

Cambrian Cannibals

Agnostid Trilobites and The Earliest Known Case of Arthropod Cannibalism

by Mark A. S. McMenamin



Association between two Agnostid trilobites, *Peronopsis interstricta*, showing a larger Agnostid overriding a smaller one.

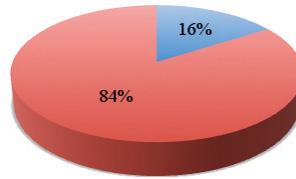
A slab from the Middle Cambrian Wheeler Formation, from Millard County, Utah

Agnostid trilobites are tiny compared to their better known and larger relatives from the Paleozoic seas. Agnostids survived for almost exactly one hundred million years, living from the Early Cambrian (beginning 542 million years ago) to the late Ordovician Period (which ended 443 million years ago). Largely due to their diminutive size, agnostid trilobites have defied attempts to properly interpret their affinities, environmental preferences, behavior, and feeding strategies (McMenamin 2010).

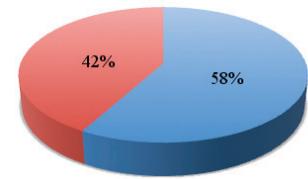
Results from a suite of 44 separate slabs bearing specimens of *Peronopsis in-*

Trilobite associations

Total sample number:	44
Total number of large (>4 mm) intact trilobites:	44
Total number of small (<4 mm) intact trilobites:	3
Number of samples with possible cannibalism events:	7
Total number of possible cannibalism events:	8
Number of slabs with just one trilobite:	32
Number of slabs with multiple trilobites:	12
Percent of total number of samples suggesting cannibalism:	7/44 = 16%
Percent of samples with multiple trilobites suggesting cannibalism:	7/12 = 58%

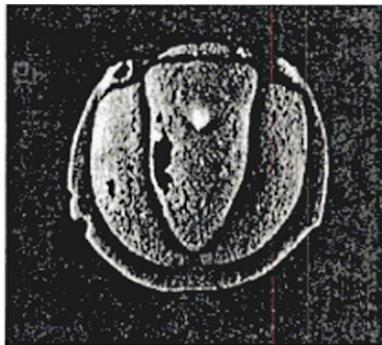


Proportion of samples showing large and small agnostids juxtaposed: $N=44$; red=no juxtaposition; blue=juxtaposition



Proportion of multi-agnostid samples showing evidence of cannibalism: red=no evidence; blue=evidence of cannibalism

terstricta have provided new data concerning agnostid behavior. Most of the specimens (43) were donated to Mount Holyoke College by an alumna, so their precise fossil locality is not known. Nevertheless, the samples are undoubtedly derived from the Middle Cambrian Wheeler Formation, Millard County, Utah. A final slab, also derived from the Wheeler Formation, Millard County, Utah, was purchased for comparison purposes in an online auction. The matrix of the auction sample shows iron staining that does not occur in the donated samples, thus the suite of samples probably represents at least two separate stratigraphic horizons within the Wheeler Formation. Seven samples out of the entire suite (16%) contain juxtapositions of large (>4 mm in length) and small (<4 mm) specimens. The small individuals of the pairs frequently appear to be damaged or partly ingested.



Bite marks to the pygidial margin. Taken from L. E. Babcock, 2003, in Kelley et al., ed., *Predator-Prey Interactions in the Fossil Record*.

In some cases a small individual is overridden by the cephalon of a larger animal, in what does not appear to be a merely chance association. These associations are interpreted here as evidence of attack by the larger member of the conspecific pair. As shown above, of the samples preserving multiple trilobites, 58% show evidence for cannibalism.

These results suggest that the agnostid trilobite *Peronopsis interstricta* was a predator. The predator interpre-

tation is supported by putative tiny bite scars on the pygidium of a specimen of *Peronopsis interstricta*, damage that may be the result of intraspecific attack (Babcock 2003). This damage looks like someone nicked the posterior edge of an agnostid trilobite with a manual hole puncher.

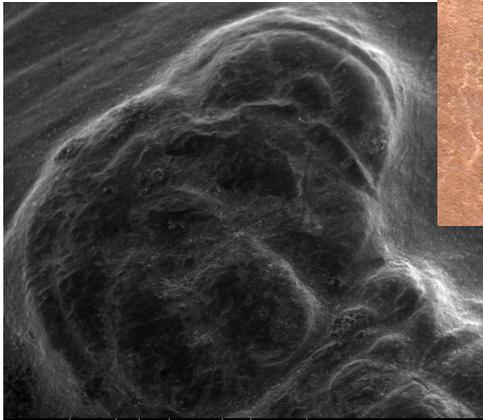
An alternative to the predatory attack interpretation holds that the attacks represent an expression of intraspecific territoriality or mating competition. Scavenging and accidental juxtaposition interpretations must also be considered. The cannibalism explanation, however, seems best supported by available data. As such, these encounters represent the earliest known examples of arthropod cannibalism, and thus add to the accumulating evidence indicating that the Cambrian biosphere experienced an unprecedented increase in marine predation pressure (McMenamin and McMenamin 1990).

As the agnostid *Peronopsis interstricta* was evidently



Agnostid damage: shredded thorax. Note, both agnostids are in the same bedding plane.

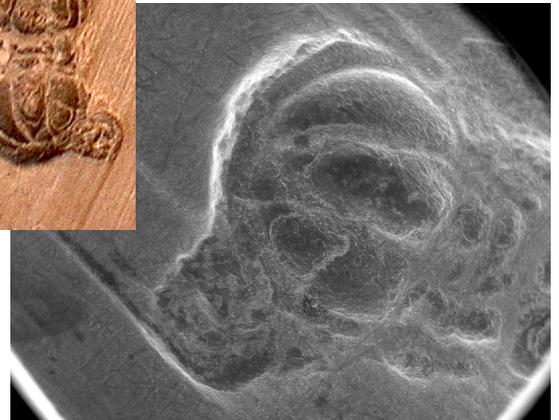
Captured small agnostid



Marian Rice



Damaged remains of smaller agnostid.



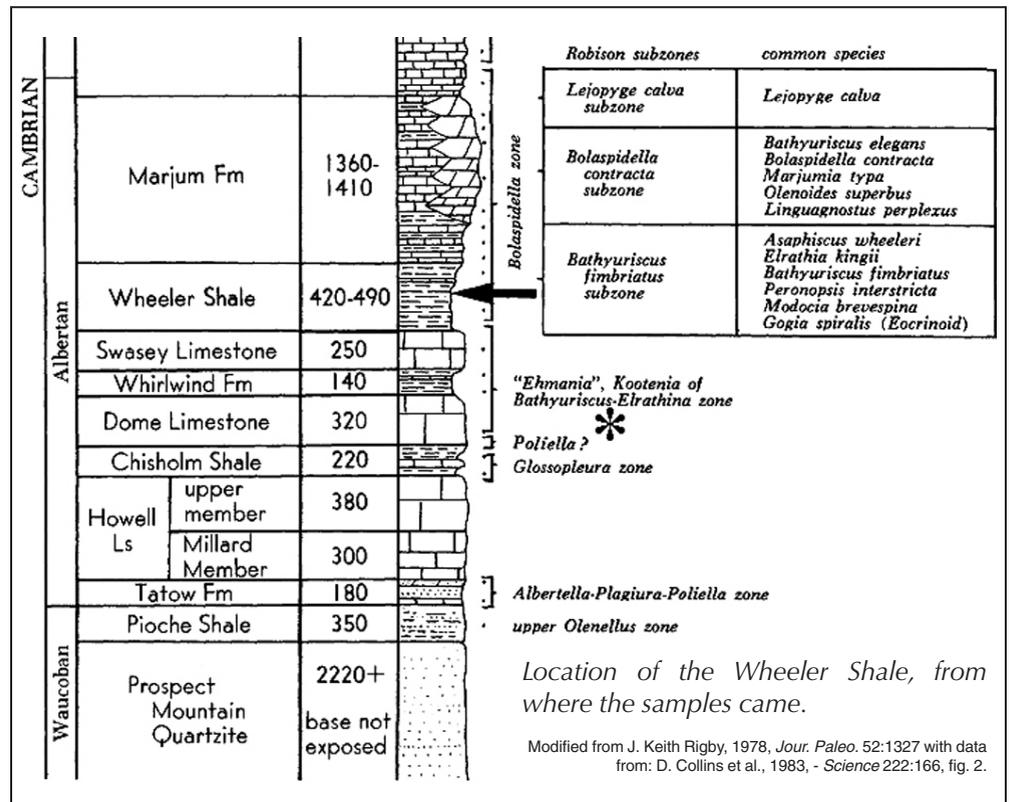
Marian Rice

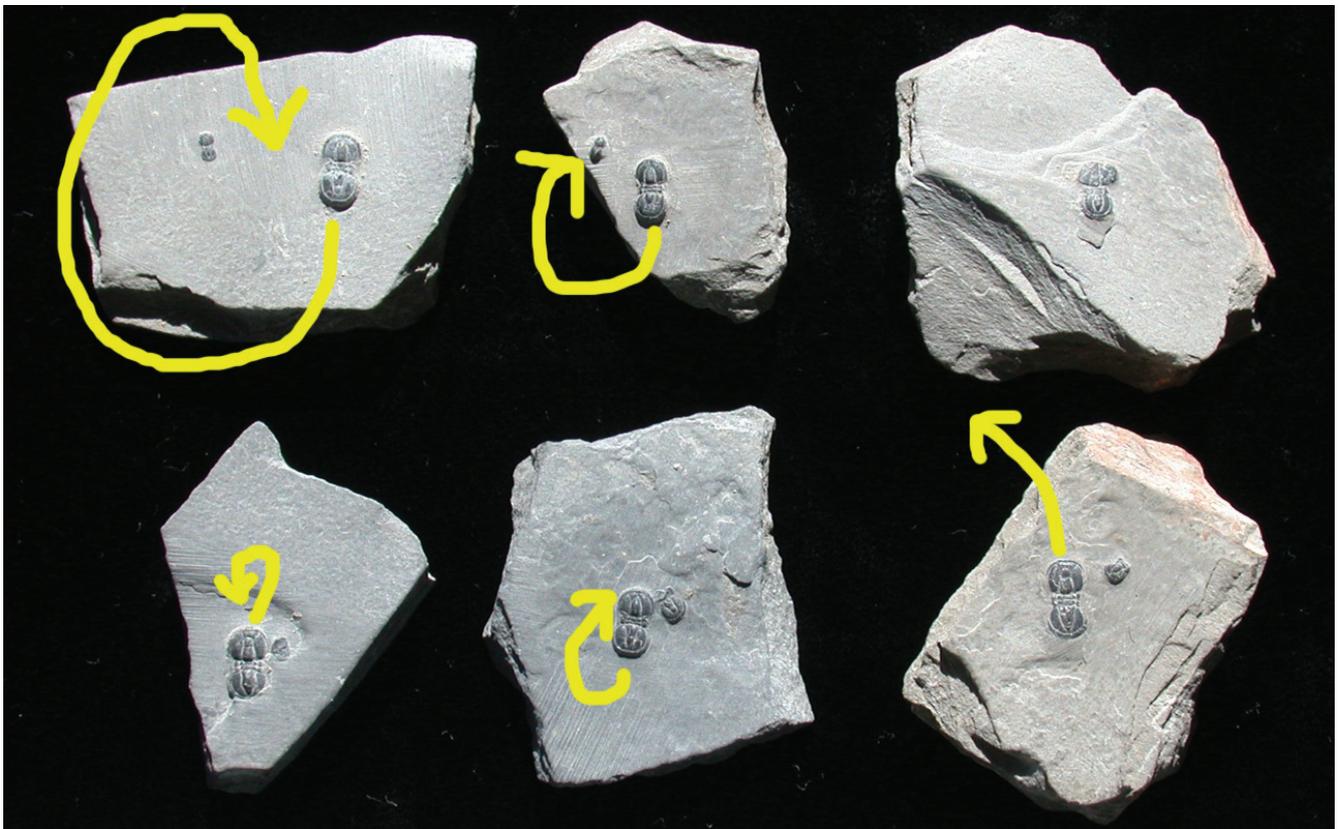
blind, these predatory trilobites must have relied on senses other than sight to locate and capture their prey. Alternate sensory modalities, such as chemotaxis, electrotaxis or phonotaxis, may have been put into play in the search for prey. The slabs may be arranged in such a way as to suggest that the attacking trilobite approached its smaller prey in a coiling trajectory, spiraling inward to eventually seize the hapless victim. Other interpretations of the seek-and-destroy pattern are also possible. We might be able to obtain an unambiguous solution to the approach pattern problem if a specimen were to be located that showed agnostid trace fossils (crawling tracks) associated with the body fossils.

The earliest known case of cannibalism, just slightly older than the case for agnostid cannibalism presented here, occurs in fossils of the Burgess Shale priapulid worm *Ottoia* (Nudds and Seldon 2008). A number of specimens are known in which a large *Ottoia* has swallowed a small *Ottoia* of the same species. Cannibalism is common in modern priapulid worms as well. No cases of cannibalism have yet been reported from the Early Cambrian; however, the trace fossil *Treptichnus pedum* may be the track of an early priapulid worm. If

so, this Early Cambrian trackmaker may have been cannibalistic as well.

Interestingly, the priapulid worm *Ottoia* and the agnostid trilobite *Peronopsis* were both apparently blind. This implies that cases of early cannibalism are not necessarily associated with vision-directed predation. Vision-directed predation has been blamed as the primary cause for the development of skeletons at the base of the Cambrian in an event known as the Cambrian Explosion (McMenamin and Schulte McMenamin 1990; Parker 2003).





A possible chemotaxis, spiralling approach pattern.

Ecological reconstructions of the Cambrian sea floor must now portray agnostid trilobites as predators. The agnostid trilobite species *Agnostus pisciformis* had antennae with regularly spaced spikes that may have served a predatory function (see the C.O.R.E. Cambrian fossil research group web site). Cannibalism should also be considered

as a potential contributing factor to the appearance of widespread Cambrian predators (McMenamin 2003). The behavioral tools associated with macropredation may have been refined within a single species before being unleashed on the rest of the biosphere. This suggests that cannibalism in animals first appeared shortly before, or right at, the beginning of the Cambrian Period.



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Burgess Shale stem-group Priapulid *Ottoia prolifica*.

References

- Babcock, L. E. 2003. "Origin and early evolution of predators: The ecotone model and early evidence for macropredation." In P. H. Kelley, M. Kowalewski and T. A. Hansen, eds., *Predator-Prey Interactions in the Fossil Record*, Kluwer Academic/Plenum Publishers, New York, pp. 55-92.
- McMenamin, M. A. S. 2010. "Cambrian cannibals: agnostid trilobite ethology and the earliest known case of arthropod cannibalism." *Geological Society of America Abstracts with Programs*, v. 42, no. 5, p. 320.
- McMenamin, M. A. S. 2003. "Origin and early evolution of predators: The ecotone model and early evidence for macropredation." In P. H. Kelley, M. Kowalewski and T. A. Hansen, eds., *Predator-Prey Interactions in the Fossil Record*, Kluwer Academic/Plenum Publishers, New York, pp. 379-400. ISBN 0306474891.
- McMenamin, M. A. S. and D. L. Schulte. 1990. *The Emergence of Animals: The Cambrian Breakthrough*. Columbia University Press, New York.
- Nudds, J. and P. Seldon. 2008. *Fossil Ecosystems of North America*. Manson Publishing, London.
- Parker, A. 2003. *In the Blink of an Eye: How Vision Sparked the Big Bang of Evolution*. Perseus Publishers, Cambridge, Massachusetts.