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## On Mazon Creek Thylacocephala

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ABSTRACT—Three species of the enigmatic arthropod group Thylacocephala are described from the Middle Pennsylvanian Mazon Creek biotas: two new species of the genus *Concavicaris*, *C. georgeorum* and *C. remipes*, and one new genus and species, *Convexicaris mazonensis*. There are problems in the study and interpretation of thylacocephalans because their form is so unusual and they appear to lack characters that would ally them with known major arthropod groups. A revision of the higher taxonomy of thylacocephalans is proposed and comments are made on possible affinities of the group.

## INTRODUCTION

The class Thylacocephala as a separate, recognized group of arthropods is a relatively recent collation. Yet species now included within this group (Arduini and Pinna, 1989) have been known since Meek (1872) described what is currently called *Concavicaris bradleyi*. However, prior to the work of Briggs and Rolfe (1983), thylacocephalans were, almost without exception, classified as phyllocarids even though neither abdomen nor appendages were known.

In 1982 and 1983, three groups of researchers, working independently of each other, published studies of different fossils that we now realize are related in some way (Rolfe, 1985, presented an excellent historical review). Each team created a new higher taxon to accommodate their species. First, Pinna *et al.* (1982) designated a class Thylacocephala to accommodate a new arthropod from the Jurassic of northern Italy, *Ostenocaris cypriformis* Arduini *et al.*, 1980, which they believed had possible cirripede affinities. Second, Secretan (1983) erected a class Conchyliocarida to recognize the aberrant position of *Dollocaris ingens* Van Stralen, 1923, from the Jurassic of France, a recognition facilitated by the study of then newly made collections (Secretan and Riou, 1983). Finally, Briggs and Rolfe (1983) described a collection of arthropods from the Devonian of Australia, but could not attribute their material to any known class and erected an order Concavicarida of uncertain affinities. The disagreements over the interpretation and higher taxonomic placement of these fossils (see Pinna *et al.*, 1985; Secretan, 1985; Rolfe, 1985) in large part reflected differences in the preservation of a combination of peculiar anatomical features unique among arthropods. Rolfe (1985) weighed the available evidence and concluded that all three groups of researchers had been working on closely related fossils, which by priority took the name of Thylacocephala.

Quite independent of the above, amateur collectors of the famous Middle Pennsylvanian Mazon Creek faunas of the Francis Creek Shale long have puzzled over peculiar fossils they referred to

by the common name "flea shrimp." Results of the study of these flea shrimp fossils reveals that they are a varied group composed of three distinct species assignable to two genera of Thylacocephala. These fossils suggest a reorganization of the higher taxonomy within the Thylacocephala.

Specimens used in this study are designated by the following prefixes: SDSNH, San Diego Society of Natural History paleontology collections; PE, Field Museum of Natural History invertebrate paleontology collections; MCP, Northeastern Illinois State University, Mazon Creek Study Center.

## SYSTEMATIC PALEONTOLOGY

CLASS THYLACOCEPHALA Pinna, Arduini, Pesarini, and Terruzzi, 1982

*Diagnosis.*—These are arthropods with a small to large bilobed carapace enclosing the entire body. Compound eyes are very well developed as either large, sessile bodies situated in optic notches or as organs that virtually cover the surface of a protrudent, sac-like cephalon. Body appendages are of two types: anteriorly 3 pairs of subchelate, raptorial limbs, and posteriorly a set of from 8 to 16 pairs of apparently paddle-like limbs. Eight sets of well-developed gills are associated with the subchelate limbs. The posterior trunk is marked with pronounced pleurites, probably developed internally as an endophragmal skeleton, associated with the posterior limbs.

*Remarks.*—This definition is emended from that implicit in Rolfe (1985), who attempted to reconcile the divergent opinions of Pinna *et al.* (1985) and Secretan (1985). The result of this study suggests that the thylacocephalans can be separated into two orders: the Concavicarida, with a large, well-developed optic notch bearing a discrete compound eye, and the Conchyliocarida, lacking the optic notch as a distinct structure and having the eyes located on the surface of a protrudent, sac-like cephalon.

Despite the fact that some 24 genera have been assigned to the Thylacocephala (see Arduini and Pinna, 1989), the affinities of

several of these still remain uncertain. These include *Dioxyaris*, *Saccocaris*, and *Tuzoia* from the Cambrian, *Galenocaris* from the Devonian, *Nothozoe* from the Cambrian through Devonian, *Coreocaris* from the Permian, and *Rugocaris* from the Jurassic.

#### ORDER CONCAVICARIDA Briggs and Rolfe, 1983

**Diagnosis** (after Briggs and Rolfe, 1983).—Thylacocephalans with a carapace bearing a prominent concave optic notch, typically developed with a fused rostrum that may curve ventrally to occlude the notch anteriorly. From 8 to 16 homonomous well-demarcated trunk segments diminish in height anteriorly and posteriorly.

**Remarks**.—This order includes such forms as *Harrycaris* from the Devonian, *Concavicaris* from the Devonian through the Carboniferous, *Dollocaris* from the Jurassic, and an undescribed form from the Silurian (Mikulic *et al.*, 1985). In addition, *Ankitokazocaris* from the Triassic, *Microcaris* from the Jurassic, and *Protozoe* from the Cretaceous might also belong in this order.

#### GENUS CONCAVICARIS Rolfe, 1961

**Diagnosis**.—The carapace has a fused hinge line, a rostrum extended anteriorly, pronounced optic notches, and up to three lateral longitudinal ridges.

**Remarks**.—This diagnosis is quite general and is based on features that essentially characterize the order. Sixteen species of *Concavicaris*, including the two described here, exhibit a wide array of sizes, shapes, and decorations (Briggs and Rolfe, 1983). Clearly the genus is a candidate for revision. However, *Concavicaris* is not unique in this regard since very few of the 25 genera of Thylacocephala currently recognized (Arduini and Pinna, 1989; Arduini, 1990) are clearly diagnosed with a concise set of apomorphic characters.

#### *Concavicaris georgeorum* n. sp. (Figs. 1–7)

**Diagnosis**.—The carapace is suboval in outline with a short rostrum, an optic notch prominently occupying about half of the anterior aspect, a ventral margin marked by a notch anterior of its midpoint, a pointed postero-dorsal aspect, and a single, dorsally situated, longitudinal ridge.

**Stratum**.—Francis Creek Shale, Desmoinesian, Middle Pennsylvanian.

**Holotype**.—SDSNH 36777; Peabody Coal Company Pit 11, Will, Grundy, and Kankakee Counties, Illinois (Fig. 1).

**Etymology**.—Named in honor of the George family, Calvin, Harriet, and Steven, well-known collectors of Mazon Creek fossils and donors of the holotype.

**Description**.—The carapace is roughly oval in outline, marked with thickened free margins, and from 9.4 to 17.0 mm long (Table 1). The anterior aspect of the carapace features a small

TABLE 1. Representative measurements of *Concavicaris georgeorum* (mm). Body length measured from tip of rostrum to posterior of carapace; carapace length measured from optic notch to posterior of carapace.

Feature	n	$\bar{x}$	Range
Body length	12	14.7	11.7–18.7
Carapace length	16	13.2	9.4–17.0
Carapace depth	16	9.8	7.0–12.0
Eye depth	5	4.3	4.0–5.0
Eye width	4	1.9	1.4–2.3
Body length/carapace depth	12	1.46	1.37–1.59



Figure 1. *Concavicaris georgeorum*. Holotype. SDSNH 36777, with compound eye (e), carapace (c), subchelate mouthparts (m), ventral carapace notch (n), 4.4 $\times$ .

rostrum (SDSNH 36768; PE 24591, Fig. 2A), a well-differentiated optic notch that occupies its dorsal half (SDSNH 36759; PE 23146, Fig. 2B), and closely spaced alternating grooves and ridges on the margin of the ventral half (MCP 596, Fig. 2C; PE 15346, Fig. 2D). The carapace appears to have been relatively thin and not particularly well mineralized, since it is commonly bent and distorted by underlying structures, but it does bear a slight dorsal longitudinal ridge extending from the optic notch to just below the pointed dorso-posterior aspect (PE 10853, Fig. 2E).

The compound eyes are large, slightly more than twice as long as they are wide (PE 24590, Fig. 3A). They are broader dorsally than ventrally such that they do not interrupt in lateral silhouette the oval outline of the body. In occasional specimens, the carapace has separated from the body and slipped posteriad during diagenesis to reveal the part of the head that bears the eyes (PE 23146, Fig. 2B; PE 31049). In these instances, the eyes are clearly seen to be sessile. Although the compound eyes are often preserved as a unit, fine detail is rarely seen. Only a few specimens (e.g., SDSNH 36762, Figs. 3B, C; PE 23144) preserve any facets on the eye surface. These facets are extremely small, a few tenths of a millimeter in diameter.

Mandibles are preserved on several specimens, and are typically in close association with the mouth just dorsal and anterior to the ventral, marginal notch of the carapace (SDSNH 36764, Fig. 3D; PE 51937; PE 30575; PE 15346, Fig. 3E). Each mandible consists of a well-developed molar process with four or five ridges that interface nicely with ridges on the opposite member of the pair (PE 24592, Fig. 3F). This interfacing is not always easy to discern, but one specimen (PE 24529, Fig. 3G) clearly preserves one mandible in natural position near the mouth while the other mandible is dislocated from this at a 90° angle.

The three pairs of raptorial subchelate limbs posterior to the mandibles are large (Fig. 4A–C). The animals, however, are so narrow that compaction of the specimens during diagenesis often superimposes right and left members of the limb pairs onto each other, complicating their study and interpretation. The most anterior set of these three is the smallest and is rarely preserved completely (PE 30556, Fig. 5A), while the most posterior pair is the largest. These subchelate limbs are often completely folded under the



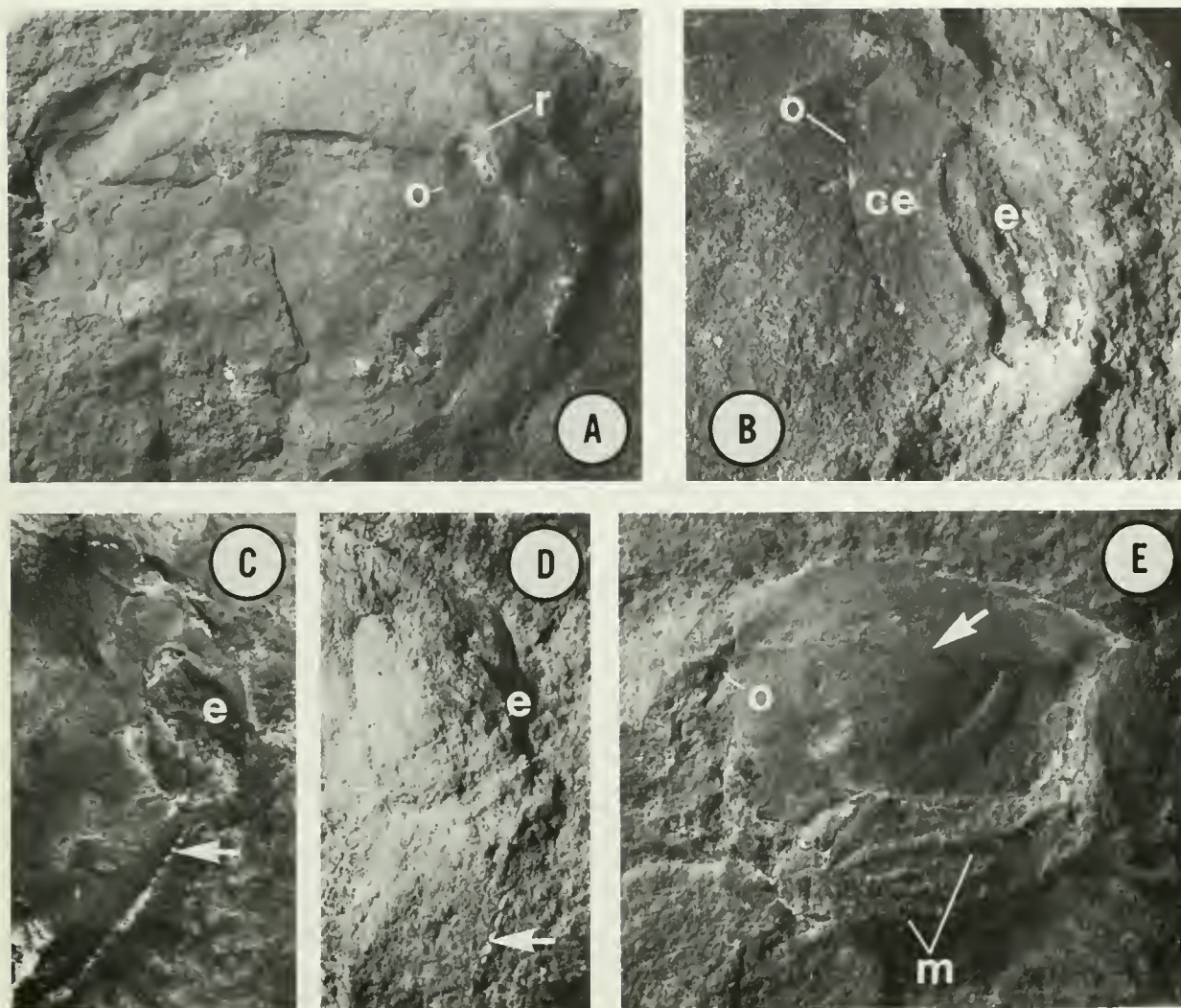


Figure 2. *Concavicularis georgeorum*. A, PE 24571, dorso-oblique preservation showing left optic notch (o) and rostrum (r), 4.3 $\times$ . B, PE 23147, close-up with optic notch (o), remnants of compound eye (e), exposed portion of cephalon (ce), 7 $\times$ . C and D, MCP 596 and PE 15346 respectively, with notched "tongue-in-groove" carapace margins (arrow) ventral to the eye (e), 6 $\times$ . E, PE 10853, displaying longitudinal carapace ridge (arrow) extending posteriorly from the optic notch (o) and tightly flexed raptorial mouthparts (m) ventral to the body, 4 $\times$ .

carapace (e.g., SDSNH 36759, PE 10853, Fig. 2E). I interpret them as a set of highly specialized mouthparts: from front to back, the maxillules, maxillae, and maxillipedes, respectively (see Discussion below).

The exact number of articles in these limbs is difficult to discern. The most distal portions clearly have three podomeres, and these appear to have been held fairly rigidly with respect to each other. The preservation of these podomeres ranges from virtually straight (SDSNH 36777, Fig. 1; PE 30556; PE 32957; PE 45696) to somewhat arcuate (PE 11020, Fig. 4A). The margins of these articles are not marked by any teeth or spines. A few specimens preserve the pronounced flexure in these limbs (PE 10916, Fig. 4D; PE 11020, Fig. 4A; PE 14105, Fig. 4C; PE 29466), and at least four or five podomeres lie proximal of those flexures (Fig. 4C). The exact number is not known because these structures are generally poorly preserved and because the articles on the ventral side of the body are crowded under the margins of the carapace. However, some specimens do preserve individual articles very clearly (most notably PE 45696, Fig. 4D). These have a punctate surface and at least

the most basal one appears to have been broader proximally than distally, like an inverted paddle (PE 23144; PE 45696, Fig. 4D). In ventral view (SDSNH 36774; PE 23145, Fig. 4E; PE 40107, Fig. 4F), these proximal segments floor the space lying ventral to the trunk proper between the ventral margins of the carapace.

As in almost all thylacocephalan fossils, the trunk (or body or abdomen; all terms have been used in the literature) is usually enclosed completely within the great carapace chamber. However, through the vagaries of preservation, a few specimens available to me do reveal something of this region. The most dorsal part of the trunk is discernible as a thick rod. Sometimes it can be seen in place under the carapace along the dorsal margin (e.g., PE 31752), but more often it becomes very noticeable when it arcs ventrad to extend toward the postero-ventral aspect of the carapace (PE 15356; PE 23144; PE 30556, Fig. 5A). In these cases, the rod often is associated with an extruded trunk.

The trunk segments are seldom clearly preserved (e.g., SDSNH 36769), and usually are visible only when their ventral portions extend beyond the margin of the carapace. The maximum number



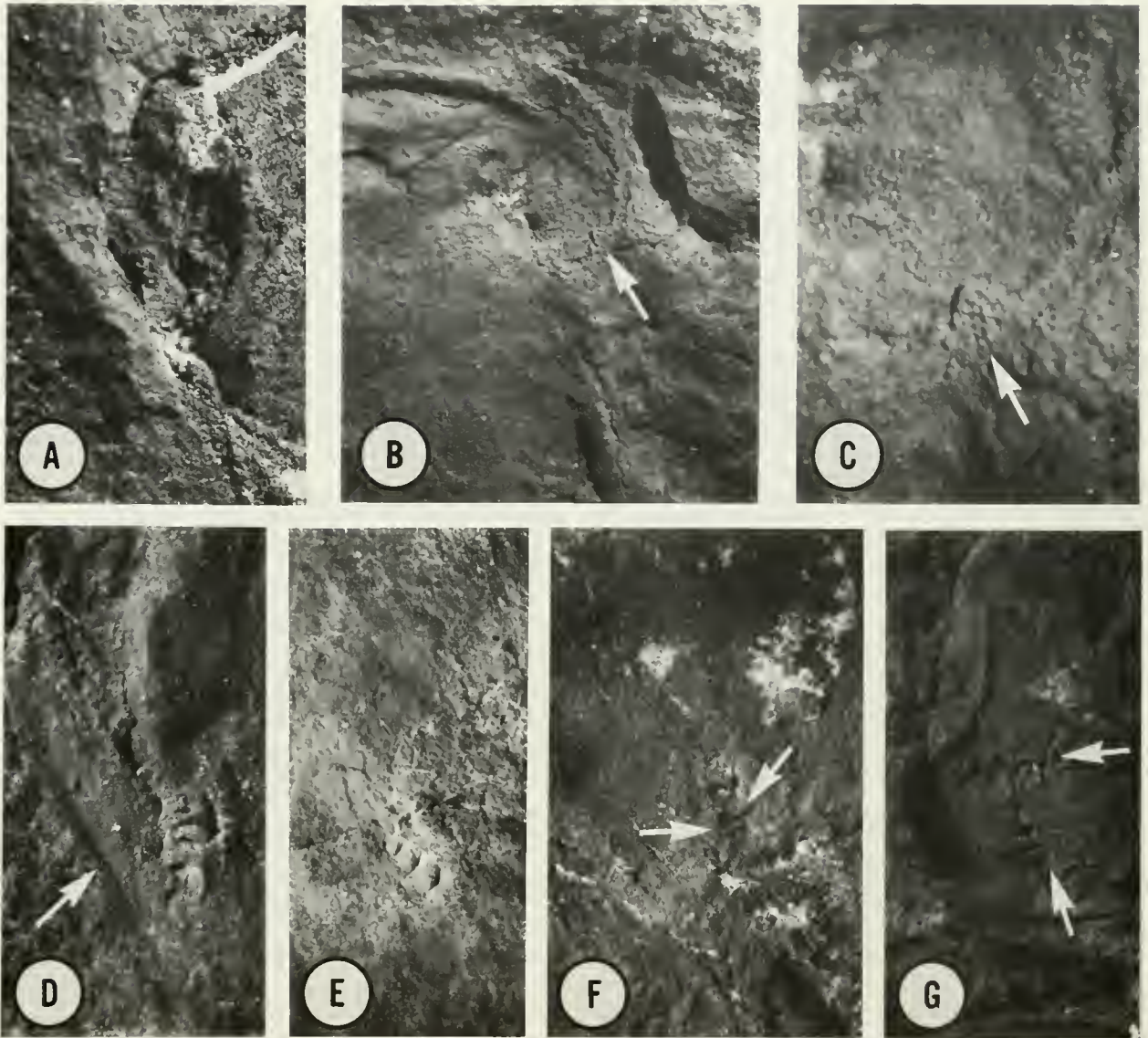


Figure 3. *Concavicularis georgeorum*. A, PE 24590, with outline of eye lobe in relation to carapace,  $2\times$ . B and C, SDSNH 36762, overall view of anterodorsal region of body (B,  $11\times$ ) showing position of fragment of eye surface (arrow) enlarged (C,  $40\times$ ) preserving facets. D, SDSNH 36764, mandible located posterior to the carapace anterior margin (arrow),  $10\times$ . E, PE 15346, mandible,  $6\times$ . F, PE 24592, pair of mandibles (arrows) in position interfacing with each other,  $8.5\times$ . G, PE 24529, with two halves of a mandible pair at right angles to each other (arrows),  $7\times$ .

of segments seen is 8 (MCP 591, Fig. 5B). These segments are associated distally with small quadrangular structures to which in turn the diaphanous remains of the trunk limbs are attached (MCP 591; PE 29469, Fig. 5D). The limbs are never well preserved, and the quadrangular structures are probably the limb bases or protopods.

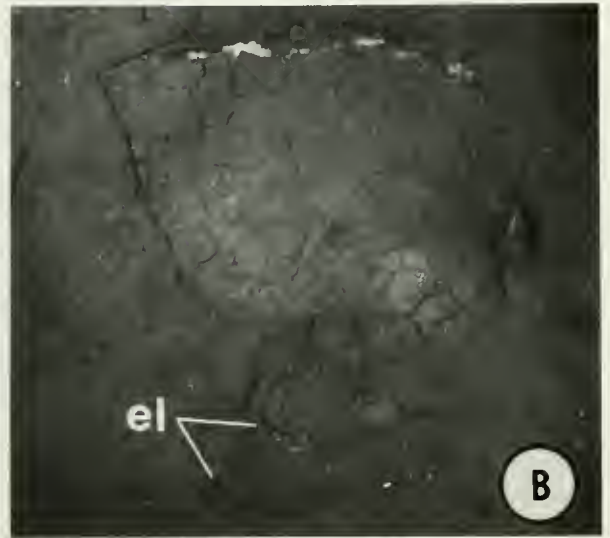
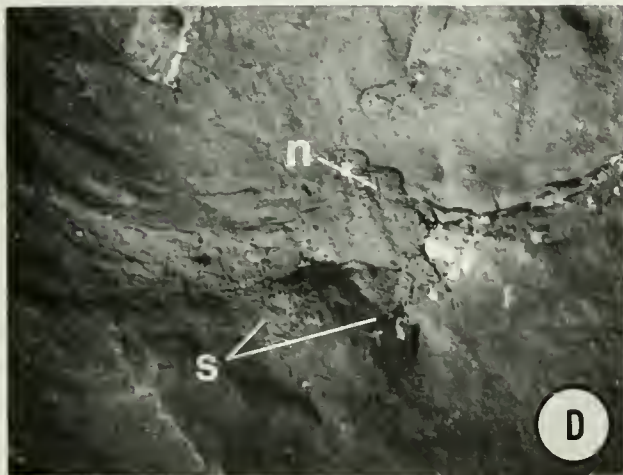
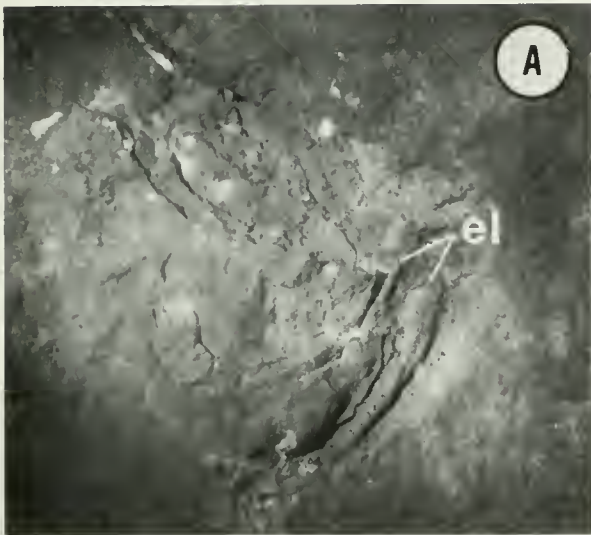
The gut seems a fairly simple structure. The anterior part of the foregut is narrow (PE 30575, Fig. 6A) and is associated with the

mandibles (as noted above). This part of the foregut extends dorsally to a large region that seems to be a posterior foregut or stomach, located posterior to the optic notch (SDSNH 36763, Fig. 6B; PE 30575, PE 45696). The mid- and hindguts extend posteriorly (SDSNH 36778, Fig. 6C; MCP 595, Fig. 6D) to an anus located near the postero-dorsal corner of the carapace.

As noted above, some specimens preserve the ventral aspect of the body (SDSNH 36774; PE 23145, Fig. 4E; PE 24589; PE 40107,

Figure 4. *Concavicularis georgeorum*. A, PE 11020, displaying a slightly arcuate positioning of the three articles distal to the elbow (el) of the second (2) and third (3) raptorial limbs,  $6\times$ . B, PE 10916, clearly preserving the elbows (el) of the raptorial mouthparts,  $4.8\times$ . C, PE 14105, flexed maxillipede with partial preservation of proximal limb segments (1–4), elbow (el), and distal segments (5–7),  $6\times$ . D, PE 45696, close-up of carapace margin near the ventral carapace notch (n) with punctate, proximal segments of the mouthparts (s),  $8\times$ . E and F, PE 23145 ( $7\times$ ) and PE 40107 ( $6\times$ ), respectively, ventral preservations showing right and left carapace valves (c), conjoined ventro-anterior margins (a), ventral opening to the ventral space beneath the body and between the ventral carapace margins (v), and flexed segments of various mouthparts (m).







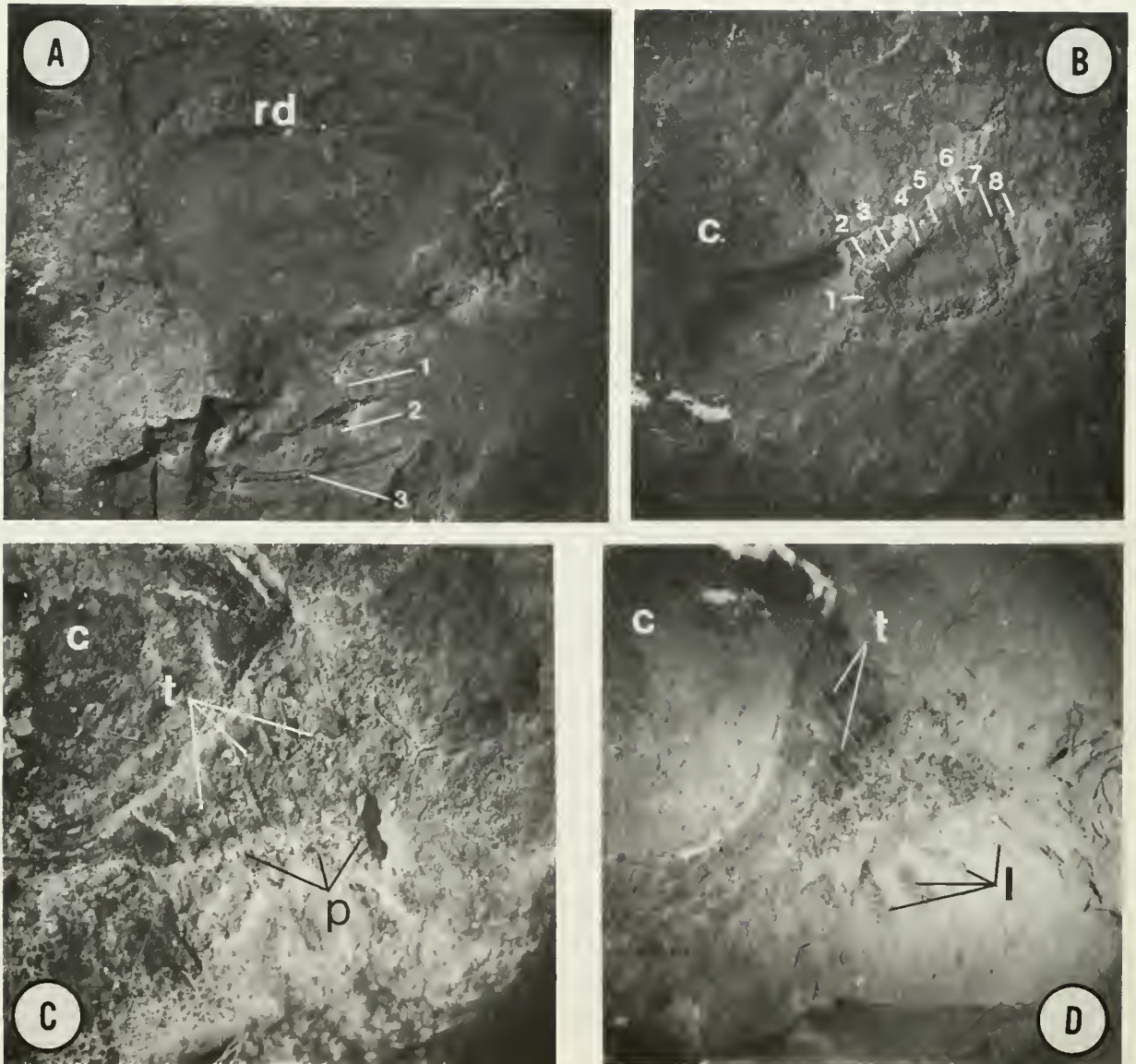


Figure 5. *Concavicaris georgeorum*. A, PE 30556, note the dorsally positioned thick rod (rd) and the maxillules (1), maxillae (2), maxillipedes (3), 5 $\times$ . B, MCP 591, with eight trunk segments (1–8) extruded from under the carapace (c), 6 $\times$ . C, MCP 590, under alcohol, note posterior carapace (c), trunk segments (t), and limb bases (p), 6 $\times$ . D, PE 29469, under alcohol, note the carapace (c), trunk segments (t), and remnants of the trunk limbs (l), 5.2 $\times$ .

Fig. 4F). Though the distortion of these fossils that arises from the compaction of the animals' deepest plane onto a thin surface at right angles to that plane makes them difficult to interpret, some tentative conclusions can be advanced. The right and left portions of the ventral margin of the carapace anterior of the ventral notch seem to lie in close proximity, if not being actually linked. This corresponds to the area of the carapace with the marginal ridges and grooves, and it is tempting to speculate that this region is held rigid by these marginal decorations not unlike the "velcro pads" that hold a jacket or pocket flap closed. The region posterior to the ventral carapace notch appears to have been more widely spaced than the anterior area, and this is the region typically occupied by the flexed rami of the subchelate mouthparts.

*Remarks.*—*Concavicaris georgeorum* is the most abundant of the Mazon Creek fauna thylacocephalans, outnumbering *Concavicaris remipes* by at least 33:1 and *Convexicaris mazonensis*

by at least 12:1. These are undoubtedly conservative figures since of all the Mazon Creek thylacocephalans *Concavicaris georgeorum* is more likely to be poorly preserved and therefore most likely to have been discarded in the field as not "worth the effort to collect" than either of the other two species. A reconstruction is offered in Figure 7.

The tiny eye facets discerned on specimens of *C. georgeorum* are similar to those on other thylacocephalans, although none exceed in detail of preservation that found on *Clausocaris* (Polz, personal communication). Both Secretan (1985) and Rolfe (1985) commented on the small size of the individual ommatidial units in thylacocephalans, and they felt that the close packing of these facets indicated a very acute sense of sight in this group of arthropods. The finely structured ommatidia of *C. georgeorum* (Fig. 3B) would appear to second those conclusions.

Secretan (1985) observed that the superimposition of the



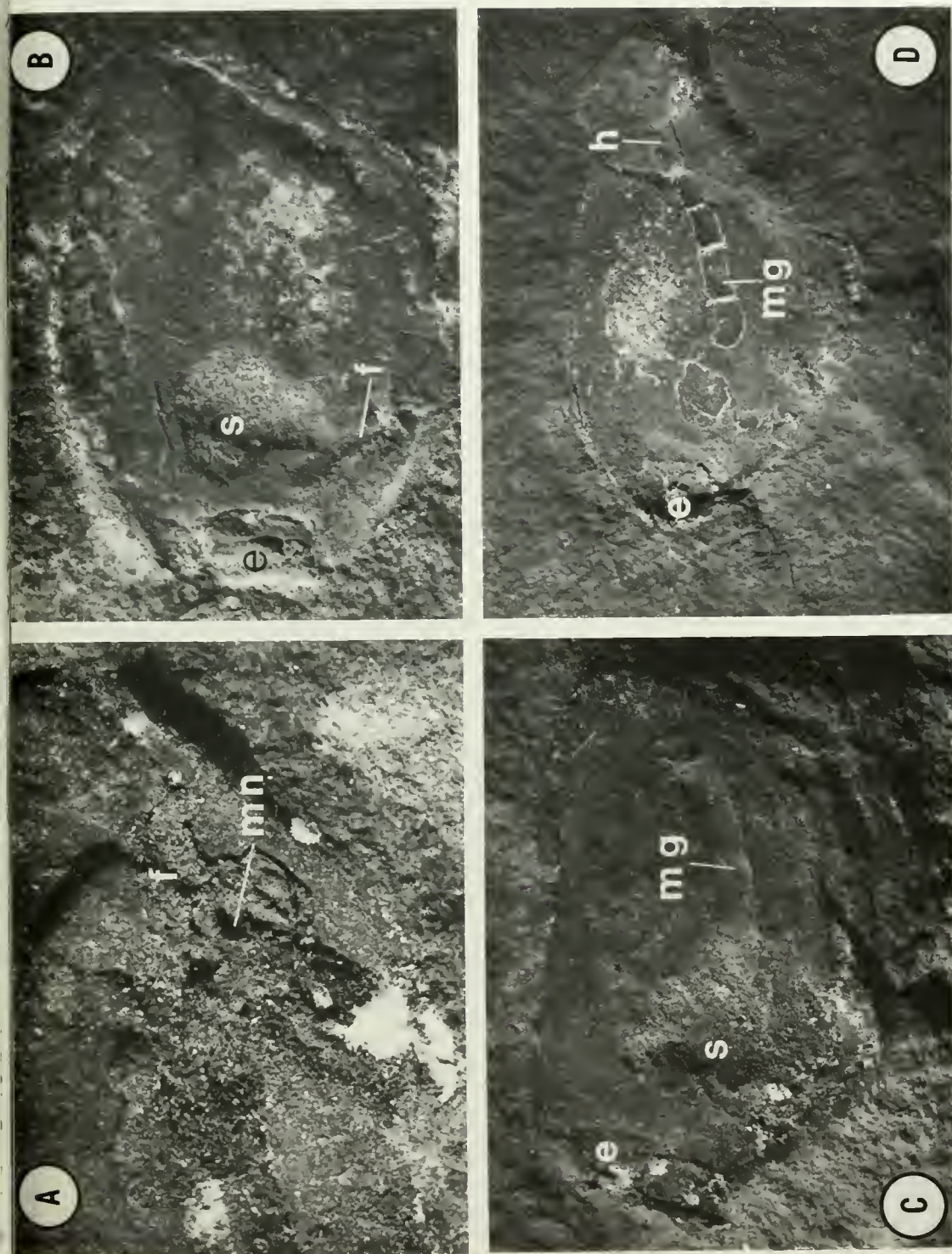


Figure 6. *Concavicularis georgeorum*. A, PE 30575, pyritized anterior gut showing anterior foregut (f) with mandibles in negative relief (mn), and portions of the stomach (s), 10x. B, SDSNH 36763, with displaying remnants of the anterior foregut (f) and the posterior foregut or stomach (s) posterior to the eye (e), 6x. C, SDSNH 36778, displaying the eye (e) and midgut (mg) extending posteriorly from the remnants of the posterior foregut (s), 6x. D, MCP 595, with the eye (e), midgut (mg), and hindgut (h), 3.7x.

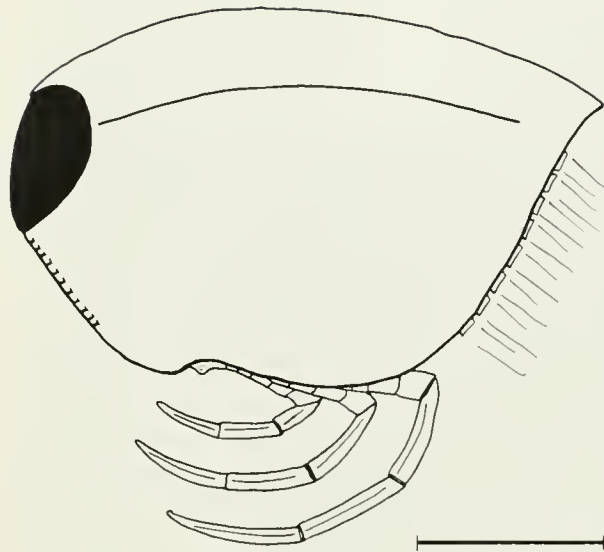


Figure 7. *Concavicularis georgeorum*. Reconstruction, 5 mm scale.

subchelate limbs in *Dollocaris* made their study difficult. This is certainly true for *C. georgeorum*, but the detection of the punctate, plate-like, basal segments of these limbs suggests a possible explanation for some peculiar features of the *Dollocaris* fossils. Secretan and Riou (1983) noted structures on their fossils that suggested to them the remnants of the most anterior cephalic limbs (see their plate 1, figs. 1 and 4); this interpretation (see their fig. 3) was incorporated into their reconstruction (see their fig. 16). In a subsequent paper, Secretan (1985) again noted these structures, confessed problems with deciding exactly what they represent other than anterior cephalic limbs, but deleted them from her updated reconstruction of *Dollocaris* (see her fig. 3). A comparison of Secretan's photographs with the punctate, basal plates seen on some specimens of *C. georgeorum* suggests that the plate-like structures of *Dollocaris* are not the remnants of antennae and other cephalic structures but are the most basal segments of the raptorial, subchelate mouthparts.

Rolfe (1985) homologized the "rods" noted by Briggs and Rolfe (1983) with the concavicularid trunk, similar to that seen in the Devonian *Concavicularis* material originally described by Böhm (1935), and maintained that the segmental structures ventral to it represent fused limb protopods. However, Briggs (1985) interpreted the dorsal rod and associated segments as a trunk. These "rods" clearly correspond to the thickened dorsal aspect of the *C. georgeorum* trunk (Fig. 5A). The segments ventral to the rod are the well-developed pleurites of the trunk; similar structures in living arthropods are often associated with an internal skeleton of apodemes to accommodate the origins of the trunk leg muscles. Careful study of other thylacocephalans may show that specializations of this region are a diagnostic feature of the genus *Concavicularis* and thus useful in some future revision of the Concavicularida.

The gut fillings of *C. georgeorum* (Fig. 6) differ from those of *Ostenocaris* (Pinna *et al.*, 1985; Rolfe, 1985), which has an inflated "stomach" region that extends into the cephalic sac. It is not clear whether this is an inflated foregut, as Pinna *et al.* (1985) suggested, or an anteriorly directed caecum, as Rolfe (1985) suggested. However, the less developed gut of *C. georgeorum* seems more primitive.

*Concavicularis remipes* n. sp. (Figs. 8–10)

*Diagnosis*.— A small concavicularid with an oval carapace, a large deep ventrally deflected rostrum, and a very small optic notch. The body terminates (?) in a large paddle-shaped foot, or abreptor.

*Stratum*.— Francis Creek Shale, Desmoinesian, Middle Pennsylvanian.

*Holotype*.— PE 21418; Peabody Coal Company Pit 11, Will, Grundy, and Kankakee Counties, Illinois. (Fig. 8)

*Etymology*.— The name refers to the paddle-shaped foot or abreptor.

*Description*.— This small concavicularid is almost twice as long as it is deep (Table 2). Of the seven specimens known, the carapace length averages 9.4 mm and the depth averages 5.6 mm. The almost perfectly oval carapace is marked externally by only a very small optic notch (PE 30579, Fig. 9). The rostrum is very deep and directed ventrally so that the anterior aspects of the optic notches are partly occluded.

Two limbs types are noted. PE 46330 (Fig. 9C, D) preserves part of a characteristic raptorial mouthpart. Little can be discerned concerning this appendage other than that the segments preserved distal to the principal flexure are well-developed. Neither the most proximal or the most distal articles of this limb are preserved.

A prominent spinose paddle extends from under the carapace at its postero-ventral aspect. The posterior margin of this organ carries a row of spines or robust setae. The anterior margin is reinforced by thickened cuticle, which terminates distally in a pair of large spines (PE 21418, Fig. 8; PE 39371, Fig. 9B).

*Remarks*.— A reconstruction of *C. remipes* is presented in Figure 10. One distinctive feature of this species is the paddle, but its exact nature is unknown. It may be a limb. One specimen, PE 39371 (Fig. 9), seems to preserve two short segments that lie proximal to the large spiny distal article. This suggests that the paddle is a specialized distal segment of some longer structure.

Although this organ is preserved on several of the specimens at hand, it occurs only singly and is not a part of some series as would



Figure 8. *Concavicularis remipes*. Holotype, PE 21418, note the postero-ventral paddle (arrow), 4.6 $\times$ .



TABLE 2. Representative measurements of *Concavicularis remipes* (mm).

Feature	<i>n</i>	$\bar{x}$	Range
Body length	7	9.4	8.6–10.3
Carapace depth	7	5.6	5.0–6.5
Body length/carapace depth	7	1.69	1.46–1.91

be expected if it were an appendage. So the paddle may be a single, median, terminal element akin to similar organs seen in ostracode, conchostracan, and cladoceran Crustacea (e.g., see Schram, 1986). In the Conchostraca, the last or anal segment of the trunk is directed ventrally as a paddle-like abreptor posteriorly bearing a row of spines and terminating in a set of large spines and spinose caudal rami. In the Cladocera, the posterior part of the trunk loses any trace

of segmentation to become a postabdomen, curves ventrally, and is decorated with posterior setae and terminal spines like the abreptor. The cladoceran arrangement is similar to that of ostracodes, whose ventrally directed terminus of the body bears an abreptor-like caudal ramus. All of these structures in living crustaceans generally assist in some way with locomotion.

The *C. remipes* paddle, while not necessarily homologous to terminal units of living crustaceans, may have had a similar function. Locomotory thrust can be generated in an aquatic organism by either uniformly coordinating limbs that beat in a single power stroke or reflexing a single rigid structure that acts as a rapidly moving, spring-loaded lever. Which of these alternatives is used depends on the fluid physics applicable around a particular animal. Larger-bodied forms of Thylacocephala would have lived in a fluid medium characterized by turbulent flow and could have relied on a single power stroke of all their trunk limbs to put them in a position to capture prey. On the other hand, the hydrodynamics of quick

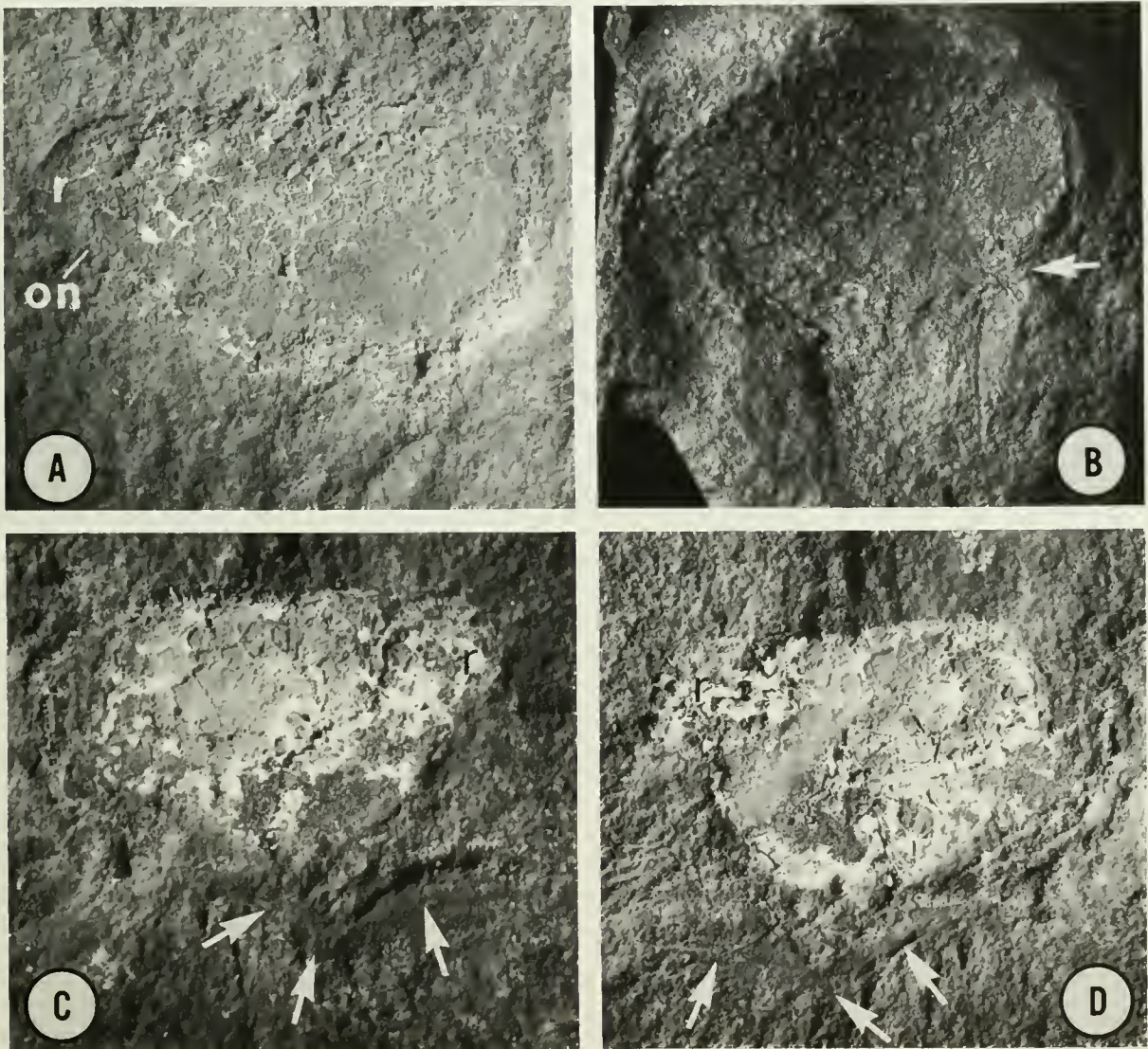


Figure 9. *Concavicularis remipes*. A, PE 30579, note the deep rostrum (r) and small optic notch (on), 7.7 $\times$ . B, PE 39371, with well-preserved paddle and an apparently, small segment proximal to it (arrow), 7 $\times$ . C and D, PE 46330, part and counterpart, note the segments of a raptorial limb (arrows), and rostrum (r), 8.5 $\times$ .

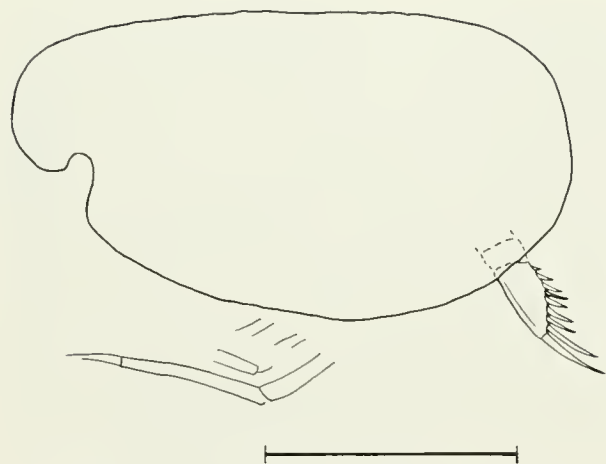


Figure 10. *Concavicularis remipes*. Reconstruction, 5 mm scale.

attack in small forms, such as *C. remipes*, a species which because of its size may have lived in a viscous medium characterized by laminar flow, could have required the use of a lever to generate the speed necessary to capture prey. Consequently, the nature of the body terminus may be another important feature to consider in any future revisions of the Concavicularida.

ORDER CONCHYLIOCARIDA  
Secretan, 1983 (emended herein)

*Diagnosis.*— These are thylacocephalans with a carapace lacking a clearly delineated optic notch, and often lacking a rostrum. The eyes are situated on the surface of a large protruding cephalic sac.

*Remarks.*— Rolfe (1985:391) anticipated that thylacocephalans might one day prove to be more diverse than could be accommodated in a single order. Indeed, it appears to me that some of the controversy over the interpretation of the Jurassic thylacocephalans from Italy (see Rolfe, 1985, for a summary) may be related to this possibility. Certainly, my examination of some of the material Prof. Pinna and his colleagues have been studying convinces me that *Ostenocaris* and related forms are quite different from *Concavicularis* and related taxa. The most obvious difference is the presence in the Italian material of a large cephalic sac almost completely covered by ommatidia versus a more typical head in the concavicularids *sensu stricto* bearing discrete compound eyes. The presence or apparent absence of the optic notch may then merely be a reflection on the degree of development of the head as a cephalic sac.

Genera that belong in this order include *Convexicularis* from the Carboniferous, *Yangzicaris* from the Triassic, and *Atropicaris*, *Austriocaris*, *Clausocaris*, *Kilianocaris*, *Ostenocaris*, and *Paraoštenia* from the Jurassic. Other genera that might belong in this order include *Isoxys*, *Probosicaris*, and *Silesicaris* from the Cambrian and *Pseuderichthus* from the Cretaceous.

GENUS CONVEXICARIS n. gen.

*Diagnosis.*— Conchyliocaridan with a sinuously shaped carapace displaying a rounded antero-dorsal aspect, a convex antero-ventral margin, and a blunt postero-ventral aspect. The subchelate raptorial limbs are very elongate, composed of narrow articles. The body terminates in long caudal rami.

*Type of genus.*— *Convexicularis mazonensis* n. sp.

TABLE 3. Representative measurements of *Convexicularis mazonensis* (mm). Specimens were oriented into assumed living position with eyes directed anteriorly. The body length was then measured along the antero-posterior axis of the body from points tangent to the antero-dorsal to postero-ventral corners of the carapace, while the carapace length was measured along an axis parallel to the longitudinal carapace ridges from those same points. The measurements of the (?) *Convexicularis* sp. specimen (see text) are included for comparison.

Feature	n	x	Range	PE 27622
Body length	8	18.3	11.2–23.3	54.2
Body depth	8	14.2	6.4–19.0	35.8
Carapace length	8	22.0	11.2–29.0	59.8
Eye depth	3	8.3	7.4–9.8	—
Eye width	2	4.3	4.0–4.6	—
Body length/carapace depth	8	1.3	1.2–1.7	1.6

*Convexicularis mazonensis* n. sp. (Figs. 11–13)

*Diagnosis.*— Since there is only one species, the diagnosis is the same as that of the genus.

*Stratum.*— Francis Creek Shale, Desmoinesian, Middle Pennsylvanian.

*Holotype.*— PE 32958; Peabody Coal Company Pit 11, Will, Grundy, and Kankakee Counties, Illinois. (Figs. 11A, B)

*Description.*— *Convexicularis mazonensis* is relatively large (Table 3). The carapace is sinuous in outline, with the anterior aspect more dorsal and the posterior more ventral (SDSNH 36781; PE 11255; PE 23525; PE 32958, Figs. 11A, B). A pair of ridges runs parallel to the sinuous axis of the carapace (MCP 594, Fig. 11C; PE 23525); the dorso-posterior ridge is more prominent than the fainter median one. These ridges extend from just posterior of the eye toward the postero-ventral region of the carapace. The carapace is rounded at its antero-dorsal aspect, not quite as developed as a full-fledged rostrum (SDSNH 36781, Fig. 11D). The antero-ventral aspect of the carapace is broadly convex (PE 38169; SDSNH 36781; MCP 594, Fig. 11C), while the postero-ventral corner is blunted (MCP 594).

The compound eyes are large, in fact enormous relative to the size of the body (SDSNH 36781, Fig. 11D; PE 45695). The eyes do not occupy any well-defined optic notch but rather appear to be part of the cephalon that protrudes anteriorly from the carapace in that area.

The thin raptorial limbs are relatively enormous (PE 45692, Fig. 12A, B). Those of the first set, or maxillules, are the shortest; the second, or maxillae, are longer; and the third set, the maxillipedes, are the longest of all. The unarmed distal three articles of each of these limbs are fairly rigid relative to each other with a slight arc noted on some specimens (PE 45695, Fig. 12C). The proximal and intermediate segments of these limbs generally are not well preserved, though PE 45695 has at least four articles proximal of the elbow, and PE 39350 (Fig. 12D) has possibly seven or eight segments that extend virtually from what appears to be the limb base to the elbow.

The trunk is only faintly preserved on a few specimens at hand, but there appear to be about eight segments in this area (PE 11255; PE 32958, Figs. 11A, B). A series of limbs is often seen attached to these segments, but the preservation is always as a color difference in the concretion and no structural details are discernable (PE



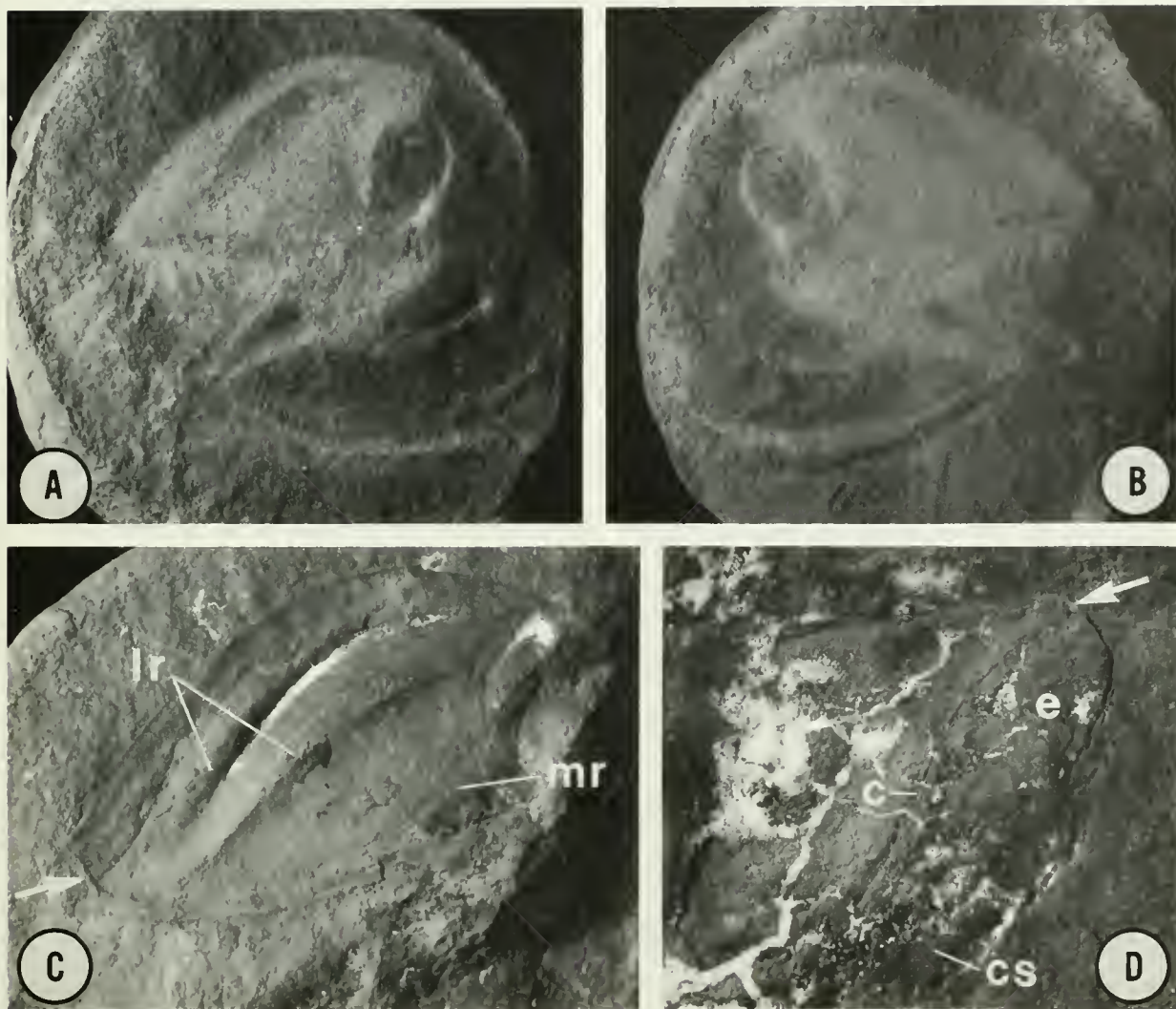


Figure 11. *Convexicaris mazonensis*. A and B, PE 32958, holotype, part and counterpart, 2 $\times$ . C, MCP 594, displaying the concave form of the carapace antero-ventral margin (mr), the double longitudinal ridges (lr), and the blunt posterior end of the carapace (arrow), 3.6 $\times$ . D, SDSNH 36781, close-up view of the head region, note the rounded anterior end of carapace (arrow), carapace margin (c), the cephalic sac somewhat disrupted during preservation (cs), and the compound eye (e), 5.7 $\times$ .

32958, Fig. 11B). Posterior to the trunk, the body terminus appears to bear a set of long caudal rami (PE 32958, Fig. 11B), but these rami too are preserved, unfortunately, only as color differences in the rock.

Some soft anatomy is evident on the specimens at hand. An anterior portion of the foregut just inside the mouth is evident as a narrow tube (PE 40076, Fig. 12E). Remnants of gills appear to be preserved on one specimen as blackened lobe-like structures under the carapace just dorsal to the bases of the raptorial limbs (PE 38169, Fig. 13F), but their preservation is not very good.

*Remarks.*— A reconstruction of *Convexicaris mazonensis* is presented in Figure 13. Though *Convexicaris mazonensis* was larger than *Concavicularis georgeorum*, specimens of the former are not preserved nearly as well as those of the latter. More often than not the structures of *Convexicaris* occur as color differences in the rock, molds or casts in the concretion, or badly preserved pieces of cuticle, patterns of preservation like those seen among fossil shells in the Mazon Creek faunas. It is possible, therefore, that the differences in preservation noted between these two thylacocephalans

may reflect qualitative differences in the nature of their cuticles in life. *Concavicularis* might have possessed a rather organic exoskeleton, perhaps with some sclerotization, but little mineralization. *Convexicaris*, on the other hand, may have had more mineral than organics in its exoskeleton. The acidic conditions that apparently prevailed during diagenesis of Pennsylvanian concretion faunas generally mitigated against good preservation of animals with much mineral content in their cuticle, whereas animals with a high organic content in their exoskeletons were relatively unaffected.

One specimen of a carapace (MCP 589, Fig. 14) is distinctly larger than any specimen of *Convexicaris mazonensis*, though its general outline resembles that species'. This specimen, however, does not preserve the characteristic features of *C. mazonensis* such as the carapace ridges, any portion of the eyes or cephalic sac, or any of the raptorial limbs. Whether this specimen represents an aberrant preservation of *C. mazonensis* or is actually some other species of thylacocephalan or other arthropod can not be determined at this time.

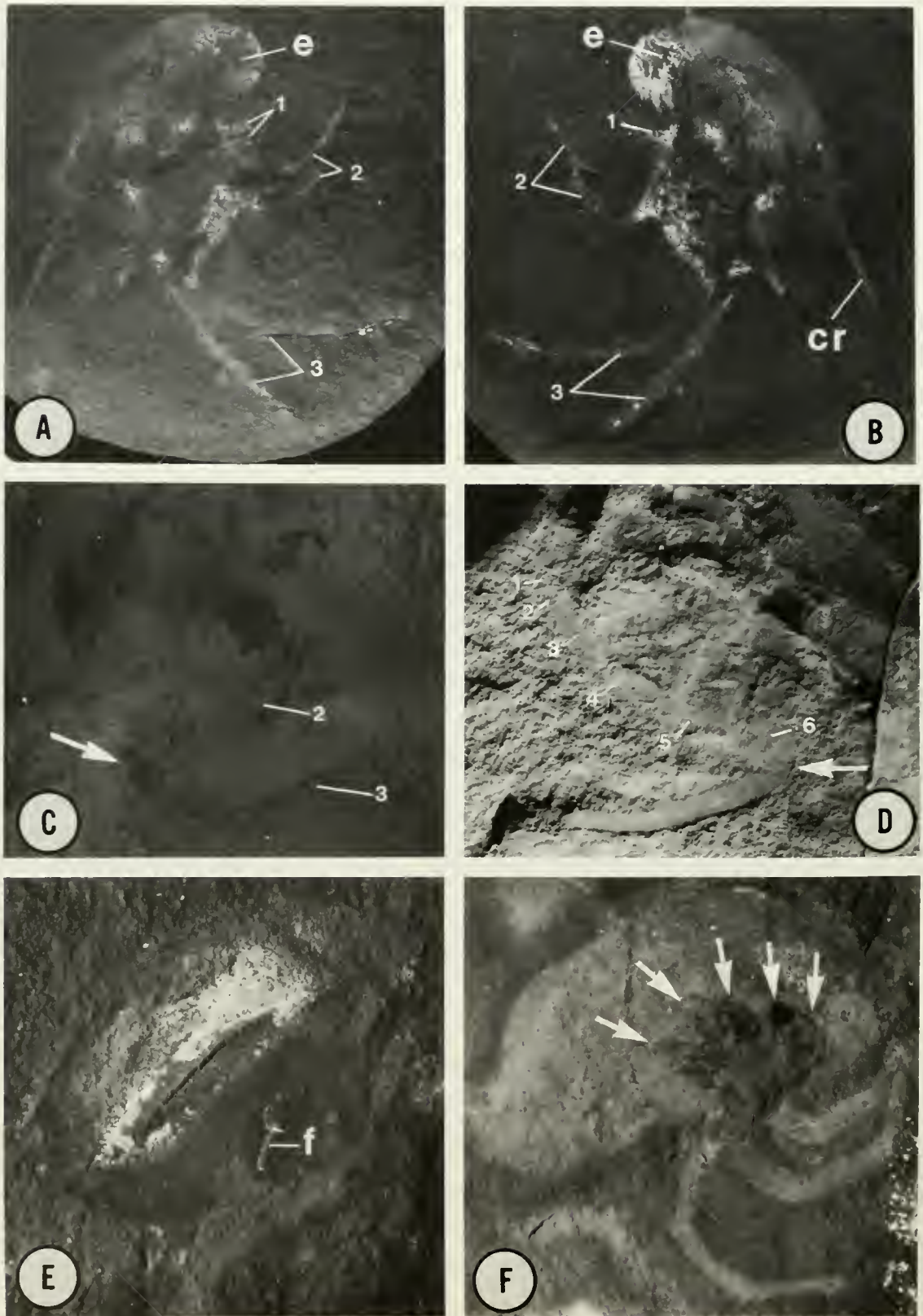


Figure 12. *Convexicaris mazonensis*. A and B, PE 45692, part and counterpart, preserving the eyes (e), the raptorial mouthparts, maxillules (1), maxillae (2), maxillipedes (3), and a caudal ramus (cr), 1.5 $\times$ . C, PE 45695, close-up under alcohol of a maxilla (2) and maxillipede (3), the latter preserving the three segments distal to the elbow (arrow), 4 $\times$ . D, PE 39350, close-up of a raptorial mouthpart (probably the maxillipede) that preserves limb segments (numbers) proximal to the elbow (arrow), 4 $\times$ . E, PE 40076, with the anterior portion of the foregut, (f), 3.2 $\times$ . F, PE 38169, under alcohol, with carbonized remains of gills (arrows) under the carapace above the raptorial mouthparts, 4 $\times$ .



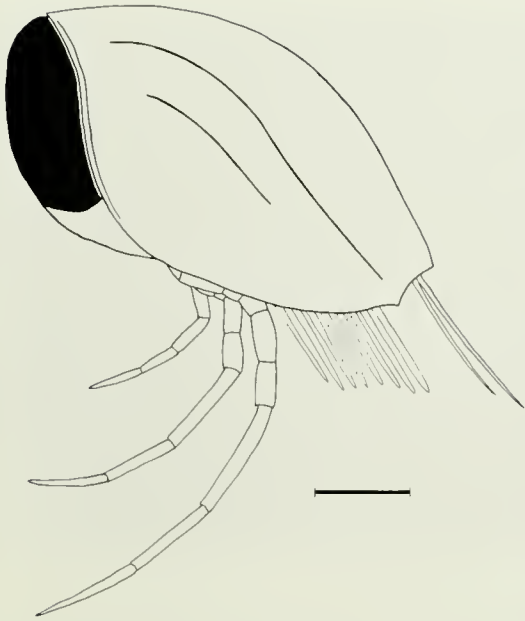


Figure 13. *Convexicaris mazonensis*. Reconstruction, 5 mm scale.

#### DISCUSSION

*Mode of Life.*— There now seems to be a consensus among students of the Thylacocephala that these animals were carnivores. Pinna *et al.* (1984), influenced by their postulated affinities of *Ostenocaris* with cirripedes, originally felt *Ostenocaris* was a filter feeder. However, the raptorial limbs, often well armed with spines, as in *Dollocaris* (Secretan, 1985) and *Ostenocaris* (e.g., Pinna *et al.*, 1982), bespeak a carnivore with limbs like those of stomatopod malacostracan and remipedean crustaceans. Secretan (1985) suggested that these animals were scavengers, but certainly the stomach residues found in *Ostenocaris* (Pinna *et al.*, 1985) imply active carnivory.

There is little agreement, however, over just how thylacoceph-



Figure 14. (?)*Convexicaris* sp., MCP 589, thylacocephalan(?) carapace, 1.3 $\times$ .



Figure 15. *Convexicaris sinuata*. Scanning electron micrograph of terrace structures on the surface of the carapace, developed from negative 1561 in the photo collection of the Field Museum Mazon Creek Project,  $\sim 75\times$ .

alans lived. Briggs and Rolfe (1983) examined the micro-ornamental terracing on the *Convexicaris* carapace and, influenced by Seilacher (1973), concluded that the Gogo thylacocephalans could have been burrowers, but they refused to rule out other options. The Gogo convexicarids are small to moderate in size, but terracing is clearly visible even on large *Convexicaris sinuata* from the Pennsylvanian black shales of North America (Fig. 15). If we postulate a carnivorous habit for thylacocephalans, then a burrowing or lurking life style is not unreasonable. As Secretan (1985) observed, the stomatopods are active, predaceous carnivores that routinely build burrows, bury themselves in sediment, or lurk in cracks and crevices while waiting for prey to pass by, whereupon they thrust forward from hiding and strike at their victim.

Rolfe (1985), however, felt that there are physiological problems with this interpretation. If thylacocephalans were denizens of low-oxygen benthic habitats, given that they almost always occur as fossils in rocks deposited under such conditions, he questioned how their physiology could have allowed them to be such active carnivores, unless there were fluctuating oxygen layers near the bottom that were responsible for mass kills. Moreover, Rolfe felt that benthic creatures would do away with the lower aspect of their huge compound eyes and limit their field of view to be directed upward only. However, the analogy to stomatopods should not be overlooked in this regard. The benthic mantis shrimps have among the most acute senses of sight of any crustacean. Stomatopods bear large, often multilobed eyes with overlapping fields of view (e.g., see Schram, 1986:52), and have recently been noted to possess acute color vision (Marshall, 1988). Eye structure in thylacocephalans is more likely governed by the requirements of their feeding habits than by the location of their resting places.

A pelagic habit for thylacocephalans remains an alternative, but serious problems might intervene here. Though streamlined, many thylacocephalans were apparently rather massive. Some, like *Convexicaris sinuata* and *Ostenocaris cypriformis*, are "huge" by

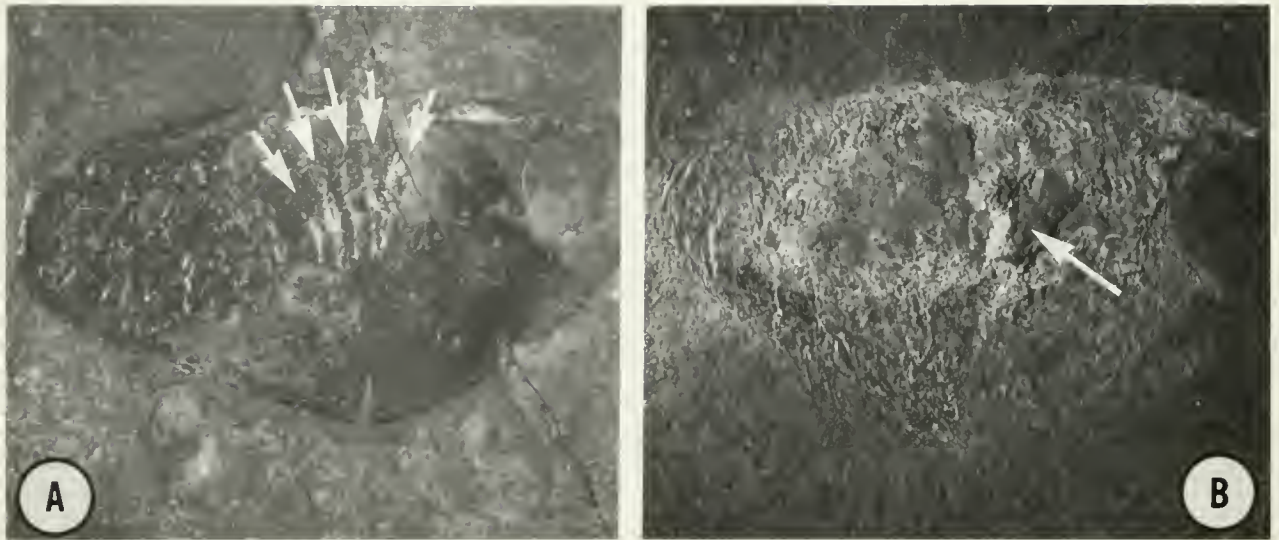


Figure 16. *Concavicaris sinuata*. A, PE 51939, from the black shale just above the coal in Peabody Coal Company Pit 15, Will Co., Illinois, displaying the outline of individual gills (arrows) preserved beneath the surface of the carapace, 1.8 $\times$ . B, PE 51940, from the Mecca Quarry Shale, Quarry Q, Park Co., Indiana, with gill area indicated as a bulge in the carapace (arrow) apparently formed by a gas bubble as the gills decayed, 2 $\times$ .

any standards, and it is difficult to conceive of such large arthropods as being neutrally buoyant. Even if they were so, they would have required a well-developed series of limbs to maintain their position in the water column and, more importantly, to engage in sustained active pursuit of prey. Except for nectiopodan remipedes (Schram, 1986:40), no large predatory aquatic arthropods seem capable of that kind of behavior, and the relatively small and presumably delicate thylacocephalan trunk limbs do not seem to have been capable of sustaining an active, massive, pelagic predator.

However, Rolfe (1985) found an analogy of the thylacocephalans in hyperiid amphipods, based mainly on the size of their eyes and bulkiness of form. Since hyperiids are mesopelagic, Rolfe suggests thylacocephalans may have been so as well. This suggestion should not be lightly discarded, but problems of scale may intervene. Hyperiids are often small animals that generally subsist in the water column by hitching rides on or in other creatures, such as tunicates. Although some of the smaller thylacocephalans may have been able to do this, it is difficult to envision just how the many larger forms of this group could have done so and thus by necessity would have to have been free swimming.

I generally favor a benthic habit for these animals. Arthropod predators more often than not exhibit lurking behaviors, waiting for their prey to come to them rather than actively seeking victims. Oxygen requirements may not have been critical for thylacocephalans. One group of active crustacean carnivores, the nectiopodan remipedes, live under almost oxygen-free conditions (see Schram, 1986). However, the diversity of size and form that is slowly becoming evident for this group may indicate that thylacocephalans occupied a variety of habitats and pursued a variety of modes of seeking prey.

*Thylacocephalan affinities.*— Despite growing interest in this group, and given what we already know about their anatomy, we still have no certain idea as to what thylacocephalans are other than that they are Arthropoda.

Since the description of *Ostenocaris* by Arduini *et al.* (1980), there has been a tendency to discuss thylacocephalans in terms of their being some kind of crustacean. Nevertheless, the issue of the higher taxonomic affinities of the Thylacocephala must remain open!

Thylacocephalans do have a carapace, but that is the only apomorphic feature currently known that could possibly ally them with crustaceans. However, given the multiplicity of ways that a carapace has independently evolved within Crustacea (see Schram, 1986), and the variety of carapaces found on all manner of non-crustacean arthropods (e.g., see Briggs, 1983; Briggs and Whittington, 1985), the carapace in thylacocephalans is not a sufficient character in and of itself to place them categorically among crustaceans.

On the other hand, a clearly defined head with two sets of antennae, a set of mandibles, and two sets of maxillae constitute an excellent suite of apomorphies that could place thylacocephalans within the Crustacea. However, this is not the case at this time. We still have no certain knowledge about thylacocephalan antennae; we do not know if they even had any. As mentioned above, Secretan and Riou (1983) observed structures on specimens of *Dollocaris* that they interpreted as possibly being the antennae and nearby mouthparts. However, Secretan (1985) was more cautious in this regard, and an alternative interpretation of these features as the most basal segments of the raptorial appendages presents itself here.

We have evidence of thylacocephalan mandibles in *Concavicaris georgeorum* as well as *Dollocaris ingens* (Secretan, 1985). Their location near the mouth and foregut is to be expected, but their association with three pairs of distinct grappling appendages, the inferred raptorial mouthparts, is interesting. This pattern recalls that of many crustaceans, suggesting that these limbs are maxillules, maxillae, and a set of maxillipedes. Indeed, the combination of mandibles with large molar processes and three sets of subchelate multiarticulated "mouthparts" is identical to that seen in remipede crustaceans (e.g., see Schram *et al.*, 1986). The interpretation of thylacocephalan raptorial limbs as mouthparts lends some credence to possible crustacean affinities for *Ilea* shrimp.

Nevertheless, the definitive identity of the postoral raptorial limbs remains a problem. Arduini *et al.* (1980) originally interpreted these limbs as antennules, antennae, and mandibles (presumably as a large palp). Subsequently, Pinna *et al.* (1982) designated these limbs as the antennules, antennae, and maxillipedes. Quite in contrast, Secretan (1985) regarded these subchelipedes as



thoracic limbs, perhaps in keeping with her analogies with stomatopods, which have a series of subchelate limbs on the anterior segments of the thorax. The association of the massive gills with these limbs might support her argument. Certainly these gills are becoming one of the diagnostic features of the thylacocephalans and when preserved always occur in this position (Fig. 16). However, the gills could equally be considered "cephalic" gills, i.e., autapomorphic features of thylacocephalans, rather than "thoracic" gills, and thus synapomorphic features with other crustaceans. Finally, Rolfe (1985) suggested that the raptorial limbs of thylacocephalans are maxillules, maxillae, and maxillipedes. Rolfe conceded, however, that if these limbs really are posterior to a possible carapace adductor muscle as Secretan (1985) observed, then they could be thoracopods. All these limb designations are predicated on the premise that the thylacocephalans are crustaceans.

Concerning the carapace adductor muscle, I recently was discussing thylacocephalans with Dr. Richard Brusca, an authority on living isopods. In the course of explaining the complex anatomy of these fossils, he chanced to see the cover illustration of *Ostenocaris* used by Arduini and Pinna (1989). "Oh, they had parasitic bopyrid isopods under their carapaces," he remarked without prompting. I pointed out that his "isopod" was usually interpreted as a muscle, but when we examined some illustrations in the literature of the supposed carapace adductor muscles he remained unconvinced. When he saw that the disputed muscles were close to the region under the carapace containing the gills, he suggested that the "adductor muscles" be reexamined to determine if they were, if not bopyrids, some kind of ectoparasite. No "carapace adductor muscles" were seen on any of the Mazon Creek flea shrimps.

The interpretation of Pinna *et al.* (1985) is worth returning to briefly. Recently, Prof. Pinna and his colleagues allowed me to examine some newly collected material belonging to an as yet undescribed thylacocephalan. The cephalic sac clearly bore tiny hexagonal facets, but on this fossil "microsclerites," much smaller than those seen in *Ostenocaris* (Pinna *et al.*, 1985), occurred at the intersection of the hexagons and were not centered below them. This arrangement is similar to that seen in larval ascothoracidan Maxillopoda (Grygiel, 1988: fig. 2), where the carapace, a structure which, as in thylacocephalans, envelops almost all of the parasite's body and is marked by hexagonal sculpturing with fine setae merging from the intersections of the hexagons. In addition, ascothoracidans are often characterized by chelate antennules. So, despite the comments attributed to Newman that reject *Ostenocaris* from consideration as a maxillopodan crustacean (Briggs and Rolfe, 1983:272), it is possible that the first and second subchelate limbs of flea shrimp are modified antennae, albeit uniquely so. If this limb identification is proven, thylacocephalans might be allied in some way to ascothoracidans, and the original concept of the Italian workers of thylacocephalan/cirripede affinities might be partially vindicated.

Finally, the nature of the posterior part of the body of thylacocephalans remains a problem in interpreting the affinities of this group. Though Briggs and Rolfe (1983) did note some variations in size of segments along the trunk, this region for the most part seems to be homonomous. The segment numbers, however, vary from taxon to taxon and create some problems. Eight such segments are noted in the Mazon Creek thylacocephalans, as well as in the Italian material and some of the Gogo specimens (though as many as 14 were recorded in the Australian material). Secretan (1985) reconstructed *Dollocaris* and indicated up to 16 trunk segments. A possible explanation for the higher numbers was advanced by Briggs and Rolfe (1985), who observed that slippage could occur between right and left halves of the body. I have seen this not only in the Mazon Creek specimens but also in *Concavicaris sinuata* from the Pennsylvanian black shales. It is possible that the

extra segments at the end of the trunk could be artifacts of right side/left side slippage. That is, *Dollocaris* might actually have only eight trunk segments instead of 16. However, this explanation should not be forced. The Gogo specimens with more than eight trunk segments clearly do not seem to be explained by slippage, and Mikulic *et al.* (1985) reported a thylacocephalan from the Silurian of Wisconsin with more than 20 trunk segments. It is possible that total trunk number may have varied in thylacocephalans.

So, what *are* the affinities of the Thylacocephala? One common theme seems to emerge from the literature. All attempts to understand this group return to comparisons with crustaceans. Certainly nothing among the uniramians and little among the cheliceriforms has anything to offer toward understanding thylacocephalans. It is conceivable that their affinities lie outside any of the "mainline" arthropod groups, but nothing among Cambrian "trilobitoids" seems relevant.

Secretan (1985) mentioned in passing that the conchostracans might be a sister group to thylacocephalans. Though the paddle of *Concavicaris remipes* recalls structures seen among some phyllopodans, the similarity is possibly only analogous, not necessarily homologous. The large eyes and subchelate limbs of thylacocephalans are not features seen among branchiopods or other phyllopodans.

The maxillopodan connection remains an option, if only because of the persistence of the Italian interpretation of thylacocephalans as cirripedes (Pinna *et al.*, 1985). However, I agree with Rolfe (1985) that the affinities of thylacocephalans do not lie with barnacles, and only by means of some liberal assumptions about possible ascothoracid affinities might we be able to draw this group into the thecostracan Maxillopoda.

Among the Malacostraca, many features of the life style of thylacocephalans are closely paralleled in stomatopods: the large eyes, raptorial limbs, and possible lurking behaviors to stalk prey. However, there is no similarity to anything seen among malacostracans that compares in this regard to the cephalon or the posterior body regions of thylacocephalans.

Some thylacocephalan features are similar to those seen among remipedes: large sessile compound eyes (at least in the fossil enantiopodans), mandibles with large molar processes, three sets of subchelate postoral grappling or raptorial limbs with many podomeres, and a homonomously structured trunk. The last feature is considered the primitive condition for arthropods and thus not particularly useful in terms of deciding thylacocephalan affinities. In addition, remipedes, as currently understood, lack gills (let alone on the cephalon) and a carapace, and generally have long trunks. However, short bodies repeatedly evolved within many lines of crustaceans, carapaces independently evolved many times among arthropods (especially crustaceans), and gills of many different forms and locations evolved many times among articulate phyla. It is not inconceivable that thylacocephalans could be highly derived remipedes.

Thus, the question of thylacocephalan relationships is unresolved. I can do no better than echo the conclusion of Briggs and Rolfe (1983:273): "...the affinities...remain obscure, but probably lie within the Crustacea."

#### ACKNOWLEDGMENTS

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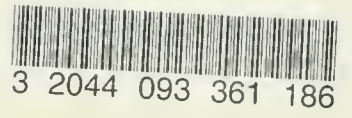
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