FIRST REPORT OF A CONCAVICARID INTERIOR (CRUSTACEA: THYLACOCEPHALA) FROM THE DEVONIAN OF NORTH AMERICA

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ABSTRACT: The first Devonian concavicarid specimen from North America with internal structures preserved is described and referred to *Concavicaris? sp. indet.* Preserved morphology closely resembles contemporaneous concavicarids previously described from the Gogo Formation of western Australia (Briggs and Rolfe 1983). This new description of interior abdominal structures augments morphological data from previous collections of isolated concavicarid carapaces from contemporaneous strata in North America. This specimen was collected from the tidal to estuarine deposits of the Oneonta Formation of New York State, USA and may also represent the oldest thylacocephalan fossil recorded from brackish water deposits.

Keywords: Devonian, Thylacocephala, Concavicarida, abdomen, New York, Oneonta Formation, soft-part preservation

INTRODUCTION

The class Thylacocephala encompasses an unusual group of extinct crustaceans characterized by a bivalved carapace covering the head, trunk, and abdominal limb region with large raptorial appendages situated anteriorly (Lange et al. 2001). The taxonomic history of the group is complex (see overview in Schram et al. 1999), and two orders are currently recognized (Schram 1990): Conchyliocariida (?Cambrian, Carboniferous to Cretaceous), and Concavicarida (Silurian to ?Jurassic) [but see Schram et al. (1999) and Vannier et al. (2006) for discussions of thylacocephalan phylogeny and origins].

Paleozoic thylacocephalans have been previously reported from North America. Both concavicarid and conchyliocarid taxa occur in the Pennsylvanian Mazon Creek Biota (Schram 1990), and an undescribed concavicarid is present in the Silurian Waukesha Biota (Mikulic et al. 1985a, b). While the Mazon Creek and Waukesha specimens include soft-part preservation, the great majority of thylacocephalan specimens from North America are restricted to isolated carapaces of concavicarids, which are most abundant in Devonian to Mississippian strata (e.g., Shimer and Shrock 1944). Although concavicarid carapaces have long been documented from the Devonian and Mississippian of North America (e.g. Meek and Worthen 1868; Meek 1872; Cooper 1932; Smith and Kenter 1975; Briggs and Rolfe 1983; Hannibal and Feldmann 1986), the preservation of internal anatomy has not been previously reported from strata of these ages. This paper presents the first description of a preserved concavicarid interior from the Devonian of North America.

LOCALITY AND GEOLOGICAL SETTING

This specimen was collected on the east side of the New York Route 30 road cut exposed about 7 km northeast of Grand Gorge, Schoharie County, New York, USA (approximately 42.38° N latitude, 74.47° W longitude) (Fig. 1) during the autumn of 2001 by a member of a Cornell University field party. The Route 30 road cut exposes two stratigraphic units that are part of the "Catskill clastic wedge" (Barrell 1913, 1914): the Middle Devonian Gilboa Formation at the base of the section and the Oneonta Formation, which may span the Middle/Upper Devonian boundary, at the top of the section. A detailed stratigraphic section for this locality was illustrated by Bridge and Willis (1994, p. 1455).

The specimen (Fig. 2), which is preserved in a maroon-colored micaceous siltstone, was collected from talus, but its lithology and sedimentary characteristics are

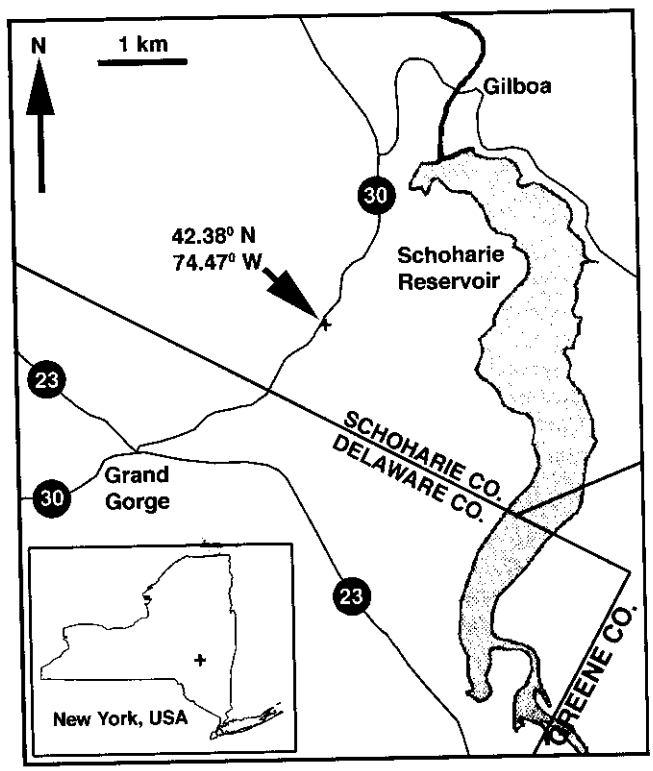

Figure 1. Map illustrating the approximate location ("+") from which the concavicarid specimen was collected. Also see Bridge and Willis (1994, fig. 1b).

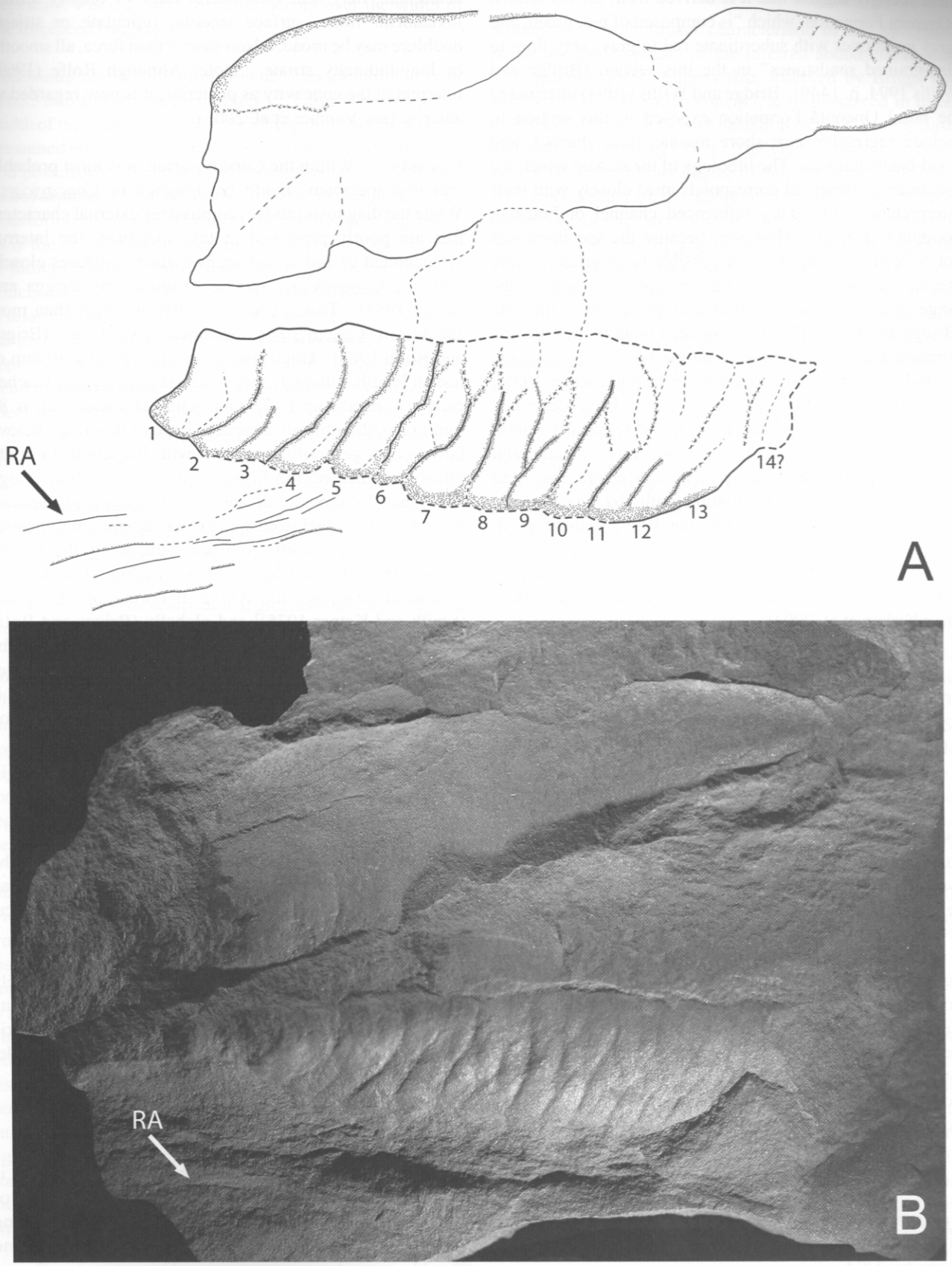

Figure 2. (A) Camera lucida drawing and (B) photograph of the Concavicaris(?) sp. PRI 54942, 1.65x. Region of specimen in upper part of picture is the dislocated carapace, abdominal region in the lower center with segments numbered from anterior to posterior, and possible raptorial appendages (labeled RA) to the lower left of the image.

inconsistent with derivation from the Gilboa Formation and strongly suggest that it is derived from the lowermost Oneonta Formation, which "is composed of red, green, and gray mudstones with subordinate red to gray, very fine- to fine-grained sandstones" in the this section (Bridge and Willis 1994, p. 1449). Bridge and Willis (1994) interpreted the basal Oneonta Formation exposed in this section to include regressive near-shore marine, tidal channel, and flood-basin deposits. The lithology of the slab on which the specimen is preserved corresponds most closely with their interpretations of tidally influenced channel or brackish floodplain deposits. However, because the specimen was not collected *in situ*, it is not possible to ascertain a more precise geological context for the specimen within the range of coastal paleoenvironments preserved at this site (Bridge and Willis 1994). Associated biota in the Oneonta Formation at this locality include the bivalve *Archanodon sp.* and plant material (Friedman and Chamberlain 1995), but other soft-bodied fossils have not been described previously. The associated biota found regionally within the Oneonta Formation, however, are more diverse and include leperditicopid ostracods, conchostracans, and lingulid bivalves in assocatiation with *Archanodon* and plant fragments (Knox and Gordon 1999; Vannier et al. 2001). The presence of these taxa further supports the interpretation of the Oneonta Formation as a brackish, tidally influenced coastal deposit (Vannier et al. 2001; Chamberlain et al. 2004).

SYSTEMATIC PALEONTOLOGY

Class THYLACOCEPHALA
Pinna, Arduini, Pesarini, and Teruzzi 1982
Order CONCAVICARIDA
Briggs and Rolfe 1983

Diagnosis (after Briggs and Rolfe 1983).– Carapace bears a prominent, concave optic notch. Rostrum fused to carapace, may curve ventrally to occlude optic notch. Between 8 and 16 homonomous trunk appendages that decrease in height both anteriorly and posteriorly.

Discussion.– The specimen collected from near Grand Gorge, New York clearly illustrates at least 13 homonomous trunk segments, which are diagnostic of the order. The presence of an optic notch cannot be confirmed since the anterior region of the carapace is incomplete (Fig. 2), but the general shape is not inconsistent with the diagnosis for the order.

Genus CONCAVICARIS? Rolfe, 1961

Type species.– *Ceratiocaris (Colpocaris) bradleyi* Meek, 1872, from the Waverly Formation (Mississippian) of Kentucky, USA.

Diagnosis (after Rolfe 1969).– Posterior excavation of carapace valves semicircular, anterior margin truncate or acuminate, may bear mesolateral ridge or bluntly serrate juxtadorsal ridge, surface smooth, reticulate or striate; doublure may be broad, telson shorter than furca, all smooth, or longitudinally striate. Note: Although Rolfe (1969) interpreted the concavity as posterior, it is now regarded as anterior (see Vannier et al. 2006).

Discussion.– Within the Concavicarida, it is most probable that this specimen should be assigned to *Concavicaris*. While the diagnosis (above) emphasizes external characters that are poorly preserved in this specimen, the internal arrangement of abdominal segmentation compares closely with the *Concavicaris* species examined by Briggs and Rolfe (1983). This specimen is slightly larger than most species of *Concavicaris* described from Gogo (Briggs and Rolfe 1983). Gogo specimens are typically 30 mm or less in length, although specimens of *C. playfordi* reached carapace lengths up to 73 mm, while this specimen is 87 mm in length. Overall carapace shape as described below, however, is generally consistent with the length to width ratios documented for *Concavicaris* species from Gogo and other locations. In addition, *Concavicaris* species have been described from approximately contemporaneous deposits both in North America [(including the nearby Cleveland Shale and Chagrin Shale of Ohio (Hannibal and Feldmann 1986) and the Woodruff Formation of Nevada (Smith and Ketner 1975)] and globally (Briggs and Rolfe 1983). Lange et al. (2001) suggested *Concavicaris* may be polyphletic. We cannot assign this specimen to a species group at this time, since comparative internal material is only known from the western Australian Gogo Formation species of Briggs and Rolfe (1983).

Concavicaris? sp. indet.
(Figs. 2A, B)

Material.– One slab containing the impressions of the abdominal somites and displaced carapace of one individual, coll. Paleontological Research Institution (PRI), Ithaca, New York, specimen PRI 54942.

Locality and horizon.– Collection locality approximately 42.38° N latitude, 74.47° W longitude. East side of Route 30, about 2.8 km northeast of Grand Gorge, Schoharie County, New York, USA. Oneonta Formation, Middle/Upper Devonian.

Description

General dimensions.– Preservation of this specimen is moldic, with no cuticle preserved. Specimen consists of three regions: an inferred abdominal interior illustrating segmentation, a portion of a displaced carapace valve, and possible appendage impressions. The entire length and maximum width of the entire specimen are 87.0 mm and 56.9 mm, respectively. At least 4 mm of vertical relief

exists across the curved surface of the preserved anterior segments, while 2-3 mm of relief occurs over the width of the displaced carapace valve.

Abdominal interior.– Outline ovoid. Length of the interior is 65.5 mm and maximum width is 17.1 mm. The maximum width of the interior occurs at the 8th segment (counting from presumed anterior, left hand side), and tapers both anteriorly and posteriorly. At least 13 abdominal segments (possibly more) separated by deep grooves can be distinguished. The anteriormost segment is broader than subsequent segments, as is the posteriormost segment. This could either be due to biological structural differences or taphonomic factors, which cannot currently be distinguished. Segment width is relatively constant; most posterior segments are between 4.5 and 4.8 mm wide, while the most anterior segments are approximately 3.8 mm. Segments exhibit a gentle oblique trend toward the inferred anterior end (left hand side) of the specimen. Segments appear to coalesce proximally along a hinge structure, while producing rounded terminations distally. Several segments (numbers 4, 7, 9, 10, 11) are longitudinally divided by a weak linear depression in the medial to distal portion of the segment, which is particularly evident on segment 10. The proximal portion of these segments is characterized by grooves which subdivide this portion of each segment into triangular regions. These grooves are best developed in segments 4 through 12, and are a distinctive feature of the anatomy of this specimen.

Possible appendages?.– Faint parallel traces occur near what is inferred to be the anterior of the specimen and may represent impressions of weakly sclerotized raptorial appendages. The longest of these traces is 31.7 mm. A slight three-dimensionality suggests that a pair of convex (possibly tubular structures) may extend outward from the region of abdominal somites approximately parallel to the trend of the hinge line.

Displaced carapace valve.– An ovoid, tapering structure with a length of 78.1 mm. The width of the valve tapers from a maximum of 25.3 mm at a fractured end to a rounded, distal terminal of approximately 6.3 mm. The shape of this body is ovoid, but the side nearest the abdominal segments is a straight edge, which may represent the hinge structure. The opposite side exhibits a smooth, rounded transition from a bulbous, inflated anterior region to the rounded distal margin. The surface is generally smooth but is penetrated by several fractures. The fractures do not extend into the matrix, which suggests fracturing of a relatively rigid (sclerotized) original biologic material rather than post depositional modification of the sedimentary unit. Indentations near the posterior distal margin may represent impressions of underlying abdominal appendages.

An additional area of smooth surface is apparent between the abdominal segments and the displaced carapace valve. This may represent the remains of another carapace fragment.

Remarks.– The dominant characteristic of this specimen is the segmented nature of the inferred abdominal region. This pattern closely reflects that observed by Briggs and Rolfe (1983) in Frasnian concavicarids preserved in three-dimensions from the Gogo Formation of the Canning Basin of western Australia (1983). The Gogo concavicarids are preserved with a higher degree of detail than this specimen, but many details of the abdominal arrangement between Gogo specimens and this specimen can be observed. Firstly, the number of segments is consistent between the taxa: 10 to 14 for the Gogo specimens, 13 for this specimen. The arrangement of the segments, in which height increases posteriorly until the 6th or 7th segment and then decreases is congruent in both cases. The dorsal regions of the Gogo pleurites are subdivided into three or four lobes which results in a V-shaped groove (Briggs and Rolfe 1983). The dorsal regions of segments of this species also exhibit a V-shaped groove (best developed in segments 5-12), which likely represents the same muscular arrangement preserved in this specimen in lower taphonomic detail. Several segments of this specimen, most notably 4 and 10, also demonstrate the presence of a groove parallel to the axis of the segment ventrally, which has also been described in Gogo concavicarids (Briggs and Rolfe 1983).

The combination of abdominal features described above is unique to the Thylacocephala (Briggs and Rolfe 1983; Schram 1990; Schram et al. 1999). These segments have been interpreted as body somites (Briggs and Rolfe 1983), elongated protopods of abdominal limbs (Rolfe 1985), and as sections of musculature to which posterior paddle-like limbs attached (Schram et al. 1999). Regardless of their interpretation, the detailed similarities between the abdominal segments in Gogo concavicarids and this specimen strongly support a concavicarid interpretation for this specimen. An interpretation of the anterior impressions as raptorial appendages (although speculative), would further strengthen the support for a thylacocephalan affinity of this fossil.

CONCLUSIONS

The description of the first concavicarid interior from the Devonian of North America creates a significant link between the isolated carapace fragments present at other Devonian localities with well preserved thylacocephalans recorded from other stratigraphic intervals. Futhermore, this specimen may be the oldest thylacocephalan to be collected from brackish strata. Although Carboniferous and younger thylacocephalan species have been described from brackish or marginal marine environments (ex. Schram 1990; Polz 1994), Devonian and older thylacocephala have been previously reported only from marine units, with most specimens from black shale deposits (e.g., Briggs and Rolfe 1983).

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