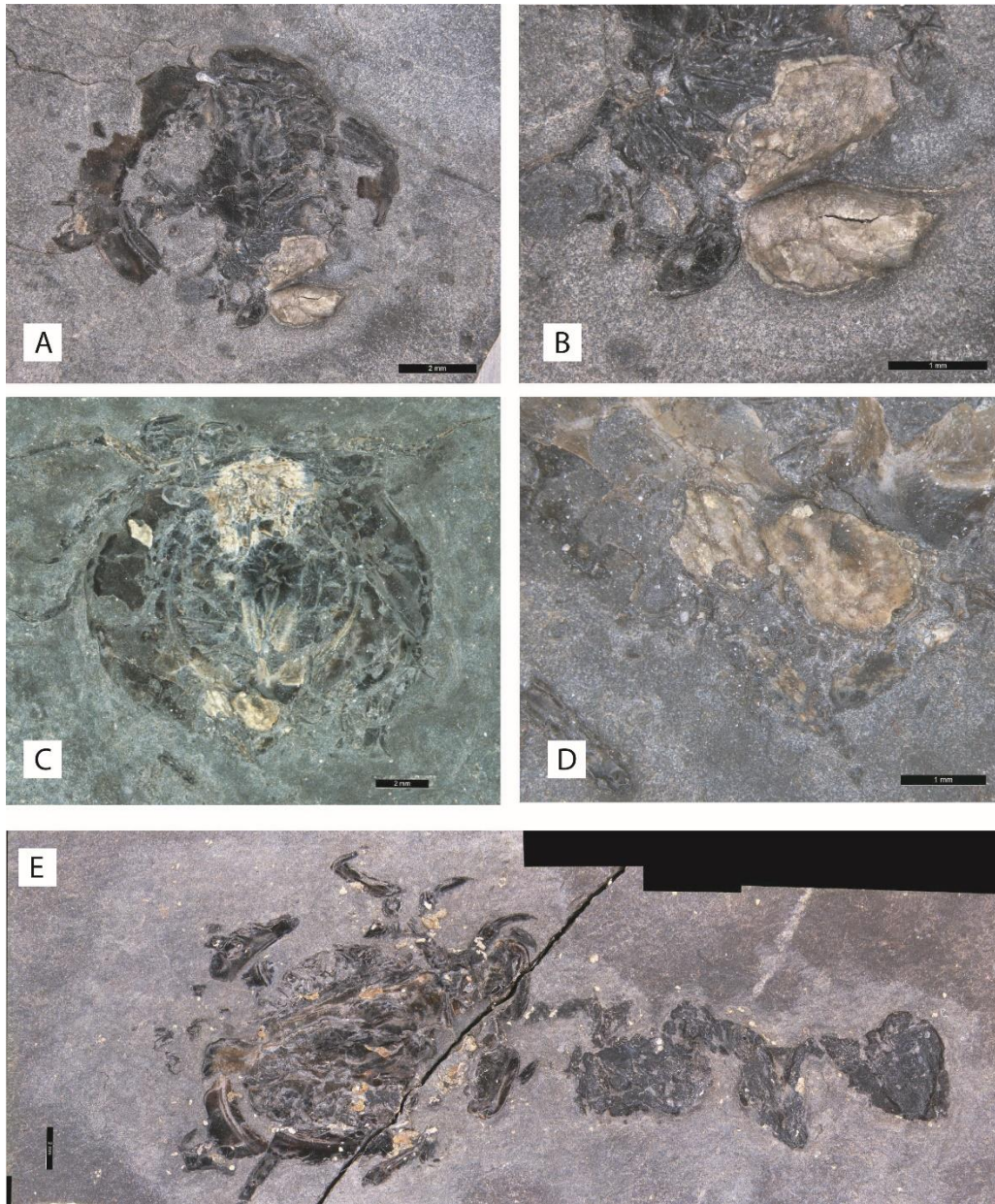


Figure 9. GLAHM A2813 with bivalves attached to rear of carapace (A) and enlarged (B); GLAHM A2814 with bivalves attached to rear of carapace (C) and enlarged (D); GLAHM A21528 with distended coprolite positioned near the mouth parts of the cyclidan (E). Scale bars A, C, E = 2 mm; scale bars B, D = 1 mm.