SYSTEMATICS AND PALEOECOLOGY OF MALACOSTRACAN ARTHROPODS IN THE BEAR GULCH LIMESTONE (NAMURIAN) OF CENTRAL MONTANA

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Abstract

The limestones of the Bear Gulch Member of the Heath Formation (Namurian, Mississippian) have become famous for the quality of their diverse vertebrate and invertebrate faunas, including numerous specimens of malacostracous arthropods. The malacostracan elements of the fauna include Dithyrocaris rolfei, Sairocaris centurion, Perimecturus rapax, Tyrannophontes theridion, Aenigmacaris cornigerum, Crangopsis eskdalensis, and Beolotelson magister. These taxa have been redescribed using known, but previously unstudied material analyzed by standard and ultraviolet photographic techniques. Major systematic changes include rendering Bairdops beargulchensis the junior synonym of Tryannophontes theridion, and transfer of the Sairocarididae to the Archaeostraca, with the consequence that the order Hoplostraca is unnecessary. Interpretations concerning trophic positions and habitat preferences based on functional morphological analyses confirm the earlier observation (Schram, 1981) that the four basic feeding types of Paleozoic Crustacea are found in this locality—rapacious carnivores, scavengers, filter feeders, and algal-detrital feeders. Paleontological, sedimentological, and stratigraphic information from the limestones of the Bear Gulch Member are interpreted to represent carbonate deposition in a calm, shallow, tropical basin with a restricted, Mediterranean-type circulation pattern. The basin margins supported growth of algal and bacterial mats, which provided micritic material to the sediment of the basin center. The water column was well oxygenated and normal marine near the surface with higher salinity bottom waters overlying sediments with anaerobic pore spaces. Sedimentological and fossil evidence indicate a vital-pantostome benthos (Schäfer, 1972).

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INTRODUCTION

The diverse fauna found in the limestones of the Bear Gulch Member of the Heath Formation in central Montana has received considerable attention since the early work of Melton (1971). The locality has become famous for the quality and diversity of its invertebrate and vertebrate fauna, which includes fish, shrimp, annelids, xiphosurans, conulariids, starfish, brachiopods, cephalopods, gastropods, bivalves, sponges, and numerous unidentified forms (Lund and Horner, 1979). Notable by their absence or rarity are corals, trilobites, stalked echinoderms, echinoids, and bryozoans.

Numerous papers describing fish morphology, taxonomy, and palaeoecology have been based on Bear Gulch finds (Lund, 1974, 1977a, 1977b, 1980, 1982; Lund and Zangerl, 1974; Zidek, 1980). Work on the invertebrate portion of the fauna is being pursued at a slower pace. Sponges (Rigby, 1979), “worms” (Schram, 1979d), conodont-eating animals (Conway-Morris, 1979), and limulines (Schram, 1979c) have received some attention. The flora of the Bear Gulch Limestone Beds is currently being prepared for publication (R. Lund, personal communication, 1985).

The malacostracan crustaceans were described (Schram and Horner, 1978; Schram and Schram, 1979) on the basis of earlier finds. A few phyllocarid arthropods are currently under study (R. Lund, personal communication, 1985).

The ecology of the Bear Gulch malacostracan assemblage, as well as recently discovered fossil material, has been virtually unexplored. The purposes of this paper are: 1, to expand upon the published descriptions of the Bear Gulch malacostracans utilizing recently collected and previously described material; 2, to re-evaluate the taxonomic position of each member of the malacostracan assemblage based on material now available; and, 3, to ascertain some of the trophic relationships and habitat preferences of these malacostracans in their environment.

STRATIGRAPHY

The Bear Gulch Limestone Beds alternate with other limestones and black shales to form the Bear Gulch Member of the Heath Formation in the Big Snowy Group (Williams, 1981) (Fig. 1). The Bear Gulch Limestone was termed a lithographic limestone or plattenkalke by Williams (1981). Fossils of marine organisms with chitinous and phosphatic hard parts of excellent quality are found throughout the rhythmically alternating massive micrite and fine-grained, platy, shaly limestone beds (Williams, 1981).

The Big Snowy Group in central and eastern Montana and the correlative Big Snowy Formation of western Montana represent sediments
Fig. 1.—Generalized stratigraphic section of the mid-Carboniferous rocks in central Montana exposed on Potter Creek Dome. After Williams, 1981.
deposited in the Big Snowy Trough during the Late Mississippian (Maughan and Roberts, 1967; Williams, 1981). The Big Snowy Trough was a long, narrow, marine embayment at this time, connecting the Cordilleran miogeosyncline with the Williston Basin (see Fig. 2;
Maughan and Roberts, 1967; Sando et al., 1975; Williams, 1981). The entire unit represents an unconformity-bounded, transgressive sequence overlying the Lower Mississippian Madison Group and underlying the Lower Pennsylvanian Amsden Group (Smith and Gilmour, 1979). The Big Snowy Group in central Montana is made up of three diachronous units, older in southwestern Montana, younger in the Big Snowy Trough, and youngest in the Williston Basin of eastern Montana, the Dakotas, and southern Canada (Sando, 1976). The Kibbey Formation at the base of the transgression represents sediments deposited at the margin of the transgressing sea. The Otter Formation was deposited offshore from the Kibbey and is comprised of shales and limestones. The Heath Formation is composed of black shale and limestone that accumulated along the axis of the Big Snowy Trough (Sando et al., 1975). The Bear Gulch Limestone Beds and laterally correlative black shale make up the Bear Gulch Member of the Heath Formation. The age and stratigraphic relationships of the Bear Gulch Limestone Beds are controversial. Some authors have assigned the Bear Gulch Limestone Beds to the overlying Amsden Group (see Maughan, 1984). Based on evidence from cephalopods (Saunders, 1973), conodonts (Scott, 1973), and palynomorphs (Cox, written communication to R. Lund, 1982 and 1984) a Namurian, Late Mississippian age seems to be the most reliable determination. The stratigraphy of Williams (1981) has been accepted for this paper.

Bear Gulch Limestone crops out only on Potter’s Creek Dome. This small dome (350 km$^2$) is located approximately 50 km southeast of Lewistown in Fergus County, Montana, and about 30 km northeast of the Big Snowy Mountains. The Bear Gulch Member covers some 5000 km$^2$, mostly in the subsurface, from T36E to T21E and from R16N to R8N (Williams, 1981) (Fig. 2).

The carbonate rocks of the Bear Gulch Member of the Heath Formation vary in thickness depending on their position relative to the depocenter of the basin. Near the depocenter, in the Atherton Creek area, the unit is about 30 m thick. Westward, in the region of Tyler Creek, the unit thins to 2 m or less. The Bear Gulch Member is composed of three carbonate lenses interbedded with, and separated vertically by, black shale. Each lens has been interpreted to represent a small, en echelon-fault-formed basin around the margins of which algae and bacteria precipitated the micrite by which the basins were eventually filled (Williams, 1981). It is in this setting that the Bear Gulch fauna, including the malacostracans, has been preserved.

**Materials**

Specimens used in this study were collected over fifteen field seasons from 1969 to 1983. Collections were made by quarrying suitable accessible pillars of Bear Gulch Member limestone on Potter’s Creek Dome.
Specimens utilized in this study are deposited in the museum collections at the Carnegie Museum of Natural History, the Museum of Paleontology at the University of Montana in Missoula, the San Diego Museum of Natural History, and the Field Museum of Natural History. Several hundred pertinent specimens from the Carnegie Museum of Natural History and the University of Montana were examined. Twenty-eight specimens from the Carnegie Museum of Natural History (CM) and 21 from the University of Montana (UM) were borrowed for detailed study. Additionally, 17 specimens were provided to the authors by Frederick Schram, San Diego Museum of Natural History. Included in the specimens from the University of Montana are the holotypes of *Aenigmacaris cornigerum*, *Bairdops beargulchensis*, *Dithyrocaris rolfei*, *Perimecturus rapax*, and *Sairocaris centurion*. Seven specimens of *Tyrannophontes theridion*, were borrowed from the Field Museum (FMNH) in Chicago for comparison to Bear Gulch material.

**SYSTEMATIC PALEONTOLOGY**

Class Malacostraca Latreille, 1802
Subclass Phyllocarida Packard, 1879
Order Archaeostraca Claus, 1888
Suborder Rhinocarina Clark *in* Zittel, 1900
Family Rhinocarididae Hall and Clark, 1888
Genus *Dithyrocaris* Scouler, 1843

*Dithyrocaris rolfei* Schram and Horner, 1978

Fig. 3

**Diagnosis.**—A large rhinocarid up to 10 cm in length; median dorsal plate elongate and narrow; carapace covered with papillae; fine setae ornament posterior half of ventral carapace margin; telson with dorsal carina, shorter than furcal rami.

**Description.**—Carapace suboval, covering entire cephalothorax and four abdominal segments. Antero-dorsal granules, anterior tubercles, cephalic, nuchal, and mesolateral carinae prominent (UM5193, CM34443, CM34444) (Fig. 3). Medial dorsal plate elongate, very narrow, extending from posterior terminus of rostral plate to near posterior margin of carapace, separated from carapace by distinct marginal groove, terminates as mid-dorsal spine extending beyond posterior carapace margin. Entire surface of carapace ornamented by posteriorly directed papillae, most dense dorsal to the mesolateral carinae and becoming less dense or absent laterally. Perimeter of carapace bordered by broad doublure; postero-lateral margin with posteriorly directed setae (CM34444). Postero-ventral spines prominent; about one-half the length of an abdominal segment.

Seven abdominal segments present. Four weakly sclerotized segments covered by carapace; outlined by longitudinal and transverse sclerotized ridges beneath carapace. Eight transverse mid-dorsal bands visible under carapace, decreasing in length anteriorly, represent boundaries of thoracic somites. Four sclerotized abdominal somites protrude beyond carapace valves, ornamented by postero-ventrally directed striae, producing a crude chevron pattern symmetrical about mid-dorsal line. Postero-ventral corners of poorly developed pleurae marked by spines (CM34444).

Telson narrowly triangular in plan view, with prominent medial carina and weak marginal ridges (CM34443). Styliform furcae with longitudinal carina along proximal margin; single row of closely spaced setal (?) pits border proximal, ventral surface of furcae; slightly longer than telson.

Appendages unknown.

**Materials and measurements.**—Measurements, in centimeters, of all *Dithyrocaris rolfei* specimens used in this study are given in Table 1.
Fig. 1.—*Dithyrocaris rolfei* Schram and Horner. 3.1, lateral reconstruction. 3.2, CM34444. 3.3, UM5193 carapace, right valve, lateral view. 3.4, UM6225, holotype, ultraviolet photographic technique. 3.5, CM34443. Bars represent 1 cm.

Fig. 3.—*Dithyrocaris rolfei* Schram and Horner. 3.1, lateral reconstruction. 3.2, CM34444. 3.3, UM5193 carapace, right valve, lateral view. 3.4, UM6225, holotype, ultraviolet photographic technique. 3.5, CM34443. Bars represent 1 cm.
Table 1.—Representative measurements of *Dithyrocaris rolfei* (in cm).

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† From Schram and Horner, 1978.
* Holotype.

*Remarks.*—*Dithyrocaris rolfei* is sometimes well preserved as entire mineralized specimens or impressions in micrite and shaly limestone. This quality of preservation makes possible comparison to two other species in the genus, *Dithyrocaris testudinea* (Scouler, 1835), and *D. paradoxoides* (de Koninck, 1844), which are also described from whole animal fossils. The surface ornamentation of the carapace on each of the species is so distinctly different that identification can be made on this basis alone. The carapace of *D. testudinea* is covered by swirling, posteriorly directed terrace lines. That of *D. paradoxoides*, as reconstructed by Rolfe (1969), has a largely smooth unornamented carapace surface. The overall setose nature of *D. rolfei* is distinctly different from either of these. Like *D. rolfei*, *D. testudinea* has a small postero-ventral spine and no carapace horn. *Dithyrocaris paradoxoides* has large postero-ventral spines, a distinct carapace horn and, like *D. rolfei*, a telson that is shorter than the caudal furcae. The telson margins of *D. rolfei* and *D. testudinea* are apparently unornamented while those of *D. paradoxoides* are setose.

The various specimens assigned to this taxon permit making some suggestions about the morphology of *Dithyrocaris* that are more detailed than those previously made. The typical dorsal view of complete animals, confirms that the axial structures of the carapace did not function as a hinge. Rather, the entire carapace seems to have been a well calcified, rigid structure which, when distorted during burial, tended to yield in areas other than along the axis (Fig. 3.2). Less commonly, the taxon is represented by specimens consisting of lateral views of one carapace valve only (Fig. 3.3). These, we interpret to represent molted fragments of the exoskeleton, perhaps the most durable and, therefore,
the most likely molt fragment to be preserved. Finally, a single specimen representing the entire organism is preserved in lateral view with only the right valve of the carapace preserved (Fig. 3.4). This specimen could be interpreted in several different ways. It might represent a normal individual preserved in lateral view or it might represent the entire molted exoskeleton. The flexed position of the abdomen might argue for this interpretation. A third interpretation, however, seems more plausible. This specimen might represent a “softshell” Dithyrocaris buried shortly after molting and while the carapace was still flexible enough to articulate somewhat about the axis. This position is reinforced by the observation that, under ultraviolet illumination, various parts of the internal anatomy are visible.

Examination of this latter specimen (UM6225) and another (CM34443) raises some doubt about the number of thoracic and abdominal segments. It would appear that the posterior-most seven segments are each characterized by pleural elements and that only the posterior four are heavily sclerotized. Anteriorad of these seven segments lies a single segment whose tergal outline resembles those of the abdomen but without tergal flaps. This, in turn, is preceded by as many as seven faintly defined segments, decreasing in size regularly toward the anterior. These, clearly, are thoracic segments. The single intervening somite simply cannot clearly be assigned either to the thoracic or the abdominal region, at least until details of the gills or the appendages are discovered. The only tangible evidence, the absence of pleural flaps, suggests placement of the segment in the thoracic region, a position we adopt.

Based on its size, bivalved, dorso-ventrally compressed carapace and ventrally directed sensory and trophic apparatus, Dithyrocaris rolfei is interpreted to have been a benthic species (Rolfe, 1969:R309). The absence of terrace lines as found on D. testudinea may indicate that while some members of the genus may have been shallowly infaunal in habit (Seilacher, 1973; Schmalfuss, 1978; Briggs and Rolfe, 1984), D. rolfei was probably, in large part, epifaunal or, perhaps, plowed through the sediment to the approximate depth of the mesolateral carinae. The absence of appendages and mouthparts in D. rolfei makes further trophic interpretation less certain.

Suborder uncertain
Family Sairocarididae Schram, 1973
Genus Sairocaris Rolfe, 1963

Sairocaris centurion Schram and Horner, 1978

Fig. 4

Diagnosis. — Bivalved phyllocarid. Elongate telson with medial longitudinal carina, longer than pretelson segment, dorsally flexed at pos-
Table 2.—Representative measurements of Sairocaris centurion (in cm).

<table>
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† From Schram and Horner, 1978.
* Holotype.

Description.—Bivalved (CM34446, Fig. 4.1, 4.3), carapace strongly alate, thin, smooth, subtriangular in profile, about one-half as long as abdomen. Anterior and ventral margins smoothly convex. Posterior margin strongly sigmoid, concave at mid-dorsum. No rostral or median dorsal plates visible. Entire margin marked by marginal ridge (CM34446).

Three thoracic and seven abdominal segments exposed behind carapace (UM6491). Thoracic segments covered by branchiostegite laterally and ventrally (UM6491, CM34446) when viewed laterally; dorsal surfaces smooth, subequal in length, shorter than first four abdominal segments. Integument of thoracic and abdominal segments finely punctate (UM6491, CM34447, CM34446). Segments increase in length posteriorly; 1 to 4 approximately one-half as long as 5 to 7 and not as tall (UM6491, CM34447). Pleura of first three abdominal segments acuminate along mid-ventral surface. Tergal margins smooth. Pleural margin of fifth segment with prominent notch in antero-ventral corner, notch extends approximately one-third segment length and to height of pleuron on preceding segment. No marginal furrow visible on pleura. Terga as on segment 1 to 3 but longer.

Telson base finely punctate, distinct dorsal flexure distally. Ornamented by longitudinal ridge. Uropods reduced to small ovate appendages visible at base of telson, approximately one-sixth telson length.

No thoracic or abdominal appendages visible. Heavily sclerotized undefinable mass in oral region (UM6491, CM34446). A triangular trace extends postero-ventrally from anterior-most part of carapace approximately one-eighth carapace length.

Materials and measurements.—Measurements, in centimeters, of all Sairocaris centurion specimens used in this study are given in Table 2.

Remarks.—Sairocaris centurion is easily recognized within the Bear Gulch fauna and appears to be distinguishable from the Scottish Visean.
S. elongata on the basis of greater segment heights, much smaller size and more rounded shape of the notch on the fifth pleomere and longer relative telson length and flexure on the latter.

One specimen (CM34446) is of particular interest. Examination of ultraviolet fluorescence photographs of this specimen (Kummel and Raup, 1965) revealed the presence of a bivalved rather than a univalved carapace (Fig. 4.3). This is the only specimen examined from the Bear Gulch that illustrated this feature. Sairocaris elongata has not been figured with this feature (Rolfe, 1969; Schram, 1979a). That a bivalved carapace has not been observed in previously studied specimens is probably due to the generally poor preservation of this structure and to the orientation of most specimens. Typically, Sairocaris is preserved in lateral aspect. Other specimens (especially UM6491) failed to fluoresce. Only CM34446 responded to the ultraviolet wavelengths by fluorescing.

In 1973, Schram erected the Order Hoplostraca (p. 78) to embrace a single family, the Sairocarididae. The basis for distinguishing the order was primarily the absence of a bivalved carapace. He also referred parenthetically to the “distinctive nature of the body tagma” (1973:78) as being of primary importance in distinguishing the order. The Sairocarididae, in turn, contained two genera—Sairocaris and Kellibrooksia. This latter genus was described as containing a single species from Mazon Creek (Schram, 1973:80) and was not clearly distinguished from Sairocaris. It would appear that the outline of the carapace and relative proportions of the abdominal somites would constitute the primary distinguishing features. Specimens of Kellibrooksia, judging from the illustrations by Schram (1973), are not well preserved which renders making distinctions very difficult. Based on our present understanding of Sairocaris, and the recognition that it and Kellibrooksia are very similar, we would suggest that the Sairocarididae is a distinct family but that the family should properly be assigned to the Archaeostraca. Thus, the Order Hoplostraca becomes void. This conclusion lends some support to Rolfe’s suggestion (1969:R328) that Sairocaris may be assignable to the Ceratiocarina. The presence of a bivalved carapace would certainly make a stronger argument for this change on purely morphological grounds.

Little is known about the feeding habits of phyllocarids or their habitat requirements. The large abdomen, reduced thorax and apparent absence of pleopods on Sairocaris centurion suggest a benthic habit as swimming in phyllocarids is indicated by flattened thoracic and abdominal appendages (Rolfe, 1969). The absence of any appendages means this interpretation is by no means certain. Rolfe’s (1969) suggestion that the large mandibles of Paleozoic Archaeostraca were used to chew up large detrital fragments seems to apply to Sairocaris cen-
turion. The large sclerotized mass in the oral region of UM6491 and CM34446 probably represents mandibles and would appear to have been capable of handling large pieces of detritus. A similar feature is preserved on a specimen of *Kellibrooksia macrogaster* from the Mazon Creek fauna (Schram, 1973:81, fig. 3).

Subclass Hoplocarida Calman, 1904
Order Palaeostomatopoda Brooks, 1962
Family Perimecturidae Peach, 1908
Genus *Perimecturus* Peach, 1908

*Perimecturus rapax* Schram and Horner, 1978

**Fig. 5**

**Diagnosis.** — Palaeostomatopod with five carinae on posterior surface of carapace and six carinae on abdominal tergites. Terminal spike more than half the length of telson; telson serrate in region of caudal furcae. Uropodal protopod serrate distally; endopod a small spine-like projection; exopod styliform, serrate along distal third of outer margin.

**Description.** — Carapace dorso-ventrally compressed, approximately as wide as long. Antero-lateral margin evenly convex; mid-dorsal anterior margin concave over rostrum (CM34448, CM34449). Postero-lateral margin slightly convex. Posterior margin sinuous, with mid-dorsal spine (CM34448, CM34450; Fig. 5). Marginal ridge surrounds entire carapace. Rostrum a separate articulated plate, spatulate, axially depressed; one-third the length of the carapace extends beyond carapace margin about one and a half times its width. Posteriorly divergent antennal carinae extend from anterior carapace margin about one-sixth length of the carapace (CM34450). A medial and two lateral pairs of carinae extend anteriorly from the posterior carapace margin about one-third to one-half its length (CM34450, CM34448, CM34449). Medial carina intersects transverse carina that is slightly concave forward at midline becoming more concave laterally; terminates in elements nearly paralleling lateral margins. Anterior-most carapace surface marked by coarse ridges and nodes; entire surface finely punctate (CM34451).

Six abdominal somites, punctate as carapace (CM34451, CM34448, CM34452); subequal in length, slightly wider in mid-abdomen, tapering anteriorly and posteriorly. Pleural margins with marginal ridge continuing to anterior tergal margins; sharp, posteriorly directed postero-lateral spines mark terminations of marginal ridge. Tergal margins straight except near mesolateral carinae with small anterior marginal ridge (CM34451). In plan view, three longitudinal pairs of ridges: one pair straddles the midline; two, closely spaced, parallel the body outline adaxial to pleurae, converging on fifth segment. Node midway between medial and first lateral ridge on segments 1 to 6 (CM34451, CM34448) and on telson (CM34449).

Telson large, marked by marginal ridge (CM34448), a medial and two pairs of convergent lateral ridges, and node near base. Base broadly triangular, axis attenuated into long sharp spine with furcal spine and two or three pairs of subterminal fixed caudal spines (CM34448, CM34451). Styliform uropodal exopods with marginal furrow nearly as long as telson. Outer exopodal margins spined along distal one-third of length. Uropodal bases with prominently spined protopods and endopods (CM34451).

Preserved appendages are short annulate antennules with two visible rami and antennae (CM34450, UM6141 [holotype]). Antennules and antennae subequal in length. Bases with two subequal segments visible (CM34450).
Table 3.—Representative measurements of Perimecturus rapax (in cm).

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† From Schram and Horner, 1978.
* Holotype.

Materials and measurements.—Measurements, in centimeters, of all Perimecturus rapax specimens used in this study are given in Table 3.

Remarks.—The genus Perimecturus has only one unquestioned species other than *P. rapax*. Two former members of the genus *P. pattoni* Peach, 1908, and *P. fraiponti* Van Straelen, 1923, have been recognized as tyrannophontids (Schram, 1979b). *Perimecturus fraiponti* Van Straelen, 1923, has been reassigned by Schram (1984) to the genus *Tyrannophontes*.

Specimens of *Perimecturus rapax* and *P. parki* from the Scottish Glencartholm Volcanic Beds are preserved most often in dorsal view. This probably reflects the species’ strong dorso-ventral compression. At least one specimen from Scotland (Institute of Geological Sciences, Edinburgh (G.S.E.) 5874) is preserved in profile with subchelate thoracopods visible (Schram, 1979a). In detail the species seem to differ mainly in the fine points of ornamentation on the carapace, abdomen and especially the tail. The carapace of *P. parki* apparently has no medial carina as found on *P. rapax*. Dorsally, the abdominal ornamentation of *P. rapax* appears to be similar to *Perimecturus parki* (Schram, 1979a) with paired carinae straddling the midline and the remaining carinae more lateral in position. The main difference is the pairing of these lateral carinae in *P. rapax* and the presence of a node between the mid-dorsal and lateral carinae (CM34449, Figs. 5.1, 5.2, 5.4).

Fig. 5.—*Perimecturus rapax* Schram and Horner. 5.1, CM34448. 5.2, dorsal reconstruction. 5.3, CM34451. 5.4, CM34449 ultraviolet photographic technique. 5.5, CM34450. 5.6, UM6141, holotype. Bars represent 1 cm.
The structure of the tail has been recognized as the easiest way to distinguish *Perimecturus rapax* from *P. parki*. The uropods and telson of *Perimecturus parki* are prominently setose. The outer margins of the uropodal exopodite and the posterior telson base margin of this species are smooth, the telson spike is less than one-half the length of the telson base. On *Perimecturus rapax* no setae have been found on the tail apparatus. The distal one-third of the outer margin on the uropodal exopodite is serrate, the telson spike is more than one-half the length of its base and the telson’s margin is serrate in the vicinity of the furcae flanking the telson spike.

*Perimecturus rapax* is interpreted to have been a low level active carnivore in the Bear Gulch area. This conclusion is based on the inferred presence of subchelate thoracopods as found on *P. parki* in Scotland which are indications of rapacious habits (Schram, 1969).

Order Stomatopoda Latreille, 1817
Suborder Archaeostomatopodea Schram, 1969
Family Tyrannophontidae Schram, 1969
Genus *Tyrannophontes* Schram, 1969
*Tyrannophontes theridion* Schram, 1969
Figs. 6–7

1978. *Bairdops beargulchensis* Schram and Horner, p. 398; pl. 1, figs. 3, 5; text-fig. 4.

*Diagnosis.* — Stomatopod; carapace extends mid-dorsally to about fourth thoracic segment; laterally at least part of sixth thoracic segment exposed. Thorax shows regionalization by size; posterior-most segments, 6–8, taller, longer than anterior segments, only slightly smaller than abdominal segments. Uropodal protopod with two small spikes; exopodite outer margin with articulated spines along distal two-thirds of length; exopodite and endopodite blade-like without diaresis, setose. Telson with terminal spike flanked by spines.

*Description.* — Carapace thin, smooth, cylindrical, subtriangular in profile, approximately one-half as tall as wide and one-half the length of abdomen. Antero-lateral margin smoothly convex. Posterior margin sigmoid, convex near postero-ventral corner and concave dorsally. Rostrum smooth, sharply pointed, down turned, about one-fourth mid-dorsal length of carapace (CM34454, UM6138). Antennules annulate triramous, base of three segments (CM34455), antennal scale large (UM6022). Margin of carapace with marginal furrow; no other grooves evident. Three thoracic segments exposed laterally posterior of carapace, two more exposed dorsally (CM34454, UM6138, UM6492). Three posterior-most thoracomeres larger than those anteriorad. Fully exposed somites increase in size posteriorly, smaller than abdominal somites. Pleurae of thoracomeres rounded with marginal rim; terga smooth with marginal furrow, rim (UM6138, CM34454). Four subchelate, subequal thoracopods on anterior thoracic segments. Propodus massive, armed with two rows of unequally sized spines. Row of larger spines more widely spaced than finer row. Dactylus thin, inwardly curved blade, one-half length of propodus, no
Table 4.—Representative measurements of *Tyrannophontes theridion* (in cm).

<table>
<thead>
<tr>
<th>Catalog no.</th>
<th>Carapace midline (cm)</th>
<th>Length last 3 thoracomers (cm)</th>
<th>Total abdomen (cm)</th>
<th>Telson (cm)</th>
<th>Uropod lateral margin (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>††FMNH25502</td>
<td>1.19</td>
<td>.83</td>
<td>2.83</td>
<td>1.05</td>
<td></td>
</tr>
<tr>
<td>††FMNH25506</td>
<td>1.07</td>
<td>.84</td>
<td>2.40</td>
<td>2.20</td>
<td>.89</td>
</tr>
<tr>
<td>††FMNH25507</td>
<td>1.71</td>
<td>1.43</td>
<td>4.30</td>
<td>2.00</td>
<td>1.46</td>
</tr>
<tr>
<td>UM6492</td>
<td>2.43</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>*UM6217</td>
<td>1.78</td>
<td>.62</td>
<td>1.99</td>
<td>.77</td>
<td></td>
</tr>
<tr>
<td>UM6138</td>
<td>.73</td>
<td>.51</td>
<td>1.66</td>
<td>.82</td>
<td></td>
</tr>
<tr>
<td>CM34454</td>
<td>.56</td>
<td>.57</td>
<td>1.63</td>
<td>.74</td>
<td>.60</td>
</tr>
<tr>
<td>CM34460</td>
<td>1.17</td>
<td>.89</td>
<td>2.96</td>
<td>1.35</td>
<td>1.05</td>
</tr>
<tr>
<td>CM34453</td>
<td>1.22</td>
<td>.94</td>
<td>3.16</td>
<td>1.47</td>
<td>1.19</td>
</tr>
<tr>
<td>CM34459</td>
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<td>1.06</td>
<td>3.15</td>
<td>1.58</td>
<td>1.16</td>
</tr>
<tr>
<td>CM34461</td>
<td>.75</td>
<td></td>
<td>2.20</td>
<td>1.78</td>
<td>1.12</td>
</tr>
</tbody>
</table>

* From Mazon Creek fauna.

† Holotype of *Bairdops beargulchensis*.

Evidence of spines (CM34456, CM34457, CM34455, CM34458). Carpus, ischiomerus small, subequal in size, basis elongate. Posterior thoracic appendages present but form indistinguishable (UM6492, CM34450).

Six subequal abdominal somites, decreasing height posteriorly; pleural lobes subquadrate, corners rounded; posteriorly directed spine on postero-lateral corner of segments 3–5; all with marginal rim and furrow. Terga smooth. Pleopods of segments 1–5 with segmented axis, flattened distally.

Telson broadly ensiform with dorsal carina (UM6492). Telson length about equal to last three abdominal segments, terminal spike flanked by spines. Blade-like uropodal exopodite with articulated spines along distal two-thirds of outer margin (UM6492); marginal furrow present. Endopodite and exopodite blade-like, setose (UM6492, UM6138). Uropodal protopod marked by two spines (CM34454).

Materials.—Specimens of *Tyrannophontes theridion* utilized in this study follow: CM34453–CM34468, UM5174, UM4976, UM6022, UM6138, UM6217 (holotype of *Bairdops beargulchensis*), UM6492, FMNH25502, FMNH25506, FMNH25507.

Measurements.—Measurements, in centimeters, of selected specimens are given in Table 4.

Remarks.—*Tyrannophontes theridion* was named by Schram in 1969. The species was represented by well-preserved material in concretions and was part of the Essex fauna of Mazon Creek. The species was envisioned to belong to a primitive suborder of stomatopods, the Archaeostomatopodea, exhibiting regionalization of the thorax, and a tail apparatus with unisegmental protopods, blade-like exopods and endopods, and a triangular telson (Schram, 1969:260). A recent re-examination of the original material used to describe the species led to the conclusion that the propodus on the subchelae was more massive than originally described, and that the uropodal exopods and endopods...
were less narrow (Schram, 1984:202). These revisions are supported by observations made on the Bear Gulch specimens of *Tyrannophontes theridion*. Bear Gulch specimens show more morphological detail than those from Mazon Creek for preservational reasons. Most Bear Gulch specimens are preserved in micrite with mineralized exoskeletal material still present. Mazon Creek specimens are preserved as impressions in more coarsely grained ironstone nodules. Morphologically, specimens of *T. theridion* from the Bear Gulch differ little from the revised concept (Schram, 1984) of the Mazon Creek material except for size (Figs. 6 and 7). Bear Gulch specimens may reach a larger size than any reported from Mazon Creek.

*Bairdops beargulchensis* Schram and Horner, 1978, was erected as a taxon based on fragmentary material from the Bear Gulch. This taxon was envisioned to represent a medium to large palaeostomatopod with a massive propodus, broadly blade-like uropodal exopods and endopods, and a triangular telson with a terminal spike flanked by furcal lobes. Newer, more complete specimens (CM34462, CM34453 (Figs. 6.4, 6.5), CM34459, and CM34455 (Fig. 6.3)), indicate that these features are found on specimens exhibiting undoubted *T. theridion* characters. These specimens exhibit a distinctly regionalized thorax with three fully exposed thoracic segments posterior to the carapace, a broad propodus armed with a double row of spines opposed by a thin, smooth
dactylus, and a tail apparatus with broad blade-like uropodal elements and a triangular telson terminating in a spike and flanked by caudal spines. They differ from published descriptions of *T. theridion* in that the outer margins of the uropodal exopodite are armed with articulated spines, the posterior uropodal and telson margins are sometimes setose, and the terminal spike of the telson is flanked by furcal lobes. Some or all of the characters may or may not occur on any one specimen. The conclusion, based on observations of these specimens, is that *Bairdops beargulchensis* is a junior synonym of *Tyrannophontes theridion*. Differences from specimen to specimen are attributed to the vagaries of preservation.

The revised description of *Tyrannophontes theridion* is of particular interest when comparing *T. theridion* to the newly described *Gorgonophontes peleron* Schram, 1984. Schram (1984) pointed out that some anatomical details necessary for morphological comparisons of *T. theridion* to *Gorgonophontes peleron* Schram, 1984, are not available in the Mazon Creek material. Comparisons of Bear Gulch *T. theridion* material to *Gorgonophontes peleron* suggests similarity of the species. Some Bear Gulch specimens, especially CM34455 (Fig. 6.3), demonstrate that the propodus of *T. theridion* had two rows of spines, one with closely spaced, fine spines, one with more widely spaced and larger spines. This feature is similar to *G. peleron* Schram, 1984. The tails of specimens of *T. theridion* from Bear Gulch differ from those of *G. peleron* in the details of their ornamentation and absence of a diuresis. They are otherwise similar. The presence of a terminal spike on the tail of *T. theridion* at Bear Gulch is significant because this is one of the diagnostic features for the genus *Gorgonophontes* as described by Schram (1984). The main morphological features remaining which separate *Tyrannophontes theridion* from *Gorgonophontes peleron* are the size of the postero-lateral carapace wings, the shape of the abdominal pleurae, presence or absence of a diuresis on the uropodal exopod, and the relative lengths of the propodus and dactylus of the thoracopods.

It should be noted here that many of the details of *Tyrannophontes theridion* morphology were made more clear by ultraviolet radiation fluorescence photography of the specimens. Many *T. theridion* specimens were particularly responsive to this technique but CM34454 and CM34455 (Figs. 6.3 and 6.6) were especially useful for study of thoracic segment regionalization, propodus shape and armament, pleural margins, and details of tail morphology.

The presence of armed thoracopods suggest a benthic, predaceous habit similar to that of modern stomatopods for these organisms (Schram, 1969, 1979b).
Order Aeschronectida Schram, 1969  
Family Aenigmatocarididae Schram and Horner, 1978  
Genus *Aenigmatocaris* Schram and Horner, 1978  
*Aenigmatocaris cornigerum* Schram and Horner, 1978  
Figs. 8–9

**Diagnosis.**—Malacostracan with thinly sclerotized carapace; prominent anteriorly directed mid-dorsal spine; antero-dorsal and antero-ventral spines present. Ventral margins of abdominal pleura triangular, smooth. Third abdominal segment with strong dorsal flexure.

**Description.**—Carapace thin, smooth, subquadrate in lateral view, about twice as long as high. Anterior with prominent anteriorly directed mid-dorsal spine arising anterior to midlength, extends to anterior carapace margin (CM34465, CM34466, UM6191, UM6146). Antero-dorsal and antero-ventral spines define limits of anterior carapace margin. Ventral margin slightly convex, greatest curvature posterior to midlength. Posterior margin sigmoid, concave at mid-dorsum. Endophragmal skeleton often visible, with 8 subequal segments apparent, no pleurobranchial openings visible (CM34465, CM34466, UM6191, UM6146).

Thinly sclerotized abdomen approximately twice length of carapace. Six segments present; segments 1 to 3 and 4 to 6 increase in length posteriorly. Third and sixth tergites longer than remaining four; overall decrease in height posteriorly. Pleurae ventrally pointed, triangular in outline; margins smooth. Terga of third segment strongly flexed ventrally. Telson poorly preserved, apparently elongate with mid-dorsal carina, shape of margins unknown (CM34467; Fig. 8.1). One specimen (CM34467) with uropods about one and a half times longer than telson with smooth outer margins, no other details visible.

Mandible heavily sclerotized (CM34465, CM34466, CM34467, UM6146). Thoracopods similar, long, with strong proximal elements. Ischium and merus marked by rows of setal (?) pits along outer margin. Distal elements more slender; no apparent developments of chelae. Pleopods present but poorly preserved (CM34467, UM6191), stenopodal, five segments, most proximal segment short, next two segments longer, two distal segments very short.

Intestine straight, dorsally positioned, anus immediately anterior to base of telson (UM6191).

**Materials and measurements.**—Measurements, in centimeters, of all specimens of *Aenigmatocaris cornigerum* used in this study are given in Table 5.

**Remarks.**—Specimens are preserved as thin, mineralized material in profile on bedding planes with only a small amount of relief. Preservation of the main body and proximal portions of the thoracopods is often very good, but other appendages and the tail are generally not well preserved. Those specimens studied which exhibited pleopods had only the appendage bases visible on all five abdominal segments (CM34467) or complete appendages on only one segment (UM6191). The slender, elongate, well-sclerotized, and jointed legs imply a benthic habit (Manton, 1977).

In the specimens preserved with the intestine visible (UM6112 and UM6191), no coarse fragments of material are visible. The gut material
appears to be identical to the matrix in which the specimens were preserved suggesting a detrital feeding habit. This interpretation is supported further by the absence of chelae on any of the thoracopods. These animals had no limbs adapted to grasping or tearing apart prey.
Table 5.—Measurements for *Aenigmacaris* cornigerum (in cm).

<table>
<thead>
<tr>
<th>Catalog no.</th>
<th>Carapace length</th>
<th>Carapace height</th>
<th>Carapace horn length</th>
<th>Abdominal segment lengths</th>
</tr>
</thead>
<tbody>
<tr>
<td>UM5889</td>
<td>2.18</td>
<td>1.95</td>
<td>1.02</td>
<td>a1</td>
</tr>
<tr>
<td>UM6112</td>
<td>.69</td>
<td>.96</td>
<td>.87</td>
<td>.94</td>
</tr>
<tr>
<td>*UM6146</td>
<td>1.80</td>
<td>.60</td>
<td>.26</td>
<td>.44</td>
</tr>
<tr>
<td>UM6191</td>
<td>3.69</td>
<td>1.75</td>
<td>.75</td>
<td>.75</td>
</tr>
<tr>
<td>CM34468</td>
<td>2.24</td>
<td></td>
<td></td>
<td>.84</td>
</tr>
<tr>
<td>CM34465</td>
<td>4.25</td>
<td>2.53</td>
<td>.79</td>
<td>.69</td>
</tr>
<tr>
<td>CM34466</td>
<td>3.29</td>
<td>1.70</td>
<td>.57</td>
<td>.45</td>
</tr>
<tr>
<td>CM34467</td>
<td>1.26</td>
<td>.38</td>
<td></td>
<td>.64</td>
</tr>
</tbody>
</table>

* Holotype.

The thin nature of the carapace reflected by the visibility of the endophragmal skeleton in specimens is typical of the genus (see Schram and Schram, 1979). While larger than *Aenigmacaris minima* Schram and Schram, 1979, the characteristics of preservation and morphology indicate that *Aenigmacaris* was a wide ranging genus in Carboniferous rocks of the western United States.

Order Aeschropectida Schram, 1969  
Family Aratidecithidae Schram, 1978  
Genus *Crangopsis*

*Crangopsis eskdalensis* (Peach, 1882)  
Figs. 10–11

1882. *Palaeocrangon eskdalensis* Peach  
1903. *Palaeocrangon eskdalensis* Peach and Horne  
1908. *Crangopsis eskdalensis* (Peach). Peach  
1911. *Crangopsis eskdalensis* (Peach). Woodward  

**Diagnosis.**—Hoplocarid, no rostrum, subtrapezohedral carapace; antennules well developed, prominent antennal scale; pleuron of first abdominal segment covered by posterior extension of carapace and inflated pleuron of second abdominal segment.

**Description.**—Small, carapace subtrapezohedral in outline, thin, approximately one-half length of abdomen. Posterior margin sigmoid; convex postero-ventral margin, concave dorsally. No rostrum, spines, carina or grooves other than faint marginal ridge on postero-ventral margins (CM34469-A, CM34469-B, Figs. 10.2 and 10.3).  
Six abdominal segments present. Pleuron of first segment hidden by branchiostegal flap of carapace and anterior portion of broadly rounded pleuron of second abdominal somite (CM34469-C). Pleuron of third segment smaller than second segment; rounded
Fig. 9.—Lateral reconstruction of *Aenigmacaris cornigerum* Schram and Horner. Bar represents 1 cm.

and attenuated posteriorly. Pleura of fourth and fifth segments forms a notch along posterior margin of segment (CM34469-B). Small marginal ridge borders the four pleura; terga and pleura otherwise smooth (CM34469-B). Terga of first four segments subequal in length, fifth and sixth increase in length. Telson apparently spike-like, uropods with two subparallel carinae (CM34469-A).

Peduncle of antennule with three segments; each narrowing terminally (CM34469-A). Antennules appear to be short, biramous. Blade-like antennal scale, longer than antennule base (CM34469-A). No other appendages preserved.

*Materials and measurements.*—Measurements in centimeters of all *Crangopsis eskdalensis* used in this study are given in Table 6.

*Remarks.*—The specimens found in the Bear Gulch which have been studied and assigned to this species are from a group of shrimp preserved on a single, broken-up slab of rock (CM34469). Preservation of most of the individuals is poor but three of the best specimens were utilized to produce the reconstruction (Fig. 11) shown.

The Bear Gulch specimens of *Crangopsis eskdalensis* differ from published descriptions of other species in similar, aeschronectid genera in a variety of readily distinguishable ways. *Kallidecthes* species were larger animals than the *C. eskdalensis* specimens studied. They had longer antennules and antennae than *Crangopsis eskdalensis*, a short rostrum and the pleuron of the first abdominal segment was not covered by the carapace and pleuron of the second abdominal segment (Schram, 1979a:237). *Aratidecthes* species were moderate sized organisms like *Kallidecthes*. They possessed enlarged antennules, had no rostrum and only a slightly enlarged pleuron on the second abdominal segment (Schram, 1969:253). *Crangopsis socialis*, like species of *Kallidecthes*
and *Aratidecethes*, was larger than *C. eskdalensis*. It is distinguishable from *C. eskdalensis* on the basis of possession of reptantian-like thoracopods, more alate carapace, a relatively longer length of its first abdominal segment, and the attenuated nature of the postero-ventral corners of the abdominal pleura on segments 3 to 5 in *C. socialis* (Schram, 1979a). *Kallidecthes* and *Aratidecethes* species and *C. socialis* appear to have led solitary lives whereas the *Crangopsis eskdalensis*

Table 6.—Representative measurements of *Crangopsis eskdalensis* (in cm).

<table>
<thead>
<tr>
<th>Catalog no.</th>
<th>Carapace</th>
<th>Total abdomen</th>
<th>Abdominal somites</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>$a_1$</td>
</tr>
<tr>
<td>†GSE5007</td>
<td>.80</td>
<td>1.98</td>
<td>.14</td>
</tr>
<tr>
<td>CM34469-A</td>
<td>.45</td>
<td>.75</td>
<td>.07</td>
</tr>
<tr>
<td>CM34469-B</td>
<td>.73</td>
<td>1.06</td>
<td>.12</td>
</tr>
<tr>
<td>CM34469-C</td>
<td>1.08</td>
<td></td>
<td>.13</td>
</tr>
</tbody>
</table>

† Schram, 1979a. Lectotype *Crangopsis eskdalensis* from Glencarholm fauna.
specimens from the Bear Gulch and the Glencartholm Volcanic Beds in Scotland are found in “schools” (Schram, 1969, 1979a:39). It is interesting to note that all the larger aescronectid genera and *Crangopsis socialis* show signs of solitary benthic adaptations, especially in thoracopod structure, while *C. eskdalensis* was smaller, gregarious, and perhaps nektonic in habit. *Crangopsis eskdalensis* may, indeed, represent adult forms but it seems only prudent to recognize that they may be natant forms as is suggested by Schram and Horner (1978).

Subclass Eumalacostraca Grobben, 1892
Superorder Eocarida Brooks, 1962
Order Eocaridacea Brooks, 1962
Family Belolotelidae Schram, 1974
Genus *Belotelson* Packard, 1886

![Fig. 12](image)

**Diagnosis.**—Eumalacostracan, shrimp-like in overall appearance, with large, smooth carapace; rostrum long; 8 pairs of long, subequal, aechalate thoracopods.

**Description.**—Carapace thin, smooth, subquadrate approximately twice as long as high. Anterior margin with deep, well-defined optic notch (UM6495, CM34470, Fig. 12); ventral margin slightly convex. Posterior margin nearly straight mid-dorsally and strongly convex near postero-ventral corner, projected over pleural lobe of first abdominal segment. Rostrum ensiform with marginal fold and mid-dorsal ridge; approximately one-half length of carapace. Carapace with narrow marginal ridge and furrow on posterior and ventral margin. Endophragmial skeleton visible (UM6495) as postero-dorsally inclined ridges and grooves on carapace.

Abdomen about as long as cephalothorax; five segments decreasing in length posteriorly; sixth elongate. Pleura of first five segments well developed, reniform anteriorly, becoming orbiculate posteriorly, nearly one-half height of the segment; inclined postero-
Fig. 12.—Belotelson magister (Packard). 12.1, lateral reconstruction. 12.2, UM6495. 12.3, CM34470 ultraviolet photographic technique. Bars represent 1 cm.
Annals of Carnegie Museum

Table 1.—Representative measurements of Belotelson magister (in cm).

<table>
<thead>
<tr>
<th>Catalog no.</th>
<th>Carapace length</th>
<th>Rostrum length</th>
<th>Body length (optic notch to telson base)</th>
</tr>
</thead>
<tbody>
<tr>
<td>UM5889</td>
<td>2.90</td>
<td>1.05</td>
<td>4.27</td>
</tr>
<tr>
<td>UM6495</td>
<td>4.06</td>
<td>1.50</td>
<td>6.24</td>
</tr>
<tr>
<td>CM34470</td>
<td>3.57</td>
<td>1.41</td>
<td>6.47</td>
</tr>
</tbody>
</table>

ventrally. Sixth pleuron subquadrate with rounded corners. Distinct marginal ridge and furrow on pleura, otherwise smooth. Terga smooth. Telson longer than sixth segment (UM6495), triangular outline marked by a medial ridge and two lateral grooves. Uropodal exopod lateral margins smooth, apparently tapering posteriorly; no other features visible.

Appendages poorly preserved. Antennule biramous, base with at least two segments, distal element small. Antenna long, single annulate flagellum; at least two segments in base, distal element shorter. Large blade-like antennal scale setose on inner margin (CM34470). Eye apparently stalked, round. Eight pairs of long, similar, achelate thoracopods. Pleopods poorly preserved with large base, blade-like exopod and endopod.

Materials and measurements.—Measurement, in centimeters, of all Belotelson magister specimens used in this study are given in Table 7.

Remarks.—Specimens of Belotelson magister found in the Bear Gulch Limestone are generally preserved as mineralized impressions and/or casts lying on their sides. This consistent feature of their preservation is unfortunate because no specimens reveal the structure of the animal's ventral surface. Specimens available from Illinois (Schram, 1974) reveal the structure of the mouthparts, development of a branchiostegal chamber, and specialization of the thoracic sternites in a fashion parallel to that of modern reptantian decapods. Despite the prominent nature of the thoracopods the exact structure of their bases is obscured in all the specimens from Illinois and Montana and remains undescribed. Belotelson traquairi (Peach) Schram, 1969, from the Glencartholm fauna of Scotland is also imperfectly preserved in this region (Schram, 1979a). Another feature not preserved because of the preservational orientation in the Bear Gulch specimens is the distinctive mid-dorsal pore found in both B. magister and B. traquairi.

None of the specimens studied exhibited details of the pleopods. Specimens CM34470 and UM6495 suggest by the fracture pattern of the rock the presence of short, paired appendages on abdominal segments 1 to 5 but no details of the structures are visible (Fig. 12). Similarly, the exopods and endopods of the tail are simply not preserved. These features may have been too delicate to preserve, but it is the preservation of just such fine features for which the Bear Gulch Limestone is notable.

The anatomical similarity of Belotelson to modern crayfish and lobsters suggests the groups occupied similar habitats as bottom dwelling scavengers (Schram, 1974). Absence of chelipeds, however, would
Table 8.—Near-shore marine crustacean assemblages of the Carboniferous. Analogous taxa are on the same line, with lack of corresponding taxon indicated by a dash.

<table>
<thead>
<tr>
<th>Trophic level</th>
<th>Dinantian Glencairnhom</th>
<th>Mississippian Bear Gulch</th>
<th>Pennsylvanian Essex fauna</th>
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<tr>
<td></td>
<td></td>
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<td>Tyrannophontes theridion</td>
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<tr>
<td>Rapacious carnivores</td>
<td>Perimpecturus parki</td>
<td></td>
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<tr>
<td></td>
<td>Bairdops elegans</td>
<td></td>
<td>Belotelson magister</td>
</tr>
<tr>
<td>Scavenger low-level</td>
<td>Belotelson traquairi</td>
<td></td>
<td>Mamayocaris jaskoskii</td>
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<td>Pseudogalathea macconnachie</td>
<td></td>
<td>Kallideichus richardsoni</td>
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<td></td>
<td>Pseudotealliocaris etheridgei</td>
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<td>Anthracophasia ingelsorum</td>
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<td>Crangopsis eskalensis</td>
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<td>Hesslerella shermani</td>
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<td></td>
<td>Joannellia elegans</td>
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<tr>
<td></td>
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<td>Aenigmaticarcs cornigerum</td>
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Modified from Schram, 1981.
probably rule out low-level predation. The prominent reptantian-like thoracopods and well-developed antennae are especially suggestive of this interpretation. The occurrence of such an organism in anaerobic sediments deposited in a water column believed to be generally hypersaline at the base (Williams, 1981) suggests that B. magister lived in localized patches of suitable habitat within this sedimentary environment or that individuals were transported in from surrounding areas.

**DISCUSSION**

The Bear Gulch malacostracan fauna is of interest because of the quality of its preservation and its diversity. The excellent preservational quality of chitinous and phosphatic residues in fossils of this unit is attributed to the rapid accumulation of very fine-grained carbonate sediments in an area of restricted circulation where the level of available oxygen in the pore spaces of the sediments was extremely low. Preservation of malacostracan material is good enough to allow some internal organs, for example the intestine of *Aenigmacaris cornigerum*, to be seen. However, fine details of anatomy are often lacking in otherwise good specimens. Appendages, for instance, while often present, are difficult to see clearly upon close inspection. Ventral surfaces are almost never visible because almost all specimens are preserved either in profile or with the dorsal surface exposed and hiding the ventral. Some of these shortcomings were reduced by maximizing the detail that is preserved by the use of ultraviolet photographic techniques (see “Remarks” in species descriptions of *Sairocaris centurion* and *Tyran- nophontes theridion*). In contrast to chitinous and phosphatic material, calcareous fossils were preserved only as casts and molds. Calcareous skeletons were apparently preferentially dissolved by pore waters (Williams, 1981).

Diversity in this malacostracan assemblage is high enough to embrace the four basic feeding types found in Paleozoic Crustacea: rapacious carnivores, scavengers, filter feeders, and algal-detrital feeders (Schram, 1981). Species assignments to the different feeding types are based on analysis of the functional morphology of appendages and by analogy with modern forms. These interpretations are summarized in Table 8.

The abundance of specimens and the diversity of the Bear Gulch fauna and flora allow some analysis of the trophic structure of the area in which these organisms lived. Malacostracans represent an intermediate trophic level in the food web of this area. Algal and bacterial mats and plankton represented the primary producers for this system. These organisms, along with sponges, provided cover and/or attachment sites for invertebrates and vertebrates. There is little or no evi-
Evidence to suggest the presence of frame builders such as corals and bryozoans. The presence, in the water column of filter feeding shrimp, such as *Crangopsis eskdalensis*, suggests that plankton were present, despite their absence in the fossil record (Table 8). *Sairocaris centurion, Dithyrocaris rolfei*, and *Aenigmacaris cornigerum* were detrital and perhaps algal consumers living at the sediment-water interface. None possessed the stout appendages necessary for scavenging or predation. *Belotelson magister* was apparently a scavenging species. *Perimecturus rapax* and *Tyrannophontes theridion* were higher level consumers as evidenced by their specialized grasping thoracic appendages. The malacostracans, in turn, were fed upon by fish. An entire 50 mm long *Tyrannophontes theridion* was found in a 150 mm coelecanth, *Cardinodon populum*. Whole shrimp have been found in three species of sharks (Lund, personal communication). Shrimp parts are often found in fish coprolites throughout the study area.

The diversity, taxonomic composition, habitat, and stratigraphic position of the Bear Gulch malacostracan fauna are of particular interest because of their relationship to other Carboniferous malacostracan assemblages in other parts of the world. The malacostracan faunas from the Glencartholm Volcanic Beds (Visean) in Scotland and the Mazon Creek (Westphalian) in Illinois are from sites of unusually good preservation. When compared to the Bear Gulch fauna (Table 8) striking similarities in diversity, taxonomic composition, habitat, and trophic position are apparent. This phenomenon of assemblages of related species occupying similar trophic positions and habitats over wide geographic areas and relatively long geologic time (70–80 million years) has been discussed by Olsen (1966). He applied the term chronofauna to assemblages exhibiting relatively little change in their ecological relationships or taxonomic composition over time. Schram and Horner (1978) made reference to the persistence of the near-shore marine malacostracan assemblage represented by the Bear Gulch, Glencartholm, and Mazon Creek Essex faunas. Schram (1981) gave a good summary of the relationships found within these three faunas and how their structure changed over time and space (Table 8). In general, species within a genus or a related genus are found living in similar habitats but are separated geographically and stratigraphically. For instance, at Bear Gulch *Perimecturus rapax* is found, not *Perimecturus elegans* of the Glencartholm fauna, and the Bear Gulch’s *Sairocaris centurion* has a functional counterpart in a related genus, *Kellibrookskia macrogaster*, at Mazon Creek. At a higher taxonomic level, the more progressive stomatopods replaced their trophic equivalents, the rapacious palaeostomatopods, in the Westphalian Mazon Creek assemblage after appearing and coexisting with the palaeostomatopods at Bear Gulch. The true nature and sequence of species changes from fauna to
fauna and over time in North America and western Europe must remain obscure due to the lack of time equivalent diverse fossil assemblages to which these faunas can be compared. The rarity of the special conditions necessary to produce high quality preservation of large numbers of individuals may preclude many new faunal comparisons.

In addition to strictly biological interpretations about the study area during the time of deposition, Bear Gulch fossils combined with sedimentological and stratigraphic information have much to contribute to our understanding of the physical conditions under which the sediments of the Bear Gulch Limestone Beds were deposited. Paleogeographic studies of Montana and Wyoming indicate that the Williston Basin and the eastern portion of the Big Snowy Trough were filling progressively westward with near-shore and off-shore sediments while the Bear Gulch Limestone Beds were being deposited. To the south, the Southern Montana Arch was rising, shedding clastic materials northward into the Big Snowy Trough (Sando et al., 1975; Maughan, 1984). Black shale and limestone were deposited along the axis of the shrinking trough (Sando et al., 1975; Williams, 1981; Maughan, 1984).

The region was tropical during the Late Mississippian and Early Pennsylvanian (Scotese et al., 1979). The deposition of sediments composed of algal- and bacterial-generated micritic muds (Williams, 1981) is typical of tropical conditions as are the clays found in the Bear Gulch Member (Schopf, 1980:196). The rapid deposition of the Bear Gulch Limestone Beds, demonstrated by abundant dewatering faults, numerous and diverse well-preserved fossils, and the short period during which deposition occurred (Williams, 1981), lend further evidence to the high biological productivity rate associated with tropical habitats.

Water depth in the area of Bear Gulch Limestone deposition was generally shallow. Certainly the mats of cyanobacteria and noncalcareous algae found preserved in the sediments lived within the photic zone. A distinct decrease in total organic carbon from marginal to basinal areas of deposition was documented by Williams (1981, table 1). She also considered the exposed sections of the limestones of the Bear Gulch Member to be complete. This shallowing upwards sequence represents about 35–40 m in the main portion of the section exposed at Potter’s Creek Dome, with much thinner outcrops, 2 m or less, to the south, east, and west. If the section is complete, then conditions do appear to have been shallow, even in the deepest part of the basin, at the time of deposition.

Wave and current energy levels responsible for deposition of Bear Gulch Limestone sediments are interpreted to have been very low because of the very fine ripple marks in the micritic sediments (Williams, 1981) and the small size of carbonate and clastic sediments in the rocks. Rippling of thin laminations composed of skeletal grains
and micrite throughout otherwise massive beds implies a variable, but still low, level of current activity. The presence of occasional platy shales and silts between massive limestones (Williams, 1981) may denote the potential for higher currents dominating the basin at times, or the incursion of the clastic source which eventually engulfed the area with a deltaic sequence.

The pattern of water circulation within the area where the Bear Gulch Limestone Beds were deposited is not easy to deduce. Schopf (1980: 98–112) discussed the possible patterns for flow of waters in a basin. The absence of any circulation would lead to a stagnant, anaerobic water column. The rich nektonic and benthic fossil assemblage of the Bear Gulch Limestone Beds rules out that possibility. The two remaining possible patterns are termed estuarine and Mediterranean. Estuarine flow is characterized by basins in which the rate of inflow of water is much greater than the rate of evaporation in the basin. Mediterranean type basins experience a greater rate of evaporation than inflow of water. Mediterranean basins tend to have a water column with elevated salinities at the base, high $pO_2$, and low nutrient levels. Sediments in these basins tend to be high in CaCO$_3$ and low in organic carbon (Schopf, 1980). The basin in which the Bear Gulch Limestone Beds were deposited seems to have exhibited a restricted Mediterranean type circulation pattern. The interpreted geographical site of deposition of the Bear Gulch would lie near the southern limit of the predictable low precipitation and high evaporation region characterizing the Mediterranean climate (Scotese et al., 1979). Total organic carbon of the CaCO$_3$ rich sediments is generally low, from 0.5 to 1.5% (Williams, 1981). The input of elastics into the area, and probably of freshwater to compensate for evaporation, was low as evidenced by 5 to 8% quartz silt content (Williams, 1981) in the Bear Gulch Beds. The general absence of benthic organisms with strict open marine requirements, that is, corals, bryozoans, and most echinoderms, coupled with the abundance of somewhat more salinity tolerant near-shore marine benthos, the crustaceans, cephalopods, and sponges, suggests that bottom conditions in the main basin were not normal marine in nature but somewhat hypersaline. Brackish and freshwater forms are found only in southern, marginal facies of the unit’s outcrop pattern (Lund and Horner, 1979; Williams, 1981).

Water temperature in the basin was almost certainly warm as indicated by the tropical position and shallow depth of the basin. Temperature apparently did not rise so high as to deplete oxygen levels to intolerably low levels because an abundant open marine fauna existed within the basin. The oxygen level of the water column within the basin, though not intolerable, may have been low and even lower yet in the sediments
on the bottom. The absence of burrowing forms in most localities is suggestive of very low oxygen level in the sediment pore spaces. However, the presence of benthic organisms in the section suggests that adequate oxygen for their existence was available at the sediment-water interface. The generally complete, undisturbed nature of deposited layers with little or no evidence of erosion by bottom currents is further evidence for low oxygen levels (Schäfer, 1972).

Salinity varied locally in the basin depending on a number of conditions. To the south, brackish and some freshwater conditions existed near the shore of the Central Montana Trough embayment. To the east, brackish and freshwater environments predominated (Maughan, 1984). The presence of terrestrial plant parts in the south suggests these areas were not a great distance removed from the Bear Gulch Basin. The Mediterranean basin type circulation pattern implies stratification of salinity levels with higher salinity water flowing seaward from the bottom of the basin which is, in turn, overlain by more normal marine surface water entering the basin. This model is consistent with the marine character of the nektonic fauna and the absence of some expected normal marine benthos.

The Bear Gulch Limestone Beds formed in a shallow tropical basin with restricted, Mediterranean type water circulation. The basin was connected to the Central Montana Trough somewhere north of Potter's Creek Dome. Algal and bacterial mats surrounding the basin precipitated CaCO$_3$ in the form of micrite which was distributed by low energy currents entering the basin. Occasional, possibly seasonal, pulses of clastics reached the basin from rivers and streams prograding from the south and east. Water in the basin was sufficiently oxygenated to support plankton, fish and nektonic shrimp. Bottom conditions were influenced by elevated salinities and anaerobic sediment pore spaces.

Sedimentological and fossil evidence permits the characterization of a vital-pantostrate biocoenosis in the sense of Schäfer (1972). This biocoenosis is characterized by: 1, the presence of a limited benthic community; 2, a taphocoenosis of nektonic, benthic, and planktonic forms; 3, complete beds only occasionally disrupted or penetrated by benthos; 4, common coprolites and fossils; 5, small sediment grain size; 6, pore water low in O$_2$; 7, large number of well-preserved, more-or-less complete fossils; 8, material record of biofacies complete throughout the record; and 9, low perturbation in an off-shore, or sometimes near-shore, sublittoral zone.

**Summary and Conclusions**

Schram and Horner (1978) made the original descriptions of Bear Gulch malacostracans. They described five new species and docu-
mented the presence of five other species or genera. Utilizing specimens discovered since 1978 and reexamining material collected earlier, re-descriptions of seven species recognized to occur in the Bear Gulch malacostracan assemblage have been made. Aenigmacaris cornigerum, Belotelson magister, Crangopsis eskdalensis, Dithyrocaris rolfei, Perimicturus rapax, Sairocaris centurion, and Tyrannophontes theridion are recognized. Bairdops beargulchensis is considered to be a junior synonym of Tyrannophontes theridion. The recognition that Sairocaris centurion has a bivalved carapace renders the Order Hoplocostraca unnecessary and permits placement of the Sairocarididae in the Archaeostraca. Anthracophausia sp. and Pseudotealliocaris sp. are not reconsidered in this study. The uniformly poor and incomplete quality of specimens previously assigned to these taxa render the assignments tentative and no new material substantially improves this situation. Nothing more can be done with these until better material becomes available.

The taxonomic composition of the malacostracan assemblage found in the Bear Gulch Limestone Beds is similar to the Glencarthurm Volcanic Bed fauna (Visean) in Scotland and the Mazon Creek Essex fauna (Westphalian) in Illinois. Similarities, especially at the generic and family levels, to these faunas fit the pattern of a Carboniferous, near-shore, marine malacostracan assemblage as discussed in Schram and Homer (1978) and Schram (1979a, 1979e, 1981).

The near-shore marine nature of this chronofauna (in the sense of Olsen, 1966) provides an initial basis for environmental interpretations of the Bear Gulch Limestone Beds. The presence of nektonic and benthic malacostracans implies that conditions in the water column and at the sediment-water interface were conducive to animal life in at least part of the basin. The quality of preservation of arthropods and the preservation of bedding laminae suggest rapid sedimentation rates and absence of organic activity in the sediment. Arthropods are found throughout the section in the limestones of the Bear Gulch Member except at the very top of the section where shallowing produced brackish and supratidal conditions (Williams, 1981). Distribution of arthropod specimens around Potter's Creek Dome is not uniform. Specimens appear to be concentrated at three collection sites, 24, 28, and 51 (see Fig. 2). This distribution is interpreted to represent a patchy distribution of sites suitable for malacostracan occupation, although selective preservation may also be a factor in controlling distribution. As a result of the conditions outlined above, it appears the museum specimens of this fossil arthropod fauna have little more to offer to detailed study of the stratigraphy and sedimentology of their basin of deposition beyond the level presented in this paper.
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