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The Influence of Spines and Size Refuge on Predation of Devonian Brachiopods from the Lime Creek Formation near Rockford, Iowa

Broc S. Kokesh
University or Minnesota, Morris

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Introduction:

Brachiopods are a common index fossil for shallow marine paleoenvironments throughout the Paleozoic (Copper, 1967). Features common to all brachiopods include dorsal and ventral valves connected at a hinge, a lophopore for filter feeding, and a pedicle for attaching to the substrate. Furthermore, some species of articulated brachiopods (subphylum Rynchonelliformes) have developed external spines on each valve. There is strong evidence suggesting that these spines evolved as a mechanism for avoiding predators (Harper *et al.*, 2009; Johnsen *et al.*, 2013; Zhang *et al.*, 2011). Fortunately, many signs of predation are well preserved in fossilized brachiopods. Injuries on the valve surface are typically identified by healed scars (Figure 1a) or boreholes (Figure 1b). In order to determine the size of an individual at the time of an injury, the length from the apex of the hinge to the growth line associated with an injury can be measured (Johnsen *et al.*, 2013). In this study, brachiopods were collected from the Lime Creek Formation near Rockford, Iowa to assess predation rates on brachiopod species where spines are absent (*Atrypa devoniana*) and present (*Atrypa rockfordensis*).

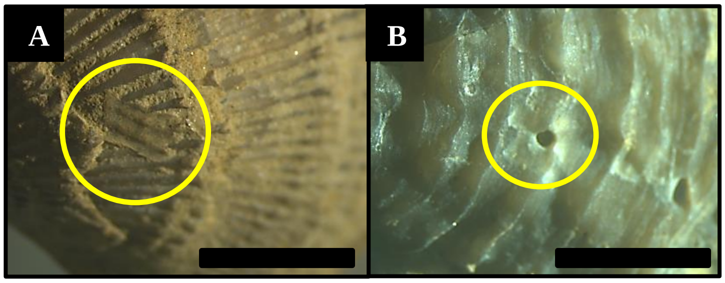

Figure 1. A) *A. devoniana* specimen with healed scar on dorsal valve. B) *A. rockfordensis* specimen with borehole on ventral valve. Circles highlight wounds. Scale bars =10mm.

Methods:

Brachiopods were collected on September 22, 2014 from the Devonian-aged Lime Creek Formation at Fossil and Prairie Park near Rockford, Iowa. Specimens of *A. devoniana* (n=183) and *A. rockfordensis* (n=89) were identified, sorted, and cleaned in the lab. Using a low-power dissection microscope, specimens were observed for signs of predation (Leighton, 2001; Zhang *et al.*, 2011). Specimens containing predation marks were measured as described by Johnsen *et al.* (2013). Additionally, the injury type and valve of injury were noted. Care was taken to ensure that identified injuries were not caused by post-fossilization processes and questionable markings were rejected from this study.

Results:

A total of 48 injuries were identified on 46 specimens of *A. devoniana*. For *A. rockfordensis*, 12 specimens were found to each have one injury. All injuries for *A. rockfordensis* occurred at valve lengths no greater than 15mm ($\bar{x}$=9.272, SD=2.895) while *A. devoniana* injuries were present up to 21mm ($\bar{x}$=13.354, SD=4.607). When sorted into size classes of 2mm (Figure 2), each species had a different peak in proportion of injuries in each size class. Proportions for each species were significantly different ($p < 0.05$) in all size classes except 11-13mm using a Z-test.

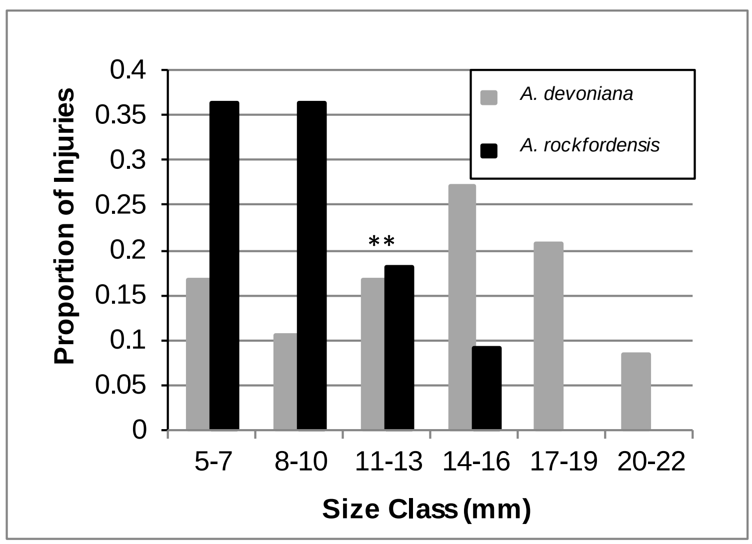

Figure 2. Proportion of injured specimens sorted by 2mm size classes. All size classes except 11-13mm (indicated by **) had proportions that were significantly different ($p<0.05$).

For *A. devoniana*, 44 out of 48 injuries were caused by scars with evidence of valve recovery (Table 1). The remaining four injuries were caused by boreholes. A Z-test shows that these proportions are significant (Z=8.165; p=0). For *A. rockfordensis,* seven injuries were caused by scars while the remaining five were due to boreholes. Scars and boreholes were found to not be significantly identified in certain size classes.

Table 1. Proportion of injured specimens sorted by wound type. Proportions are calculated by the count of each injury type divided by total injuries for *A. devoniana* (n=48) and *A. rockfordensis* (n=12).

	Healed Scar		**Borehole**	
	Count	**Proportion**	**Count**	**Proportion**
A. devoniana	44	0.917	4	0.083
A. rockfordensis	7	0.636	5	0.364

<u>Discussion</u>:

Signs of predation were found to be rather common among *A. devoniana* with approximately 25% of collected specimens showing at least one injury. In contrast, approximately 13% of *A. rockfordensis* specimens were injured. Injuries for *A. rockfordensis* do not occur in size classes greater than 14-16mm, suggesting that *A. rockfordensis* may experience size refuge beyond this size class (Figure 3). This is likely due to the presence of spines on *A. rockfordensis* since *A. devoniana*, a spineless species, experiences predation up to at least 20mm. Spines make it more difficult for predators to reach the surface of the valve, meaning well-developed spines that come with growth can ultimately prevent all predation (Johnsen *et al.*, 2013). Nevertheless, boring predators may have an easier time reaching the valve since they tend to be smaller and require less surface area to attack (Copper, 1967; Leighton, 2001). A higher proportion of *A. rockfordensis* experienced borehole injuries (Table 1), suggesting that boring predators are capable of preying on spiny brachiopods beyond the point when other predators are incapable of doing so.

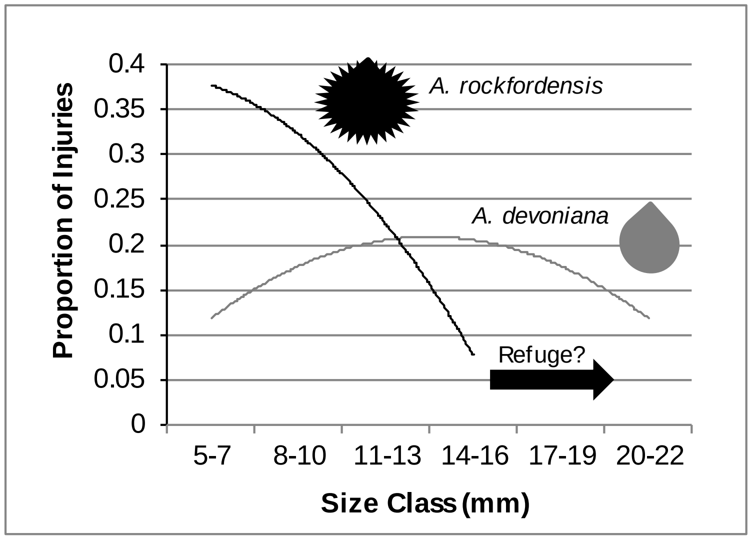

Figure 3. Polynomial trendlines of data from Figure 2. Black line for *A. rockfordensis* and grey line for *A. devoniana*. Trends show that each species has a different peak in injury proportion. Trendline for *A. rockfordensis* ends in the 14-16mm size class, suggesting that *A. rockfordensis* may experience refuge from predators due to size.

Although predation to *A. rockfordensis* by proportion is most frequent in the smallest size classes, it should be noted that more specimens of *A. devoniana* are still found to have injuries at these size classes despite peak frequency for *A. devoniana* being 14-16mm. This suggests that *A. devoniana* may have been more common than *A. rockfordensis*, and was more vulnerable to predation at any point in development. Future work should emphasize using a larger sample size with more similar numbers of each species since this study used approximately twice as many specimens of *A. devoniana* as *A. rockfordensis*.

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