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Type Collection References

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MAZON CREEK CYCLOIDEA

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ABSTRACT—The Mazon Creek Cycloidea contain four taxa: *Cyclus americanus* Packard, 1885, *Cyclus obesus,* new species, *Halicyne max,* new species, and *Apionicon apioides,* new genus, new species. We conclude, based on a cladistic analysis, that cycloids are specialized maxillopodan crustaceans and a possible sister group to the Copepoda. They may have filled a niche similar to modern-day crabs.

INTRODUCTION

CYCLUS AMERICANUS PACKARD, 1885, is among the most common of Pennsylvanian arthropods from the Essex biota of the Mazon Creek area of northeastern Illinois. Packard's original description employed only a single specimen from the famous Lacoe Collection, now in the National Museum in Washington. At that time, despite a lack of good illustrations in the literature for the European species of *Cyclus* with which to compare his fossil, Packard managed to relate those previously known species to his specimen, interpreting *C. americanus* as a larva of some kind of horseshoe crab. However, Packard's effort stands as only a single incident in a long history of confusion and debate over the affinities of these enigmatic arthropods.

Phillips (1835) described the first cycloid based on a single example from the Carboniferous Limestone of Yorkshire, England, assigning his peculiar little nut-shaped species, *Agnostus radialis,* with radiating grooves and ridges, to the trilobites. Not long afterward, de Koninck (1841) concluded that Phillips' specimen was not a trilobite and created a new genus, *Cyclus,* for it and other material of his own from the Carboniferous of Belgium. To de Koninck, the genus *Cyclus* clearly possessed a symmetrical round to oval shell with depressed margins, anterior paired ocular tubercles, and posterior longitudinal and radial sinuous ridges. Nevertheless, de Koninck did not have a clear understanding of *Cyclus* because later (de Koninck, 1842) he erected a second species (*C. brongniartianus*) that Woodward (1870) subsequently recognized as a trilobite hypostome.

Phillips' and de Koninck's confusion of their fossils with the agnostid trilobites was not an isolated case. Quite independently, von Meyer (1838) rather casually recognized a new species of what he thought was a trilobite from the Triassic Muschelkalk, naming it *Limulus agnotus.* He subsequently decided in 1844 that this species was neither a trilobite nor a *Limulus* and erected

for it the genus *Halicyne*. However, this genus remained rather vaguely diagnosed until von Meyer (1847) named a second, somewhat smaller, sister species to *H. agnota* from the same beds, *H. laxa*. Although these *Halicyne* occurred as steinkerns, i.e., interior molds of the shell or carapace, the genus clearly was about as wide as long, possessed a truncated front margin, had a rather vaulted shell with its height being about ⅓ the length, and displayed a wide, flat, posteriorly pointed margin.

So, by the middle of the 1800s two distinct cycloid morphotypes occurred: a small, nut-like, ridged "skull cap," viz., *Cyclus*; and a flattened "shield," viz., *Halicyne*. In 1857, von Seebach collected three poorly preserved specimens from the Triassic Lettenkohle of Thuringia near Weimar and named them *Halicyne plana*. However, subsequent authors largely overlooked this work. Schafhäutl (1863, p. 423) recorded a form similar to *Halicyne*, which he named *Carcinaspis pustulosus*, with a highly papillose surface and sculpted margin from the Upper Triassic of the Alps. Both *H. plana* and *C. pustulosus* broadly conformed to the flattened shield morphotype.

In 1868 and 1870, Henry Woodward began to describe cycloids in considerable numbers. Besides *C. radialis*, Woodward recognized five species from the Carboniferous rocks of the British Isles: *C. harknessi, C. bilobatus, C. rankini, C. torosus, C. wrightii* and *C. jonesianus*, and these conformed in broad outline to the morphotype of Phillips' *C. radialis*, i.e., small, cap-like forms. All but the first of these, though, rather lacked the distinctive radiating grooves and ridges, features which *C. radialis* and *C. harknessi* shared. Because the non-radiating cap-like forms resembled the shield-like genus *Halicyne*, Woodward demoted *Halicyne* to a subgenus within the genus *Cyclus*. Woodward thus began the confusion among cycloid genera that persists to this day.

As we noted, Packard (1885, 1886) described the first American species of *Cyclus, C. americanus*, from the famous Pennsylvanian Mazon Creek deposits of Illinois. Packard compared his little fossil to larval *Limulus*, but in this he merely followed upon himself since his own earlier published commentary (Packard, 1872) treated *Cyclus* as a late larva of, or possibly an adult, *Limulus*. The Mazon Creek fossil itself (see Figure 1.1, 1.2) certainly preserved little that would have justified saying so. Unwittingly, however, Packard introduced yet a third morphotype into the cycloid pantheon, not recognized as such at the time. This morphotype possessed not only the flattened and shield-like form evocative of *Halicyne*, but also had a rounded or concave posterior margin and an anteriorly extended rostral plate.

Woodward (1893) erected another species, *Cyclus scotti*, and the first elucidation of the great array of preservational variations in *Cyclus* came from Woodward (1894). Peach (1883) influenced Woodward in this regard, by first recognizing that *C. rankini* preserved a ventral surface, and then describing a species of his own from the Coal Measures of Scotland, *C. testudo*, that supposedly had biramous limbs. From this work of Peach, Woodward then recognized that 1) his species *C. torosus* in reality preserved the ventral surface; 2) *C. jonesianus* had many preservational variants; and 3) one preservational variant of *C. radialis* displayed a broken carapace in such a way as to show part of the radiating grooved and ridged dorsal surface of the segments that lay beneath the shield. Woodward also speculated for the first time on cycloid functional morphology, suggesting that *Cyclus* had an enormously developed labrum with either the mouth moved way posteriad and the leg bases serving as jaws (as in *Limulus*), or the labrum developed as a sucking tube (as in *Argulus*). Finally, Woodward's publication characterized *Cyclus* for the first time as ". . . undoubtedly . . . crustacean" (Woodward, 1894, p. 534). Woodward also added two new species to the growing list, *C. scotti* (1893) and *C. johnsoni* (1894), which matched the general rounded shield-like form of *C. americanus* and *C. testudo*.

Reed (1893) described another nut- or cap-like form with radiating grooves and ridges, *C. woodwardi*. Thus by the turn of the century, the British *Cyclus* assemblage exhibited great diversity.

In parallel with this work on Coal Measure *Cyclus* and Triassic *Halicyne*, descriptions of an enigmatic array of smaller, highly vaulted cap-like species appeared. Von Schauroth (1854) presented a small granulate shell, *Hemitrochiscus paradoxus*, from Upper Permian rocks in Germany. Gemmellaro (1890) demonstrated a distinctly different, spinous form from the Permian strata of Sicily, *Oonocarcinus insignis*, as well as a form more akin to rounded shield-like *Cyclus* originally called *Paraprosopon reussi*. Stolley (1915) discovered in Triassic rocks of the Alps and the Balkans a tiny, cap-like form, *Cyclocarcinus serratus*, and a very peculiar, possibly spinose species, *Mesoprosopon triasinum*.

Despite the fact that by this time three distinctively different forms of cycloid occurred in rocks of either Carboniferous or Triassic age, the general consensus viewed them as closely related species. As an example, Rogers (1902) described some additional highly vaulted, cap-like, papillose forms from the Pennsylvanian limestones of Missouri, *Cyclus communis* with supposedly large compound eyes and *C. permarginatus*. Clearly, Rogers attached no significance to the vaulting since he also described some flattened *Cyclus* forms, *C. packardi, C. limbatus* with distinctive spines on the margin, and *C. minutus*.

Woodward (1905) re-entered the field again with a short note on *C. johnsoni* and *C. rankini* in which he asserted, with apparently little basis except for Peach's earlier interpretation, that all cycloids had biramous limbs; he also reiterated his view that cycloids were limuloid-like crustaceans (not mutually exclusive terms at that time in history because *Limulus*, and even trilobites, were thought of as "crustaceous" in nature). Reed (1908) described an Irish cycloid, *C. simulans*.

Bill (1914) noted specimens of *Halicyne* from the Alsatian Buntsandstein, and Trauth (1918) also found *Halicyne* in Upper Triassic rocks of the Alps. Neither of these authors formally assigned their specimens to distinct species.

Hopwood (1925) finally tried to deal with the three distinct morphotypes and re-separated *Halicyne* from *Cyclus*. However, he focused on characters somewhat at odds with the original diagnoses of the genera. Hopwood viewed *Halicyne* as a large form with a bifurcate or bilobed posterior margin possessing punctate ornament; whereas he perceived *Cyclus* as a small form with a posterior median ridge that could bifurcate to enclose a triangular area anteriorly and with lobate, ridged, nodular, or papillose ornament. Hopwood sorted out all known species of that time based on these characters. The genus *Halicyne* contained the species *agnota, americana, johnsoni, limbata, packardi, permarginata*, and *scotti*. The genus *Cyclus* contained the species *radialis, bilobatus, communis, harknessi, woodwardi, jonesianus, minutus, torosus* and *wrightii*. Hopwood (1925, p. 308) could not determine the affinities of *H. laxa*, and decided that *C. rankini* was merely the ventral side of one of the other species. He also believed that the affinities of the cycloids lay with Branchiura, parasitic crustaceans also known as the fish lice.

Müller (1955) clearly re-established the differences between the two genera. Returning to the work of von Seebach (1857), and prompted by some new material, Müller identified the truncated anterior margin and the pointed median, posterior margin as the distinctive features of the genus *Halicyne*.

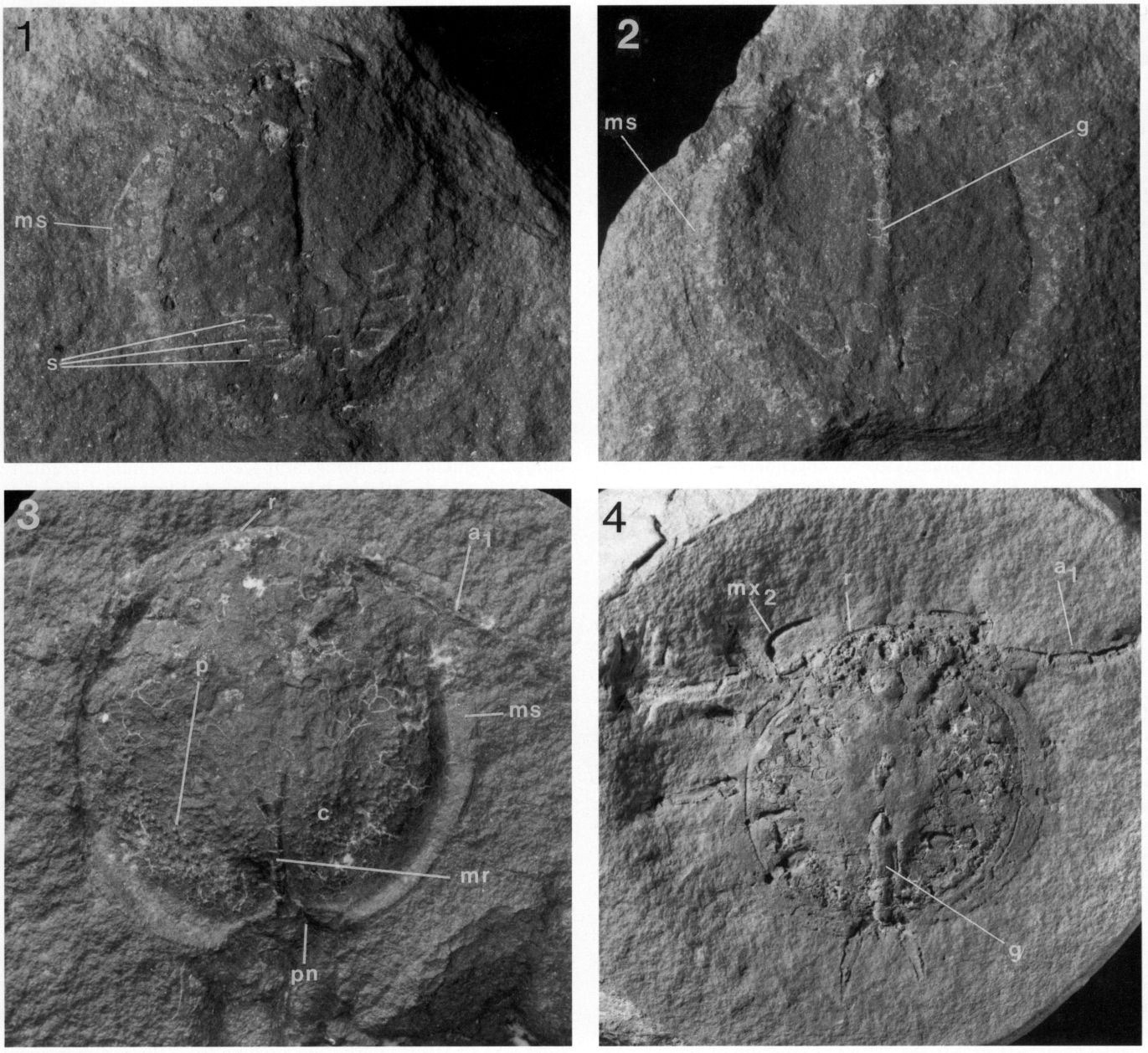

FIGURE 1—*Cyclus americanus* Packard. *1,2,* Part and counterpart of the holotype, USNMP 38863, × 4.3. *3,* Note carapace shield showing anterior lobe bearing antennules and antennae, posterior median notch, broad marginal shelf, median posterior ridge, lateral and posterior course papillation, PE 22462, × 5. *4,* Displaying trunk limbs impressed from below the carapace, antennules, geniculate maxillae, and caudal rami, PE 31712, × 3. a1 = antennule, c = carapace, g = gut, mr = medial ridge, ms = marginal shelf, mx2 = maxilla, p = papillae, pn = posterior notch, r = rostral lobe, s = sternites.

Trümpy (1957) promptly took up this definition when he erected a species from the Muschelkalk, *Halicyne ornata.* Trümpy also pointed out the great variation in shape within the genus *Cyclus* and called attention to the difference between the flattened species as opposed to highly vaulted taxa, suggesting that separate generic names might eventually be necessary to distinguish these two morphotypes. Thus Trümpy recognized as distinct the third cycloid morphotype introduced by Packard in 1885 when he described *C. americanus.*

Kramarenko (1961) extended the geographic range for *Cyclus* when he described *C. milaradovitchi* from Lower Permian rocks of the southern Urals.

Goldring (1967) introduced a new *Cyclus* species from Upper Viséan strata of England, *C. martinensis.* He determined that coral thickets formed probably the natural habitat of this species.

Meanwhile, Gall (Gall and Grauvogel, 1967; Gall, 1971) found *Halicyne ornata* in the Buntsandstein (some specimens originally alluded to in Bill, 1914), a classic *konservat lagerstatt.* This material occurred in greater abundance and with better preservation than that which Trümpy found in the Muschelkalk. Although the wealth of information available from the Buntsandstein specimens allowed a detailed reconstruction of *H. ornata,* Gall could say nothing about the higher level relationships of these cycloids other than "Crustacés aux affinités in-

certaines" (Gall, 1971, p. 55). However, Gall and Grauvogel did erect a subclass for cycloids, the Halicyna, and they clearly believed in biramous trunk limbs.

Glaessner (1969) provided a summary review of the cycloids, but their status within the Crustacea remained uncertain. He also took the opportunity to correct some generic names. Schafhäutl's *Carcinaspis* became *Carcinaspides,* and Stolley's *Cyclocarcinus* changed to *Cyclocarcinides.* Glaessner also sorted the genera known at that time into three families. The Cyclidae contained the more or less flatter forms *Cyclus, Halicyne,* and *Carcinaspides*; the Hemithrochiscidae included the small, highly vaulted taxa *Hemitrochiscus, Cyclocarcinides,* and *Oonocarcinus*; and the peculiar *Mesoprosodon* earned its own family, the Mesoprosopidae.

Clark (1989) conducted the most recent study of *Cyclus* based on material from the Namurian shales of Scotland. He produced a detailed reconstruction of *C. rankini* and, more importantly, attempted the first rigorous character analysis of known *Cyclus* in combination with various other crustaceans, concluding that cycloids belong within the Copepoda.

In addition to the above problems engendered by over a century of taxonomic confusion concerning cycloids among professional paleontologists, confusion also occurs among modern collectors of Mazon Creek fossils about what name to use when referring to their cycloids. These collectors variously call these fossils *Cyclus, Halicyne,* or "trilobitomorphs." Use of the term trilobitomorph harkens to the vague similarity of cycloids (albeit without tails) to forms like the Burgess Shale creatures *Burgessia* or *Waptia.* As to the origin of the confusion among collectors about generic names (though Packard placed his species *americanus* within the genus *Cyclus*), for some time the late Gene Richardson and one of us (FRS) used the generic designation of *Halicyne* for Mazon Creek cycloids. This usage developed from some contacts we had in 1967 with Prof. H. K. Brooks, who mistakenly equated the name *Cyclus* with *Halicyne.* Richardson, before his death, had begun a study of the Mazon Creek cycloids. He recognized that the fauna contained at least three species of cycloids, but remained confused as to their taxonomy and mistaken as to certain details of their anatomy. In point of fact, *Halicyne* differs significantly from *Cyclus,* and we now realize that both genera occur in the Mazon Creek fauna in addition to some previously unrecognized new species.

For this study, we used specimens in the fossil invertebrate collections of the Field Museum of Natural History in Chicago (PE), the Mazon Creek Project at Northeastern Illinois University in Chicago (MCP), the Natural History Museum of Los Angeles County (LACM), the National Museum of Natural History in Washington (USNMP), and the Nationaal Natuurhistorische Museum, Leiden (St).

SYSTEMATIC PALEONTOLOGY

Class MAXILLOPODA Dahl, 1956

Diagnosis.—No more than 12 postcephalic trunk segments, uniramous antennules, at most six thoracic segments, abdomen lacking most or all limbs, heart small and bulbous, with "maxillopodan" naupliar eye with tapetal cells.

Remarks.—This diagnosis comes from that provided for Maxillopoda in Schram (1986), and a few items in the definition (e.g., heart and naupliar eye) do not occur in any known fossils. Many crustacean workers place the Maxillopoda among the most derived of all the crustaceans. The maxillopodans exhibit a clear trend to reduce various parts of the body, often linked to repeated evolution of a parasitic life style. However, the reader should realize that if the number of trunk and thoracic segments in a crustacean does not exceed the respective numbers specified above, then one almost automatically considers it a maxillopodan by default—not a particularly desirable situation.

Subclass HALICYNA Gall and Grauvogel, 1967

Diagnosis.—With only one order recognized at present, the subclass definition is the same as that of the order.

Order CYCLOIDEA Glaessner, 1928.

Diagnosis.—Maxillopodans with flattened bodies, carapace oval to subcircular in outline and typically covering entire body, uniramous antennules large, uniramous antennae reduced in size, antennules and antennae laterally attached on the anteriormost part of the head, abdomen reduced to no more than one or two segments, maxilla and anterior thoracopod(s) developed as geniculate claspers.

Family CYCLIDAE Packard, 1885.

Diagnosis.—Dorsal surface shield-like in appearance and often highly convex; carapace with margin entire or denticulate and with central regions smooth, longitudinally keeled, or papillose; segments underlying carapace appear somewhat radially arranged; abdomen bears terminal, blade-like caudal rami.

Remarks.—The above definition modifies that of Glaessner (1969). The range of structural diversity in carapace form, as well as in genicula number and their anatomical variations in the Mazon Creek cycloids, may in fact be the basis some day for splitting this single family into several. Future discoveries about these features in other genera and species of the cycloids will undoubtedly lead to complete taxonomic revision of the group.

The preservation of these fossils can confuse the casual observer. The carapace can occasionally appear intact (e.g., PE 22462, Figures 1.3, 2.2). More often one or more surfaces of the original body can appear on the same specimen. The dorsal surface of the carapace often breaks away in the central area, displaying portions of the cephalothoracic segments underneath (USNMP 38863, Figure 1.1). One can often see traces of the cephalothoracic limbs impressed from below (e.g., PE 31712, Figure 1.4; PE 22472, Figure 3.4). In some specimens, the lateral portions of the carapace are missing to reveal the lateral portions of the thoracic tergites and limbs PE 34759, Figure 5.4). The ventral surface can also display variations in their preservation, e.g., as a ventral view of the sternites without legs (PE 22478, Figures 6.1,2) or as a ventral view of the legs lying over the sternites (PE 34954, Figure 5.2). Preservation commonly occurs in negative, i.e., a mold of the original (PE 21013, Figure 6.5). Fossils may exhibit variations ranging from three-dimensional preservation of the original form (e.g., PE 22495, Figure 6.3) to mere color differences in the rock (e.g., the antennae on MCP 507, Figure 4.1), or retain a lot of clay mineral such as kaolinite (PE 24959, Figure 3.1) or pyrite (PE 20601, Figure 6.4). Because of the variations in preservation that one can find on these fossils, no one specimen preserves all the anatomy in perfect array. Thus, reconstructions offered by us are composites based on examination of several specimens for each feature. Material actually illustrated here represents only a small portion of what one can see on the 876 specimens available for this study.

Genus CYCLUS de Koninck, 1841.

Diagnosis.—Carapace oval to subcircular except for a large rectangular plate over a frontal extension of cephalon, not very convex and somewhat flattened in lateral or cross-sectional view, surface papillose or smooth, margin either smooth or decorated with fine crenulations. Antennules and antennae attached laterally to frontal extension. Mandibles small and serrate, maxillules small and bearing reflexed palps. Maxillae as large gen-

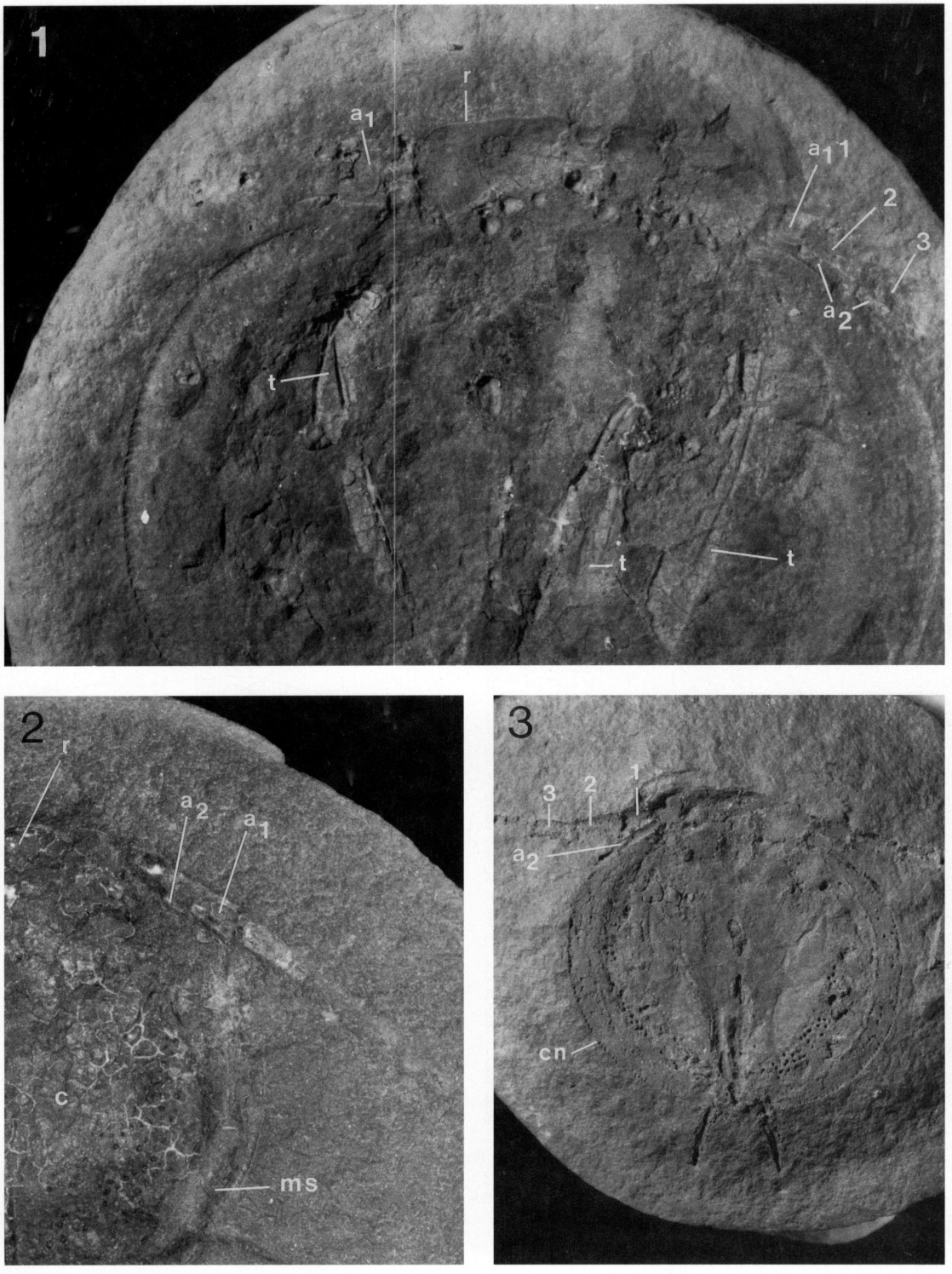

FIGURE 2—*Cyclus americanus* Packard. *1,* Close-up of the anterior half showing the rostral lobe, antennule (segments numbered) and antennal peduncles, crenulated carapace margin and the proximal segments of some of the trunk limbs, PE 20985, × 6.9. *2,* Close-up under alcohol of the antennule peduncle with the proximal portion of the flagellum and a small antenna, PE 22462, × 6. *3,* Anterior part of the body displaying the antennular peduncle segments and antennae, counterpart of PE 31712, × 3.2. a1 = antennule (peduncular segments numbered), a2 = antenna, c = carapace, cn = crenulated edge of carapace, ms = marginal shelf, r = rostral lobe, t = thoracic limbs.

icula, commonly preserved outstretched beyond frontal or rostral plate. First thoracopod as geniculate maxillipede, last five thoracopods as robust walking legs.

Type species.—*Agnostus radialis* Phillips, 1835.

CYCLUS AMERICANUS Packard, 1885
Figures 1–8.

Diagnosis.—Carapace subcircular; margins as a broad shelf, postero-lateral edges of shelf crenulate, margin bearing postero-

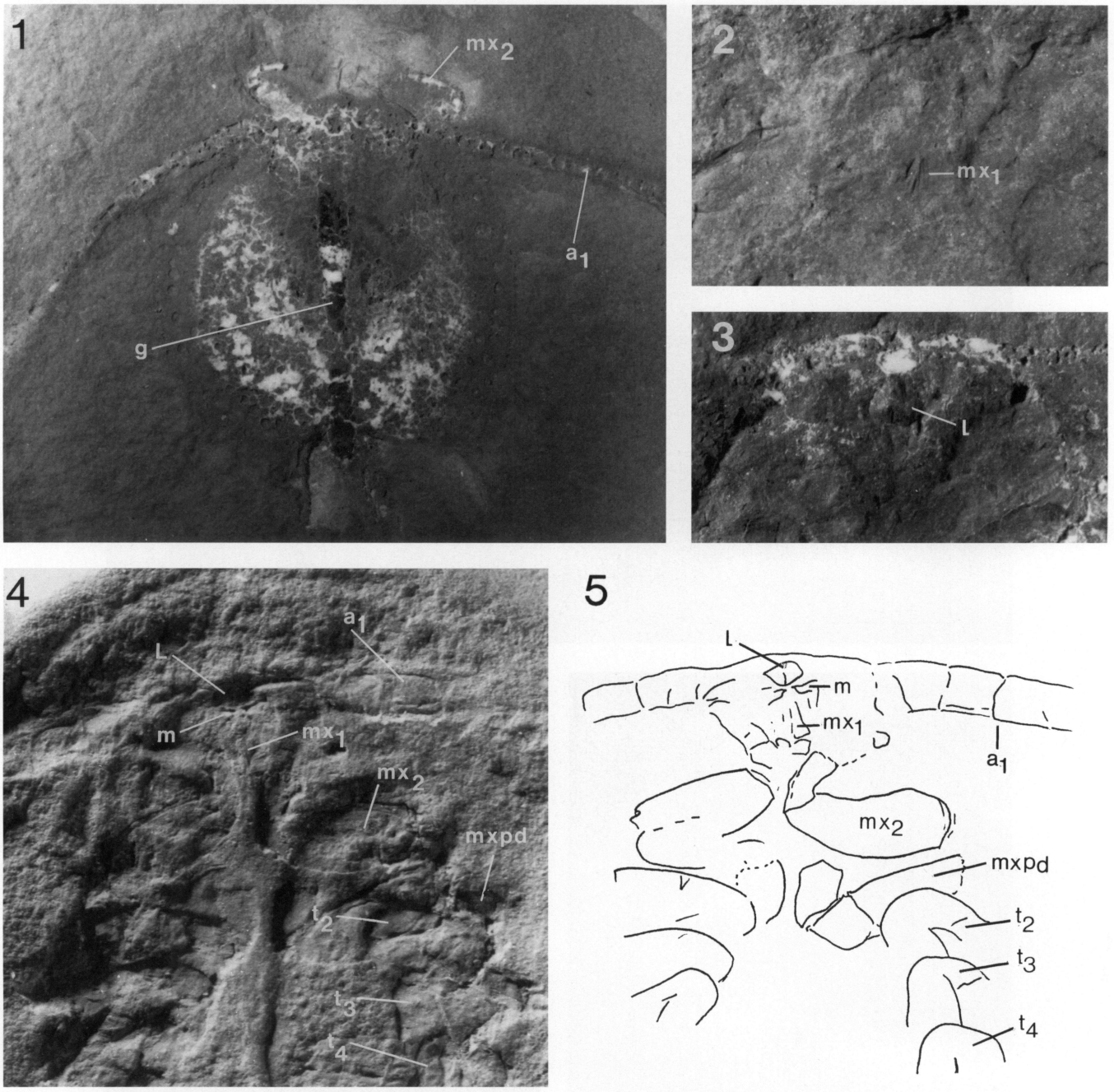

FIGURE 3—*Cyclus americanus* Packard. *1,* PE 24959 with antennular flagella and maxillary geniculum, × 4. *2,* PE 22498, maxillulary palp, × 10.6. *3,* PE 34763, close-up of anterior ventral area with labrum, × 7. *4,* PE 22472, displaying a negative impression of the labrum, of the maxillules, the proximal segments of the maxillary geniculum, the proximal segments of the maxillipedal geniculum, and the first walking legs, × 6.4. *5,* Line drawing of 4. a1 = antennule, g = gut, l = labrum, m = mandible, mx1 = maxillule, mx2 = maxilla, mxpd = maxillipede, t"n" = thoracic limbs.

median semicircular notch that dorsally exposes part of abdomen; central region of carapace marked posteriorly with broad median ridge and decorated postero-laterally with coarse papillae.

Description.—The body is roughly subcircular in outline. The length/width ratio is 0.98 (see Table 1).

The carapace has the form of a circular shield except for an anterior frontal extension, or shelf-like rostrum, that covers that part of the head that bears the antennules and antennae (e.g., PE 22462, Figure 1.3; PE 31712, Figure 1.4) and a posterior, broadly rounded, median notch (PE 22462, Figure 1.3). The carapace margin forms a broad shelf (USNMP 38863, Figure 1.2; PE 22462, Figure 2.2) that laterally and posteriorly displays crenulations, which resemble the scoring of a pie crust with a fork (PE 31712, Figure 2.3). The surface of the central part of the carapace shield has a broad, subtriangular ridge on its posterior half, as well as fields of coarse papillae located laterally and posteriorly (USNMP 38863, Figure 1.2; PE 22462, Figures 1.3, 2.2).

The large antennules extend laterally from the frontal exten-

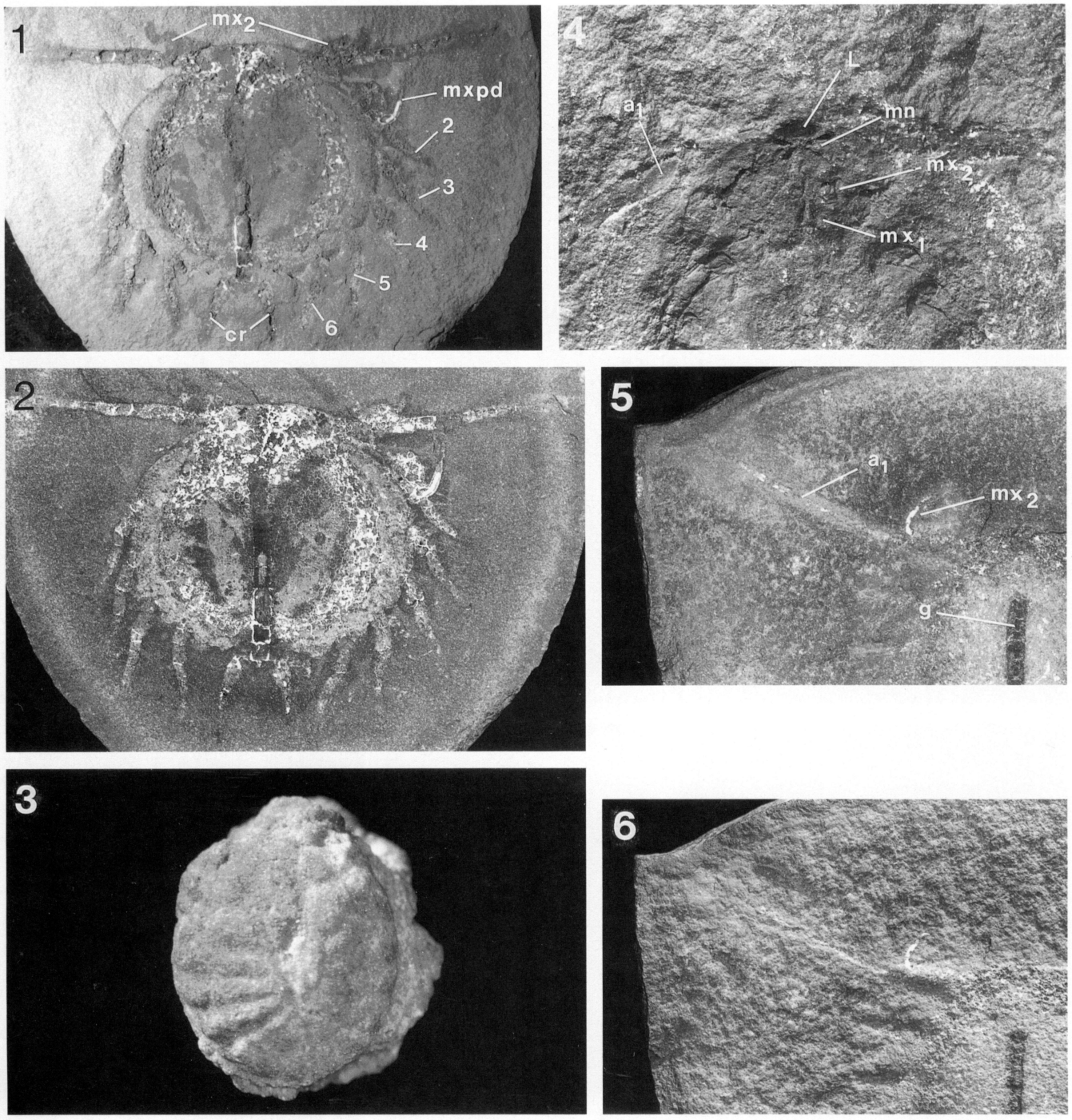

FIGURE 4—*1, 2, Cyclus americanus* Packard, MCP 507, *1,* Under alcohol , showing maxillae, maxillipedes, five thoracopods, caudal rami, and gut cast, × 2.4; *2,* under direct light, × 2.7. *3, Cyclus rostratus* Phillips. St 39783, showing the characteristic highly-vaulted body with thoracic segments visible, × 8.4. *4–6 Cyclus americanus* Packard. *4,* MCP 557 showing cephalic structures, × 5.0. *5,6,* MCP 556, with antennular flagellum segments, maxilla, and gut cast, *5,* under alcohol, *6,* under direct lighting, × 3. a1 = antennule, cr = caudal rami, g = gut, l = labrum, mn = mandible, mx1 = maxillule, mx2 = maxilla, mxpd = maxillipede, 2–6 = 2nd–6th thoracopods.

sion of the head (PE 20985, Fig 2.1). The basal segment of the peduncle is roughly subquadrangular in outline (PE 20985). The second peduncular segment, more than twice as long as the first, distally bears another short segment subequal to the first (PE 20985, Figure 2.1; PE 31712, Figure 2.3). The distal portion of the antennule possess numerous short segments (PE 24959, Figure 3.1). However, only a few specimens (PE 24959, Figure 3.1; MCP 556, Figures 4.5, 4.6) preserve these segments well enough along the entire length of the appendage that we can attempt to count them. It appears that this portion of the limb has 25–27 segments, which when added to the three peduncular segments totals 28–30 for the whole appendage (Figure 8.1).

The very small antennae appear just dorsal and posterior to the antennules (PE 20985, Figure 2.1). The peduncles possess

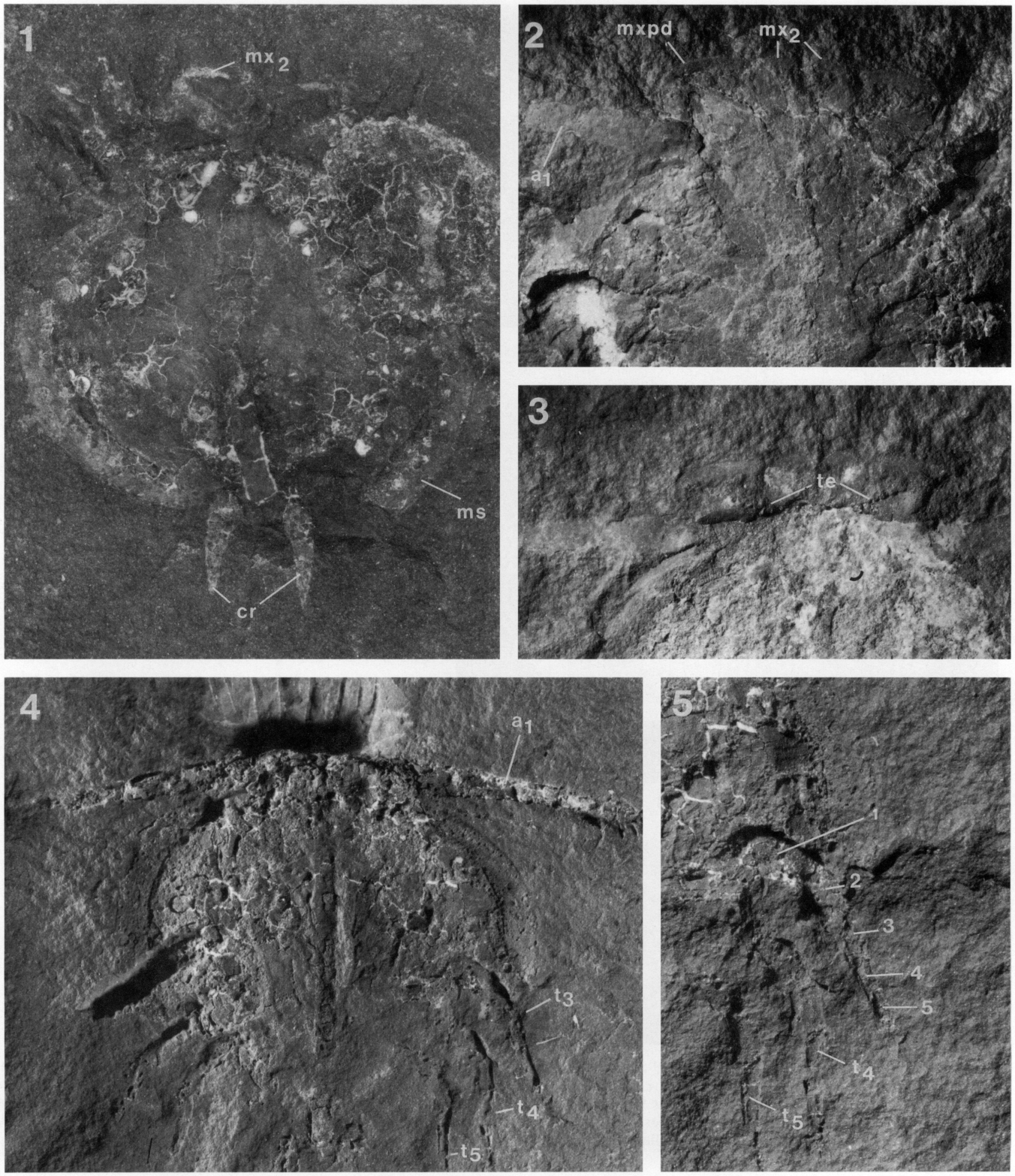

FIGURE 5—*Cyclus americanus* Packard. *1,* PE 22421 with maxillary geniculum extended to display scimitar-like terminal segment, blade-like penultimate segment, and caudal rami, × 5. *2 ,3,* PE 34954 (part and counterpart) × 4.8, *2,* Medial-most maxillary genicula and maxillipede distal segment. *3,* Clear view of teeth on penultimate blade of maxillipedal geniculum. *4 ,5,* PE 34759, *4,* Showing general body form and placement of thoracic legs, × 4.3. *5,* Close-up revealing leg segments distal to knee, × 7.8. a1 = antennule, cr = caudal rami, ms = marginal shelf of carapace, mx2 = maxillae, te = teeth, t "n" = thoracopods, 1–5 segments on third thoracopod.

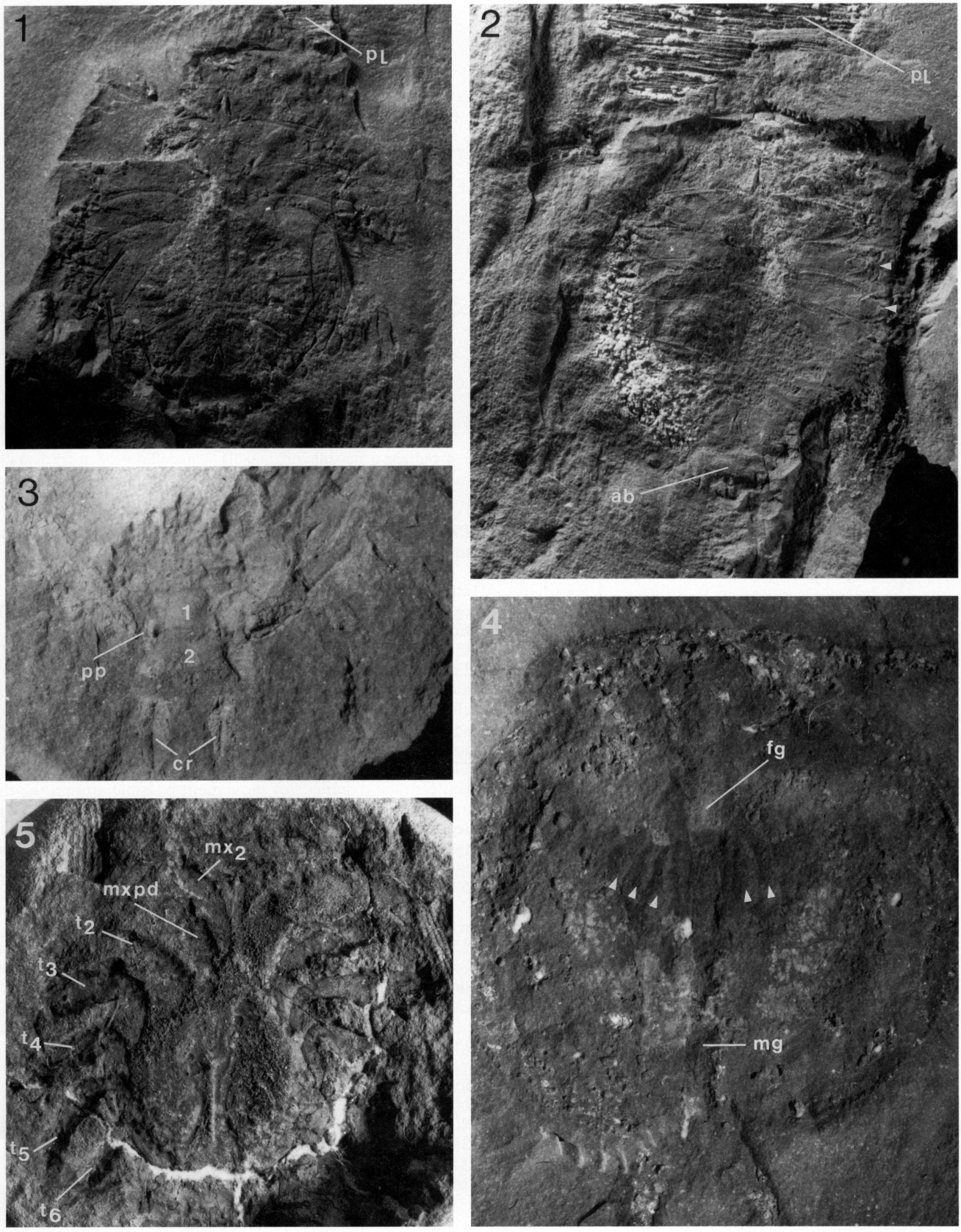

FIGURE 6—*Cyclus americanus* Packard. *1,2,* PE 22478, part and counterpart with associated plant remains and displaying ventral surface, note long proximal leg segments and apparent basal-most ring segments (arrow heads), × 5. *3,* PE 22495, posterior portion of body with abdomen, caudal rami and portions of posterior thoracic limbs, × 6. *4,* PE20601, under alcohol, with foregut, pyritized gut dilator muscles (arrow heads), midgut, × 5.7. *5,* PE 21013, ventral surface, printed reversed to heighten relief, × 4.7. cr = caudal rami, fg = foregut, mg = midgut, mx2 = maxilla, mxpd = maxillipede, pl = plant material, pp = "genital" posterior papillae, t "n" = thoracopods, 1–2 = abdominal segments.

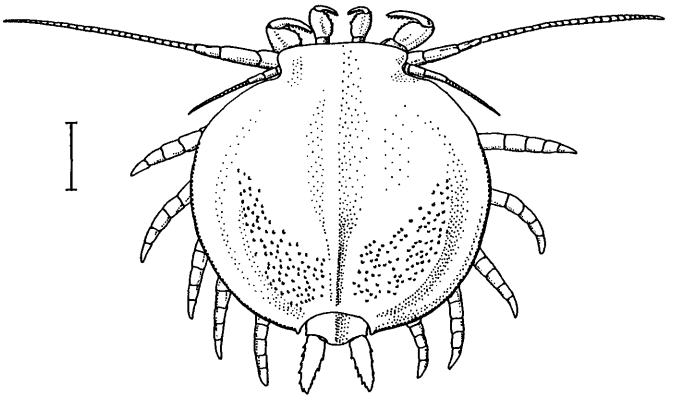

FIGURE 7—*Cyclus americanus* Packard. Reconstruction of dorsal surface. Scale = 2 mm.

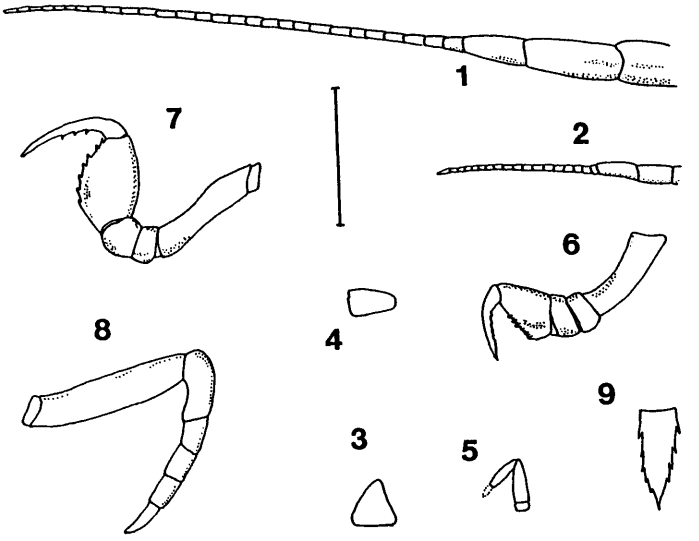

FIGURE 8—*Cyclus americanus* Packard. Reconstruction of appendages and associated structures: *1*, antennule; *2*, antenna; *3*, labrum; *4*, mandible; *5*, maxillule; *6*, maxilla; *7*, maxillipede; *8*, thoracic walking leg; *9*, caudal ramus. Scale = 2 mm.

3 segments: a short basal one and two longer more distal articles. The last of these carry a short flagellum (PE 20985, Figure 2.1; Figure 8.2).

The small and delicate mouth parts occur on only a few specimens. The small labrum displays a somewhat triangular structure (PE 34763, Figure 3.3; Figure 8.3). Just posterior to these, the mandibles (Figure 8.4) appear as blades (PE 22472, Figure 3.4; MCP 557, Figure 4.4). Whether these bore palps can not be determined.

What appears as the small maxillules (Figure 8.5), lie just posterior to the mandibles, and each bear a pronounced, reflexed palp. The small basal segment (PE 22498, Figure 3.2) carries a long article, which in turn distally connects to another long segment directed medially and posterior, effectively bending back on the proximal segment (MCP 557, Figure 4.4).

The large, robust maxillae (Figure 8.6) apparently could collapse on themselves, like multiple-jointed jackknives, but they frequently extend beyond the anterior edge of the rostral plate (PE 24959, Figure 3.1; MCP 507, Figures 4.1, 4.2). The terminal segment, shaped like a scimitar (PE 22421, Figure 5.1, PE 31713, and PE 15167), apparently bears robust setae on its medial terminus and flexes against a large, blade-like, penultimate segment with large setae on its medial margin (PE 34940, PE 34954, Figure 5.2) to form a geniculate claw or clasper. Proximal to the claw, two short segments connect to a very long segment (PE 22421, Figure 5.1) that in turn may articulate with a short basal-most segment.

The first pair of thoracopods, or maxillipedes (Figure 8.7), greatly resemble the geniculate maxillae (PE 34954, Figure 5.2). The maxillipedes, like the maxillae, also were capable of extending anteriorly beyond the edge of the front of the head. The geniculate claw is somewhat larger than that seen on the maxilla (PE 34954, Figure 5.3) and bears more robust setae on the penultimate blade-like segment. Two intermediate segments connect the geniculum to a long proximal segment (PE 1280, PE 22472, Figure 3.4), which in turn seems to attach proximally to a very short, ring-like segment.

Thoracopods two through six, virtually identical, tend to become somewhat shorter posteriorly in the series. Although we examined almost 900 specimens from several museum collections in this study, of these we found that very few preserve the thoracopods adequately (e.g., PE 22495, Figure 6.3; PE 34759, Figures 5.4, 5.5; PE 34954, Figure 5.2). These limbs apparently all articulate on the margin of the thoracic sternites. It is not clear whether a very long, often medially directed, proximal segment attaches directly to the sternites. Some evidence seems to indicate in this regard that a small ring-like article (PE 22478, Figures 6.1, 6.2) connects this long segment to the sternite. (Indeed, the dynamics of movement possible around the thoracopod/sternite joint would seem to require a small "coxal" segment.) The distal end of the long segment marks a knee in the thoracopods (Figure 8.8), and five moderate to short segments compose the distal aspect of the thoracopod (Figures 5.4, 5.5).

The abdomen possesses two segments, a short anterior one, which bears a pair of large papillae laterally (PE 22495, Figure 6.3), and a somewhat larger posterior segment exposed dorsally by the median posterior carapace notch. This last segment bears the anus as well as the marginally serrate (PE 22421, Figure 5.1) caudal rami (PE 22495, Figure 6.3).

Occurrence.—Francis Creek Shale, Desmoinsean, Middle Pennsylvanian.

Material examined.—USNMP 38863. Some 876 specimens in the fossil invertebrate collections of the Field Museum of Natural History, but especially PE 15167, 15191, 20601, 20616, 20985, 21013, 22421, 22444, 22462, 22472, 22478, 22495, 22498, 23397, 24949, 24959, 31712, 31713, 32159, 32173, 34940, 34759, 34763, 34791, 34797, 34822, 34842, 34925, 34935, 34954. MCP 452, 507, 554, 555, 556, 557, 558.

Holotype.—USNMP 38863 (Figures 1.1, 1.2) ; from along Mazon Creek, Grundy County, Illinois.

Remarks.—We offer a reconstruction of the dorsal aspect of *C. americana* in Figure 7 and our interpretation of the appendages in Figure 8.

A problem exists regarding the identity of the antennules and

TABLE *1*—Size in cm of a representative array of 55 well-preserved specimens *Cyclus americanus* in the collections of the Field Museum of Natural History.

	Carapace		
	Length	Width	Length : width
Range	0.96–2.02	0.90–2.0	
Av. length	1.40	1.43	0.98
St. dev.	0.23	0.27	
St. error	0.03	0.04	

antennae. Although the large size of the anterior-most limbs might suggest antennae, we denoted these long limbs as the antennules, initially only because of their location. We thus identified the much shorter and somewhat more posterior limbs as the antennae. Clark (1989), however, believed that the opposite was true based on his work with *Cyclus rankini,* viewing the large limbs as the antennae and the smaller ones as the antennules. Although antennules generally occur as the smaller of the two limbs in crustaceans, in many groups just the opposite prevails. This in fact commonly happens within the Maxillopoda, as within many copepod orders, the branchiurans, and the mystacocarids. Huys and Boxshall (1991) have advanced a new interpretation of copepod evolution in which they hypothesized that antennules had in their most plesiomorphic state 28 segments—virtually identical to what we found on those limbs we identify as the antennules of *Cyclus.* So, Clark not withstanding, we hold to our original designation.

These fossils can preserve internal soft-part anatomy. The gut often occurs as a detritus-filled cast (e.g., see Figures 1.2, 1.4, 3.1, 4.5, 4.6). Occasionally, one can discern a somewhat wider anterior region of the gut. In one particular specimen (PE 20601, Figure 6.4), this transition appears not only as a change in gut diameter, but also as a difference in gut content. The foregut in this specimen (the anterior, wider region) contains slightly coarser sediment than the midgut (the posterior, narrow region) and, when examined under alcohol, this specimen appears to preserve pyritized remnants of the foregut dilator muscles associated with that region. *Cyclus americanus* is the most common of the cycloids in the Mazon Creek biotas. Of the 876 specimens in the collections of the Field Museum examined for this study, all of them came from the Peabody Coal Company, Pit 11 mine, in Will and Kankakee counties, northeastern Illinois. This is the principle collecting site for the marine-like Essex fauna. The holotype specimen that Packard described from the Lacoe Collection had to have come from the fresh- to brackish-water Braidwood fauna localities along Mazon Creek itself, the principal source of classic Mazon Creek specimens in the last century. However, one hardly ever sees examples of *Cyclus* in any of the Braidwood fauna collections examined by many researchers over the years. This would indicate that, although *Cyclus* could have occurred in the Braidwood habitat, in life *Cyclus americanus* preferred more marine conditions.

Some question has arisen in the literature as to what *Cyclus* fed upon. The loosely stated consensus of past workers has more or less opted for some kind of parasitic mode, based mostly on the gross similarity of cycloids to branchiuran fish lice. However, the relatively large size of *Cyclus* argues against a parasitic habit (at 1 cm in diameter these purported parasites match in size many of the fish in the fauna they supposedly would have fed upon). On the other hand, the only consistent association within the Mazon Creek concretions of *Cyclus,* other than with other examples of itself, occurs with plant material (e.g., see Figures 6.1, 6.2). Such associations inevitably have the plant material lying close to or attached to the head. The geniculate claws and slicing mouth parts not only could have served a parasite, but also could have provided equally good service to a plant or detritus eater. We believe this latter possibility much more likely than parasitism.

CYCLUS OBESUS new species
Figures 9, 10

Diagnosis.—Carapace oval in outline, much wider than long, surface smooth bearing no decoration, margin demarcated by a narrow shelf, edges smooth and entire (no posterior notch), central region of carapace shield elevated as a plateau and delineated by a pronounced circular ridge.

Description.—*C. obesus* possesses a strikingly wide carapace (see Table 2), with a surface not marked with any textured decoration (PE 30630, Figure 9.2), but with a margin set off by a narrow brim or shelf. The central area is flattened, higher than the margin and set off by a distinct circular ridge (PE 23041, Figure 9.3). The cephalon has a very wide frontal extension or rostral plate, and the area of the carapace just posterior to the antennular bases bears a slight, raised, ocular ridge (PE 23041, PE 30630 , Figure 9.1, 9.3). The carapace displays neither posterior median nor anterolateral ocular notches.

The large and very long antennules (PE 34834; PE 34880, Figure 9.5) possess a basal peduncular segment of moderate length, slightly longer than wide. The second peducular segment appears shorter than the first. Presently we have little knowledge concerning the rest of the limb.

We known nothing about the labrum, mandibles, or maxillules. The geniculate maxillae have a robust, club-like, terminal segment that folded back onto a rather wide penultimate segment (PE 39056, Figure 9.4). We have no knowledge about the rest of the limbs.

The caudal rami appear as long blade-like processes on only a single specimen (PE 34834, not illustrated).

The thoracic tergites have a subparallel, largely laterally directed, linear arrangement and express only a slight posteriad orientation (PE 34880, Figure 9.5).

Occurrence.—Francis Creek Shale, Desmoinsean, Middle Pennsylvanian.

Material examined.—PE 23041, 24975, 30630, 34834, 34880, 39056.

Holotype and locality.—PE 30630 (Figure 9.1, 9.2), Peabody Coal Co. Pit 11, Will and Kankakee counties, Illinois.

Remarks.—We present a reconstruction of the dorsal aspect of *C. obesus* in Figure 10.

A few specimens of *C. obesus* (notably PE 39056, Figure 9.4, PE 34880, Figure 9.5) preserve gut casts. However, the gut appears to terminate in a position relatively more anterior to that seen for the position of the anus of *C. americanus.*

The arrangement of the thoracic segments differs from that of *C. americanus.* Rather than "radiating" out from an area somewhat posterior to the center of the cephalothorax, they have a somewhat more linear and subparallel array, with the posterior deflection not nearly as pronounced as that seen in *C. americanus.* Thus, the thorax, wide like the carapace, may accommodate the short abdomen such that the terminus of the abdomen may lie well beneath the carapace.

The lack of a posterior median notch on the carapace shield distinguishes *C. obesus* from what is known of other species of *Cyclus.* However, the relatively flattened shape of the body, the character of the geniculate maxillae, the prominence of the frontal extension, and the nature and orientation of the antennules, resemble the better known *C. americanus* and *C. rankini.* The above features would seem perhaps more diagnostic at a family rather than a generic level, and some future revision of the cycloids may place *C. obesus* into a separate genus.

Genus HALICYNE von Meyer, 1844.

Diagnosis.—Carapace with moderately convex and shield-like outline distinctly truncated anteriorly and either slightly acute or distinctly pointed posteriorly, with distinct optic notches, anteriorly articulated to a separate rostral plate; geniculate maxillae modest to small in size; first two thoracopods at least modified as maxillipedes; post-maxillipedal thoracic legs directed laterally and anteriorly; underside of carapace in the thoracic region marked by densely packed transverse rugae or lamellae.

Type of genus.—*Limulus agnotus* von Meyer, 1838.

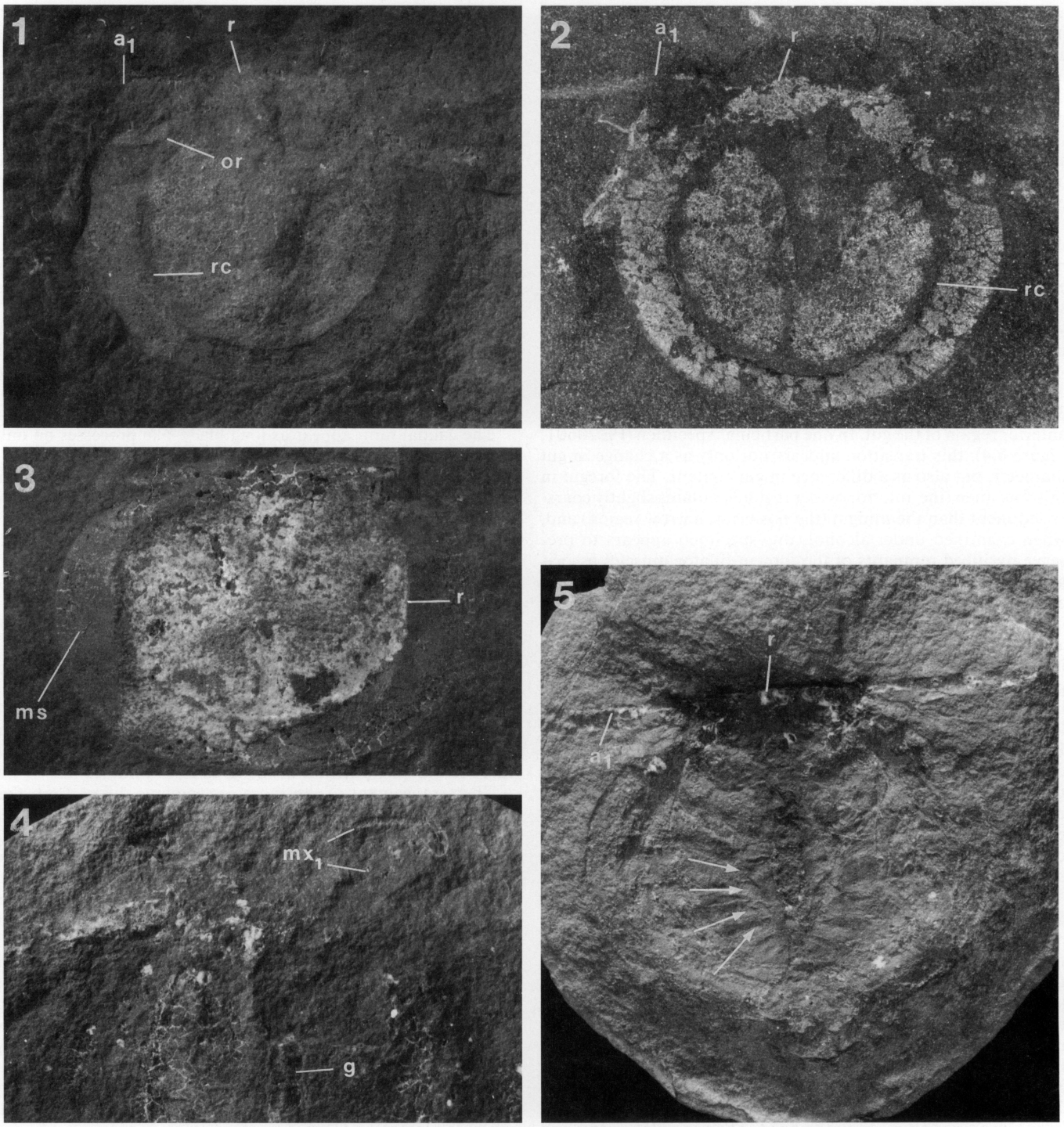

FIGURE 9—*Cyclus obesus* new species. *1,2,* PE 30630, holotype, *1,* Under direct lighting, × 4.3; *2,* Under alcohol, × 4.5. *3,* PE 23041, note circular central ridge and lack of a median 'posterior notch', × 4. *4,* PE 39056, with distal elements of maxillary genicula and gut trace, × 5. *5,* PE 34880, displaying proximal portion of the antennule and body segments (arrows), × 4. a1 = antennule, g = gut, or = orbital ridge, ms = marginal shelf, r = rostral plate, rc = circular ridge, mx1 = maxilla.

Remarks.—One can recognize members of the genus *Halicyne* by their moderately convex yet distinctly shield-like carapace that bears a clearly delineated margin, a rather truncated anterior aspect, and an articulated or hinged rostral plate. In addition, the posterior margin of the carapace shield can display a somewhat pointed apex at the midline. The carapace surface may or may not possess any decoration; *H. max,* H. ornata, and *H. plana* do exhibit such decoration, whereas *H. agnota* and *H. laxa* do not. All the thoracic legs may have a somewhat geniculate character (not at present clear), but at the very least the more anterior of the post-maxillipedal limbs have a distinct lateral and anterior orientation.

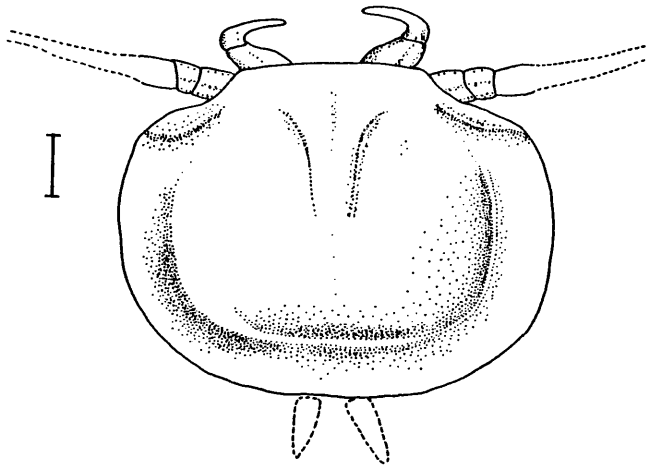

FIGURE 10—*Cyclus obesus* new species. Reconstruction of the dorsal surface. Scale = 2 mm.

Another fossil species should probably figure into these comparisons, the poorly known taxon *Carcinaspides pustulosus* Schafhäutl, 1863. This species more than likely seems related to *Halicyne,* because it shares with that genus a truncated anterior area and lobate decoration on the anterior and median areas of the carapace. The *Carcinaspides* fossils, however, appear to lack a clearly defined optic notch and a rostral plate. Nevertheless, they display a distinct, dense, and robust array of papillations on the carapace surface and a highly scalloped margin. Although *Carcinaspides pustulosus* should remain a distinct species for now, one might make a convincing argument for placing it within the genus *Halicyne* if the holotype ever becomes available for study.

HALICYNE MAX new species
Figures 11–16

Diagnosis.—Carapace shield almost circular in outline, slightly vaulted in cross section, bearing distinct papillose decoration (especially on antero-medial parts), with distinctly thickened submarginal rim bearing thin, scalloped, serrate, shelf-like edge; underside of carapace with lamellae; distinct optic notches antero-laterally with small stalked compound eyes; rostral plate well developed with a distinct ventrally directed anterior-most portion bearing a pair of rounded knobs or bosses; terminal segments of all geniculate claws long and thin, two sets of maxillipedes, maxillepedal genicula distinctly larger than those of the maxillae.

Description.—The almost completely circular and vaulted carapace appears about as long as wide (see Table 3) and bears a distinctly papillose surface (e.g., PE 13445, Figure 11.2; PE 34772, Figure 11.1; PE 34772, Figure 12.3). The quite complex margin of the carapace folds to form a distinct submarginal rim (PE 15233, Figure 11.3, PE 34772, Figure 11.1) that bears a thin, shelf-like, scalloped, and robustly spinose edge (e.g., PE 22453, Figure 13.1; PE 24954, Figure 13.2; PE 24061, Figures 13.3 and 13.4). The distinct optic notches occupy places at the anterior ends of the submarginal rim and anteriorly bear a laterally directed process (PE 15233, Figures 11.3 and 11.4; PE 34772, Figure 11.1). Stalked compound eyes lie in these notches (PE 34772, Figure 14.1). A wide, papillose rostral plate extends forward from the anterior margin of the carapace shield (PE 34772, Figure 12.3; PE 22453, Figure 13.1). Composed of two portions, the dorsal part of the rostral plate bends ventrally to form a separate "bumper" along the anterior-most facade of the head (PE 15233, Figures 11.3, 11.4; PE 22552, Figure 15.1). We cannot determine exactly whether this ventrally directed portion forms a solid part of the rostral plate or movably articulates with the basal portion. This ventrally directed plate bears distinct paired bosses (Figures 11.4, 12.3) and a median raised area that has a finely reticulated, reflective surface similar to that seen on the optic areas of the compound eyes (Figure 14.1).

TABLE 2—Measurements in cm of specimens of *Cyclus obesus*; * indicates holotype.

Specimen	Carapace		
	Length	Width	Length : width
PE 23041	1.22	1.70	0.72
PE 24975	1.32	1.70	0.78
PE 30630*	1.20	1.44	0.83
PE 34834	1.05	1.45	0.72
PE 34880	1.33	1.67	0.80
PE 39056	1.35	1.74	0.78
Average	1.24	1.62	0.76

The underside of the carapace in the region of the thorax has a dense arrangement of subparallel lamellae or rugae (Figure 11.1; PE 25662, Figure 12.1, Figure 15.1; Figures 14.1, 14.2, 14.3). These occur as thin double-walled plates (PE 22552, Figure 14.3). These plates appear to arise as a series of folds or flaps from the underside of the carapace proper rather than growing out from the lateral thoracic body wall. The preservation of these fossils precludes definitive conclusions, but it appears that these plates lie in a U-shaped chamber formed by the body wall and carapace and possibly partially enclosed by a flange from the posterior and postero-lateral sternites and the edge of the carapace (PE 22552, Figure 14.2, 14.3).

None of the specimens we have seen preserve much of the antennules and antennae. We know only the geniculate limbs completely. The maxillae have a short delicate terminal segment (PE 28958, Figure 15.2) and serrations on the medial edge of the moderately long penultimate segment (PE 13445; PE 34772, Figure 12.3). Although well developed and directed distinctly anteriad, the maxillae appear smaller than the maxillipedes (Figures 15.1–15.3).

The very large first maxillipede has a long and delicate terminal segment, subequal to the single-segmented, somewhat more robust, penultimate segment (PE 25662, Figure 12.2; PE 28958 Figure 15.2). These seem to have a distinct anterior orientation extending out in front of the head. The second maxillipede has a more antero-lateral orientation of its subchelate geniculum (PE 13445, Figure 11.2; PE 11451, Figure 15.3). The second maxillipede appears as somewhat shorter than the first but still longer than the maxillae (PE 34772, Figure 11.1).

The well-developed walking legs extend laterally from the body but are concentrated in the anterior portion of the thorax (PE 34772, Figure 11.1). Furthermore, at least the anterior-most of these have their distal segments directed anteriad (PE 25662, Figure 12.1). Thus the posterior thoracopods appear to be somewhat geniculate.

We know nothing concerning the abdomen or caudal rami of this species.

Occurrence.—Francis Creek Shale, Desmoinsean, Middle Pennsylvanian.

Material examined.—PE 11451, 13445, 15233, 20613, 21610, 22464, 22552, 22471, 24061, 24954, 25662, 28958, 34764, 34772.

Holotype and locality.—PE 34772 (Figures 11.1, 12.3), Peabody Coal Company Pit 11, Will and Kankakee counties, Illinois.



FIGURE 11—*Halicyne max* new species. *1,* PE 34772, holotype, × 4.6. *2,* PE13445, clearly preserving the carapace in one plane and in a different plane portions of the thoracic limbs, × 4.8. *3,4,* PE 15233, *3,* Part, with optic notch and inflated rim, papillated dorsal surface of carapace missing, × 4; *4,* Counterpart, under alcohol, canted with posterior edge higher than anterior so that the rostral plate, at an angle to plane of carapace, can be more fully seen, × 6. ms = marginal shelf, mx2 = maxillae, mxpd1, 2 = first and second maxillipedes, on = optic notch, r = rostral plate, ru = gill lamellae or rugae.

Remarks.—We offer in Figure 16 a dorsal and anterior reconstructions of this species.

Halicyne max takes its place as one of the better known species of the genus. Yet it pales in comparison with the amount of information available for *Cyclus americanus.* Even so, the variations in preservation between the various known *Halicyne* taxa make it difficult to compare species, especially those for which we know so little. *H. agnota* and *H. laxa* have smooth surfaces

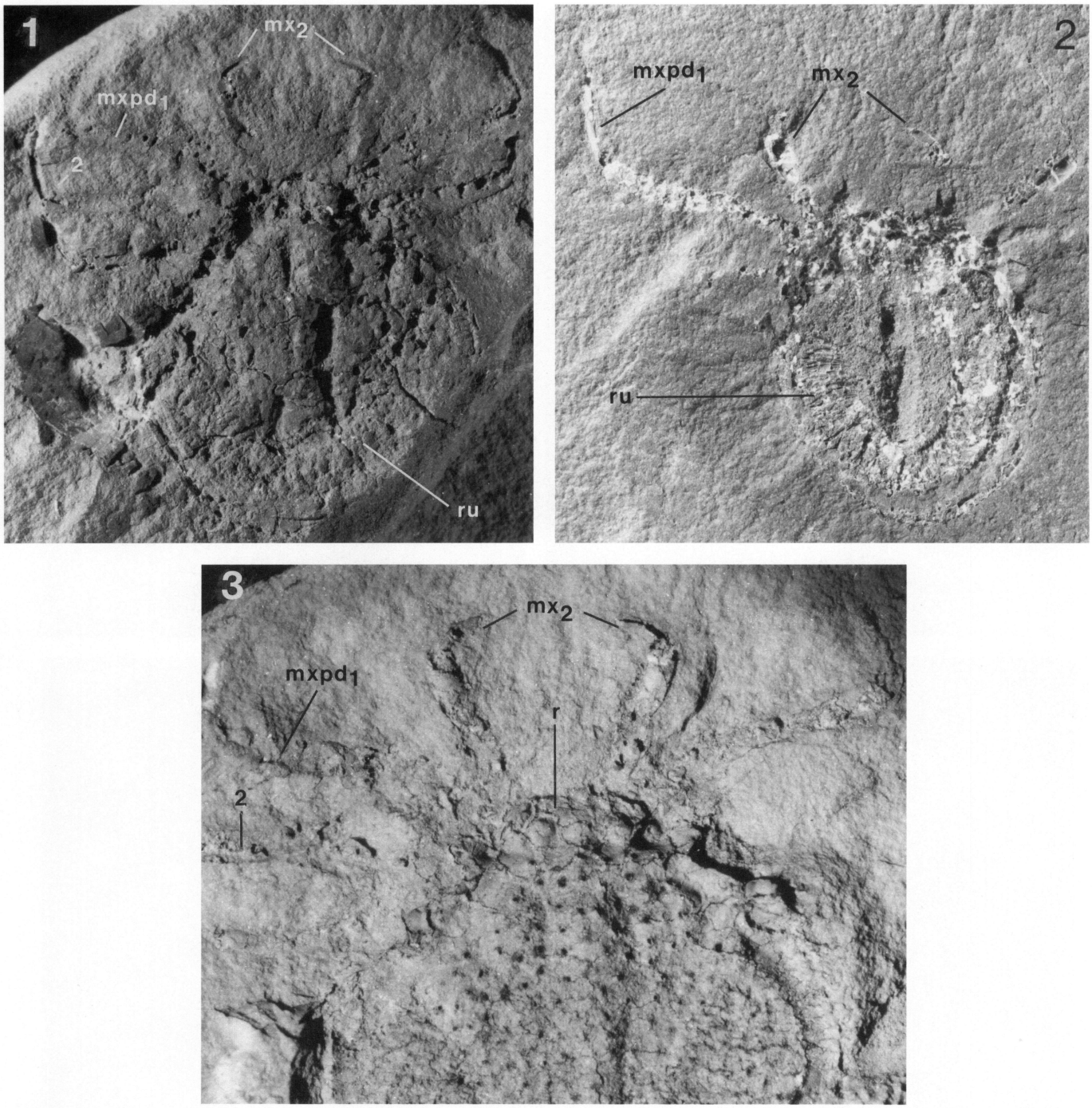

FIGURE *12*—*Halicyne max* new species. *1,* PE 25662, counterpart, with maxillae and maxillipedal genicula and laterally/anteriorly oriented thoracopod, × 5.2. *2,* PE 25662, with fully extended maxilla and first maxillipede genicula and showing rugae or lamellae in carapace chamber, × 3.8. *3,* PE 34772, close-up of Figure 11.1 printed in reverse to better illustrate surface papillation, rostral plate, optic notch, and genicula, × 8.3. mx2 = maxillae, mxpd1,2 = maxillipedes, r = rostral plate, ru = gill rugae or lamellae.

on the carapace, and the anterior and median portions of the carapace shield possess prominently inflated bumps and folds. All other species of *Halicyne* have papillated carapace surfaces. *H. plana* possesses a body more narrow than long, inflated areas on the anterior part of the carapace, and a postero-medial distinctly pointed margin. *H. ornata* may resemble *H. max* most closely in that it has an almost circular outline; but it exhibits large optic notches and a pointed postero-medial margin, and the ventral part of the rostral plate appears to lack bosses on the surface.

The lamellae under the carapace of *Halicyne* pose problems for interpretation. These structures may constitute a diagnostic feature for this genus. We do not notice lamellae such as these on any other cycloids. Aside from *H. max,* similar lamellae also occur in *H. ornata.* The thin, double-walled nature of the plates possibly suggests an interpretation of these as "gills." One might

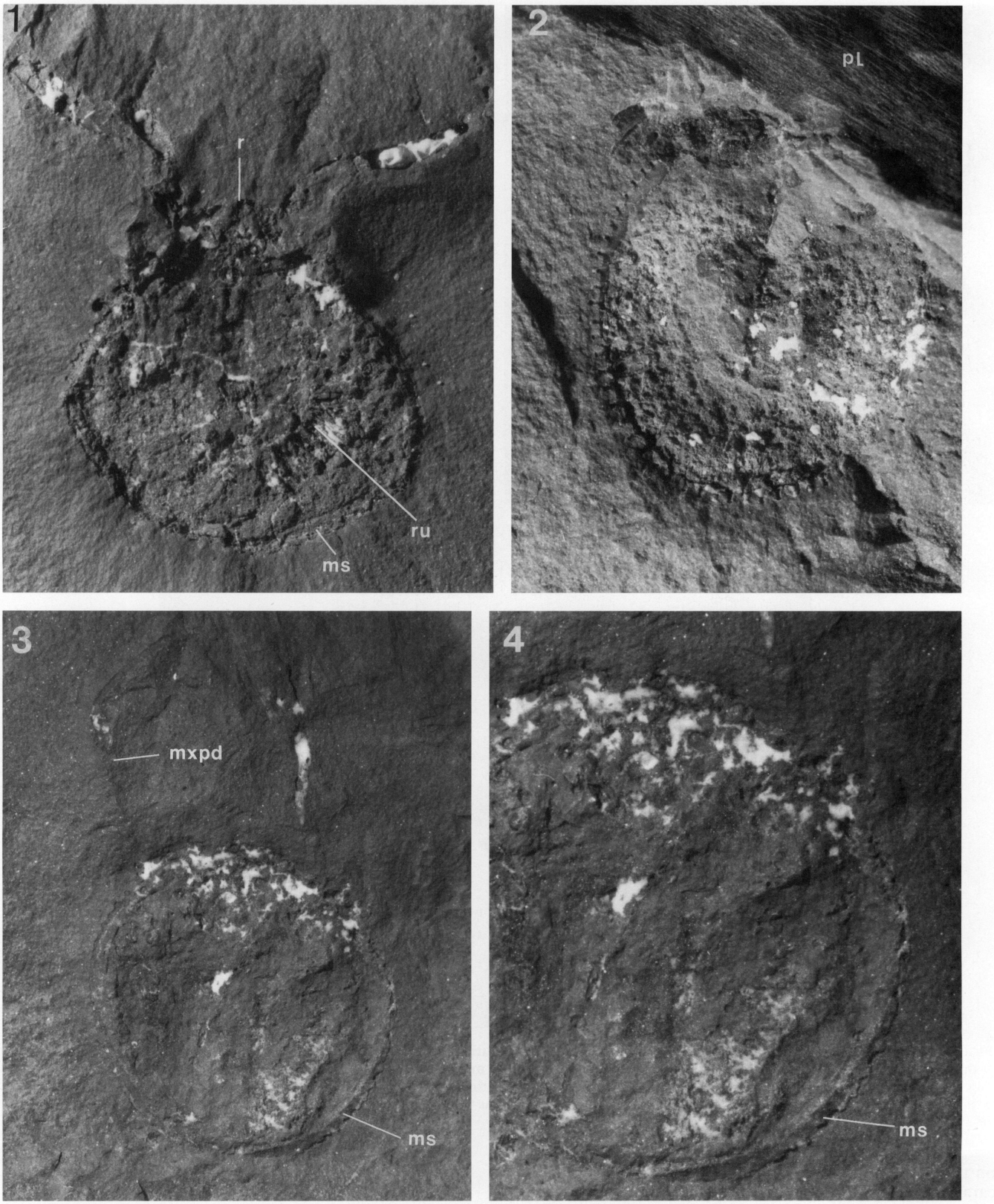

FIGURE *13*—*Halicyne max* new species. *1,* PE 22453, with sculpted ring-like marginal shelf, × 6. *2,* PE 24954, note plant material adjacent to rostral plate and sculpted margin, × 8. *3,4,* PE 24061, *3,* with extended maxillipede, × 5.4; *4,* Close-up showing sculpted margin, ×9.3. ms = marginal shelf, mxpd = maxillipede, pl = plant material, r = rostral plate, ru = gill rugae or lamellae.

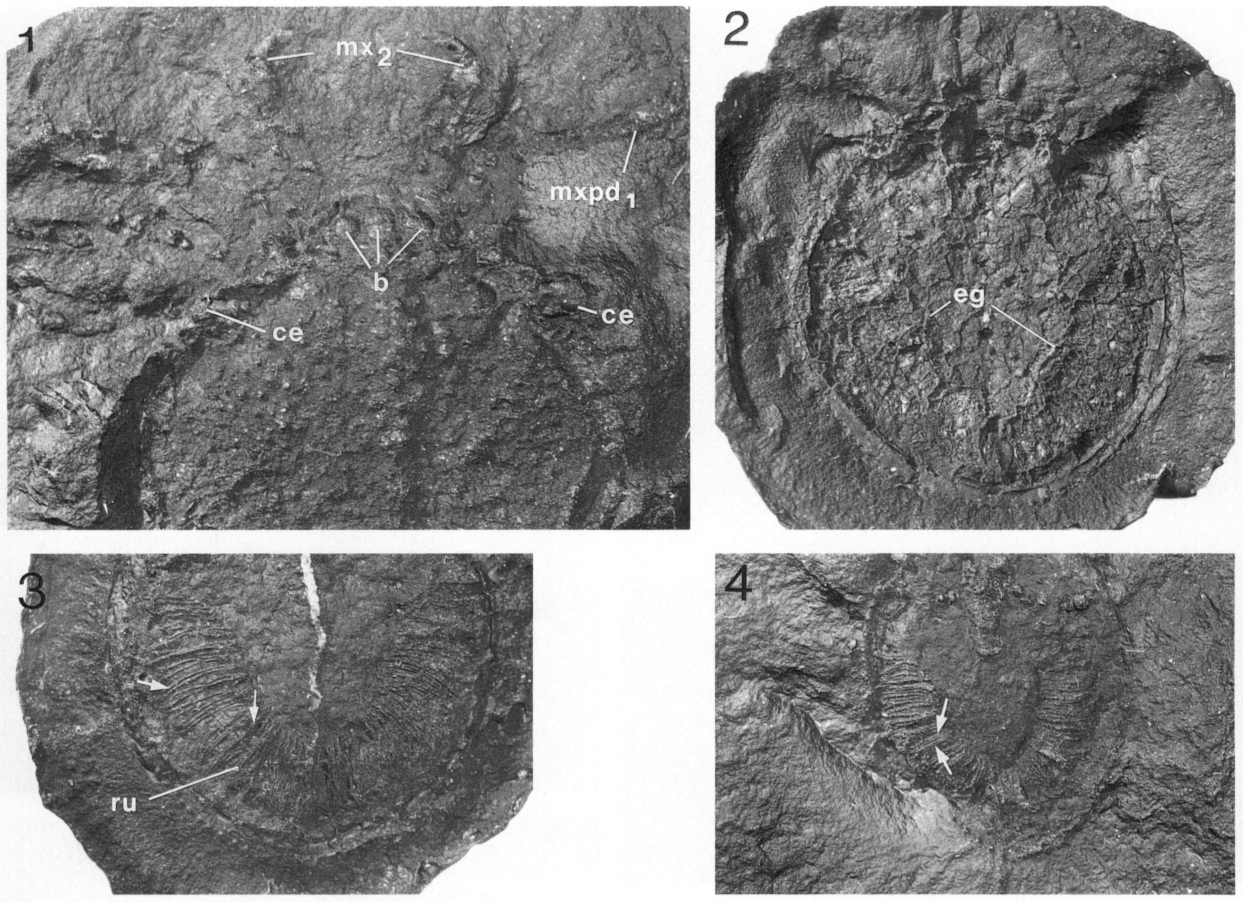

FIGURE *14*—*Halicyne max* new species, latex molds. *1,* PE 34772, displaying the extended genicula, the rounded bosses on the rostral plate, and the stalked eyes in the optic notches, × 5.7; 2,3, PE 22552, *2,* Featuring the underside of the body and the opening to the "gill chamber," note also serrated marginal shelf, × 4.0; *3,* Counterpart of 2 with the underside of the carapace and the gill lamellae, note that the lamellae are paired (arrows) which we believe indicates they were folded each member of a pair forming a wall of the fold, × 4.0. *4,* PE 20812, clearly showing the paired nature of these lamellae, × 4.0. b = bosses on rostral plate, ce = stalked compound eye, eg = edge of gill chamber, mx2 = maxillae, mxpd1 = maxillipede, ru = gill lamellae or rugae.

look for parallels in the densely packed thoracopodal epipodites seen among many branchiopods or the lamellae of phyllobranchiate gills in eucarid malacostracans.

The reflective bosses on the anterior bumper raise questions. As noted above, upon close examination they appear similar to sessile eyes. However, we hesitate to call them so because we note a perfectly good set of stalked compound eyes located in the antero-lateral optic notches of the carapace. More and better preserved material may subsequently confirm these bosses as eyes. If that occurs, the only parallel we can draw upon comes from the unusually large ocelli of naupliar eyes seen in pontellid copepods (Park, 1966), so large in fact that at one time Parker (1891) mistakenly reported them as compound eyes.

Genus APIONICON new genus

Diagnosis.—Carapace distinctly oval and anteroposteriorly elongate, with no well-developed marginal shelf; small rostral plate extending from anterior portion of carapace; antennules directed laterally.

Type of genus.—*Apionicon apioides* new species

APIONICON APIOIDES new species
Figures 15.4, 17, 18.

Diagnosis.—Carapace marked by median and lateral longitudinal ribs and furrows, posterolaterally lightly decorated with papillae, margin slightly crenulate.

Description.—The carapace envelops the body, and displays an elongate, oval form with a medial and some paired longitudinal ribs flanked by slight furrows and a posterolateral field of papillate ornament (PE 22464, Figure 15.4). The anterior part of the carapace has a rounded rostral extension from which a well-developed set of antennules and smaller antennae extend laterally (PE 22471; PE 34764, Figure 17.1). The margin of the carapace exhibits some faint crenulation (PE 22464, PE 34764).

The specimens studied preserve few of the remaining appendages. PE 20613 may preserve some remnants of one of the geniculate limbs, whereas LACM 1052 preserves some faint outlines of long thin caudal rami (Figure 17.2).

Occurrence.—Francis Creek Shale, Desmoinsean, Middle Pennsylvanian.

Material examined.—PE 20613, 22464, 22471, 34764.

Holotype and locality.—PE 22464 (Figure 15.4); Peabody Coal Company Pit 11, Will and Kankakee counties, Illinois.

Remarks.—With only five poorly preserved specimens of this species available for study, the species description must remain minimal for now. However, one should not conclude that this scarcity indicates any unimportance for this species in the original Late Pennsylvanian Mazon Creek biotas. Amateur and professional collectors through the years have tended to keep only better preserved specimens gathered from Mazon Creek localities. The generally poor preservation of *A. apiodes* may have produced a bias against this species in museum and private

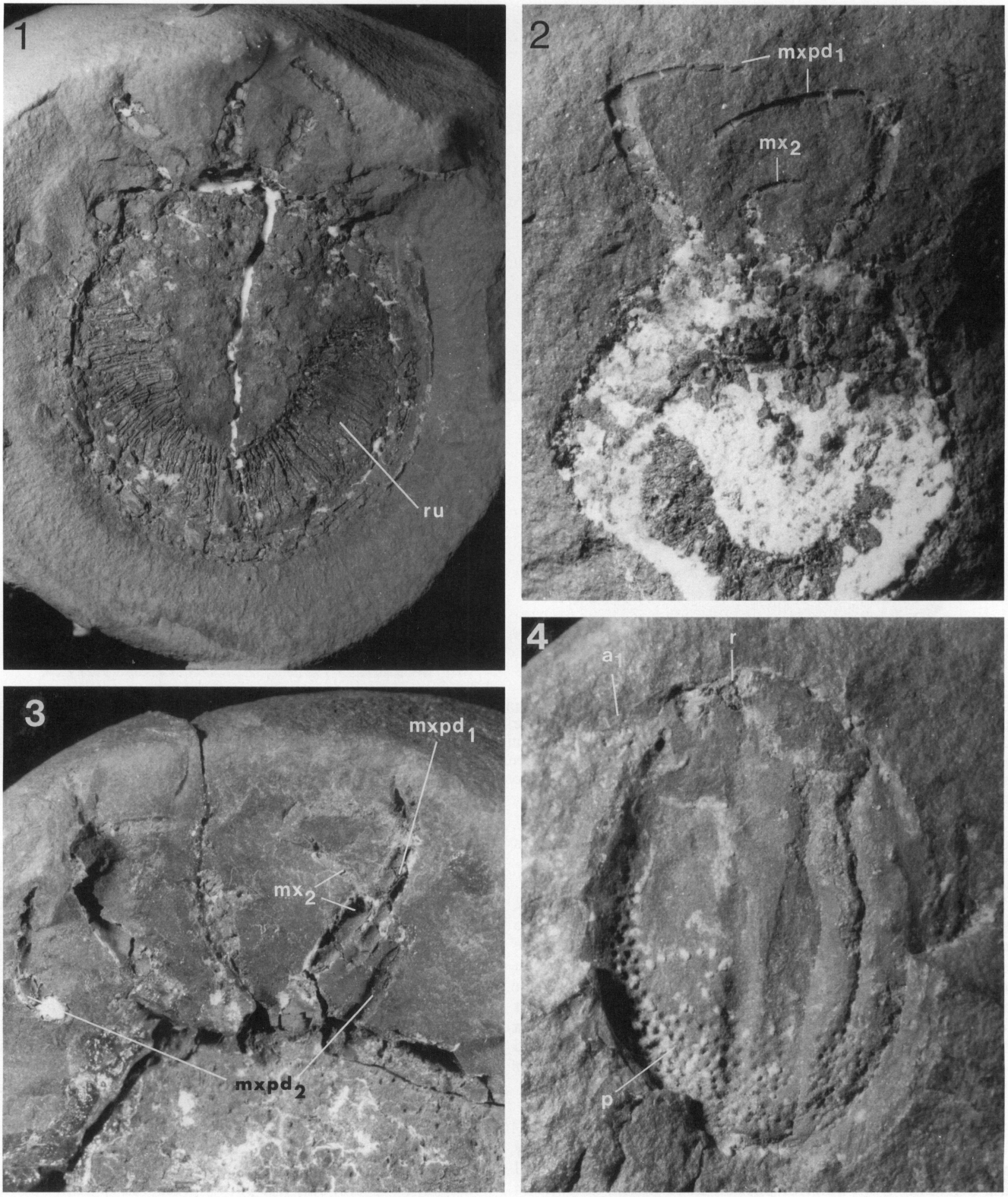

FIGURE *15—1–3, Halicyne max* new species. *1,* PE 22552, note gill rugae on posterior and lateral areas of carapace underside, × 4.8; *2,* PE 28958, with well-preserved maxilla and first maxillipede, × 6.4; *3,* PE 11451, close-up showing portion of maxillae, first and second maxillipedes, × 6. *4, Apionicon apioides* new genus, new species, PE 22464, holotype, × 8.4. a1 = antennule, mx2 = maxilla, mxpd1 = maxillipedes, p = papillations, r = rostral plate, ru = gill rugae or lamellae.

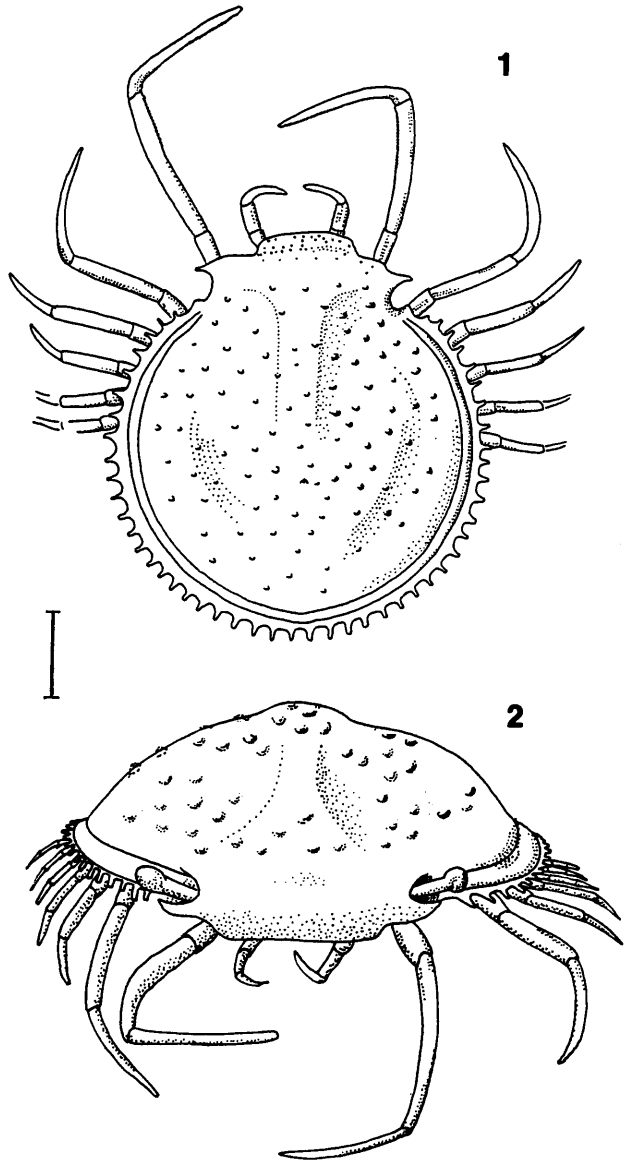

FIGURE 16—*Halicyne max* new species. Reconstruction of dorsal (1) and anterior views (2). Scale = 2.5 mm.

collections. As a typically structureless, color-fossil, *A. apiodes* displays the kind of preservation generally discarded in the field by collectors and which can cause casual sorters of Mazon Creek collections to misidentify these fossils as belonging to some other group, e.g., jellyfish. This kind of preservation in other Mazon Creek fossils more often than not occurs in groups that were highly calcified in life, such as molluscs, and this may indicate that *A. apioides* also may have had a high degree of cuticular mineralization.

DISCUSSION

Earlier workers on cycloids were obviously uncertain about the taxonomic affinities of the group. As we have seen above, within the first 16 years of work on the group, various workers had suggested every major higher category of arthropods as a repository for cycloids. This confusion has continued down to the present.

The reason for so much disagreement regarding not only higher taxonomic placement, but also the generic affinities of the species described, centers on problems with taphonomy. The forms found in limestone appear as small, highly convex fossils with little or no information concerning appendages, whereas those collected from shales appear generally flatter and often preserve additional information concerning limbs and internal anatomy. The question then becomes whether these differences arise from varying modes of preservation, or do they reflect some real structural variants. Trümpy (1957) believed them real, although Clark (1989) thought them to be taphonomic. We believe that proper consideration of both taphonomy and real morphology will play equal roles in any future revision of the cycloids.

TABLE 3—Measurements in cm of specimens of *Halicyne max*; * indicates the holotype.

Specimen	Carapace		
	Length	Width	Length : width
PE 11451	—	1.35	—
PE 15233	1.30	1.23	1.06
PE 22552	1.45	1.43	1.01
PE 24954	~0.84	0.80	1.05
PE 24061	1.05	1.00	1.05
PE 25662	1.24	~1.10	1.13
PE 34772*	1.13	1.10	1.03
Average	1.17	1.14	1.03

However, we see clearly distinct body types within the genus *Cyclus* alone. Many species of *Cyclus* at least superficially more closely resemble species in other cycloid genera than they do each other (Figure 19). We can distinguish at least three body types within *Cyclus*: 1) a form characterized by *C. radialis* (the "type" form; see also Figure 4.3), a highly vaulted cap-like body and including *C. bilobatus, C. communis, C. harkensii, C. jonesianus, C. martinensis, C. milaradovitchi, C. minutus, C. permarginatus, C. simulans, C. torosus, C. woodwardi,* and *C. wrighti*; 2) a form represented by *C. rankini,* very flat, wide, with a weakly developed rostral plate, and a distinctly raised margin on the carapace including *C. johnsoni, C. scotti,* and *C. testudo*; and 3) the form characterized by *C. americanus* with moderate vaulting and a well-developed rostral plate and that also includes *C. obesus.* The affinities of *C. limbatus* and *C. packardi* may actually lie with the *Halicyne/Caracinaspides* complex, but the type specimens of these species, as well those as of *C. communis, C. minutus,* and *C. permarginatus* appear to be lost.

The issue of taphonomy cannot be ignored in all of the above. The *radialis* cluster of species occurs in limestones, whereas the *rankini* and *americanus* clusters occur in shales and coal-measure deposits. Without examining all the material available for all species, clearly beyond the scope of this paper, we cannot hope to make any reasonable judgements as to the status of these groups. Consequently, rather than erect new genera, we believe it more prudent for now to refer to these clusters of taxa within *Cyclus* as species groups.

Specimens of *Halicyne max* also demonstrate the clear association of cycloids with plant remains. Figure 13.2 illustrates one such specimen with the cycloid clearly attached by the head to a plant. When we build on this association to indicate a diet of herbivory, or possibly scavenging, and combine this with general features of the cycloid habitus (viz., broad, round, flat bodies; small antennae and possibly small antennules; laterally placed, stalked, compound eyes; claws; laterally located, robust, uniramous, walking limbs; broad sternites; and greatly reduced abdomen), we come to a startling conclusion. Cycloids bear striking, convergent similarities to the body plan of crabs! The

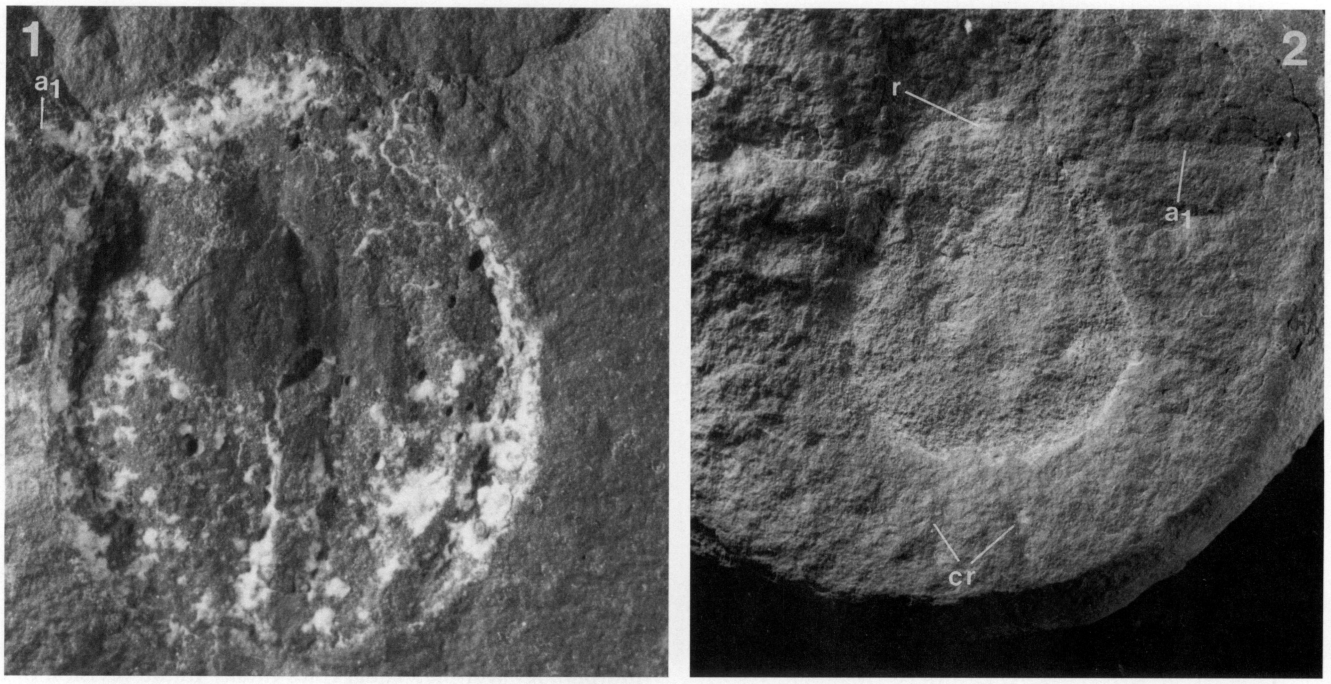

FIGURE 17—*1,2, Apionicon apioides* new species. *1,* PE 34764, with antennules from rostral extension, × 6; *2,* LACM 1052, with antennules and faint remnants of caudal rami, × 3. a1 = antennule, cr = caudal rami, r = rostral plate. IP 12383

only true crab from the Paleozoic, *Imocaris tuberculata* Schram and Mapes, 1984, apparently has affinities to the dromiaceans. In light of well-developed lobsters appearing in Late Devonian time (e.g., Schram et al., 1978), paleocarcinologists have had problems explaining why crabs came into full development relatively late (from Jurassic and Cretaceous onward). The answer may lie in the fact that cycloids occupied the niche, and crabs could not really begin to radiate until cycloids became extinct after the Triassic—an interesting speculation.

The above taxonomic issues notwithstanding, we can advance a clear hypothesis about the higher taxonomic affinities of Cycloidea. First, there now appears little doubt that the Cycloidea belong among the crustaceans. The possession of two sets of antennae, mandibles, and two sets of maxillae with maxillipedes clearly places at least the genus *Cyclus* squarely within the Crustacea. This would strongly infer that genera such as *Halicyne*

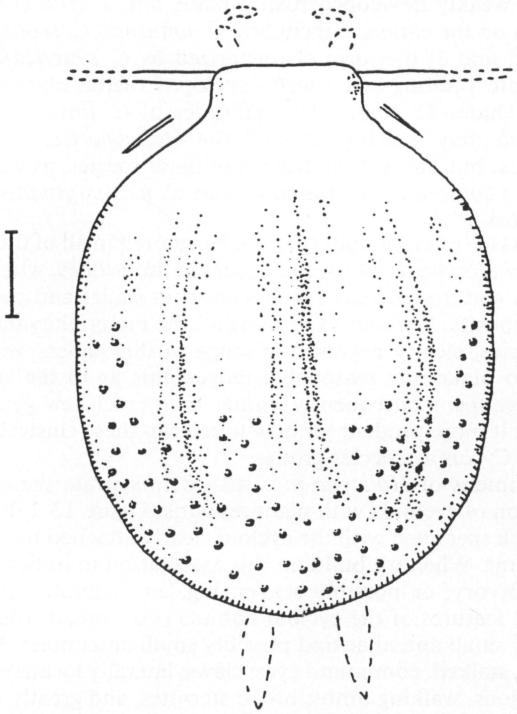

FIGURE 18—*Apionicon apioides* new species. Partial reconstruction of dorsal surface. Scale = 2 mm.

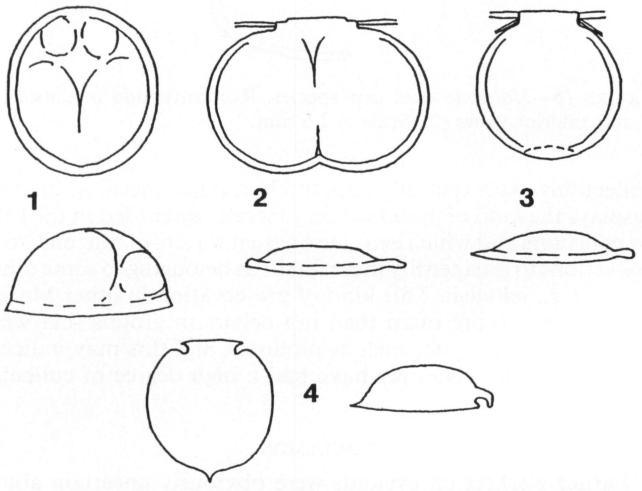

FIGURE 19—Outline diagrams of generalized dorsal (anterior towards the top) and lateral (anterior to the right) body forms in the currently recognized species groups in the genus *Cyclus* and the genus *Halicyne*. *1,* The highly vaulted, button-like *C. retractata* species group; *2,* The flattened, bilobed *C. rankini* species group; *3,* The flattened, shield-like *C. americanus* species group; *4,* The highly vaulted, shield-like, anteriorly blunted *Halicyne*.

TABLE 4—Measurements in cm of specimens of *Apionicon apioides*; * indicates the holotype.

Specimen	Carapace		
	Length	Width	Length : width
PE 20613	1.45	—	
PE 22464*	~1.29	~0.90	1.43
PE 22471	1.46	1.17	1.25
PE 34764	~1.27	1.57	0.81

and *Apionicon* belong there as well, even though currently known specimens of these and other genera do not always preserve pertinent information concerning the antennae, mandibles, and maxillules. Nevertheless, the form of the maxillae in these more poorly known species, with two sets of maxillipedes and caudal rami, agrees with what we now known about *Cyclus americanus.*

In addition, a combination of other features discernible on these fossils places them squarely inside the Class Maxillopoda. These include uniramous antennules and, most importantly, the body tagmosis pattern in accord with that seen in maxillopodans, viz., a classic 5–6–5 (head, thorax, and abdomen) segment pattern. The maxillopodans often reduce the abdomen (and in some cases the posterior thorax). *Cyclus* clearly has a 5–6–2 pattern, and thus falls within a maxillopodan *bauplan.* In addition, the anterior abdomen segment may bear some reproductive structures. Clark (1989) reported apparently paired penes extending forward from the abdomen in *Cyclus rankini,* and we have noted possible genital papillae similar to those seen in female branchiurans (see above) on the first abdominal segment in *C. americanus,* another common feature of maxillopodans.

We disagree, however, with the opinions of previous authors about where the cycloids belong *within* the array of the various Maxillopoda. Though cycloids have a large, shield-like carapace and apparently serrate mandibles like branchiurans, they lack other apomorphic features of the branchiuran fish lice. First, cycloids do not bear antennules and antennae modified for attachment to a host. Cycloid antennules, at least for *Cyclus* proper, are actually rather plesiomorphic, albeit large; and the antennae, while uniramous, are well within what one would expect for a basically sensory appendage. Second, cycloids do not bear sucker-like or hook-laden maxillules modified for attachment to the host. Cycloid maxillules appear to be typical crustacean mouthparts. Third, cycloids do not have maxillae that would have functioned strictly as grooming structures, although grooming could have been another function of the geniculate cycloid maxillae and maxillipedes. And fourth, cycloids do not have the abdomen reduced to a single, unsegmented lobe. At least some cycloids, although having a reduced abdomen, still display segmentation in that region. Thus, chances of branchiuran affinities for the cycloids appear negligible.

Although cycloids share with copepods several features, such as fusion of the first thoracic segment into the head, development of the first thoracopod as a maxillipede, and specialization of the maxillipede as a uniramous limb, these two groups bear distinct differences. Cycloids posses several unique characters that include: the presence of the carapace and its apparent fusion to all the thoracic segments, the uniramous antennae, the large geniculate maxillae and maxillipedes (this latter in some forms also including the second thoracopods as maxillipedes), the posterior thoracopods as robust and uniramous "walking" limbs, an abdomen reduced to two segments, and the development of wide sternal plates in the cephalothorax. Cycloids also lack the intercoxal sclerites used as couplers on the thoracic limbs (an important apomorphy of copepods).

We can now assess cladistically where the Cycloidea fit with the Maxillopoda. Schram (1986, p. 538) made the first attempt at a cladistic analysis of the class Maxillopoda and felt, given

TABLE 5—Characters used in the cladistic analysis of maxillopodan taxa. Multistate characters denoted with variations. Plesiomorphic state essentially represented by those characters found in the Malacostraca as the outgroup.

Character	Plesiomorphic state	Apomorphic state(s)
1. Antennule	biramous	uniramous
2. Trunk-limb number	14	(1) = 7, (2) = 6, (3) = 5, (4) = 4, (5) = 2, (6)1
3. Trunk somite number	15	(1) = 12, (2) = 11, (3) = 8, (4) = 5
4. Male pore location	thoracomere 8	(1) tmere 7, (2) tmere 4 or 5
5. Naupliar eye	without tap. cells	with tapetal cells
6. 1st thoracopod	unmodified	as a maxillipede
7. Maxillipedes	biramous	uniramous
8. Carapace	present	absent
9. Compound eye	present	absent
10. Male trunk limb 7	not as a penis	(1) paired penes, (2) median penes
11. Female trunk limb 7	present	absent
12. Thoracopodal endite	absent	present
13. Thoracopodal exopod	3 segments or more	(1) 1–2 segs., (2) absent
14. Thoracopod number	2–6 present	(1) 5–6 absent, (2) 2–6 absent
15. Caudal rami	single segment	three segs.
16. Antennal exopod	at least 14 segs.	(1) ≤9, (2) absent
17. Mandibular exopod	at least 11	(1) ≤7, (23) absent
18. Antennule segments	9 or more	eight or less
19. Thoracopods 2–5	biramous	(1) uniramous, (2) buds, (3) absent
20. Intercoxal sclerites	none	sclerites as couplers
21. 1st thoracomere	free	fused to head
22. Cephalic appendages	present	absent
23. Oral disc	none	present
24. Bipartite pigment cells	none in cmpd. eyes	present in compound eyes
25. Naupliar carapace	none	present
26. Carapace gut caeca	none	present
27. Al attachment organ	none	present
28. Poison spine	none	present
29. Naupliar postmaxillary limb buds	present	absent
30. Frontal filaments	not with cmpd. eye	associated with cmpd. eye
31. Lattice organ	none	present
32. Female pore location	thoracomere 6	(1) tmere = 7, (2) tmere = 4 or 5, (3) tmere = 1

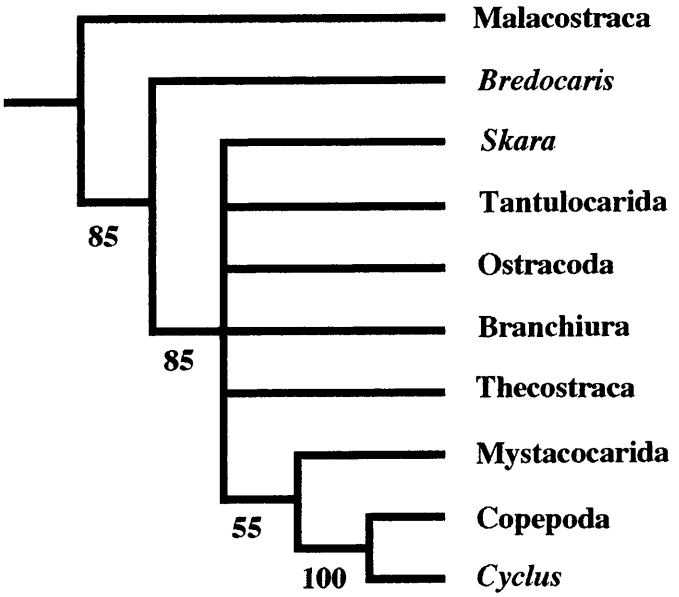

FIGURE 20—A 50% majority-rule consensus obtained from 20 equally parsimonious trees from the cladistic analysis of the data matrix in Table 6; characters as in Table 5. Numbers represent the percentage of times a particular bifurcation appeared. Analysis of data ran unordered, unweighted, and with the uninformative characters (1,2,5,15,19,20,22–24,27–31) deleted.

the limited data base available to him then, that there was much irresolution at the base of the tree. Grygier (1987), in trying to clarify the position of the Facetotecta (= y-larvae forms), developed a data base utilizing 20 features focusing on larval maxillopodans. Grygier excluded from consideration the mystacocarids, tantulocarids, and ostracodes. Boxshall and Huys (1989), building on both Schram and Grygier, produced another arrangement using some 35 characters identifiable in adult forms, and as a result they had to exclude the facetotectans. Abele et al. (1992), using 18S ribosomal RNA, concluded that the branchiurans and their sister group the Pentastomida (Abele et al., 1989) may have sister-group affinities outside the maxillopodans (Walossek and Müller [1994], however, advocated a stem-group crustacean position for the Pentastomida). We cannot resolve in this paper issues of larval affinities or evaluate the role of molecular sequencing. We only wish to assess the affinities of Cycloidea.

To this end we modified slightly the data base of Boxshall and Huys (1989) by reconfiguring some features into multistate characters and incorporating some more recent knowledge concerning fossil and Recent forms uncovered in the last few years (e.g., Huys et al., 1993). The list of these characters appears in Table 5. We used the taxa essentially as Boxshall and Huys presented them, adding of course *Cyclus*. Thus we included the branchiurans, and our scoring of ostracodes continues to consider the phosphatocopines as part of that group. This does not necessarily reject other options concerning the affinities of these groups (e.g., see Boxshall, 1992), but these issues do not concern the immediate matter at hand. Finally, we have also included into the data base the Cambrian *Bredocaris* (Müller and Walossek, 1988) to offer a complete cladistic analysis of all the potential maxillopodan forms.

Figure 20 presents the results of this analysis, based on the matrix of Table 6. The analysis utilized malacostracans as an outgroup, unordered all the data so as not to inject preconceived

TABLE 6—Character matrix used in the cladistic analysis of maxillopodans, based on the character list of Table 5.

Taxa	11111111112222222222333 12345678901234567890123456789012
Malacostraca	00000000000000??000000000000000
Bredocaris	11???0000000110?00000000?1?000???
Skara	161??001101012100030000???00????
Mystacocarida	1322?10110102101112000000000002
Copepoda	12211111100000011001100000000001
Cyclus	123??110??10200220101100???00????
Tantulocarida	1231?0011211100???00111000000003
Ostracoda	15211000011012010100000110000001
Branchiura	14421000001011012100000001010002
Thecostraca	12211000011000021100000001101113

ideas about polarity, and deleted the uninformative characters. Twenty equally parsimonious trees resulted using the exhaustive search option of PAUP 3.1.1, length = 48, consistency index = 0.604, homoplasy index = 0.396, retention index = 0.441, and rescaled consistency index = 0.267. The fifty-percent, majority-rule, consensus tree reveals a high degree of certainty about the copepod/cycloid clade.

The examination of the data with MacClade 3.0 revealed some interesting issues. The location of *Bredocaris* (even to outside the Maxillopoda) does not effect the length of the tree, as might be expected in an animal that appears to exhibit a great many plesiomorphic features. This proved true to a large extent with the other Cambrian taxon in the analysis, *Skara*. However, every alternative analysis we performed, whether it included the fossils or not, or whether we used the data matrix exactly as Boxshall and Huys (1989) had outlined it, always placed *Cyclus* as a sister group to the Copepoda.

Despite the analysis above, which focuses *solely on maxillopodans,* different data bases could come up with alternative schemes. Schram and Hof (in press) used a much larger data base for all fossil and Recent "crustaceoids" and noted two things of relevance. First, that data base indicated a possibility that the maxillopodans could occupy a *paraphyletic* position on a cladogram of all crustaceoids. Second, under those circumstances cycloids may yet prove to bear some affinity to branchiurans. The results from any analysis of such a larger data base, however, should not necessarily negate the results of the analysis here. Such results merely indicate that there still exists a fair amount of uncertainty about the sister-group relationships of extinct groups, such as cycloids.

Many aspects of the anatomy of the cycloids remain unclear. We need more comparative information about the head appendages in all the cycloid genera. We still need to resolve interpretations of biramous limbs in some cycloid species such as *Halicyne ornata* and *Cyclus torosus,* and we need reliable information concerning the abdomen in all genera and the structure of possible penes. New information concerning these characters could effect the location of cycloids within a crustacean cladogram. Although our understanding of these peculiar fossil arthropods has taken a giant step forward, we still have much more to discover about these creatures.

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