Epizoans and Predation Traces of Devonian Hay River Formation Brachiopods: Indicators of Complex Ecosystems and Ties to the Iowa Basin

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Summary
Two brachiopod communities from the Devonian Hay River Formation units B and C are moderately to heavily encrusted by epizoans. The unit B community bears evidence of predatory attacks. This community was much more diverse in terms of host brachiopods and attached epizoans; furthermore, epizoans were highly abundant. Predation traces occurred only on brachiopod species that were heavily encrusted. The unit C community is much less diverse in encrusters and epizoans, and brachiopods were smaller on average. In this community, low epizoan abundance may have arisen from influences of nearby biostromes or from brachiopod size effects. Using Bray-Curtis polar ordination, we compared epizoan and brachiopod diversity to those from four stratigraphic units and nine localities from Iowa and Ohio, USA. Our results suggest that Hay River epizoan assemblages are most similar to those from Iowa, regardless of age, and support interbasin exchange patterns recovered from studies of brachiopod migration.

Introduction
In the Western Canada Sedimentary Basin, Devonian brachiopod paleontology is a valuable tool for biostratigraphy and facies interpretation; however, few studies expand beyond the diversity or abundance of brachiopod species. In the Midcontinent, brachiopods also play a critical role in paleontological reconstruction, but over the past few decades, the focus has shifted to include their role in ecosystem dynamics, such as predator-prey interactions and as hosts for a myriad of encrusting organisms. Herein, we investigated not only the diversity of brachiopods in two communities from the Hay River Formation, but also their influence on ecosystem complexity and their ecological ties to the Midcontinent Epicontinental Sea.

Epizoans are organisms which encrust other organisms, such as a modern barnacle attaching to a scallop, or as in the present study, bryozoans attaching to brachiopods. In the fossil record, usually only calcified epizoans preserve well; however, in the Hay River Formation, some “fragile” epizoans, such as lightly calcified hederellids (Phoronida) and moulds of *Ascodictyon* (incertae cedis), are also preserved on brachiopod hosts. Furthermore, Hay River epizoans are unusually well preserved despite taphonomic erosion of host shell surface layers. Brachiopod specimens also bore traces of predatory attacks, such as drill holes and crushing scars.

Methods
With the assistance of Dr. James Day and Dr. Shilong Mei, we sampled the brachiopods of the Frasnian Hay River Formation along the Hay River in the Northwest Territories. Two units produced abundant brachiopod specimens: a floatstone to grainstone carbonate bed capping unit B and a biostromal floatstone to bindstone capping unit C. Each unit produced a distinctive brachiopod assemblage, including distinct associations of epizoans and predation traces. All brachiopods are reposited in the Leighton collection at the University of Alberta.

We tested differences in epizoan abundances on brachiopod taxa and frequency of predatory traces using chi-square tests. To examine brachiopod diversity and evenness, we used the

Shannon Diversity Index (SDI), which relates richness (number of species) to evenness (even abundance distributions among species):

$$H' = -\sum_{i=1}^{S}(p_i \ln p_i) - [(S-1)/2N]$$

Where p_i is the relative abundance of each species i, S is the richness, and N is total number of specimens. A low value indicates low evenness and/or richness; a typical high value in Paleozoic fossil ecosystems is 4 to 5.

We used Bray-Curtis polar ordination with relative Sorensen distance measure in city-block space to compare Hay River epizoans on brachiopod taxa with those from the Givetian Cedar Valley Group (Solon and Rapid Formations), the Frasnian Shell Rock Formation, and the Frasnian Lime Creek Formation (Owen and Cerro Gordo Members) of Iowa, USA; as well as the Givetian Silica Formation of Ohio, USA. We performed Q-mode ordination, setting each brachiopod taxon per locality as samples and the epizoans as the species within (or attached to) the samples. Brachiopod morphology and carbonate lithology of the Cedar Valley Group samples are most similar to that of the Hay River unit B limestone bed in terms of large atrypides, large spiriferides and abundant *Schizophoria* and floatstone carbonates. The Solon Formation of the Cedar Valley Group also has similarities to Hay River unit C, in that brachiopods occur in the sediments between small biostromes. Lime Creek and Silica shales most resemble the dominant lithology of the Hay River Formation; however, the Lime Creek brachiopods are small like the Hay River unit C specimens, and the Silica Shale brachiopods are large and bear a similar epizoan diversity and abundance to Hay River unit B brachiopods. The Shell Rock Formation is a carbonate unit containing large brachiopods, but unlike Hay River unit B, epizoans are rare.

Results and Discussion

The Hay River unit B assemblage was the more diverse in terms of brachiopods, epizoans, and predation traces. A total of twelve brachiopod taxa (Shannon Diversity Index of H=1.88) were recovered from surface collecting of an abandoned quarry. Four brachiopods (*Variatrypa, Schizophoria, Cyrtospirifer, Douvillina*) dominated the assemblage in terms of abundance; these same four brachiopod taxa supported the majority of the epizoans and bore all of the predation traces.

A total of 15 epizoan taxa encrusted the brachiopod shells (Shannon Diversity Index, H'=1.51). The enigmatic "worm" *Microconchus* was by far most abundant, but sheet-like bryozoans and hederellids were also common. Ninety-five percent of the shells of the most abundant brachiopod, the orthide *Schizophoria*, were encrusted by at least one or more epizoans. The three next most abundant brachiopods bore epizoans on at least 75% of their shells. When brachiopod taxa are corrected for abundance, epizoans preferentially recruited onto the four most common species (Chi-square; $p << 0.01$).

Predators attacked the four most abundant brachiopods, with the majority of predation traces occurring on *Schizophoria*, of which 26% bore predatory traces. Brachiopod taxa with over 50% of individuals encrusted were more likely to be attacked than those with few epizoans (Chi-square; $p=0.025$), while taxa that lacked encrusters never bore traces of predation. Predation and encrustation frequencies of unit B brachiopods were strongly positively correlated (Speaman's Rank Correlation, $r = 0.87$, $p < 0.01$). In modern ecosystems, epizoans confer visual or chemical camouflage to their hosts; in ancient ecosystems, the same antipredatory protection may be inferred for encrusted shells. This correlation between encrustation and predation arises either from (a) the complete destruction by crushing predators of unencrusted, uncamouflaged shells, suggesting that those bearing epizoans were less likely to be mortally damaged (and thus more likely to preserve scars from the encounter), or (b) predators were attracted to the same brachiopod taxa that were suitable substrate for epizoans.

Hay River unit C carbonates produced a less diverse and more uneven brachiopod assemblage (SDI, H'=1.136) with fewer epizoans and significantly lower encrustation rates (Chi-square, p< <0.01) than Hay River unit B and no predation traces. Only eight brachiopod taxa were recovered from the inter-biostromal facies, which were dominated by *Spinatrypina*.

Unit C brachiopods were generally smaller than their unit B counterparts, and there was little taxonomic overlap between the two brachiopod assemblages. The lower encrustation rates of unit C (< 30% of the shells of each taxon were encrusted) may be due to the smaller size (thus, less available surface area of the potential hosts) or possibly due to the greater availability of other hard substrates in the biostromal environment of unit C.

Eight epizoan taxa, all of which were also recovered in the underlying Hay River unit B, had a higher SDI (H'=1.64) than the lower unit. Although epizoans were less diverse, abundances were more evenly distributed among the encrusting taxa.

In the Bray-Curtis ordination with Midcontinent localities, the first two axes accounted for 88% of the variation among samples. Most of the Hay River unit B brachiopods and their epizoans formed a moderately tight cluster within the junction between clouds of Cedar Valley Group and Lime Creek Formation data points (Figure 1). Hay River unit C samples were more dispersed within the Cedar Valley-Lime Creek overlap. These results suggest similarities between the Cedar Valley-Lime Creek epizoans and those from the Hay River Formation.

We propose that geographic region has a greater influence on encruster-community similarity than age or depositional environment. Although Hay River unit B brachiopod sizes, epizoan abundance and epizoan diversity most resemble that of the Givetian Silica Formation, ordination analyses support an affinity between the Hay River epizoan assemblages and the Givetian Cedar Valley Group and Frasnian Lime Creek Formation of the Iowa Basin. Our results on epizoan diversity corroborate the existence of interbasinal connections between the Western Canada Sedimentary, Iowa, and Appalachian Basins previously inferred from brachiopod lineages.

Conclusions

The Hay River unit B benthic marine community experienced a greater degree of ecological complexity than that of Hay River unit C. The Hay River unit B brachiopods bore a high abundance and diversity of epizoans, which not only increased community diversity but enhanced ecosystem three-dimensionality. Furthermore, Hay River unit B contained evidence of predators which attacked encrusted brachiopod prey; however, why predation scars were found only on taxa prone to encrustation is unknown, and will be the focus of future work.

Both Hay River communities of brachiopods and epizoans are most similar to those of the Cedar Valley Group and Lime Creek Formation of Iowa, USA and least like the Shell Rock Formation of Iowa and the Silica Shale of Ohio, USA. We attribute the pattern of similarity derived in ordination space as reflecting a gradient of basin interconnection, where basin proximity influences ecosystem similarity. This ecological similarity between the Western Canada Sedimentary Basin and the Iowa Basin mirrors known patterns of brachiopod migration.

These results set the groundwork for improved understanding of off-reef, benthic marine ecosystem complexity in the Devonian of the Western Canada Sedimentary Basin. Future work will focus on exploring the dynamics of Devonian marine ecosystems in the Western Canada Sedimentary Basin and further generalization to stratigraphically and economically important units in the Elk Point Sub-Basin in Alberta.

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Figure 1. Results from Bray-Curtis ordination of brachiopods from each locality. Each data point represents one brachiopod taxon from a particular stratigraphic unit. Stratigraphic units are color coded to display relationships of encrusted brachiopods within and between each unit. Brachiopod labels have been omitted to better illustrate geographic patterns. Clusters of data points for four units are outlined below; Hay River units fall within the junction of Cedar Valley Group and Lime Creek Formation clusters.

Si Sh = Silica Formation shale; CVG = Cedar Valley Group; LC O = Lime Creek Formation, Owen Member; LC CG = Lime Creek Formation, Cerro Gordo Member; Sh R = Shell Rock Formation; Hay B = Hay River unit B carbonate bed; Hay C = Hay River unit C carbonate bed.