

# Bioimmuration and what it tells us about the systematics and paleoecology of encrusting organisms in the Cincinnati Group (Upper Ordovician, Ohio, Indiana, and Kentucky)

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## INTRODUCTION

In certain environments there are organisms which undergo rapid postmortem decay and or shell dissolution and are rarely (perhaps never) represented in fossil assemblages. One commonly overlooked process of preservation is bioimmuration, whereby soft-bodied organisms and those with aragonite shells are covered and imprisoned in the calcitic shells of others (Taylor 1990). Bioimmurations are an important resource of paleoecological information, such as overgrowth and competition.

My hypothesis is that repeatable ecological relationships exist between types of hosts and encrusters, which reveal competition between encrusters, and which also depict a predictable ecological succession of encrusters. This extends into an examination of the connection between types of hosts and successions of encrusters in situations where there has been soft-bodied preservation. Results derived from this working hypothesis can be used to make connections between paleontological relationships and ecological theory, providing insight into the Cincinnati ecosystem.

## STUDY AREA

The study is concentrated on the upper Whitewater Formation of the Upper Ordovician, three kilometers south of Richmond, Indiana (sites IN-WY-0001, and IN-WY-0002; sites are from Davis and Cuffey 1998) (Figure 1). Several specimens were also collected from the same or equivalent formations at different locations throughout the Cincinnati of Kentucky (Grant Lake Limestone at site KY-MS-0006 in particular). These specimens, along with an existing collection of Dr. Mark Wilson's at The College of Wooster, were used for both comparison and study.

## METHODS

Specimens were collected in the field and prepared for laboratory study first by washing, and then by ultra-sonication. Identification of hosts, encrusters, and soft-bodied preserved material

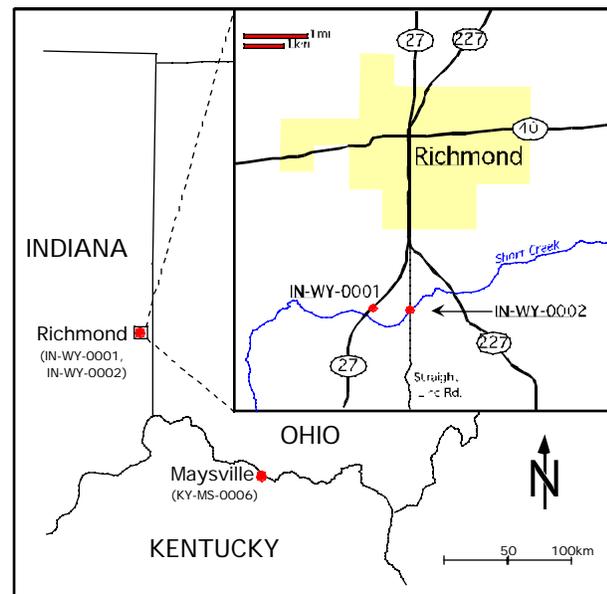


Figure 1. Location of study areas within the tri-state region

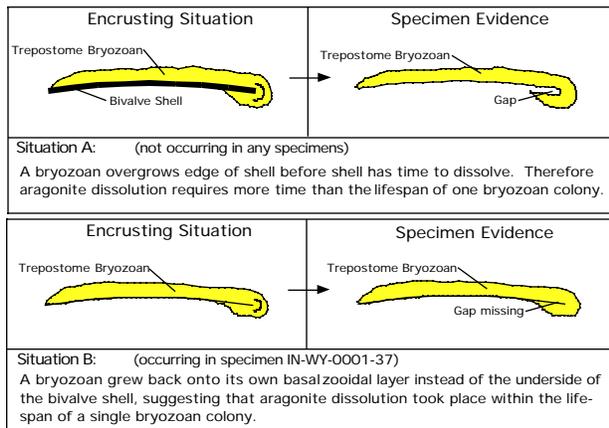
was done by comparing specimens to those from published monographs, and from collections at the Cincinnati Museum of Natural History.

Relationships between encrusters were observed under the binocular microscope, with a hand lens, and with the naked eye. Crosscutting, overgrowth, and bordering relationships between encrusters were examined. For a different perspective, I used a modified version of the acetate peel technique described by Wilson and Palmer (1989). Peels of specimens made by applying the acetate paper directly to an uncut surface, reveal that encrusting relationships are still recorded because of preferential weathering of the rock in the outcrop. A petrographic microscope was used to examine the acetate peels. Photographs and photomicrographs were taken of specimens and peels to document relationships.

## ARAGONITE DISSOLUTION

This study was dependent on the early dissolution of aragonitic shells to reveal the undersides of those encrusters first on the substrate, particularly if they were overgrown by later encrustation. If it were not for the dissolution of aragonitic shells, the bioimmuration phenomenon would not reveal much because the shells would cover any paleoecological evidence. Aragonite is the primary carbonate precipitate in modern seas. However, this was not always the case. During the Ordovician, low Mg:Ca ratios and variable CO<sub>2</sub> concentrations may have changed the relative solubilities of aragonite and calcite, causing calcite to be the primary

precipitate. This means that Ordovician seas would have been undersaturated in terms of aragonite, and therefore aragonite of biologic origin would have gone into solution after the organism (Wilson and Palmer 1992). This idea is often supported by the extreme rarity of specimens with aragonite shells found in Ordovician rocks (Palmer et. al. 1988).



**Figure 2.** Bioimmuration evidence for rapid aragonite dissolution in Ordovician calcite seas

Aragonite dissolution is very important for revealing the relationships and situations in which organisms first arrived on the substrates. Bioimmurations also provide insight into the aragonite dissolution process. The rate of aragonite dissolution in Ordovician calcite seas seems to have been relatively rapid. Some bioimmuration

specimens have lips that were created when the bryozoan colony grew around the edge of the bivalve shell and back upon itself. In order for a bryozoan colony to overlap onto its own basal layer without any gap (where the shell would have been), the shell must have dissolved during the time it took for the colony to grow around the edge of the bivalve (Figure 2). This means that aragonite dissolution in Ordovician calcite seas was quite rapid, occurring within the lifetime of a single bryozoan colony.

## HOSTS AND ENCRUSTERS

Bioimmurations record the substrate in great detail, allowing for surprisingly good identification of the past hosts. Thick trepostome and fast-growing cyclostome bryozoans are

common shell encrusters in the Cincinnatian (Wilson et. al. 1992). A variety of hosts acted as substrates for encrusting bryozoans. The bivalve *Ambonychia* is the most common. Bivalves *Anomalodonta gigantea*, *Opisthoptera casei*, and an unidentifiable bivalve species with concentric plications, also yield good bioimmurations. The remaining hosts are gastropods and nautiloids, both possessing aragonitic shells. Nautiloids may have been particularly good substrates for encrustation because their shells are smooth.

The types of encrusters found immuring the hosts include runner-type bryozoans *Cuffeyella* and *Corynotrypa*, sheet-like bryozoans *Heterotrypa* and *Homotrypella*, and spotty type bryozoans. There is also evidence for cornulitids and sphenothallids encrusting but not immuring the hosts.

## **ENCrustING IN CRYPTIC AND EXPOSED SPACE**

Bioimmuration specimens come in two varieties: external molds and internal molds. An external mold, made by an encrusting bryozoan, details the outer side of the shell surface, whereas an internal mold details the inner shell surface. Internal molds form as follows: the host dies and encrusting organisms that prefer cryptic spaces attach themselves to the inside of the host. The shell fills in with sediment, covering the encrusters, and eventually forming a hardened internal mold or steinkern. Finally the shell dissolves, and the underside of the encrusters' skeletons is left visible on the exterior of the internal mold. Regardless of the type of mold, if the shell dissolves, the undersides of the encrusters are now exposed. So examining bioimmurations reveals the order in which the shell substrates were encrusted.

Bioimmuration specimens representing internal molds show organisms that preferred to grow in primary cryptic space, while specimens representing external molds represent those organisms that prefer primary exposed space. In this study, specimens of internal molds are dominated by the delicate encrusters *Cuffeyella*, *Corynotrypa*, and spotty type bryozoans. Because primary cryptic space would have been protected from most predation and from faster moving currents, it is not surprising that more delicate encrusters attached there. The external molds of bivalves, which represent species that preferred primary exposed space, tend to be sheet-like, sometimes even employing erect growth forms that are much more robust and able to withstand a harsher environment, as found in exposed space.

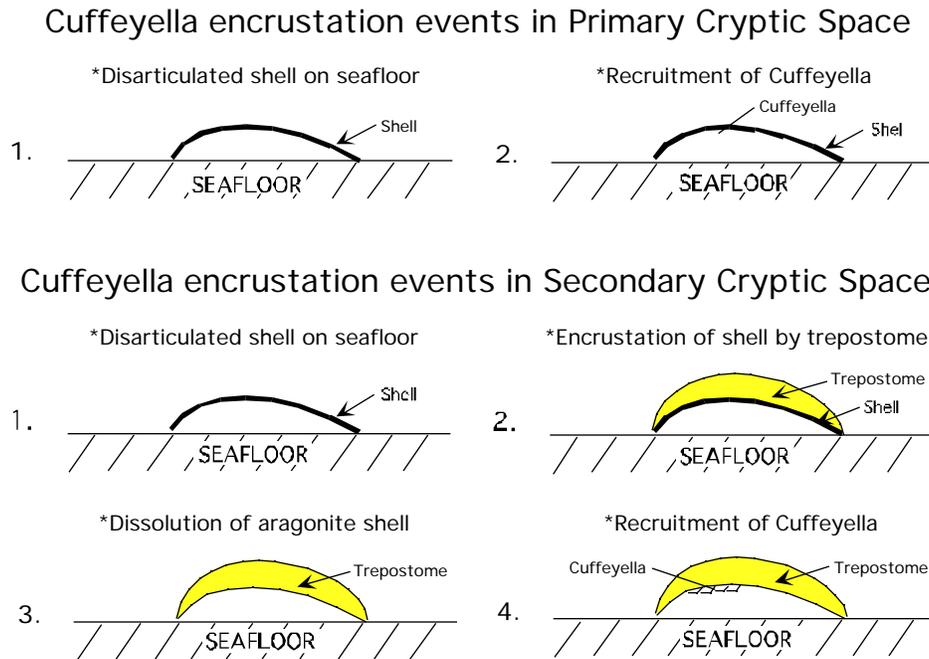
Problems arise when the type of mold is regarded as the sole indicator of environment. Occasionally *Cuffeyella* is found doubly encrusted on the inside of external molds. Because *Cuffeyella* is a delicate encruster, this suggests that an external mold can also define secondary cryptic space (Figure 3). For instance, after shell dissolution, a bryozoan mold of a bivalve shell that is resting convex up on the seafloor creates a secondary cryptic space within its points of contact with the bottom. This environment is again favored for further encrustation by *Corynotrypa*, *Cuffeyella*, and spotty type bryozoans, because it offers shelter from predation and fast moving currents.

## **COMPETITION AND SUCCESSION**

Succession refers to the biological reorganization occurring in an ecological community following a perturbation that opens up free space (Connell and Slatyer 1977). In this case free space is limited to shelly substrates, and perturbations could be anything from the first encrustation of a particular shell to a shell being flipped over during a storm.

In this study, a unique and predictable succession was established between encrusters, regardless of the type of substrate. On shell substrates, in both primary and secondary cryptic

space, runner-type bryozoans such as *Cuffeyella*, *Corynotrypa*, and some spotty forms were often overgrown by sheet-like forms, *Homotrypella* and *Heterotrypa*. However, in some situations where there is free space available in primary and secondary cryptic space, both *Cuffeyella* and sheet-like forms may have experienced growth side-by-side without any overgrowth textures.



**Figure 3.** Description of *Cuffeyella* encrustation in primary and secondary cryptic space

### BRYOZOAN GROWTH FORM VARIABILITY

Free space is a large driving factor in competition and succession between organisms on any substrate. The amount of free space on the substrates is clearly limited because on any particular shell or preexisting bioimmuration there is a fixed amount of area available for encrustation. However, encrusters vary greatly in growth strategies and their abilities to take advantage of the limited space on the substrates.

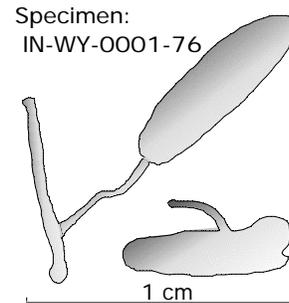
The majority of growth strategy variation is due to the difficult environment inherent to exposed space. It was stated earlier that only sheet-like forms and erect forms are found encrusting exposed space because of their ability to cope better with predation and fast moving currents. The encrusters of exposed space have adopted growth strategies that fall into four categories. Category 1 describes a sheet-like encruster having covered the entire substrate in thin sheets. Category 2 describes a sheet-like encruster having grown in thick mounds over the entire substrate. Category 3 describes a situation where a sheet-like encruster covered the substrate first in a thin sheet, and then when it reached the end of free space on the substrate it branched. Category 4 describes an encruster having grown into an erect form before the substrate is covered (free space still existing when branching occurred).

Particular encrusters utilized different growth strategies. For example, in several specimens, the sheet-like encruster *Homotrypella* employed both thick encrusting and branching growth strategies. Although the growth forms of encrusters may be quite variable, they are likely a function of several factors. The growth form taken by any particular encruster in exposed space is conceivably a result of the amount of free space on the substrate, and nature of the surrounding environment.

### SOFT – BODIED PRESERVATION

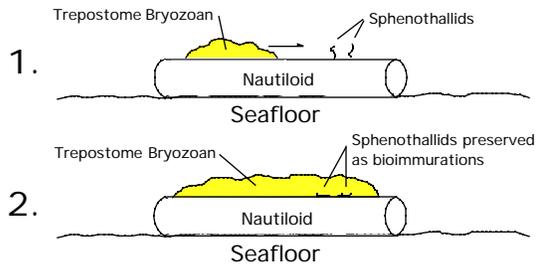
Several specimens studied have evidence of soft-bodied preservation. Cyclocrinoids and sphenothallids are among the types preserved. The sphenothallids are preserved as impressions on an external mold of a nautiloid, which also had an aragonitic shell. The sphenothallids were attached at one end to the surface of the nautiloid. As the bryozoan grew over them, they were pushed down against the substrate and bioimmured (Figure 4).

One intriguing bioimmuration of the bivalve *Ambonychia* shows an interesting texture that appears to be related to soft-bodied preservation (Figure 5). It is difficult to identify the ancient organisms. They are simply too large to be hydroids. Since the forms are found on an external



**Figure 5.** Unusual Soft-bodied organisms

mold, one can speculate that they were soft-bodied encrusters of exposed space.



**Figure 4.** Bioimmuration of sphenothallids

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