New 3-D Arthropods from Cambrian Sandstones

By Joseph Collette III

A new suite of soft-bodied arthropods – animals with jointed appendages, like modern crabs and insects – have been uncovered from Upper Cambrian layers in Wisconsin and Quebec. One of them, a small shrimp-like crustacean called a phyllocarid, almost certainly is the earliest undisputed appearance of this group in the fossil record. The other, larger fossils are intermediate between two other enigmatic arthropod groups, the aglaspidids and the euthycarcinoids. These fossils are remarkable for being preserved in three dimensions, in fine- to medium-grained sandstone and orthoquartzite, with little or no compaction by the weight of time and rock.

Sandstones don't usually allow detailed preservation of soft tissues from the Phanerozoic. These rocks typically preserve only trace fossils – the footprints, burrows, and body impressions of organisms. This is because sandstones are fossilized shore environments, or "beaches," in which energy, well-oxygenated water actively breaks down remains of animals. However, as my research shows, certain Paleozoic "sheet sandstones" provide windows of exceptional preservation – if you know where to look for them.

Cambrian Geology & the Formation of Fossils

The Cambrian beaches of what would ultimately become North America were drastically different than those of today. Vast, shallow, tropical seas covered much of the continent. There was no vegetation on land, and very few animals ventured out of the water to leave their traces on the dunes. With a very low slope (only a 0.02-millimeter rise in elevation per meter) and a tidal range of 1 to 2 meters (3 to 6 feet), the distance between the high and low tide marks in these Cambrian intertidal zones would have been enormous – between 50 and 100 kilometers (30-60 miles). One might think that streams passing through such a flat, low-gradient, sand-dominated area would be shallow and meandering. But because mud and roots – that act as "glue" to secure the cut banks of modern meandering streams – are absent from such settings, these streams formed channels during the changing tide. It is these channels, and their associated fine-grained muds, that played a crucial role in the preservation of the arthropods.

Although this style of sandstone preservation is rare in the Phanerozoic, similar preservation is known from the earlier Ediacaran Period (the last geological period before the beginning of the Cambrian, or about 600 million years ago). In the Ediacaran, such unusual preservation was probably assisted by microbial films. Microbes might have also been involved in preserving my Cambrian arthropods, but they are not necessary. My taphonomic model requires only the presence of mud, and – like so much of the fossil record – a series of fortuitous events.

Channelized water flow is a common feature of the sandstones of both central Wisconsin and Quebec. The meandering tidal channels and their associated overbank levees allowed the accumulation of fine-grained mud and clay. During high tide, our arthropods went about their lives on an expansive sand flat wider than the state of Rhode Island. But when the tide retreated, they had to follow the water or

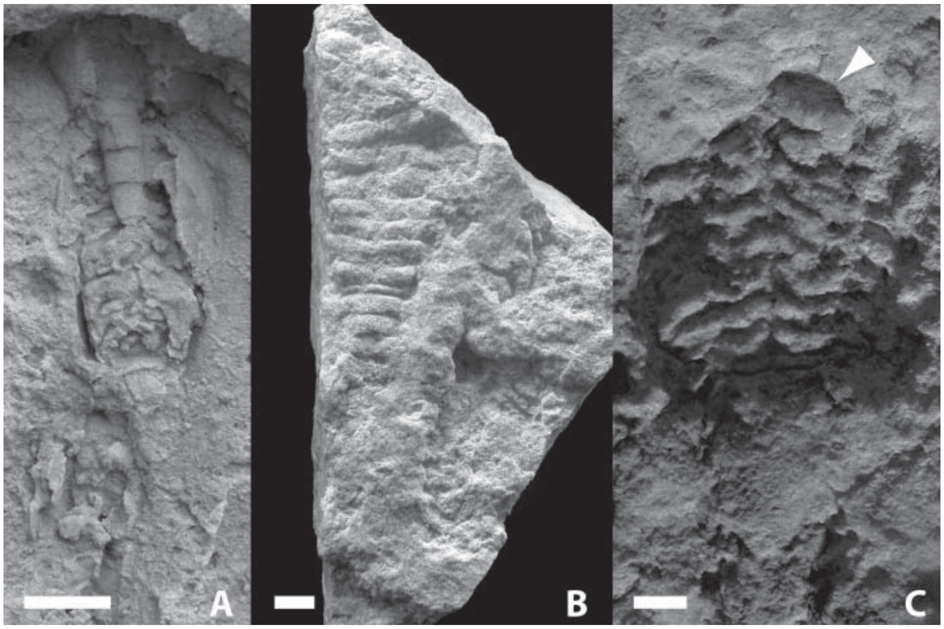

Fig. 1. Arthropods from central Wisconsin and Quebec. (A) A phyllocarid from Wisconsin. Three individuals are present in this photo. From top: a partial carapace with abdominal segments; an entire carapace with limbs and abdominal segments preserved; a partial carapace with some limbs preserved. (B) An euthycarcinoid-like arthropod from Wisconsin, one individual. (C) An euthy- or aglaspidid-like arthropod from Quebec. The arrow shows what appears to be a forward-articulating limb present near the head area. All scale bars = 1 cm.

perish. In some low-lying areas, standing water would have formed life-saving "tide pools." But more importantly for us, there was mud.

As the water within these tide pools evaporated, the arthropods "hunkered down" in the wet mud to avoid drying out. Large cracks now present in the fossil slabs tell us that desiccation took place below as well. This hardened the mud around the arthropods, forming a mold. Next, the entire surface must have been covered by a veneer of sand, perhaps brought in by a storm. As microbes within the sand gradually decomposed the arthropod carcasses, the overlying sand gradually filled the voids left in the mud mold. The well-rounded quartz sand grains reached the deepest parts of the mold, preserving the limbs of the arthropods in crisp detail. Lithification – the process by which sand becomes rock – then ensured their preservation.

Identifying Ancient Arthropods

The broader relationships of these fossils is clear – they were distinctly segmented, with exoskeletons and limbs of many joints. In some (Fig. 1A), a significant number of characters of subclass Phyllocarida occur: they have bivalved carapaces hinged along the dorsal surface, seven abdominal segments, and phyllopodus (leaf-like) limbs. On a single surface from Wisconsin, more than 44 arthropods were collected, of which all but three were phyllocarids. The carapaces are rounded in front, with a slightly convex ventral margin. The posterior margin is usually partially obscured, but generally appears linear. Some individuals have a well developed *doublure*, a portion of the carapace that folds and continues on the underside of the carapace for a short length. The more complete specimens are approximately 5 cm long and 0.7 cm wide. The arthropods have are oriented in one of two ways, either toward 190 or 310 degrees.

The second type of arthropod from Wisconsin (Fig. 1B) is much more euthycarcinoid- or aglaspidid-like. These much larger arthropods are preserved in 3-D, occur on bed soles, and are casts of the ventral side of the animals. However, it is much more difficult to assign these specimens to either of the mentioned suborders. They did not have bivalved carapaces, but did seem to have wider "thoracic" areas of at least 7 segments, and narrower "abdominal" areas of at least 5 segments, most likely ending in a telson. Less information on the arrangement and morphology of the appendages is preserved because this type of fossil occurs infrequently, but at least 7-8 appendages appear to be present on the "thorax," and probably none on the "abdomen."

Arthropods from Quebec (Fig. 1C) are approximately 14 cm long and 6.5 cm wide. Each has a "thorax" and "abdomen," with the most anterior and posterior extremities absent (possibly present within the matrix). The number of segments comprising the thorax is not clear, but there are at least 8 appendages, so at least this many segments are likely present. Seven of the appendages appear to be rear-facing, and are interpreted as walking legs. The anteriormost appendage on the right side (Fig. 1C, arrow) appears to be articulated differently than the rest – it appears to articulate forward. Whether this is an artifact of damage before death and burial remains unclear. The appendages insert close to the centerline of the body and thus appear to be gnathobases – extensions of the limbs that are used to manipulate food – but known euthycarcinoid appendages are not gnathobasic. Aglaspidid appendages are only known from three fossils, and there is some evidence that their legs could have been gnathobasic. However, the presence of a narrower five-segmented "abdomen," possibly terminating in a telson, is problematic, because aglaspidids did not have this feature.

What's Next?

Although problematic now, the features of these arthropods will hopefully soon be revealed by X-ray CT scanning at the University of Texas at Austin. This nondestructive technology produces a three-dimensional image of the interior of a rock based on subtle differences in the matrix, such as pore space, mineralogy, or texture. In many of the rocks from Wisconsin and Quebec, a clay layer visibly continues into the surrounding rock. Because this clay was responsible for the preservation of the parts of the fossil that we can see, there is a reasonable chance that additional anatomical detail is still present, locked away from view within these rocks.

I will return to my field site in Wisconsin in July 2008 to do more fieldwork and reconnaissance in hopes of locating more of the large euthycarcinoid-like fossils, and to examine trackways that could have been made by these arthropods. I am also working on a phylogenetic tree of the Phyllocarida, begun by Stigall and Lieberman in 2002 using Devonian phyllocarids. The tree that I will produce will include Stigall and Lieberman's data, plus data on earlier Cambrian-to-Silurian material that I have collected from museum collections, including the Yale Peabody, the Smithsonian, and the Royal Ontario Museum. To date, I have found at least three additional, undescribed, unnamed phyllocarids in these collections. This work will help solidify the taxonomic position of the fossil members of Phyllocarida, and will likely result in the reassignment of some fossils to different families or genera. The work on the larger arthropods is important as well, because it offers new insight into our knowledge of two very poorly understood groups of arthropods.

Joe Collette is the 2008 recipient of PRI's Student Award in Systematic Paleontology. He a graduate student in the Department of Geosciences, University of Massachusetts, Amherst, studying under Dr. James W. Hagadorn. Email collette@geo.umass.edu.