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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 Lacoë 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 $\frac{1}{3}$ 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. Schaffhäutl (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 ser-ratus*, 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*.