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GULCH LIMESTONE OF CENTRAL MONTANA

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CYCLOIDEA OF THE MISSISSIPPIAN BEAR GULCH LIMESTONE OF CENTRAL MONTANA

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ABSTRACT. A new species of cycloid crustacean, *Halicyne montanaensis*, is described from the uppermost Mississippian locality at Bear Gulch, in central Montana. Although the species is a rare component of the fauna and the specimens at hand are not well preserved, the material does allow comparison to other species in the genus. The addition of *H. montanaensis* to the species list of the Bear Gulch fauna strengthens similarities to other Carboniferous Konservat-Lagerstätten in Europe and North America and reinforces ideas about a persistent nearshore marine chronofauna in this time period.

INTRODUCTION

The strata of the Bear Gulch Limestone deposits are part of the Big Snowy Group dated as Late Mississippian, Chesterian, in age (Cox, 1986; Jenner *et al.*, 1998) just below the Mississippian–Pennsylvanian boundary. The Bear Gulch fossils are noted for their generally high quality of preservation (Melton, 1971) and suggest an anoxic environment and rapid burial of the organisms, although this would seem to be contradicted by the presence of a large array of burrowing and benthic fishes. The history of deposition has been reconstructed in great detail (Williams, 1983; Cox, 1986; Feldman *et al.*, 1994); it represents a bay at latitude approximately 10°N in an arid, monsoonal climate comparable to the present-day Sahel. Depending on the prevailing winds and circulation, the bay appears to have developed seasonally an anoxic bottom layer associated with high rates of cyclic deposition. This would explain the extraordinary preservation, the presence of those problematic bottom-dwelling fishes and other benthos, and the peculiar, regularly alternating size and coloring of the sediments.

The first cycloid described was under the name *Agnostus radialis* (Phillips, 1835). From that time on, the higher taxonomic placement of cycloids has shifted from group to group with numerous conflicting suggestions as to their affinity (for an overview, see Schram *et al.*, 1997). It appears that the cycloids belong within the crustaceans and most likely within the class Maxillopoda. They were quite diverse in the Paleozoic (see the reviews in Clark, 1989; Schram *et al.*, 1997; Brambilla *et al.*, 2002) and are now known to have survived through the close of the Cretaceous (Fraaije *et al.*,

2003). The most recent cladistic analysis places the cycloids near the Copepoda (Schram *et al.*, 1997).

There is a moderate degree of diversity in shapes and numbers of taxa within the group. Three distinct morphotypes are now recognized within the genus *Cyclus* alone and, in addition, *Halicyne* shows yet another divergent morphology. However, some of these divergences in shape may be a result of taphonomy, since the vaulted, convex specimens are in general found in limestones, whereas the flattened specimens are mainly found in shales (Schram *et al.*, 1997). Nevertheless, a number of distinct characters unite the cycloids, for example, the shieldlike carapace fused to all thoracic segments, uniramous antennae, large subchelate maxillae and maxillipeds, posterior thoracopods as robust uniramous walking limbs, and a short one- or two-segment abdomen.

Cycloids are found in Austria, Belgium, Bosnia, France, Germany, Ireland, Italy, Russia, the Netherlands, the United Kingdom, central Asia, and the United States (Glaessner, 1969; Schram *et al.*, 1997) and are mainly associated with marine to brackish environments. Cycloids frequently co-occur with plant material. Schram *et al.* (1997) suggested cycloids might have had an herbivorous or scavenging life style, that is, that they perhaps occupied a niche equivalent to modern crabs (Brachyura).

MATERIALS AND METHODS

This study is based on only six specimens: five collected in the 1970s near Beckett, Montana, USA (Natural History Museum of Los Angeles County, Invertebrate Paleontology [LACMIP] locality 15424), and one specimen (CM 45816) from the collections of the Carnegie Museum of Natural History (CM). The specimens were examined with a variety of light microscopic techniques by using various lighting strategies in both a dry state and submerged under water. Digitized photographs and camera lucida drawings were made under these varying conditions.

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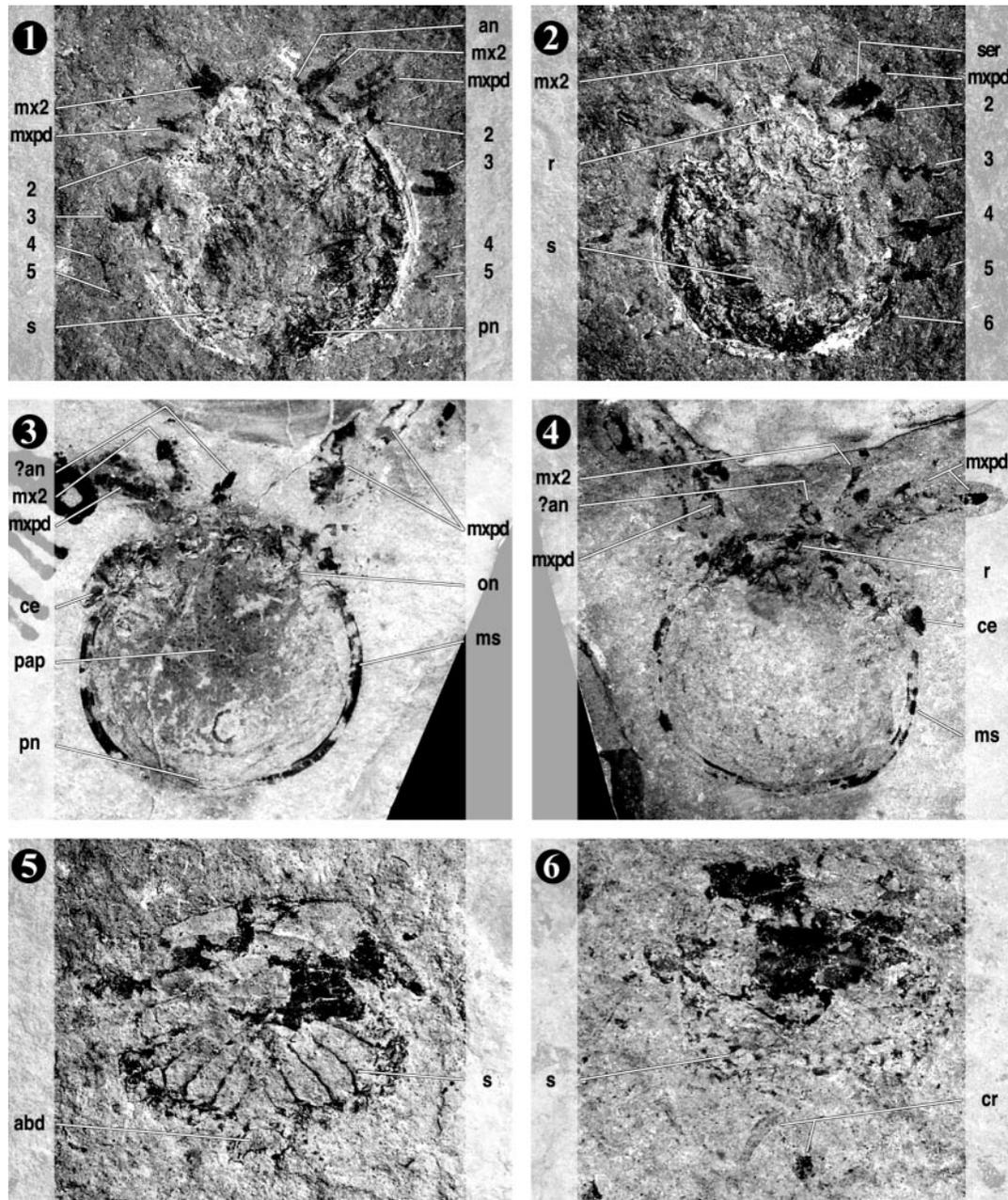


Figure 1 *Halicyne montanaensis* n. sp. 1, 2, LACMIP 7310 part and counterpart (holotype), under direct light, showing vaulted trunk, thoracic appendages, segmentation, and rostral plate, $\times 5$ (see Figs. 2.1, 2.2). 3, 4, CM 45816 part and counterpart, under water, showing cephalic appendages, compound eyes, and rostral plate, $\times 4$. 5, 6, LACMIP 7311 part and counterpart, under direct light, showing part of the posterior thoracic segmentation and caudal rami, $\times 4.5$ (see Figs. 2.3, 2.4). ABBREVIATIONS: abd = abdomen, an = antenna fragment, ce = compound eye, cr = caudal rami, ms = marginal shelf, mx 2 = second maxilla, mxpd = maxilliped, on = optic notch, pap = papillae, pn = posterior notch, r = rostral plate, s = posterior thoracic segmentation, 2/6 = thoracic appendages

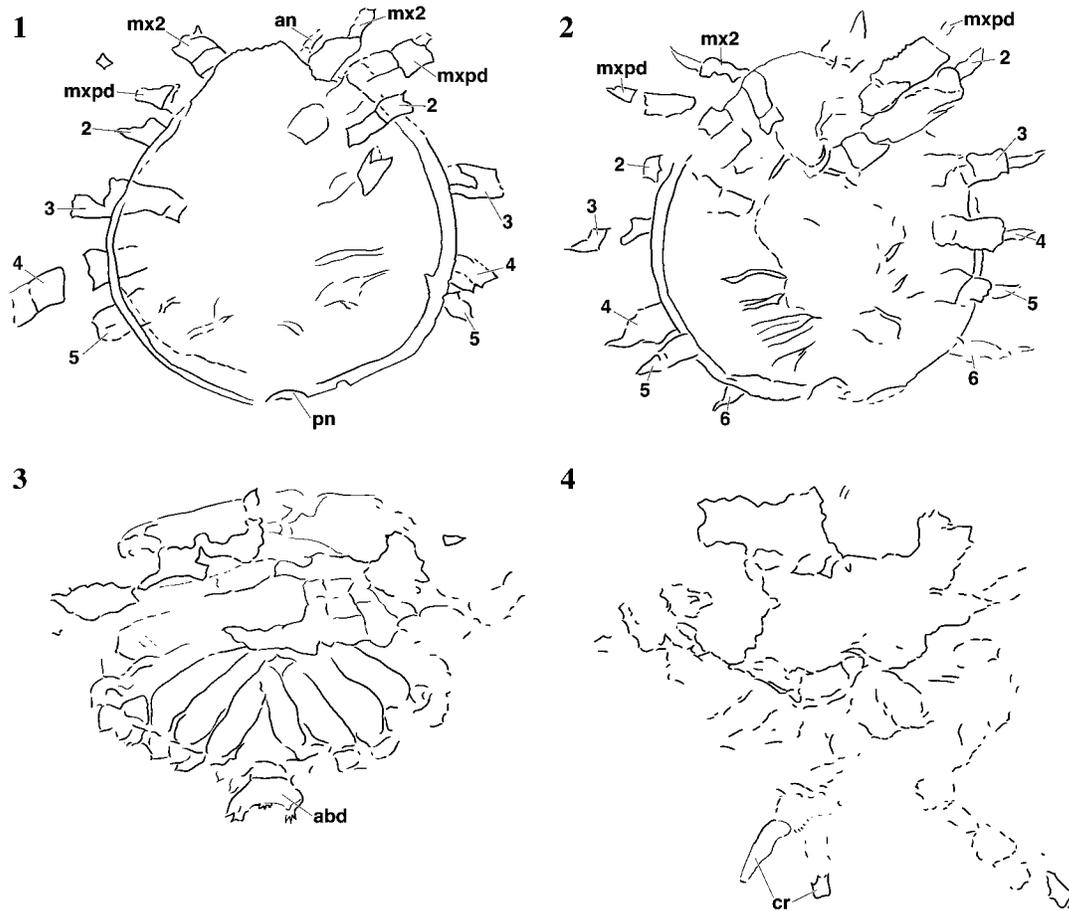


Figure 2 Camera lucida drawings of specimens of *Halicyne montanaensis* n. sp. 1, 2, LACMIP 7310 part and counterpart (holotype), corresponding to the photographs of Figures 1.1, 1.2. 3, 4, LACMIP 7311 part and counterpart, corresponding to photographs of Figures 1.5, 1.6. ABBREVIATIONS: abd = abdomen, an = antenna fragment, ce = compound eye, cr = caudal rami, ms = marginal shelf, mx 2 = second maxilla, mxpd = maxilliped, on = optic notch, pap = papillae on carapace shield, pn = posterior notch, r = rostral plate, s = posterior thoracic segmentation, 2/6 = thoracic appendages

SYSTEMATICS

Maxillopoda Dahl, 1956

Cycloidea Glaessner, 1928

Cyclidae Packard, 1885

Halicyne von Meyer, 1844

Halicyne montanaensis new species

DIAGNOSIS. Carapace round to oval in outline, slightly vaulted in cross section. Surface papillose, marginal shelf distinctly thickened with a smooth to slightly irregular edge. Carapace excavated posteriorly. Distinct optic notches with large, stalked, compound eyes. Rostral plate broadly fused with carapace and anteriorly truncated. Antermost part of carapace bearing rounded knobs or bosses. Terminal segments of all geniculate claws moderate

in size and relatively narrow, penultimate segments wide.

HOLOTYPE. LACMIP 7310 (Figs. 1.1, 1.2)

MATERIAL EXAMINED. LACMIP 7310, 7311, 7312, 7313, 7314; CM 45816

DESCRIPTION. The carapace shield is round to oval in outline ranging from 10.8 to approximately 25 mm in length, with a distinct thickened marginal shelf (LACMIP 7310a, Figs. 1.1, 1.2; LACMIP 7313, Fig. 3.2; CM 45816, Figs. 1.3, 1.4) and distinct cross-sectional vaulting (LACMIP 7310a, LACMIP 7313) characteristic of the genus. The edge of the carapace shelf is smooth (CM 45816) to irregular (LACMIP 7310) in outline. The surface of the carapace is distinctly papillated (LACMIP 7311a, Figs. 1.5, 1.6; LACMIP 7313, Fig. 3.2), the midanterior surface especially so (CM 45816) where the patterning consists of almost rhombo-

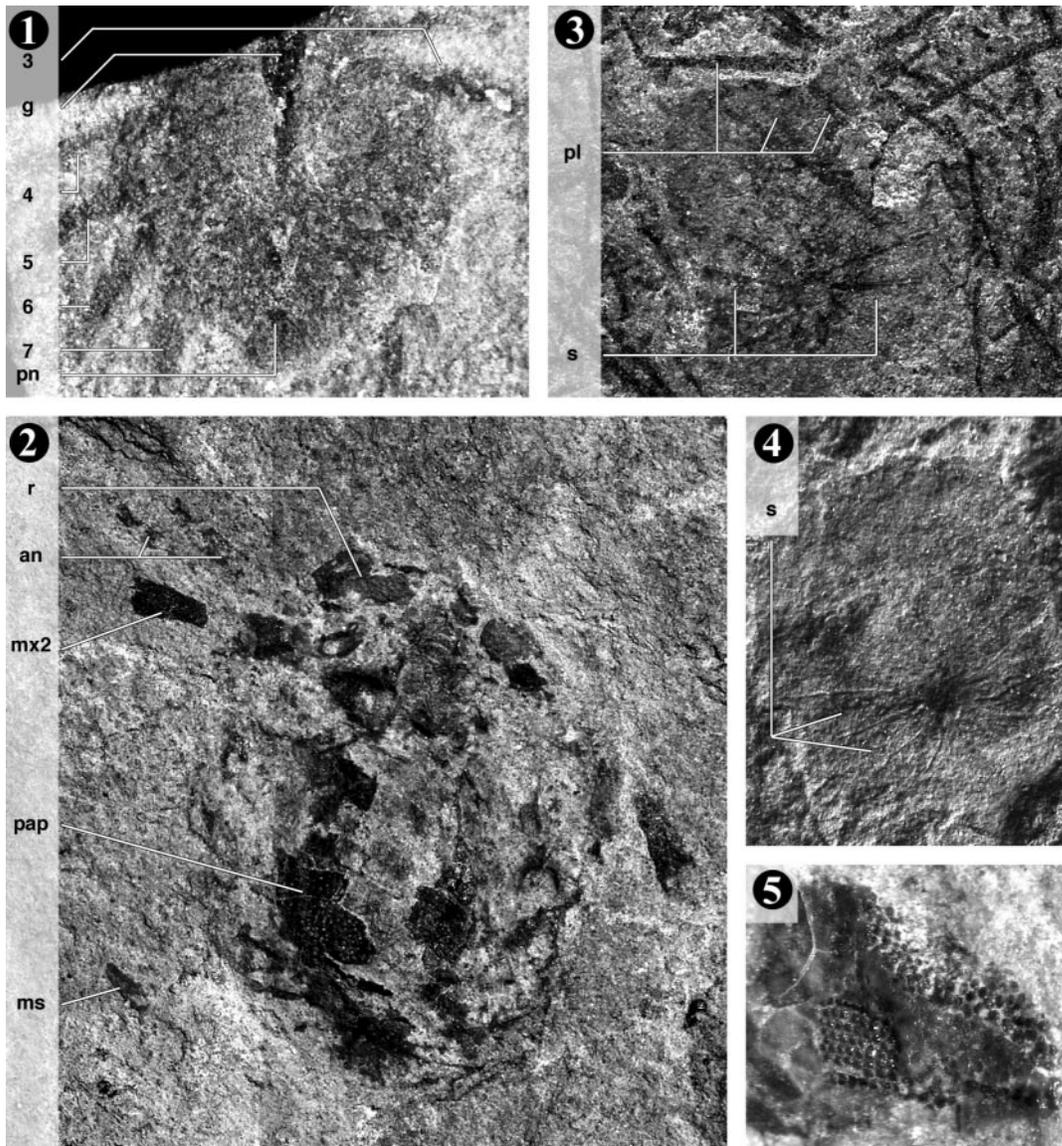


Figure 3 *Halicyne montanaensis* n. sp. 1, LACMIP 7314, photographed with green filter to enhance contrast, showing thoracic appendages, abdomen, and gut cast, $\times 6.8$ (see Fig. 4.1). 2, LACMIP 7313, under direct light, showing papillated carapace surface, fragment of marginal shelf, maxillipeds, and antenna, $\times 9.5$ (see Fig. 4.2). 3, 4, LACMIP 7312 part and counterpart, revealing part of posterior thoracic segmentation, surrounding plant material, 3, under direct high-angle light (see Fig. 4.3), 4, under direct low-angle light, $\times 5.3$. 5, CM 45816, close-up of compound eye with facets, $\times 30$. ABBREVIATIONS: abd = abdomen, an = antenna, g = gut cast, ms = marginal shelf, mxpd = maxilliped, pap = papillae carapace surface, pl = plant material, r = rostral plate, s = posterior thoracic segmentation, 2/6 = thoracic appendages

hedral knobs or bosses. The center of the carapace shield displays two faint ridges running anterior–posteriorly and delineating a V-shaped area (LACMIP 7310). The carapace shield covers virtually the entire body (Figs. 1.1–1.4) and includes an anterior extension or rostral plate that is truncated and covers the cephalon proper (LACMIP 7310a, LACMIP

7313, CM 45816). The carapace directly over the optical notches is slightly raised; between these areas is a semioblong elevated area just posterior to the rostral plate (CM 45816). The anteriormost rostral aspect of the carapace has an irregular margin.

Optical notches (Figs. 1.3, 1.4) are located just

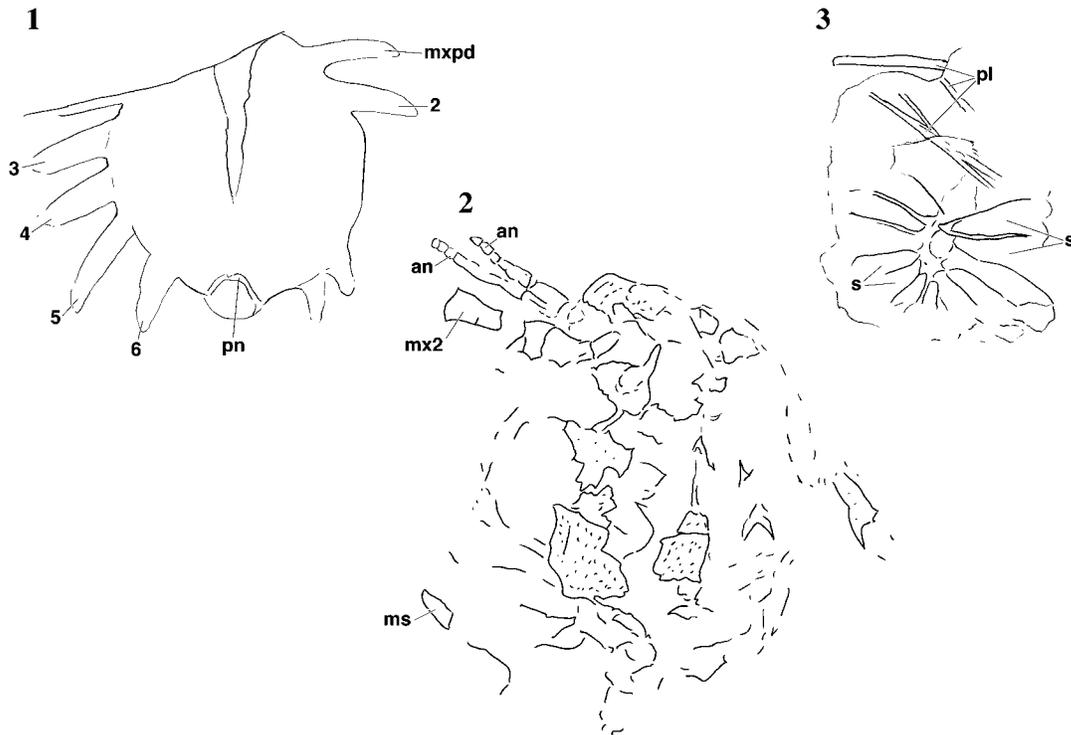


Figure 4 Camera lucida drawings of specimens of *Halicyne montanaensis* n. sp. 1, LACMIP 7314, corresponding to photograph in Figure 3.1. 2, LACMIP 7313, corresponding to photograph in Figure 3.2. 3, LACMIP 7312, corresponding to photograph in Figure 3.3. ABBREVIATIONS: abd = abdomen, an = antenna, g = gut cast, ms = marginal shelf, mxpd = maxilliped, pap = papillae carapace surface, pl = plant material, pn = posterior notch, r = rostral plate, s = posterior thoracic segmentation, 2/6 = thoracic appendages

anterior to either end of the marginal shelf (CM 45816, LACMIP 7310). Within these notches are stalked compound eyes that are exceptionally well preserved, with up to 45 hexagonal to rounded ommatidia visible (CM 45816, Fig. 3.5).

Both pairs of antennae are very poorly preserved. One set may be partly visible on the anterior lateral left side of specimen LACMIP 7313 protruding from where the edge of the rostrum and carapace would have been (Figs. 3.2, 4.2). These seem to consist of the peduncular segments and the proximal portions of the flagella. The holotype, LACMIP 7310, also shows a slight trace of antennae (Figs. 1.1, 2.1).

Anteriorly, a pair of large uniramous second maxillae (Figs. 1.1–1.4) extend anterolaterally from the frontal portions of the head. Also, at least one set of rather broad maxillipeds is present. Both these limbs bear serrate armature along the anterior margins of the dactylus and propodus (LACMIP 7310b, CM 45816). It is not entirely clear if the second set of thoracopods were developed as maxillipeds as well. The segmentation of the cephalic appendages is obscured, but the cuticle of these limbs seems to be finely papillated (LACMIP 7313, Fig. 3.2). The flexion of the dactyl of the maxillae

and maxilliped back onto the serrate anterior edge of the propodus probably facilitated grasping.

The uniramous thoracic limbs 2 through 6 (LACMIP 7310a, LACMIP 7310b, Fig. 1.2; LACMIP 7314, Fig. 3.1) are robust, short, and terminally pointed, with the narrow dactyls generally directed anteriorly, especially on thoracopods 2 and 3. The penultimate segments are relatively thick (LACMIP 7310). Little is discernable concerning the more proximal segments of these limbs. Only on the right-hand side of LACMIP 7310, where part of the carapace is missing, can one see parts of the thoracic tergites and proximal segments of the thoracopods (Figs. 2.1, 2.2), which appear to be less robust, yet longer than either of the two distal segments. These thoracopods were probably used for walking or pushing along the substrate.

The major feature in common among all the specimens is the fan-shaped pattern of the posterior thoracic segments, clearly evident on LACMIP 7311a (Fig. 1.5), LACMIP 7312a (Figs. 3.3, 3.4), and LACMIP 7313. LACMIP 7311 shows only a small part of the posterior end of the animal, whereas the anterior half was not well preserved. More anteriorly, the trunk shows traces of segmentation that is either chevron shaped, with the lateral

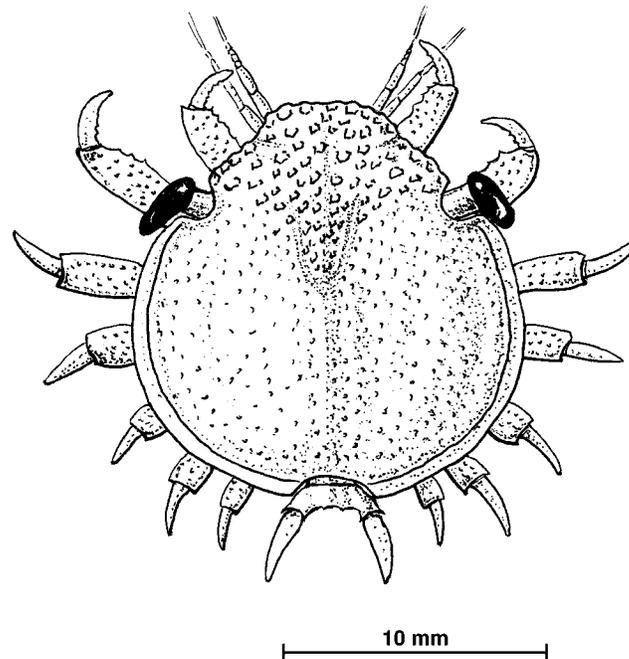


Figure 5 Reconstruction of *Halicyne montanaensis* n. sp.

aspect directed anteriorly (LACMIP 7313, Fig. 2.3) or parallel, laterally directed segmentation (LACMIP 7310a, LACMIP 7312, Fig. 4.3). What one actually sees in all these instances are the endophragmal partitions between the segments themselves.

A large subtriangular area is visible (Fig. 2.2) on the central aspect of the trunk (LACMIP 7310a, CM 45816), which corresponds to the V-shaped area of the carapace and probably marks where the carapace was attached to the underlying segments. The gut or digestive tract (Figs. 3.1, 4.1) is preserved in only one specimen as a dark, irregularly shaped cast (LACMIP 7314).

There is a short, apparently two-segment abdomen (LACMIP 7311a, Figs. 1.5, 2.3; LACMIP 7314, Figs. 3.1, 4.1), exposed because of the posterior notch of the carapace. Only one specimen (LACMIP 7311b) displays distinct caudal rami (Figs. 1.6, 2.4). These rami appear to be uniramous, long (up to 5 mm), thin, bladeliike, and attached to the posteriormost abdominal segment.

REMARKS. Most specimens at hand are of relatively poor quality. Only the holotype specimen is fairly complete. Specimens LACMIP 7310, 7311, 7312, and CM 45816 comprise both parts and counterparts.

One can note differences among the specimens, for example, in quality or amount of organic material preserved, and these are undoubtedly due to taphonomy, which probably also explains the variation visible in the differential coloring of the sur-

rounding rock matrix and the degree of preservation of associated plant material (LACMIP 7312, Fig. 3.3).

A reconstruction of *Halicyne montanaensis* is offered in Figure 5.

DISCUSSION

Currently, five species are easily recognized in *Halicyne*, and most of the characteristic features for the genus are clearly present in the specimens in this study including the round to oval shape, the marginal shelf and the papillated surface of the carapace, the distinct optical notches, and the truncated anterior part of the rostral plate. [The affinities of a sixth species, *H. plana* (Müller, 1955), is uncertain; the described material consisted only of poorly preserved carapace shields.] The large maxillipeds, which also are found in *H. max* Schram, Vonk, and Hof, 1997, and *H. gondwanae* Brambilla *et al.*, 2002, are preserved in other species of the genus such as *H. ornata* Gall and Grauvogel, 1967, *H. agnota* (von Meyer, 1838), or the enigmatic genus *Carcinaspides* (Schafhäutl, 1863). The elevated pattern of bosses on the dorsal surface of the carapace, including the anteriormost bosses or knobs, is similar to those in *H. ornata* and *H. agnota* from the Triassic Muschelkalk. Although it is not certain whether the edge of the marginal shelf is smooth or irregular, there is no indication of a regularly sculpted margin as seen in *H. max*. The postero-medial edge of the carapace, which is rounded in

H. max but pointed in *H. ornata* and *H. agnota*, although obscured in most of the specimens at hand, possesses a posterior notch. There is a small abdomen or telson with two caudal rami, bearing some resemblance to the posterior part of *H. gondwanae* (Brambilla *et al.*, 2002).

The stout, robust thoracopods on *H. montanaensis* are quite different from the limbs of *H. max*, which are longer and thinner. The thoracopods of *H. montanaensis* resemble the robust, supposedly biramous limbs of *H. ornata*, but there is no indication of any biramous limbs on the Bear Gulch species. The presence or absence of biramous limbs has been both important and controversial in discussions of the affinity of the cycloids (Glaessner, 1969; Schram *et al.*, 1997), but there is no indication of exopods in *H. max* or *H. gondwanae*, nor in the specimens under study here. In addition, the orientation of the limbs with respect to the trunk differs. In *H. max* they are concentrated in the anterior portion of the thorax, whereas in the specimens here they are positioned more evenly along the trunk. The strongest resemblance of *H. montanaensis* seems to be to *H. ornata* as reconstructed by Gall and Grauvogel (1967) and Gall (1971) and *H. gondwanae*.

The radial lamellae or radiating grooves observed in *H. max* and *H. ornata* are not preserved on *H. montanaensis*. Schram *et al.* (1997) referred to these structures as a possible diagnostic feature to help distinguish between *Halicyne* and other cycloid genera. It is conceivable that the specific taphonomic conditions at the Bear Gulch locality were unsuited to preserve these particular soft tissues.

Little is known about segmentation patterns in cycloids, except some clues from the position of the proximalmost segments of the limbs (Schram *et al.*, 1997). The distinctly fan-shaped segmentation seen in these specimens, for example, LACMIP 7311 (Fig. 1.5), might be a general character of the genus (or even the family) that was not recognized previously. Reinvestigation of the specimens described in Schram *et al.* (1997) showed that this feature is present in *Cyclus americanus*, but it was not explicitly recognized or mentioned. This pattern is probably convergent to the segmentation seen in crabs (Brachyura), where the strongly reduced abdomen causes the laterally oriented, parallel pattern of the endophragmal structures to be disrupted in the posterior part of the thorax. In crabs, the solid ventral endophragms between the segments like those seen in LACMIP 7311 (Fig. 1.5) are used for attachment of the extrinsic musculature of the legs.

Based on the fauna of malacostracan crustaceans, for example, a characteristic diversity of hoplocaridans and primitive eumalacostracans, the Bear Gulch biota was recognized by Schram (1985) and Briggs and Gall (1990) as part of a spatiotemporally extended, marine, nearshore, faunal continuum. The biota found in Bear Gulch shows strong similarities to both the biota of the Glencartholm deposits of Scotland (Viséan age) and the Essex bi-

ota of the Middle-Pennsylvanian Mazon Creek deposits (Illinois, USA). These similarities are also reflected in other taxa, including polychaete worms and other invertebrates (Schram, 1979) and suggest that the chronofauna had existed virtually unchanged for millions of years. However, note that chronofaunas (Olson, 1966) did not remain completely unchanged, especially at the species level, but rather only at higher taxonomic levels. Species did evolve, became extinct, and were replaced, but the general higher taxonomic composition and particular combination of feeding types remained stable (Schram, 1981; Briggs and Gall, 1990). The crustaceans of the Bear Gulch Konservat-Lagerstätte have long figured as among the most interesting assemblages in the Carboniferous (Schram and Horner, 1978; Factor and Feldmann, 1985; Schram, 1985; Jenner *et al.*, 1998). We can now add the Cycloidea to the faunal list of the crustaceans of Bear Gulch, although cycloids at Bear Gulch remain very rare.

In conclusion, the specimens at hand provide support for two hypotheses about the Cycloidea. First, the pattern of the segments in the posterior thorax reinforces analogous similarities between crabs and cycloids proposed by Schram *et al.* (1997). Second, the presence of a member of the genus *Halicyne* in Bear Gulch supports the Late Paleozoic chronofaunal continuum described by Schram (1981).

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