Skeletal Overgrowths among Epizoans from the Silurian (Wenlockian) Waldron Shale
Author(s): W. David Liddell and Carlton E. Brett
Reviewed work(s):
Source: Paleobiology, Vol. 8, No. 1 (Winter, 1982), pp. 67-78
Published by: Paleontological Society
Stable URL: http://www.jstor.org/stable/2400568
Accessed: 15/02/2013 15:09
Skeletal overgrowths among epizoans from the Silurian (Wenlockian) Waldron Shale

W. David Liddell and Carlton E. Brett

Abstract.—Substra for numerous epizoans in the Silurian Waldron Shale were provided by the toppled and overturned calyces of camerate crinoids. These were inhabited by a skeletonized fauna consisting of at least 25 species; including several bryozoans, tabulates, inarticulate brachiopods, worms, and echi- noderms.

Many of the encrusting bryozoans exhibit skeletal overgrowths which appear to reflect competitive interactions for space. Coexistence of certain of the bryozoans involved in such interactions is suggested by skeletal features such as inflated growth forms and upturned margins at junctions between colonies (both representing attempts to avoid being overgrown). In addition, the occurrence of overgrowth reversals within individual encounters indicates contemporaneity of that pair. Species may be ranked according to their relative overgrowth success; however, this ranking is far from rigid as lower ranked species may on occasion overgrow more highly ranked species. Such nontransitive patterns appear similar to those described from Recent cryptic bryozoan faunas.

W. David Liddell. Department of Earth Sciences, University of New Orleans, Lake Front, New Orleans, Louisiana 70148. Present Address: Department of Geology, Utah State University, Logan, Utah 84322

Carlton E. Brett. Department of Geological Sciences, University of Rochester, Rochester, New York 14627

Accepted: September 23, 1981

Introduction

Living space is often an important limiting resource for organisms inhabiting hard substrata in modern seas (Connell 1961a; Dayton 1971; Paine 1974; Jackson 1977). Competition for space in hard substratum communities has been well documented for temperate intertidal (Connell 1961a,b, 1975; Paine 1966, 1974; Dayton 1971; and others) and subtidal systems (Stebbing 1973; Osman 1977; Sutherland and Karlson 1977; Karlson 1978) and for tropical subtidal systems, including cryptic communities (Lang 1973; Jackson and Buss 1975; Buss 1976; Jackson 1977, 1979; Buss and Jackson 1979). The fossil record includes representatives of many groups, such as sponges, corals, bryozoans, brachiopods, various “worms” and others, which are adapted to life on or in hard substrata, yet, with few exceptions (Fritz 1976; Palmer and Palmer 1977; Meyer 1978; Liddell and Brett 1979; Taylor 1979; Gault and McKinney 1980), spatial competition within fossil hard substratum faunas has been rarely documented. Most paleontological studies which have dealt with epizoans (Clarke 1908, 1921; Bowsher 1955; Seilacher 1960; Ager 1961; Hurst 1974; Richards 1974; Thayer 1974; Thomsen 1977; Pitrat 1982) have been concerned only with the relationships existing between epizoans and their hosts or substrata.

Encrusting faunas of hard substrata provide paleoecologists with a unique opportunity to examine the relationship between substratum and its inhabitants as well as the interrelationships existing between faunal members. This applies whether the substrata are inorganic hardground surfaces or the skeletal remains of organisms. Original spatial relationships of the encrusting faunas are retained as they are not subject to transportation or sorting and the encrusting or endolithic life habit of many members also ensures their preservation and representation in the fossil assemblage.

The present study deals with epizoans inhabiting calyces of Silurian crinoids in the Waldron Shale and analyzes some of the biological interactions which took place on these substrata as well as documenting the composition of the epizoan fauna.

Materials and Methods

The Silurian (Wenlockian) Waldron Shale extends from southeastern Indiana into Ohio, Kentucky and Tennessee. Throughout its ex-
tent, the Waldron Shale is quite uniform and easily recognized as a 2–3 m thick, gray calcareous shale to mudstone with scattered and laterally discontinuous thin limestone bands. The fossil content of the Waldron differs markedly from site to site.

Over 200 calyces of camerate crinoids from the Waldron Shale were censused in detail during the course of this study. Crinoid species examined include *Eucalyptocrinites crassus* (Hall), *E. magnus* (Worthen), *E. elrodi* (Miller) and *Lyriocrinus melissa* (Hall). Of these, specimens of *E. crassus* and *E. magnus* were by far the most common crinoids in the collections used. All specimens were collected from a limestone quarry located near Newsom Station, Decatur Co., Tennessee (Kingston Springs 7.5′ Quadrangle). Specimens were obtained from an interval between approximately 25 and 45 cm above the base of the Waldron Shale and are housed in the collections of the University of Michigan Museum of Paleontology (UMMP).

Analyses were directed toward determination of the composition of the epizoan fauna and dynamics of interactions occurring between members of the fauna. Data were gathered on the diversity of epizoans present, relative preservation, frequency of skeletal overgrowths, ubiquity (number of calyces with species present/total number of calyces examined) and abundance (area covered) of the various species. Areas covered by epizoans were estimated under the microscope by using metric grids on clear acetate sheets.

**Biostratinomy**

The Waldron Shale crinoids are quite abundant on certain bedding surfaces, reaching densities of 13/m². After death and toppling to the seafloor the crinoids apparently underwent rapid disarticulation of stem, arm and partition plates. The rigidly sutured dorsal cups of camerate crinoids such as *Eucalyptocrinites*, however, evidently remained intact and exposed for a long time as suggested by their prolific associated epizoan faunas. The majority of calyces (90% of specimens observed in situ) were oriented in the apparently stable position of resting upon the radial facets with the stem facet upwardly oriented. Crushing of specimens buried on their sides and geopetal structures allowed estimates of orientations from loose specimens and further confirmed the above orientation for most. That many of the epizoans preserved on the crinoid calyces represent postmortem encrustations is suggested by epizoan overgrowths of both stem and radial facets as well as corroded regions of the calyces which would not be possible if the crinoids had been alive at the time of settlement.

**Composition of Epizoan Fauna**

The fauna of epizoans inhabiting the crinoid calyces consists of at least 27 species which are distributed among 6 or more phyla and includes bryozoans, inarticulate brachiopods, serpulid and cornulitid “worms,” tabulates, rugose corals, pelmatozoan echinoderm holdfasts and boring organisms of unknown affinity (possibly sponges) (Table 1; Fig. 1). It is certainly possible that soft-bodied encrusters were also present, as in Recent hard substratum communities (Jackson 1977), yet were not preserved. While high ubiquity values are distributed among several phyla, bryozoans are the most prominent epizoans on the basis of both percent cover (total area covered by epizoan species on all calyces examined/total surface area of all calyces examined) and total numbers of species present.

Bryozoans account for 16 of the 27 epizoan species noted (refer to Appendix 1). While several distinct taxa of bryozoans were readily recognizable, often species and occasionally generic identifications were not possible due to the thinness of the encrusting zoaria and recrystallization of skeletal calcite. Therefore, the examination of competitive patterns among the bryozoans required the use of an operational classification, in part.

The bryozoans are clearly dominated (based on percent cover) by *Berenicea consimilis* Lonsdale (Cyclostomata), a cosmopolitan and long-ranging genus. *Berenicea* (Figs. 2, A; 3, D–F) is related to forms such as *Hederella* and *Rep-taria* which are known to encrust relatively smooth, even substrates. Several species of ceramoporid bryozoans (Cystoporata) (Figs. 2, C, E; 3, A–D, G–I) also occur commonly on the *Eucalyptocrinites* calyces, frequently forming elevated, circular patches. It is noteworthy that ceramoporids are also important components of hardground faunas, especially in the cryptic and
Table 1. Ubiquity and percent coverage of epizoans on *Eucalyptocrinites crassus* and *E. magnus*. Ubiquity = number of calyces with epizoan species/total number of calyces examined, based on census of 50 calyces of *E. crassus* and 50 calyces of *E. magnus*. Percent cover = percentage of surface area based on measurement of 510.0 cm² surface area of *E. crassus* 628.5 cm² surface area of *E. magnus*. Values not listed under percent cover are those < 0.1% of substratum surface area. Refer to Appendix I for diagnoses of bryozoan taxa.

<table>
<thead>
<tr>
<th>Bryozoans</th>
<th>Ubiquity</th>
<th>E. crassus</th>
<th>E. magnus</th>
<th>Percent cover</th>
<th>E. crassus</th>
<th>E. magnus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Berenicea consimilis</td>
<td>52.9</td>
<td>43.8</td>
<td></td>
<td>23.5</td>
<td>6.9</td>
<td></td>
</tr>
<tr>
<td>Berenicea sp.</td>
<td>0.0</td>
<td>4.7</td>
<td></td>
<td>0.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fistulipora sp.</td>
<td>43.2</td>
<td>56.3</td>
<td></td>
<td>1.8</td>
<td>1.4</td>
<td></td>
</tr>
<tr>
<td>Leioclema sp. 1</td>
<td>13.7</td>
<td>12.5</td>
<td></td>
<td>0.5</td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td>Leioclema sp. 2</td>
<td>0.0</td>
<td>2.1</td>
<td></td>
<td>0.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ceramopora sp. 1</td>
<td>58.8</td>
<td>66.7</td>
<td></td>
<td>1.1</td>
<td>2.3</td>
<td></td>
</tr>
<tr>
<td>Ceramopora sp. 2</td>
<td>25.5</td>
<td>27.1</td>
<td></td>
<td>2.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ceramopora sp. 3</td>
<td>0.0</td>
<td>2.1</td>
<td></td>
<td>0.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ptilodictyid</td>
<td>19.6</td>
<td>14.6</td>
<td></td>
<td>0.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stomatopora sp.</td>
<td>17.6</td>
<td>6.3</td>
<td></td>
<td>0.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Monotrypa sp.?</td>
<td>11.8</td>
<td>6.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hallopora sp.</td>
<td>7.8</td>
<td>35.4</td>
<td></td>
<td>0.2</td>
<td>0.6</td>
<td></td>
</tr>
<tr>
<td>Hallopora ? sp.</td>
<td>31.4</td>
<td>43.8</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>fistuliporid</td>
<td>0.0</td>
<td>2.1</td>
<td></td>
<td>0.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>undt. bryozoan 1</td>
<td>0.0</td>
<td>&lt;1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>undt. bryozoan 2</td>
<td>2.0</td>
<td>0.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Echinoderm holdfasts</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Eucalyptocrinites</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Stephanocrinus</em> sp.</td>
<td>33.3</td>
<td>27.1</td>
<td></td>
<td>0.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Dimerocrinites</em> sp.?</td>
<td>13.7</td>
<td>3.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>undt. holdfast</td>
<td>0.0</td>
<td>2.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>“Worms”</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Spirorbis</em> sp.</td>
<td>60.8</td>
<td>79.2</td>
<td></td>
<td>0.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cranites</em> sp.</td>
<td>11.8</td>
<td>18.8</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brachiopods</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Crania</em> sp.</td>
<td>17.6</td>
<td>10.4</td>
<td></td>
<td>1.0</td>
<td>0.9</td>
<td></td>
</tr>
<tr>
<td>Corals</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Favositites</em> sp.</td>
<td>3.9</td>
<td>0.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Enterolasma</em> sp.</td>
<td>&lt;1</td>
<td>0.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Miscellaneous</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>sponge? borings</td>
<td>0.0</td>
<td>2.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>undt. borings</td>
<td>19.6</td>
<td>12.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

underledge surface subcommunity (Palmer and Palmer 1977; Brett and Liddell 1978). Another common cystoporate is *Fistulipora* (Fig. 2, B). Abundant trepostomes include encrusting sheets of *Leioclema* (Figs. 2, C, E; 3, G, I), *Monotrypa* and basal expansions of *Hallopora* (Fig. 2, C, E, F). Cryptostomes are represented by the minute fibrous holdfasts of a ptilodictyid bryozoan.

Two distinctive types of crinoid holdfasts were commonly observed—dendritic radices with pentalobate lumens (Fig. 2, C), belonging to *Eucalyptocrinites*, and small simple discoidal holdfasts (Fig. 2, E). The latter closely resemble holdfast disks of *Stephanocrinus* from the Silurian Rochester Shale of New York. *Stephanocrinus gemmiformis* Hall is very abundant in the Waldron Shale at Newsom and is tentatively correlated with the small holdfasts. Two additional echinoderm holdfasts, one possibly belonging to *Dimerocrinites*, are also found in the encrusting fauna.

Spirorbid worm tubes (Fig. 2, F) are abundant on the calyces, where they frequently occur on other epizoans. The spirorbids do not exhibit marked aggregation as observed in some mod-
ern *Spirorbis* (Knight-Jones 1951). The other worm taxon, *Cornulites*, is considerably less common.

Due to its large size the inarticulate brachiopod *Crania* (Fig. 2, D) may cover a relatively high percentage of total calyx surface area. However, these brachiopods exhibit low ubiquity and are typically clustered, with three or four specimens occurring on a single calyx. That more than one generation of *Crania* is present in some cases is evident from overgrowths of worn ventral valves by unworn specimens retaining both valves.

The tabulate *Favosites* (Fig. 3, G) and coral *Enterolasma* occur on the calyces but have low ubiquity values and occupy negligible amounts of surface area. Finally, certain pittings and borings which occur on the calyces are tentatively attributed to sponges, although others cannot be assigned to a known taxon.

**Epizoan Interactions**

Encrusting organisms commonly compete for space via skeletal overgrowth (Connell 1961a, b; Stebbing 1973; Jackson 1979). Mechanisms influencing the outcome of encounters leading to overgrowth of one organism by another include differential growth rates (Connell 1961a,b), shading or overtopping (Dayton et al. 1974), production of allelochemicals (Bryan 1973;...
Jackson and Buss 1975), extracoelenteric digestion (Lang 1973) and feeding interference (Buss 1979). The documentation of competitive interactions in the fossil record must be based upon evidence provided by skeletal features. The paramount problem associated with interpreting competition in the fossil record is that of the relative timing of events (i.e. did the overgrowth occur contemporaneously with the growth of the subordinate organism or after its death?). The possibility of mistaking the superposition of non-contemporaneous organisms for competitive interactions may be reduced, although not eliminated, by considering only those overgrowths involving specimens of equally good preservation. In certain instances skeletal modifications related to competitive interactions, such as upwardly directed colony margins or inflated growth forms in bryozoans (Stebbing 1973; Jackson and Buss 1975; Palmer and Palmer 1977) (Figs. 2, B; 3, C), may be observed. That other of the observed overgrowths represent unequivocal competitive interactions between two living organisms is indicated by reversals—such that colony “A” overgrows colony “B” at one point while being overgrown by colony “B” at another point (Fig. 3, D, F). Seven percent of the 225 interaction pairs examined exhibited such reversals. Even in those cases where contemporaneous growth of two bryozoans cannot be proven, the consistent overgrowth of one species by another provides information about life histories. The consistently overgrown species must be competitively inferior in actual interactions or, alternatively, an early colonizer.

Although almost all epizoan groups from the Waldron Shale exhibited occasional skeletal overgrowths, only the bryozoans were sufficiently common to allow quantification of such interactions. Additionally, problems of scale are encountered when attempting to compare the competitive abilities of such diverse groups as crinoids (involving only their holdfasts), brachiopods, spirorbids and bryozoans. All cases of overgrowths involving unworn bryozoan specimens were entered into a pairwise matrix (Table 2). Species involved in fewer than 10 total interactions were included together in a miscellaneous category. The ratio of “wins” (successful overgrowths)/total interactions or W/T provides an index of overgrowth abilities for a particular species.

Table 2 displays both overall W/T values and values for specific interaction pairs based upon 225 interspecific bryozoan encounters involving well preserved pairs. Based upon the overall W/T values it is apparent that the bryozoans are divisible into three broad groups of differing overgrowth abilities (Table 3). A value of approximately 0.5 (Ceramopora species and others) suggests that the bryozoan is intermediate in overgrowth abilities, whereas lower values (Berenicea) indicate that the bryozoan is relatively subordinate and greater values (Hallopora species and others) indicate that the bryozoan is competitively superior. The ranking of the different bryozoan species on the basis of overall W/T values might appear biased as most of the interactions involve an encounter between some species and the typically subordinate and very abundant Berenicea. A similar pattern emerges, however, when interactions involving Berenicea are excluded from determinations of overall W/T. When this is done, the two Hallopora species and the ptildictyd

---

**Figure 3.** Interactions among epizoan species on Eucalyptocrinites calyces (insets show enlargements of epizoan interactions). A. Oblique lateral view of small calyx of E. crassus heavily encrusted by bryozoans; majority of surface covered by Berenicea constimilis Lonsdale with smaller patches of ceramopodid species also present; ×2; UMMP 64091. B. Overgrowth of ceramopodid colony (right) by another ceramopodid and a few zooecia of Berenicea (lower right) although the latter is for the most part subordinate in this interaction; ×6.0. C. Ceramopodid colony overgrowing Berenicea; note raised and thickened lip at leading edge of ceramopodid colony; ×6.0. D. Additional lateral view of UMMP 64091; note characteristic fan-like growth form of Berenicea; ×2.0. E. Contact between leading edges of two colonies of Berenicea apparently resulting in a standoff; ×6.0. F. Overgrowth of thick ceramopodid colony by Berenicea; note that portions of the Berenicea colony have been overgrown by the same ceramopods in other areas of the calyx; ×6.0. G. Lateral view of additional E. crassus cup showing encrustation by Favosites sp. (left center) and several bryozoans including Berenicea (right of center and upper right), Leiolema (upper center) and ceramopods (lower center and just below Leiolema); ×1.5; UMMP 64092. H. Ceramopodid (left) overgrowing Berenicea at leading edge; ×4.5; I. Leiolema (upper left) overgrowth on ceramopodid species (lower left) with both specimens overgrowing Berenicea; ×4.5.
receive values between 0.80–1.00, while the other bryozoans (excluding Berenicea) show values falling between 0.22–0.66.

Within each of the three groupings of overgrowth ability (high, intermediate, low) it is unlikely that minor differences in W/T are significant. In fact, the rankings of overgrowth ability (Tables 2 and 3) appear to be far from rigid. Inspection of the values for specific interaction pairs (Table 2) reveals that lower ranked species may on occasion overgrow more highly ranked species. The occurrence of overgrowth reversals within individual encounters further supports the existence of a flexible pattern of overgrowth dominance.

When rankings of bryozoans on overall W/T values are compared with rankings based upon percent cover or ubiquity (Table 3) it is apparent that the bryozoans with superior overgrowth abilities are not the most abundant members of the fauna. In fact, an inverse relationship appears to exist between overgrowth abilities and percent cover and, to a lesser degree, ubiquity. The subordinate (based on overgrowth abilities) Berenicea if by far the most abundant member of the epizoan fauna (based on both percent cover and ubiquity). The possibility exists that the high W/T values for smaller, less abundant (based on percent cover) bryozoans such as Hallopora may be, in part, an artifact due to complete overgrowth of these smaller forms when they are subordinate, thereby preventing observation of cases where the smaller bryozoans are competitively subordinate. It should be noted in this context that smaller, pimple or lump-shaped bryozoans such as Hallopora would appear as bumps or irregularities when overgrown by flat laminate bryozoans such as Berenicea—a condition that is very rarely observed.

**Discussion**

Although the paleontological literature contains many examples of studies dealing with epizoan faunas (cited earlier) studies of competitive interactions between epizoan species are relatively few in number. Palmer and Palmer (1977) described skeletal overgrowths in an encrusting fauna inhabiting an Ordovician hardground, although the observed number of interactions for each species pair was low. Meyer (1978) studied spatial competition in Devonian patch reefs and found a competitive hierarchy in which dominant organisms (stromatoporoids and blue-green algae) could consistently exclude those lower in the hierarchy (corals), presumably

### Table 2. Outcomes of 225 interspecific bryozoan interaction pairs expressed as “Wins”/Total Interactions. “Wins”/Total displayed are for species “A” when involved in interactions with species “B.”

<table>
<thead>
<tr>
<th>Species B</th>
<th>Berenicea sp.</th>
<th>Ceramopora sp. 1</th>
<th>Ceramopora sp. 2</th>
<th>ptilodictyid</th>
<th>Leioclema sp. 1</th>
<th>Monotrypa?</th>
<th>Fistulipora sp.</th>
<th>Hallopora sp. 1</th>
<th>Hallopora? 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Berenicea</td>
<td>(0.93)</td>
<td>(0.92)</td>
<td>(0.92)</td>
<td>(0.91)</td>
<td>(0.68)</td>
<td>(0.5)</td>
<td>(0.63)</td>
<td>(0.67)</td>
<td>(0.5)</td>
</tr>
<tr>
<td>Ceramopora 1</td>
<td>(0.33)</td>
<td>(1.8)</td>
<td>(0.5)</td>
<td>(0.4)</td>
<td>(0.4)</td>
<td>(0.3)</td>
<td>(0.67)</td>
<td>(0.8)</td>
<td>(0.8)</td>
</tr>
<tr>
<td>Ceramopora 2</td>
<td>(0.63)</td>
<td>(0.8)</td>
<td>(0.7)</td>
<td>(0.2)</td>
<td>(0.17)</td>
<td>(0.5)</td>
<td>(0.67)</td>
<td>(0.67)</td>
<td>(0.67)</td>
</tr>
<tr>
<td>Ptilodictyid</td>
<td>(0.2)</td>
<td>(0.17)</td>
<td>(0.17)</td>
<td>(0.17)</td>
<td>(0.17)</td>
<td>(0.17)</td>
<td>(0.17)</td>
<td>(0.17)</td>
<td>(0.17)</td>
</tr>
<tr>
<td>Leioclema 1</td>
<td>(0.68)</td>
<td>(0.63)</td>
<td>(0.63)</td>
<td>(0.63)</td>
<td>(0.63)</td>
<td>(0.63)</td>
<td>(0.63)</td>
<td>(0.63)</td>
<td>(0.63)</td>
</tr>
<tr>
<td>Monotrypa?</td>
<td>(0.67)</td>
<td>(0.67)</td>
<td>(0.67)</td>
<td>(0.67)</td>
<td>(0.67)</td>
<td>(0.67)</td>
<td>(0.67)</td>
<td>(0.67)</td>
<td>(0.67)</td>
</tr>
<tr>
<td>Fistulipora</td>
<td>(0.33)</td>
<td>(0.33)</td>
<td>(0.33)</td>
<td>(0.33)</td>
<td>(0.33)</td>
<td>(0.33)</td>
<td>(0.33)</td>
<td>(0.33)</td>
<td>(0.33)</td>
</tr>
<tr>
<td>Hallopora 1</td>
<td>(0.3)</td>
<td>(0.3)</td>
<td>(0.3)</td>
<td>(0.3)</td>
<td>(0.3)</td>
<td>(0.3)</td>
<td>(0.3)</td>
<td>(0.3)</td>
<td>(0.3)</td>
</tr>
<tr>
<td>Hallopora? 2</td>
<td>(0.3)</td>
<td>(0.3)</td>
<td>(0.3)</td>
<td>(0.3)</td>
<td>(0.3)</td>
<td>(0.3)</td>
<td>(0.3)</td>
<td>(0.3)</td>
<td>(0.3)</td>
</tr>
<tr>
<td>Misc.</td>
<td>(0.67)</td>
<td>(0.67)</td>
<td>(0.67)</td>
<td>(0.67)</td>
<td>(0.67)</td>
<td>(0.67)</td>
<td>(0.67)</td>
<td>(0.67)</td>
<td>(0.67)</td>
</tr>
</tbody>
</table>

**Table 3.** Overall W/T, percent cover and rank (based on area covered) for bryozoans commonly involved in competitive interactions (derived from Tables 1 and 2).

<table>
<thead>
<tr>
<th>Wins/total interactions</th>
<th>Bryozoan</th>
<th>% Cover</th>
<th>Rank based on % cover</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.93</td>
<td>Ptilodictyid</td>
<td>0.8</td>
<td>6</td>
</tr>
<tr>
<td>0.92</td>
<td>Hallopora? 2</td>
<td>0.4</td>
<td>8</td>
</tr>
<tr>
<td>0.91</td>
<td>Hallopora sp. 1</td>
<td>0.9</td>
<td>5</td>
</tr>
<tr>
<td>0.68</td>
<td>Ceramopora sp. 1</td>
<td>7.0</td>
<td>3</td>
</tr>
<tr>
<td>0.67</td>
<td>Ceramopora sp. 2</td>
<td>0.6</td>
<td>7</td>
</tr>
<tr>
<td>0.67</td>
<td>Monotrypa sp.</td>
<td>0.3</td>
<td>9</td>
</tr>
<tr>
<td>0.63</td>
<td>Leioclema sp. 1</td>
<td>1.7</td>
<td>4</td>
</tr>
<tr>
<td>0.62</td>
<td>Fistulipora sp.</td>
<td>7.3</td>
<td>2</td>
</tr>
<tr>
<td>0.17</td>
<td>Berenicea consimilis</td>
<td>76.3</td>
<td>1</td>
</tr>
</tbody>
</table>
through more rapid growth rates. Gault and McKinney (1980) described skeletal overgrowths occurring in Ordovician sponge—bryozoan bioherms and Fritz (1976) described bryozoan—stromatoporoid interactions, also from the Ordovician. In the most comprehensive study to date, Taylor (1979) examined interactions among epizoans inhabiting Jurassic bivalves and documented lateral overgrowths among 22 taxa (including sponges, bryozoans, spirorbids, brachiopods, forams and others).

The skeletonized faunas of Recent tropical cryptic communities provide an interesting comparison with the fauna which inhabited calyces of crinoids in the Waldron Shale with the exception that the former lack larger, holdfast bearing forms such as crinoids. Although exposed hard substrates in tropical subtidal systems may be covered by a variety of organisms such as foraminifers, calcareous algae (Corallinacea), sponges, scleractinians and zoanthids, bryozoans are still the main skeletonized encrusters of hard substrata in cryptic communities. The cryptic faunas described by Jackson (1977, 1979) are dominated by colonial organisms (occupying 95% of substratum covered) and include chelostome bryozoans (occupying approximately 17% of the substratum), coraline algae, demosponges and other colonial organisms, as well as occasional spirorbid worms and brachiopods.

Jackson (1977, 1979) reported only 2% bare space in the cryptic communities studied. Similarly low percentages of bare space are reported for non-cryptic subtidal communities from the tropics (Jackson 1977; Ohlhorst 1980). This is in marked contrast to the percent coverage determined for the Waldron Shale calyces, which typically varies from negligible amounts to a median of 20% and, rarely, much higher. This may reflect nonpreservation of soft-bodied organisms, such as sponges and algae, in the fauna. It is of interest to note that Palmer and Palmer (1977) and Brett and Liddell (1978) similarly described low (5% and 25%, respectively) coverage on two Ordovician hardgrounds. Taylor (1979) also described very low (not quantified) coverage of bivalve shells by epizoans from the Jurassic.

The competitive patterns displayed by the Silurian bryozoans appear not to be a hierarchy (e.g. Connell 1961a,b; Lang 1973) in which higher ranked species can “triumph” over all lower ranked species. The bryozoans may be divided into three broad groups (high, intermediate, low) based upon overgrowth abilities (Tables 2 and 3) but within groups there are no clear dominants. Also, higher ranked species may on occasion be overgrown by much lower ranked species (e.g. Berenicea over Hallopora). Finally, overgrowth reversals were observed to occur within individual encounters. Therefore, the competitive pattern which emerges is flexible and perhaps more similar to nontransitive patterns (networks?) described for modern bryozoans (Jackson and Buss 1975; Buss 1976; Osman 1977; Jackson 1979), rather than a transitive hierarchy. It must be stressed that interpretations of species-specific interaction pairs should be tentative due to the small sample size for any particular pair. Nonetheless, the nontransitive nature of overgrowth competition within the Silurian fauna is well documented by these data.

Studies of modern bryozoans have shown that the outcome of any given encounter may depend not only on the species involved and such species-characteristic features as possession of defensive armature (Stebbing 1973), colony form, or growth rates but also on other factors such as angle of encounter (Jackson 1979), size-thickness (Buss 1980), and density (Buss 1981). Stebbing (1973) has shown that possession of structures such as spines serves as defense against overgrowth. Additionally, Buss (1980) has demonstrated that the outcome of overgrowth competition may be dependent upon relative vertical relief of the interacting colonies. The low overgrowth success rate of Berenicea may be due to a combination of these factors as Berenicea possesses thin, flat, and relatively smooth zoaria in contrast to other members of the fauna which exhibit thicker and often lumpy (e.g. Fistulipora and others) or pimple or stump-shaped (e.g. Hallopora, ptilodictiyid) colonies which may have rough, rasp-like surface textures (e.g. Ceramopora). Finally, although a bryozoan may be able to resist overgrowth by another when encountered at a growing edge, it is less likely to do so if encountered on a flank (Jackson 1979). This may be an additional factor in the determination of
the outcomes of interactions involving Berenicea. Although many Paleozoic bryozoans possessed fan-shaped colonies in early astogeny (Boardman and McKinney 1976; Pachut and Anstey 1979) the colonies often assumed different shapes during later development. Berenicea (Fig. 3:D) however, maintained a fan-shaped colony form during later astogeny. Thus, on a random basis, Berenicea is likely to be involved in a much higher proportion of flank encounters than other radially growing bryozoans (e.g. ceramoporids, Leio clema) which may have contributed to the overall low W/T values of Ber enicea.

Jackson (1979) found that competitively superior bryozoans (based on overgrowth abilities) in modern cryptic communities are also the most abundant in terms of area covered. In contrast, the encrusting bryozoans from the Silurian Waldron Shale exhibit an opposite trend as the more competitively superior species (high W/T values) cover relatively little area within the community (Tables 1 and 3). This pattern appears more analogous to that displayed by Recent scleractinian corals from the Caribbean which show a negative correlation between digestive dominance abilities (Lang 1973) and abundance in the reef community (Porter 1974; Ohlhorst 1980). Organisms such as Berenicea, with apparently limited overgrowth abilities, are somehow capable of maintaining high abundance within the community perhaps due to rapid growth and/or high recruitment or, alternatively, early colonization. Other less common bryozoans such as Hallopora or the pitidioidid species may rely upon their dominant overgrowth capabilities to ensure their existence within the community. Thus, it is suggested that among the bryozoan members of the epizoan fauna two very different strategies may exist for maintaining the existence of species within the community.

This study describes a Silurian fauna adapted to life on hard substrata. Further, skeletal overgrowths within bryozoan members of the fauna are documented; the occurrence of such overgrowths may have played a role in influencing community structure. The patterns of overgrowth competition delineated appear to be nonhierarchical.

Acknowledgments

We wish to acknowledge the efforts of D. B. Macurda, Jr. who initially collected many of the crinoid specimens used in this study. We also extend our appreciation to J. B. C. Jackson and S. L. Ohlhorst who have provided comments on the manuscript. Field work was supported, in part, by a Turner Research Grant (administered by the Department of Geology and Mineralogy, The University of Michigan). Laboratory facilities and access to collections of Waldron Shale crinoids were provided by the Museum of Paleontology, The University of Michigan.

Literature Cited


DAYTON, P. K. 1971. Competition, disturbance, and community
SILURIAN EPIZOOANS

LIDDELL, W. D. AND C. E. BRETT. 1979. Calyces of Eucalyptobryozoo-
PACHUT, J. F. AND R. L. ANSTEY. 1979. A developmental explana-
PALMER, T. J. AND C. D. PALMER. 1977. Faunal distribution and colonization strategy in a Middle Ordovician hardground com-
PITRAT, C. W. AND F. S. ROGERS. 1978. Spinocyrtia and its epi-
blasts in the Traverse Group (Devonian) of Michigan. J. Paleon-
tol. 52:1315–1324.
TAYLOR, P. D. 1979. Palaeoecology of the encrusting epifauna of some British Jurassic bivalves. Palaeogeog., Palaeoclimatol., Pal-
aeocol. 28:241–262.

Appendix 1

DIAGNOSES OF ENCIRCLING BRYOZOAN TAXA

ORDER CYCLOSTOMATA Busk, 1852

FAMILY DIATROPIDAE Gregory, 1899

Berenicea consimilis (Loudsle.)

Diagnosis.—Zoaria consisting of thin unilaminar encircling expansions, flabelliform to nearly circular in outline. Zoocoe tubes flattened, cylindrical, non-
tapering (except at distal terminus), subequal in diameter (0.20 mm) and ranging in length from 1.0 to 2.0 mm; tubes ornamented with transverse ridges. Ap-
portures circular and approximately 0.30 mm in diameter.

Comments.—By far the most abundant bryozaan in the fauna.

Berenicea sp.

Diagnosis.—Differs from B. consimilis in having somewhat broader more rounded tubles with large circular apertures. Also, possesses a more irregular digitate growth form.

Comments.—Uncommon.

FAMILY TUBULIPORIDAE Johnston, 1838

Stomatopora sp.

Diagnosis.—Very characteristic vine-like growth form with small (approx. 0.30 mm diam.) uniserially arranged zoecia; zoaria branch dichotomously.

ORDER CRYPTOSTOMATA Vine, 1883

FAMILY TILLOTJIDAE Zittel, 1880

Ptilodictidioida fallstafes.

Diagnosis.—Circular to elliptical-shaped fibrous expansions up to 15 mm across, often with irregular lobate margins; lacks visible zoecia. Zoarium at-
tached to central depression.

ORDER CYSTOPORATA

FAMILY CERAMOPORIDAE Ulrich, 1882

Ceramopora sp. 1

Diagnosis.—Zoaria discoidal, 0.5–1.0 mm thick and up to 10 mm in diam-
eter, slightly depressed mediately (maculae) and frequently with slightly upward flaring borders. Zoecia large (up to 1.0 mm dia.) and prostrate proximally with irregular and relatively thick walls; no diaphragms observed. Zoocoeal apertures large (0.25–0.30 mm in maximum dimension), oblique, subtriangular, radially
arranged; apertures bear prominent lunaria which give zoaria a rasplike texture.

Comments.—This is one of the most distinctive bryozaan taxa because of the circular zoarial outline and the rasplike texture.

Ceramopora sp. 2

Diagnosis.—Small (1.0–1.5 mm) circular zoaria composed of 10–15 radially arranged trumpet-shaped zoecia with oblique lunate apertures.

Comments.—These may represent very small colonies of C. imbricata.

Ceramopora sp. 3

Diagnosis.—Similar to C. sp. 1 except colonies smaller in diameter, distinctly discoidal and more convex (not as flattened); zoaria with distinct central mac-
ulae and large (0.4 mm) triangular radial apertures with lunaria.

Comments.—This form most closely resembles C. imbricata Hall from the Rochester Shale of New York and may be conspecific.

Undetermined bryozaan 1

Diagnosis.—Large irregular patches up to 15 mm across with hummocky surface and irregular upturned margins. Surface of colony bears well-defined muncticles which are 1 mm in diameter and spaced approximately 3.0 mm apart. Zoocoeal apertures roughly circular, 0.15 mm in diameter, with lunaria and separated from one another by thick (0.1–0.2 mm) walls. Zoecia are re-
cumbent proximally, curving upward distally; in tangential section zoecia ap-

This content downloaded on Fri, 15 Feb 2013 15:09:37 PM
All use subject to JSTOR Terms and Conditions
FAMILY FISTULIPORIDAE Ulrich, 1882

Fistulipora cf. F. concentrica (Hall)

Diagnosis.—Irregular lumpy crustose form, commonly with upturned margins; underside frequently separated from direct contact with hard substrate, demonstrating an upward arching of the zoarium. Where visible, the underside bears a thin concentrically-wrinkled coenosteum. Zoarial surfaces possess scattered (up to 5 mm apart) irregular maculae. Zoecial apertures large (0.25 mm), circular or roughly rhomboidal where intersecting zoarium obliquely; may be surrounded by a slight peristome. Zoecia separated by very thick (0.25–0.50 mm) interspaces occupied by large vesicles with sides convex toward zoarial surface. Zoecia cylindrical, straight-walled with few and very thin diaphragms. Autozoecia and acanthostyles are absent.

Comments.—This bryozaon occurs both loosely attached to the crinoid calycyaes and as isolated patches in the surrounding sediment. Colonies show great plasticity in form and an evident capacity to arch over obstacles.

ORDER TREPOSTOMATA Ulrich, 1882

Monotrema? sp.

Diagnosis.—Roughly circular domical patches up to 3 mm thick at center. Zoecia large (0.5 mm dia.), regularly hexagonal and angulate. Zoecia bear thin slightly sinuous walls and thinner, gently convex upward, widely spaced diaphragms. Mesopores and acanthostyles lacking.

Comments.—The simple large zoecia of this bryozaon make it highly distinctive; it is tentatively identified as a species of Monotrema although the zoecial walls are not as crenulate as those of the genotype M. undulata.

FAMILY STENOPORIDAE Waagen & Wentzel, 1886

Leioclema sp. 1

Diagnosis.—Zoaria irregular thin encrusting patches. Autozoecia small (0.25 mm), roughly circular (but tending to become petaloid), surrounded by irregular polygonal mesopores (0.05–0.10 mm dia.). Acanthostyles not observed.

Leioclema? sp. 2

Diagnosis.—Small irregular lumpy encrusting patches, somewhat thicker than L. sp. 1 and rarely domical in form. Autozoecial apertures small (0.10 mm dia.) and petaloid due to being surrounded by large acanthostyles. Zoecal tubes sinuous, thick-walled with very few and widely spaced diaphrags in immature regions. Mesopores irregular and polygonal (0.05–0.08 mm dia.).

FAMILY HALLOPORIDAE Bassler, 1911

Hallopora elegans (Hall)

Diagnosis.—Ramos cylindrical zoarium with expanded conical basal attachment. Autozoecia large (0.40–0.45 mm), circular, frequently with structures resembling opercula and surrounded by polygonal mesopores (0.05–0.10 mm dia.).

Hallopora? sp.

Diagnosis.—Small (2–3 mm) mound-like zoaria with large autopores and smaller polygonal mesopores, as in H. elegans.

Comments.—These may represent incipient colonies of Hallopora.

Undetermined bryozaon 2

Diagnosis.—Zoaria thin with digitate expansions, zoecia large (up to 0.5 mm dia.), subequal, irregularly hexagonal with thin walls, lacking diaphragms. Mesopores and acanthostyles present.

Comments.—This bryozaon may belong to the genus Paleschera.