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Epibionts from the Cerro Gordo Member of the Lime Creek Formation (Upper Devonian), Rockford, Iowa

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Epibionts and borings are common on brachiopods from the Cerro Gordo Member of the Lime Creek Formation (Upper Devonian) at Rockford, Iowa. Occurrences and distributions of epibionts are best explained by attachment and subsequent growth on either living or dead brachiopods. Distribution of *Spirorbis*, a calcareous worm tube, is best explained by random attachment of worm larvae on living or dead brachiopods. *Cornulites*, a conical shell of uncertain affinity, commonly occurs with its aperture oriented toward the anterior commissure of brachiopods, suggesting attachment to living shells and subsequent growth in response to the feeding currents of the brachiopod. Some tabulate corals (auloporids) and some bryozoa (*Hederella* sp.) display growth patterns toward, or parallel to, the plane of commissure of brachiopods. Such patterns are understandable if these colonial epibionts grew on living brachiopods, taking advantage of the brachiopods' feeding currents. Circular borings and dendritic grooves are common on the brachiopod shells and may have caused the death of some brachiopods. Because the Cerro Gordo Member of the Lime Creek Formation was deposited on a muddy seafloor, attachment sites for small suspension feeders were limited. In this environment, brachiopod shells and horn corals provided relatively mud-free sites where epibionts could attach, grow, and survive.

INDEX DESCRIPTORS: Paleocology, brachiopods, Devonian, Lime Creek Formation, Cerro Gordo Member, epibionts, epifauna.

The fauna of the Cerro Gordo Member of the Lime Creek Formation is well known, particularly from the Rockford and Bird Hill localities in Floyd and Cerro Gordo Counties, Iowa. Fenton and Fenton (1924) described the fauna in a monograph and Belanski (1931) reported on the stratigraphy. At the time of these publications, the Cerro Gordo and Owen Members of the present-day Lime Creek Formation were assigned to the Hackberry Stage (or Hackberry Formation). The basal member of the present-day Lime Creek Formation, the Juniper Hill Member, was considered to be a separate formation (Fenton, 1919; Belanski, 1931).

Megafossils reported by Fenton and Fenton (1924), particularly the ammonoid cephalopod *Manticoceras regulare* and conodont faunas described by Anderson (1966), document the Late Devonian (Frasnian) age of the Cerro Gordo Member. Mallory (1968) conducted a detailed paleoecological study of the Cerro Gordo Member of the Lime Creek Formation in which he did bed-by-bed collecting. Mallory's work provides valuable information about the occurrence and distribution of taxa at three localities in Floyd and Cerro Gordo Counties (Rockford Brick and Tile pit, Bird Hill roadcut, and Hackberry Grove exposure). European geologists have compared the fauna of the Cerro Gordo Member of the Lime Creek Formation with similar faunas in Europe (see Wallace, 1978).

The present study reports on epibionts from the Cerro Gordo Member of the Lime Creek Formation at Rockford, Iowa (locality 11 of Anderson, 1966, p. 298). In this investigation, particular attention is paid to the interesting association between epibionts and brachiopods.

PROCEDURE

Specimens utilized in this study include those collected specifically because they contained epibionts, and specimens collected on a random basis to estimate the percentage of brachiopods that bear epibionts and/or borings. All of our specimens represent loose specimens collected from the weathered face of the Cerro Gordo Member of the Lime Creek Formation at the Rockford Brick and Tile pit (center of the NW 1/4 sec. 16, T. 95 N., R. 18 W.). More than 1750 brachiopods with epibionts and/or borings were collected for this study. Additional material was studied at the repository of the Geology Department, University of Iowa.

In order to estimate the percentage of brachiopods that bear epi-

bionts and/or borings, 12 one-meter square grids were measured along the surface of the exposed Cerro Gordo Member of the Lime Creek Formation at the Rockford Brick and Tile locality. All of the specimens present in the 12 grid areas were collected, and brachiopods from the collections were studied and examined for the presence of epibionts and borings. Intact brachiopods (both valves preserved) from these collections were used to determine the percentages of specimens that bear epibionts and/or borings. Shown below are data for the 10 brachiopod species utilized in this study (Table 1).

Table 1. Occurrence of epibionts and/or borings on 10 common brachiopods from the Cerro Gordo Member of the Lime Creek Formation. Data from intact specimens.

Brachiopod species	Total specimens from 12 plots (specimens preserved intact)	Percentage of specimens with epibionts and/or borings
<i>Atrypa devoniana</i>	77	18.2
<i>Atrypa rockfordensis</i>	45	9.0
<i>Cranaenella navicella</i>	7	28.6
<i>Cyrtospirifer whitneyi</i>	44	45.5
<i>Devonoproductus walcotti</i>	8	37.5
<i>Douvillina arcuata</i>	228	39.0
<i>Schizophoria iowaensis</i>	16	37.5
<i>Strophonella hybrida</i>	4	25.0
<i>Tenticospirifer cyrtinaformis</i>	23	39.1
<i>Theodossia hungerfordi</i>	74	28.4

Our collections also included brachiopods preserved as isolated pedicle and brachial valves. Obviously, those brachiopods preserved with shells intact provide more complete information. If one studies the positions and growth patterns of epibionts in reference to the inferred life positions of these brachiopods, it is possible to reach some conclusions as to whether the epibionts attached to a living or dead brachiopod.

All of the intact brachiopods in our study collection that contained

epibionts and/or borings were examined under a binocular microscope, and an outline drawing was made of each brachial and pedicle valve, showing the location of epibionts and borings. Directions of growth of colonial organisms (*Aulopora* sp. and *Hederella* sp.) were indicated on the drawings, as were the orientations of apertures of horn corals, *Cornulites* sp., and unidentified conical tubes. Data from individual specimens were combined on master plots (separate plots for brachial and pedicle valves) to see if specific epibionts showed preferred locations, or characteristic patterns of growth. These observations and collations were made for each of the 10 brachiopod species utilized in this study.

Observations and drawings were also made of separate pedicle and brachial valves, in addition to those done for the brachiopods preserved with both valves intact. In doing this, we noticed that many of the isolated pedicle and brachial valves have epibionts and/or borings on their exterior surface, but only rarely do they display epibionts and/or borings on their interior surface. It is our interpretation that most of the epibionts and borings were originally located on valves that were intact and, therefore, observations of positions and patterns of epibionts on separate valves are also included in our study. It is possible, however, that some disarticulated valves assumed hydraulically-stable positions with their exterior surfaces positioned upward, providing sites for epibiont attachment only on the exterior surface of the valves.

In order to estimate the extent to which epibionts attached to living brachiopods, all of the brachiopods preserved with both valves intact were studied in detail and assigned to one of three categories. One category was utilized for brachiopods that contain epibionts positioned in such a way as to suggest that they grew on living brachiopods. A second category was used for brachiopods that contain epibionts with orientations and positions that are inconclusive; the locations and growth positions of the epibionts can be explained by attachment to either living or deceased brachiopods. A third category was reserved for brachiopods that contain epibionts in positions more logically explained by attachment to dead brachiopods.

Brachiopods were assigned to the first category if they possessed interareas and umbos that were free of epibionts (excluding borings of possible infaunal borers) and also exhibited at least one of the following: 1) colonial epibionts (chiefly aulopodid corals or the bryozoan *Hederella*) that displayed a direction of growth toward the anterior or anterior-lateral margin of the brachiopod's shell; 2) horn corals, *Cornulites*, or other conical shells with apertures that opened toward the anterior or anterior-lateral margin of the brachiopod's shell; 3) *Spirorbis* worm tubes located at or near the anterior or anterior-lateral margin of the shell. It was our interpretation that the epibionts on "category 1" brachiopods attached to living brachiopods and then grew in such a way as to take advantage of feeding currents set up by the brachiopod at its anterior or anterior-lateral margin (see Figure 1).

Those brachiopods assigned to "category 2" displayed inconclusive orientations and growth patterns. According to our interpretation, the positions and growth patterns of these epibionts were not necessarily related to the orientation (inferred life position) of their hosts. Such epibionts may have attached to dead brachiopods or brachiopods that toppled from their normal growth position.

Brachiopods were assigned to "category 3" if they contained epibionts that showed a preferred direction of growth toward the posterior margin of the brachiopod's shell, and/or contained epibionts in the umbo or interarea regions.

Observations of three brachiopod species for which we have sizable numbers of specimens preserved with both valves intact suggest that about 50 percent of the *Theodossia hungerfordi* and *Atrypa devoniana* that bear epibionts can be assigned to "category 1". For *Cryptospirifer whitneyi*, the percentage is even higher—approxi-

mately 75 percent.

OBSERVATIONS

Epibionts, or epifauna, are creatures that attach to the exoskeletons of living or dead contemporaries. During the time of deposition of the Cerro Gordo Member of the Lime Creek Formation, articulate brachiopods served as hosts for several different epibionts. Common epibionts on brachiopods include worm tubes (*Spirorbis* sp.), bryozoa (*Hederella* sp.), tabulate corals (*Aulopora* sp.), horn corals, conical shells (*Cornulites* sp.), and inarticulate brachiopods (*Petrocrania* sp.). Other epibionts include unidentified conical tubes, *Palescara* sp. (an encrusting bryozoan), other encrusting bryozoa, lacy bryozoa, and encrusting stromatoporoids. In addition, single occurrences of each of the following were noted on brachiopod shells: the colonial coral *Pachyphyllum* sp., the spiriferid brachiopod *Tenticospirifer* sp., a crinoid holdfast, and an ostracod.

For the most part, epibionts were suspension feeders—creatures that obtained their sustenance from the micro-organisms and detritus of the surrounding waters. Suspension feeders cannot tolerate large amounts of mud; muddy bottom conditions tend to clog their feeding structures (Rhoads and Young, 1970).

The Cerro Gordo Member of the Lime Creek Formation is composed of shales and argillaceous limestones, deposits of a muddy shelf environment. Because of widespread muddy conditions during deposition of the Cerro Gordo Member, living space was at a premium for small suspension feeders. These creatures, the epibionts of this study, found brachiopod shells to be excellent sites for attachment. Epibionts also affixed to horn corals and probably attached to gastropods, cephalopods, and pelecypods as well. The gastropods, cephalopods, and pelecypods of the Cerro Gordo Member are preserved as internal molds, however, and thus do not have preserved exoskeletons, the sites where epibionts attached.

Fossils from the Cerro Gordo Member are well preserved; many of the brachiopod valves are intact. Separated valves also occur, and the interior of a few bear epibionts—an indication that valve separation and epibiont attachment took place on the seafloor while the beds of the Cerro Gordo Member were being deposited.

In addition to hosting epibionts, brachiopods from the Cerro Gordo Member exhibit a variety of borings. Cylindrical borings of the kind assigned to polychaete worms by Ausich and Gurrola (1979) are common, as are branch-like borings of the type assigned to clionid sponges by Fenton and Fenton (1924; 1932). A variety of irregularly-shaped borings occur as well.

The associations of the epibionts and borings with 10 common brachiopods from the Cerro Gordo Member of the Lime Creek Formation are described in this report. Brachiopods studied included the following: *Atrypa devoniana*, *Atrypa rockfordensis*, *Cranaenella navicella*, *Cryptospirifer whitneyi*, *Devonoproductus walcotti*, *Douvillina arcuata*, *Schizophoria iowaensis*, *Strophonella hybrida*, *Tenticospirifer cyrtinaformis*, and *Theodossia hungerfordi*.

Theodossia hungerfordi

The morphology of *Theodossia hungerfordi* suggests that an upright orientation for the plane of commissure would have been expected in living specimens. *T. hungerfordi* probably rested on its umbo region, attached to the substrate with a functional pedicle.

Seven hundred and six selected specimens of *Theodossia hungerfordi* were found to contain epibionts and/or borings (Table 2). Data include observations of both intact and separate valves. *Spirorbis*, a serpulid worm tube, was the most common epibiont, occurring on 210 (30 percent) of the specimens.

The collection of *Theodossia hungerfordi* included a high percen-

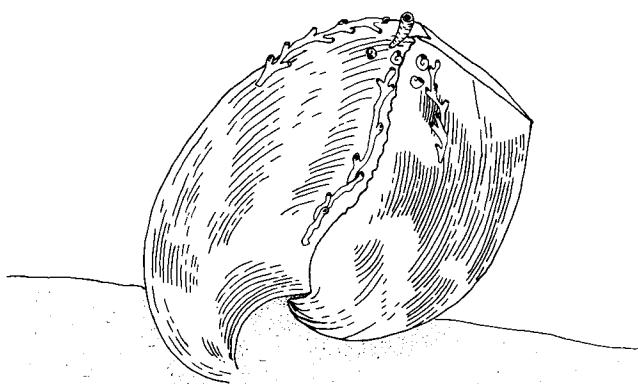


Figure 1. Idealized brachiopod with colonial epibionts (auloporid corals and the bryozoan *Hederella*) that display growth toward the anterior margin of the brachiopod's shell. Also shown are the conical shell (*Cornulites*) and worm tubes (*Spirorbis*), both with positions near the brachiopod's commissure.

tage of specimens known from pedicle valves only. In order to estimate the relative abundance of specimens of *T. hungerfordi* that were preserved with both valves intact, a collection was made of all specimens in one-meter square areas from 12 stratigraphic intervals of the Cerro Gordo Member of the Lime Creek Formation at the Rockford Brick and Tile pit. (Similar collections were made for the other brachiopod species utilized in this study). Of the 380 specimens of *T. hungerfordi* so collected, 288 (76 percent) consisted of pedicle valves only; 74 (19 percent) were represented by both valves; and 18 (five percent) consisted of brachial valves only.

Forty-nine percent of 288 specimens known from separate pedicle valves contained epibionts and/or borings. Twenty-eight percent of the separate brachial valves were found to have epibionts and/or borings. Likewise, 28 percent of the specimens with both valves intact contained epibionts and/or borings.

Eleven specimens were observed in which epibionts grew across the commissure of *Theodossia hungerfordi*. Such growth, if established on living brachiopods, would have locked the valves of the brachiopod shut, killing the brachiopod. Observations of selected epibionts and borings found on *T. hungerfordi* are summarized below.

Spirorbis—Calcareous tubes of the genus *Spirorbis*, a serpulid polychaete worm, were found to be approximately twice as abundant on pedicle valves of intact *Theodossia hungerfordi* in comparison with occurrences on brachial valves (see Figure 2). The difference in abundance is probably explained in part by the larger surface area of *T. hungerfordi*'s pedicle valve. The location of *Spirorbis* on pedicle valves was rather random, although a slight preference was shown for the anterior and lateral margins of the shell. The position of *Spirorbis* on brachial valves showed a slight preference for locations near the anterior margin of the shell.

The distribution of *Spirorbis* on disarticulated pedicle valves of *Theodossia hungerfordi* is shown on Figure 3. This distribution appears to be completely random. Overall, the position of *Spirorbis* on *T. hungerfordi* suggests a random attachment of serpulid worm larvae.

Spirorbis probably used either living or dead *Theodossia hungerfordi* as attachment sites. For the most part, the position of *Spirorbis*

Table 2. Relative abundance of epibionts and borings on 706 specimens of the brachiopod *Theodossia hungerfordi* that bear epibionts and/or borings. Data from observations of both intact and separate valves.

epibiont or borings	number of brachiopods with a particular epibiont or boring	percent of total
<i>Spirorbis</i>	210	30.0
clionid-like borings	123	17.0
<i>Hederella</i>	106	15.0
auloporid corals	81	11.5
conical tubes	75	10.6
horn corals	73	10.3
various borings	65	9.2
<i>Cornulites</i>	50	7.1
<i>Petrocrania</i>	19	2.7
<i>Palescara</i>	10	1.4
other bryozoa	8	1.1
lacy bryozoa	4	0.6
encrusting stromatoporoids	4	0.6
crinoid holdfast	1	0.1

does not appear to have been dependent on the biological processes of its host. This conclusion is in basic agreement with that of Pitrat and Rogers (1978) and is in contrast with that of Trueman (1942). Trueman reported a preferred location of *Spirorbis* on Carboniferous bivalves and explained their location in reference to the feeding currents of the bivalve.

Spirorbis was found both as the only epibiont present on *Theodossia hungerfordi* and with other common epibionts as well. No preferred associations were apparent.

Sequences of attachment were determined for eight specimens, but patterns are inconclusive: *Spirorbis* predated *Aulopora* and *Hederella* (two specimens each); *Spirorbis* postdated clionid borings (two specimens), *Petrocrania* (one specimen), and an encrusting stromatoporoid (one specimen).

Conical tubes—Conical tubes of unknown affinity are present on *Theodossia hungerfordi* and most of the other common brachiopods from the Cerro Gordo Member. The tubes are roughly conical in shape and are often somewhat contorted. The conical tubes, approx-

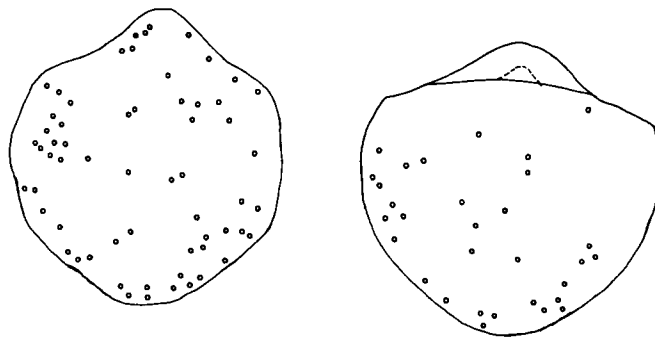


Figure 2. Distribution of the calcareous worm tube *Spirorbis* on intact *Theodossia hungerfordi*: A comparison of pedicle and brachial valves. Each circle represents the location of one *Spirorbis*. Data from 80 brachiopods. Pedicle valve shown on the left; brachial valve on the right.

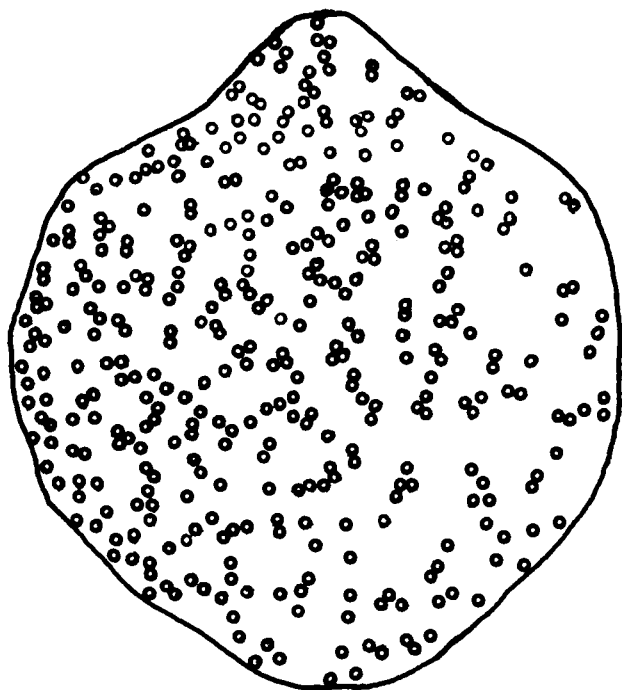


Figure 3. Distribution of *Spirorbis* on disarticulated pedicle valves of *Theodossia hungerfordi*. Each circle represents the location of one *Spirorbis*. Data from 194 specimens.

imately 1 to 3 mm. in length and 0.1 to 0.2 mm. in diameter, are generally smaller than *Cornulites*.

Seventy-five specimens of *Theodossia hungerfordi* were found to bear conical tubes such as described above. The tubes, possibly from serpulid worms, had no preferred orientation and displayed a random distribution. The position of the conical tubes does not appear to relate to the life position of the brachiopod. Instead, the conical tubes probably used both living and dead brachiopod shells as substrates for attachment.

Cornulites—*Cornulites* sp., a small conical shell of uncertain affinity, was observed on 50 specimens of *Theodossia hungerfordi*. The bulk of these *Cornulites* (77 percent) have their apertures oriented toward the anterior margin of *T. hungerfordi*. This suggests that *Cornulites* derived some benefit from the feeding currents of its hosts. *Cornulites* in our samples do not lie exclusively along the commissure of *T. hungerfordi*, however. Schumann (1967) found *Cornulites* to have preferred locations along the commissure of the brachiopod *Mucrospirifer*.

Kesling and others (1980) suggest that *Cornulites* settled near the shell margin of the Devonian brachiopod *Paraspirifer bownockeri*, used the brachiopod's shell for anchorage, and consumed the soft tissues located at the mantle edges of the brachiopod. They found that *Cornulites* invariably extended toward the anterior edges of *P. bownockeri* and terminated at the margin between the two valves.

Horn corals—Horn corals were observed on 73 specimens of *Theodossia hungerfordi*. About one-half of the corals were oriented with their apertures opening toward the anterior margin of the brachiopod's shell. Such a position can be explained by the attachment of coral larvae on living brachiopods, followed by the subsequent upward growth of the corals. Other corals showed directions of growth suggestive of attachment to dead or disarticulated brachiopods (see Figure 4).

One specimen (a disarticulated pedicle valve) was observed with a horn coral that grew from the valve's exterior onto the valve's in-

terior, unequivocal evidence that the coral's final growth was on a dead, disarticulated brachiopod.

Auloporida corals—Auloporida tabulate corals, mostly the genus *Aulopora*, occurred on 81 specimens of *Theodossia hungerfordi*. About one-half of the corals exhibited growth toward the anterior margin of the brachiopod shells; the other half displayed growth toward the umbo area. It appears as though the auloporida corals used both living and dead *T. hungerfordi* as attachment sites. The positions and growth patterns of auloporida suggest that their survival benefited from, but was not totally dependent on, the life processes of *T. hungerfordi*.

One specimen of auloporida displayed growth from the exterior of a pedicle valve onto the sediment-filling of the valve's interior, a clear indication that the coral's final growth was on a dead, disarticulated brachiopod.

Auloporida corals on *Theodossia hungerfordi* show slight preferences for orientation parallel to the anterior margin of the shell and along the medial portion of the sulcus of the pedicle valve. Corals in these positions may have been so positioned to take advantage of the feeding currents of *T. hungerfordi*.

Pitrat and Rogers (1978) found auloporida corals with preferred attachment sites on the medial ditch of the fold of brachial valves of the Devonian brachiopod *Spinocyrtia clintoni*. They suggested that the pioneering corallites arrived at the attachment site in the feeding stream of the brachiopod (an anteromedial inhalant current). The

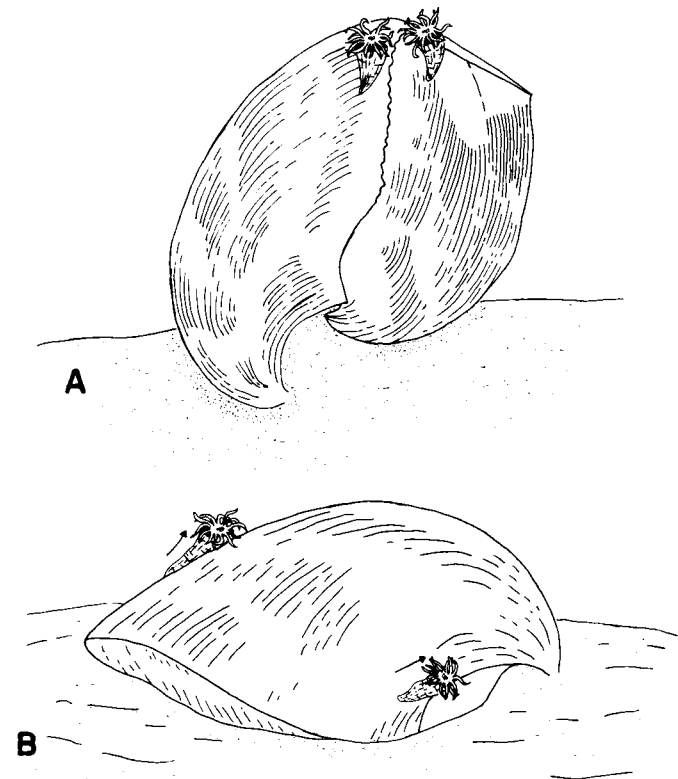


Figure 4. Contrasting patterns of growth of horn corals on the brachiopod *Theodossia hungerfordi*. "A" shows horn corals with locations and orientations that allowed them to benefit from the brachiopod's feeding stream. "B" shows horn corals that probably attached and grew on dead brachiopods. Representative specimens are repositied in the Department of Earth Science, University of Northern Iowa.

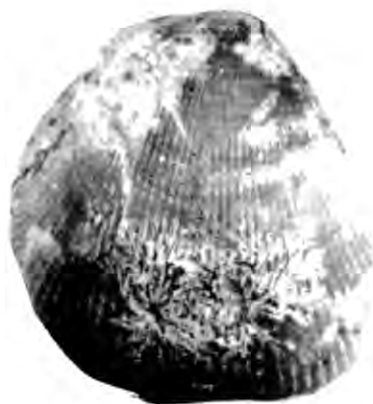


Figure 5. Dendritic grooves, of the type formerly assigned to clionid sponges, shown on the brachiopod *Theodossia hungerfordi*. Brachiopod measures 20 millimeters in width.

positions of auloporids on our specimens are more varied and are best explained by attachment of pioneering corallites on either living or dead brachiopods.

Hederella—*Hederella*, an encrusting bryozoan with a branching pattern, occurred on 106 specimens. Direction of growth of bryozoa colonies was evenly divided, with approximately one-half of the colonies showing growth toward the posterior margin of the brachiopod shells and one-half showing growth toward the anterior margin of the shells. *Hederella* commonly displayed a growth pattern parallel to the anterior shell margin of *Theodossia hungerfordi*. A plausible explanation of such growth is that the colonies of *Hederella* grew along the anterior edge of the brachiopod shell to take advantage of the brachiopod's feeding currents.

Clionid-like "borings"—Dendritic channels of the type classified as *Cliona* or *Clionolithes* by Fenton and Fenton (1924; 1932) occur on 123 specimens of the study material (Figure 5). *Cliona* was once considered to be a boring sponge but is now classified with "Miscellaneous" in the Treatise on Invertebrate Paleontology (Hantzschel, 1975). All occurrences of these "borings" were on disarticulated pedicle valves. On 75 specimens, the clionid-like borings were the lone epibiont; on the other 48 brachiopod shells, the borings occurred with various other epibionts, namely: *Aulopora*, *Cornulites*, *Hederella*, horn corals, *Spirorbis*, conical tubes, and stromatoporoids.

Borings on six of the pedicle valves penetrated the shells. Two borings were found in interareas. Although the borings were found on all areas of pedicle valve exteriors, they were slightly more abundant in the region of the pedicle beak.

The near-exclusive occurrence of clionid-like borings on disarticulated pedicle valves of *Theodossia hungerfordi* and the observation that some borings penetrate shells raise the question: did the borings cause the death and subsequent disarticulation of the brachiopod?

Other borings—In addition to the clionid-like borings, various other borings occur on *Theodossia hungerfordi*. Circular or near circular borings, approximately 0.5 to 0.6 mm. in diameter, are present. Two such borings were observed that penetrate the shells of *T. hungerfordi*. Similar borings elsewhere are interpreted to be borings by polychaete worms (Ausich and Gurrola, 1979). Borings with other shapes (elliptical, irregular, and elongate) were also observed.

Petrocrania—The inarticulate brachiopod *Petrocrania* was found on 19 specimens of *Theodossia hungerfordi*. *Petrocrania* was found on both brachial and pedicle valves and no preferred location was discernable; its occurrence on *T. hungerfordi* is probably best ex-

plained by the initial chance distribution of larvae. Shells of *T. hungerfordi* appear to have served as a suitable site for fixation and growth of *Petrocrania*, but the position of *Petrocrania* does not appear to be related to the life processes of its host.

Cyrtospirifer whitneyi

A collection of all brachiopod specimens in one-meter square areas from 12 stratigraphic intervals of the Cerro Gordo Member at the Rockford Brick and Tile pit provided the following data for *Cyrtospirifer whitneyi*: 117 total specimens of *C. whitneyi*, including 70 pedicle valves (60 percent of total), three brachial valves (2.5 percent of total), and 44 intact (37.5 percent of total).

Of the specimens of *Cyrtospirifer whitneyi* known from both valves, 67 percent contained at least one epibiont and/or boring. For the disarticulated pedicle valves, 30 percent contained at least one epibiont and/or boring. Only three disarticulated brachial valves were present in the sample, but two of these had epibionts.

The morphology of *Cyrtospirifer whitneyi* is similar to that of *Theodossia hungerfordi* and suggests that an upright orientation for the commissure would have been expected in living specimens. *C. whitneyi* probably rested on the umbo regions of both valves and attached to the substrate with a functional pedicle.

The relative abundances of epibionts and borings on 163 selected specimens of *Cyrtospirifer whitneyi* is shown on Table 3. Observations of *C. whitneyi*'s epibionts and borings follow.

Hederella—*Hederella* occurred on brachial and pedicle valves of *Cyrtospirifer whitneyi* in approximately equal numbers and displayed a preferred location parallel to the plane of commissure (Figure 6). The position of nearly all of the *Hederella* in our samples could be explained by attachment of larval bryozoa to living *C. whitneyi*. *C. whitneyi* probably rested on its umbo area, and this region, as one would expect, is characteristically free of *Hederella* colonies. The preferred location of *Hederella* along the anterior margin of *C. whitneyi*'s shell is interpreted as being influenced by the feeding currents of the brachiopod. Some *Hederella* do show growth toward the posterior margin of *C. whitneyi*; these individuals could have grown on dead brachiopods or specimens that toppled from their normal position of growth.

No clear-cut sequences of attachment for epibionts could be determined from our specimens. *Hederella* was observed to grow over

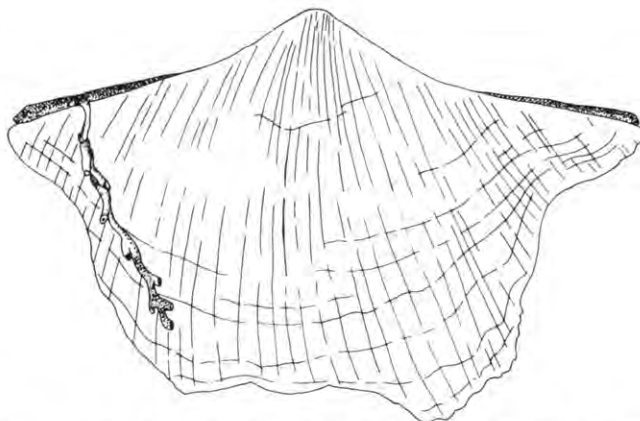


Figure 6. The bryozoan *Hederella* displays growth parallel to the commissure of the brachiopod *Cyrtospirifer whitneyi*. *Hederella* colony is approximately 15 mm. in length.

Table 3. Relative abundance of epibionts and borings on 163 specimens of the brachiopod *Cyrtospirifer whitneyi* that bear epibionts and/or borings. Data from observations of both intact and separate valves.

epibiont or boring	number of brachiopods with a particular epibiont or boring	percent of total
<i>Hederella</i>	41	25.2
<i>Cornulites</i>	35	21.5
conical tubes	34	20.9
aulopodid corals	31	19.0
<i>Spirorbis</i>	30	18.4
various borings	30	18.4
<i>Petrocrania</i>	15	9.2
clionid-like borings	11	6.7
horn corals	10	6.1
<i>Palescara</i>	7	4.3
other bryozoa	3	1.8
<i>Tenticospirifer</i>	1	0.6

Spirorbis on one specimen. In another case, however, *Spirorbis* was found attached to *Hederella*.

Aulopodid corals—Aulopodid corals, primarily of the genus *Aulopora*, were found on pedicle and brachial valves of *Cyrtospirifer whitneyi* in nearly equal numbers. The coral colonies showed a tendency for growth parallel to the anterior and lateral commissures of *C. whitneyi*, particularly on brachial valves. Aulopodids on the pedicle valves showed preferred growth toward the lateral and anterior commissure. Another preferred location was in, and adjacent to, the sulcus of the pedicle valve. Overall, the locations and orientations of aulopodids on *C. whitneyi* suggest that the corals were influenced by the feeding currents of their host.

One aulopodid was observed on the interior of a disarticulated pedicle valve of *Cyrtospirifer whitneyi*, an obvious post-mortem attachment. Another aulopodid colony covered the entire brachial valve of *C. whitneyi* and then grew onto the pedicle valve, an action that would have locked the valves shut, killing the brachiopod (unless it was already dead). *Aulopora* was observed to post-date the encrusting bryozoa *Palescara* on one specimen.

Horn corals—Most of the horn corals on *Cyrtospirifer whitneyi* were oriented with apertures that opened toward the brachiopod's anterior commissure. This suggests attachment and growth on living brachiopods, possibly to utilize feeding currents.

Spirorbis—*Spirorbis* was found on pedicle and brachial valves in about equal abundance. No preferred location was noted, and a random attachment of larvae would best explain their position.

Conical tubes—No preferred location or orientation was noted.

Borings—Circular borings, approximately 0.4 mm. in diameter, were found on seven specimens of *Cyrtospirifer whitneyi*. One boring was found to penetrate the shell. Similar borings, possibly from polychaete worms, were present on *Theodossia hungerfordi*.

Borings with irregular shapes were also observed. Three of these were found to penetrate brachial valves, and one penetrated a pedicle valve. The origin of these borings is unknown.

Petrocrania—A disk-like inarticulate brachiopod, *Petrocrania*, was found attached to 15 specimens of *Cyrtospirifer whitneyi*. *Petrocrania* used both brachial and pedicle valves of *C. whitneyi* as attachment sites. The location of all *Petrocrania* can be explained by attachment to living *C. whitneyi*.

One specimen of *Cyrtospirifer whitneyi* contained a *Petrocrania* that grew from the pedicle valve, across the commissure, to the

brachial valve. If this growth took place on a living *C. whitneyi*, it would have locked the brachiopod's valves shut, causing death.

Most *Petrocrania* displayed a preferred location along the commissure of *Cyrtospirifer whitneyi*, perhaps to take advantage of their host's feeding currents. Some *Petrocrania* show growth up to, but not across, the shell margin of *C. whitneyi*.

Palescara—The encrusting bryozoan *Palescara* was found on seven *Cyrtospirifer whitneyi*. The bryozoan colonies showed a slight tendency for location near the anterior margin of the brachiopod's shell.

Cornulites—Conical shells, assigned to *Cornulites* sp., were found on both brachial and pedicle valves of *Cyrtospirifer whitneyi* and displayed a common orientation with apertures oriented toward the brachiopod's plane of commissure. Preferred locations were the sulcus area of pedicle valves and near the anterior shell margin of brachial valves. The position of *Cornulites* is best explained by their attachment to living specimens of *C. whitneyi*, possibly to utilize the feeding currents of the brachiopod or to consume soft tissues at the mantle edges of the brachiopod.

Clionid-like borings—Borings of the type formerly assigned to clionid sponges (see previous discussion) were found on 11 specimens of *Cyrtospirifer whitneyi*. *Tenticospirifer*, an articulate brachiopod, was affixed over one patch of clionid-like borings.

Atrypa devoniana

The distribution of *Atrypa devoniana* from samples collected from 12 one-meter square areas was as follows: 100 total specimens, including 77 with both valves, 17 with pedicle valves only, and 6 with brachial valves only.

The morphology of *Atrypa devoniana* suggests that two modes of orientation were possible: Living brachiopods could have rested on their pedicle valves with the larger brachial valve oriented upward; or living brachiopods may have rested on their umbo area, achieving a somewhat upright commissure. In part, the greater surface area of the brachial valve of *A. devoniana* explains the greater number of epibionts on brachial valves compared to the number of epibionts on pedicle valves. Also, a greater number of epibionts would be expected on brachial valves, if brachial valves were oriented upwards on living *A. devoniana*. According to Cooper (1967), most, if not all, sedentary atrypids appear to have oriented in a brachial-valve upwards position.

Data on borings and epibionts on *Atrypa devoniana* are shown on Table 4. Generalizations follow.

Table 4. Relative abundance of epibionts and borings on 116 specimens of the brachiopod *Atrypa devoniana* that bear epibionts and/or borings. Data from observations of both intact and separate valves.

epibiont or boring	number of brachiopods with a particular epibiont or boring	percent of total
<i>Spirorbis</i>	43	37.1
various borings	31	26.7
conical tubes	24	20.7
aulopodid corals	19	16.4
horn coral	14	12.1
clionid-like borings	9	7.8
<i>Petrocrania</i>	8	6.9
<i>Cornulites</i>	7	6.0
<i>Hederella</i>	6	5.2

Table 5. Relative abundance of epibionts and borings on 237 specimens of the brachiopod *Douvillina arcuata* that bear epibionts and/or borings. Data from observations of both intact and separate valves.

epibiont or boring	number of brachiopods with a particular epibiont or boring	percent of total
various borings	168	70.9
<i>Spirorbis</i>	42	17.7
horn corals	33	13.9
<i>Hederella</i>	13	5.5
clionid-like borings	12	5.1
various bryozoa	10	4.2
conical tubes	6	2.5
<i>Petrocrania</i>	5	2.1
auloporid corals	2	0.8
lacy bryozoa	2	0.8
<i>Cornulites</i>	1	0.4

Various borings—Circular borings, normal to the shell, occur on both valves of *Atrypa devoniana*. Five such borings were observed on pedicle valves, versus ten on brachial valves. Borings that penetrate shells were seen on the central area of two brachial valves. The position of these borings is suggestive of emplacement from above, perhaps by a crawling worm. Irregular borings, oriented approximately normal to the shell, are also present on *A. devoniana*, and some were observed that penetrated the brachiopod's shell. Tangential borings, one of which penetrated the shell of *A. devoniana*, are present, too.

Horn corals—Horn corals are more abundant on brachial valves than on pedicle valves (13 on brachial valves versus one on a pedicle valve). The growth direction of the horn corals appears to be related to the curvature of the strongly-biconvex brachial valve of *Atrypa devoniana*. Some corals apparently attached as larvae to specimens of *Atrypa devoniana* that rested on their pedicle valves. The orientation of other corals suggests a near vertical plane of commissure for some *Atrypa devoniana*.

Cornulites—Only five specimens of *Cornulites* were noted, and all of these were oriented with their apertures toward the anterior commissure of *Atrypa devoniana*. Four of the five *Cornulites* were located near the anterior shell margin, suggesting that such a position provided a favorable location—possibly to take advantage of the brachiopod's feeding currents.

Spirorbis—*Spirorbis* was five to six times more abundant on brachial valves of *Atrypa devoniana* than on pedicle valves. A possible explanation for this is that mature *A. devoniana* probably rested on their pedicle valves while living; therefore, brachial valves had a much greater opportunity to serve as attachment sites for the mobile larvae of spirorbid worms. The distribution of *Spirorbis* is fairly random and suggests that the worms merely used the brachiopod shells as a suitable substrate, rather than attaching on the brachiopod to take advantage of its feeding currents.

The hydraulically-stable position of a dead intact *Atrypa devoniana* is with the brachial valve oriented upward. Thus, one would expect a greater number of *Spirorbis* of brachial valves on intact *A. devoniana*, even if the attachments were on dead brachiopods.

Auloporid corals—Seven colonies of auloporid corals were observed on pedicle valves of *Atrypa devoniana*, and five of these grew toward the lateral or anterior commissure. Sixteen auloporids were noted on brachial valves, with most showing growth toward the lateral or anterior margins of the brachiopod shells. The initial posi-

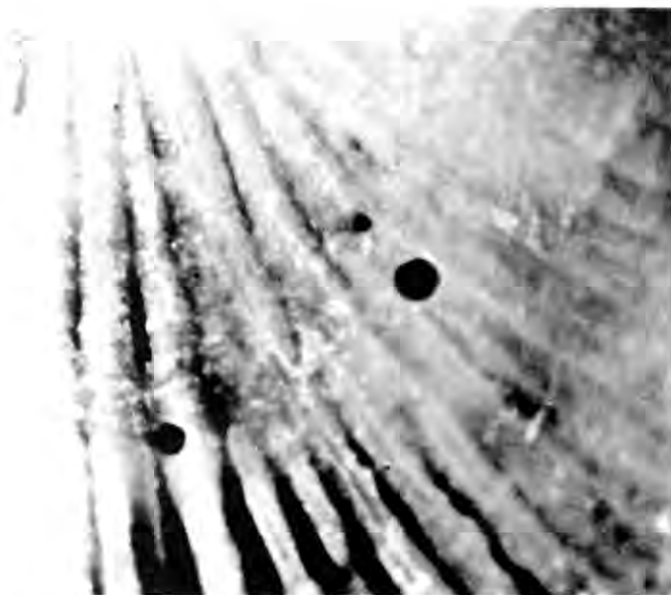


Figure 7. Circular borings, approximately 0.5 mm. in diameter, on *Douvillina arcuata*. Similar borings are found on other brachiopod species from the Cerro Gordo Member of the Lime Creek Formation.

tion of the corals appears to have been controlled by the chance arrival of larvae; there was no discernable preferred location for the coral colonies, but a tendency for growth toward the brachiopod's lateral and anterior shell margins was evident. This suggests that the corals may have grown toward the anterior and lateral margins of brachiopod shells to take advantage of the brachiopod's feeding currents.

Petrocrania—*Petrocrania* used shells of *Atrypa devoniana* as attachment sites. Brachial valves were preferred over pedicle valves (12 versus one). This would be expected if *A. devoniana* rested on their pedicle valves with brachial valves oriented upward as suggested previously. Such a distribution, however, would also be expected on dead intact *A. devoniana* in hydraulically-stable positions.

Clionid-like borings—Nine such borings were found on brachial valves, compared to one on a pedicle valve. This suggests that the borer bored from above, rather than from underneath (assuming that the model of *Atrypa devoniana* resting on its pedicle valve is correct).

Other epibionts—*Hederella* bryozoa, *Palescara* bryozoa, lacy bryozoa, and other bryozoa were observed on the shells of *Atrypa devoniana*. Their positions show no clear-cut patterns.

Atrypa rockfordensis

The number of specimens of this species, a spiny articulate brachiopod, was limited and does not allow for drawing many conclusions. Twenty-five specimens of *Atrypa rockfordensis* were studied that contained epibionts and/or borings. The following occurrences were noted (numbers refer to the number of specimens of *A. rockfordensis*): various borings (14), conical tubes (4), ostracod (1), clionid-like boring (1), auloporid corals (2), *Hederella* (2), *Spirorbis* (6), and other bryozoa (1).

Collections from the 12 one-meter square plots produced 45 *Atrypa rockfordensis* with valves intact, three pedicle valves, and nine brachial valves. Epibionts were not found to be abundant on *A.*

rockfordensis when compared to the other common brachiopods of the Cerro Gordo Member (Table 1).

Possibly, the spines of *Atrypa rockfordensis* served to restrict the attachment of epibionts and borers. Irregular borings were found to penetrate the shells of three specimens (one on a pedicle valve and two on brachial valves). One specimen showed a brachial valve penetrated by a circular boring. Although borings and epibionts were reduced in number on this spiny brachiopod, they were not eliminated altogether.

Douvillina arcuata

The thin-shelled strophomenid brachiopod *Douvillina arcuata* contained numerous borings. Random collections of 435 *D. arcuata* yielded the following distribution: valves intact, 52.4 percent; pedicle valves, 47.4 percent; and brachial valves, 0.2 percent.

Strophomenid brachiopods like *Douvillina* probably rested on their convex pedicle valves so that the valves curvature kept the anterior plane of commissure off the muddy substratum. A concave-upward life orientation for *Douvillina* seems plausible for a muddy substratum. Because feeding currents were drawn in at the anterior margin of the brachiopod's shell, it was important to keep that area free from sediment.

Just the opposite orientation (convex-upward life orientation) has been suggested for the Ordovician strophomenid *Rafinesquina* (Meyer and others, 1978). *Rafinesquina*, however, was found on a shelly substratum, whereas the strophomenids in our study are associated with muddy substrates.

A dead *Douvillina*, either intact or disarticulated, would assume a stable position on the sea floor resting on the concave side of either its brachial or pedicle valve. Such a position is the expected position of stability in an area with wave action.

A collection of 237 selected specimens of *Douvillina arcuata* was studied, and the positions of epibionts and borings were assessed as described previously. The occurrence of epibionts and borings is listed on Table 5. Generalizations are discussed below.

Petrocrania—Five specimens of *Petrocrania* were found on *Douvillina*. All specimens occurred on pedicle valves. Three of the *Petrocrania* were found on disarticulated pedicle valves of *Douvillina arcuata* and two were found on specimens of *D. arcuata* preserved with valves intact. If a living *Douvillina* were oriented as suggested above (concave-upward), attachment of epibionts to the pedicle valve of living *Douvillina* would have been impossible, other than at the anterior shell margin. Thus, we propose that *Petrocrania* were affixed to overturned specimens of *Douvillina*. Such specimens would be hydraulically stable with their convex pedicle valves oriented upward.

Spirorbis—*Spirorbis* are more abundant on pedicle valves of *Douvillina arcuata* than on brachial valves. The positions of the *Spirorbis* on pedicle valves are near the anterior edges of valves and could have found attachment on living *D. arcuata*. Attachment of *Spirorbis* on overturned, or disarticulated and overturned *Douvillina* is also plausible.

Various borings—Circular borings, approximately 0.4 to 0.6 mm. in diameter, are common on the pedicle valves of *Douvillina arcuata* occurring on specimens preserved with valves intact as well as on individual pedicle valves (Figure 7). Pedicle valves of seven intact *D. arcuata* were penetrated by borings. One intact *D. arcuata* displays a circular boring that penetrates a brachial valve; six disarticulated pedicle valves exhibit such borings.

If the concave-upward model of orientation of living *Douvillina arcuata* is correct, borings on pedicle valves would have been emplaced from below. An infaunal organism, such as a polychaete worm, may have inflicted the borings.

Table 6. Relative abundance of epibionts and borings on 44 specimens of the brachiopod *Schizophoria iowaensis* that bear epibionts and/or borings. Data from observations of both intact and separate valves.

epibiont or boring	number of brachiopods with a particular epibiont or boring	percent of total
conical tubes	14	31.8
<i>Spirorbis</i>	13	29.5
various borings	9	20.5
clionid-like borings	5	11.4
aulopodid corals	4	9.1
horn corals	4	9.1
<i>Petrocrania</i>	3	6.8
ctenostome broyoza	3	6.8
other bryozoa	2	4.5
<i>Cornulites</i>	1	2.3

Horn corals—The position and orientation of horn corals on *Douvillina arcuata* can be explained by attachment to either living and overturned, or disarticulated *Douvillina*. Disarticulated pedicle valves, oriented with their convex side upward, probably provided favorable sites for the attachment of some horn corals; overturned *D. arcuata* with both valves intact appear to have provided attachment sites for horn corals as well.

Conical tubes—The positions of conical tubes on *Douvillina arcuata* are inconclusive.

Clionid-like borings—These borings were found exclusively on pedicle valves. They occur on both disarticulated pedicle valves and on specimens with valves intact.

Hederella—The positions and growth patterns of *Hederella* are not conclusive. Attachment to both living and dead *Douvillina* probably took place.

Aulopodid corals—Only two specimens of aulopodid corals were found on *Douvillina arcuata*. One colony was found on a brachial valve and interarea, and the other colony occurred on a pedicle valve. Because of limited data, no conclusions were drawn for this group.

Schizophoria iowaensis

Forty-four specimens of *Schizophoria iowaensis* were found to host epibionts and/or borings (Table 6). Of the 44 *S. iowaensis* bearing epibionts, 23 are represented by both valves, 17 by separate pedicle valves, and four by brachial valves only.

Twenty-two *Schizophoria iowaensis* were collected from the 12 grid plots. Of these, 16 were represented by both valves, and six of these brachiopods hosted epibionts.

The pedicle opening of *Schizophoria iowaensis* is relatively small; this brachiopod probably did not have a functional pedicle at maturity. In early life stages, *S. iowaensis* may have rested on the umbo region of its brachial valve, partially supported by its pedicle. Later, after the pedicle became non-functional, the brachiopod probably assumed a stable position by resting on its pedicle valve (Figure 8). Generalizations about epibionts and borings on *S. iowaensis* follow.

Clionid-like borings—Twenty-two clionid-like borings were studied on specimens of *Schizophoria iowaensis*. All were found on pedicle valves. Only two of these 22 borings were found on intact brachiopods. No preferred location of borings was noted.

Petrocrania—Seven specimens of *Petrocrania* were found on *Schizophoria iowaensis*. All occurrences were on brachial valves, with

Table 7. Relative abundance of epibionts and borings on 29 specimens of the brachiopod *Strophonella hybrida* that bear epibionts and/or borings. Data from observations of both intact and separate valves.

epibiont or boring	number of brachiopods with a particular epibiont and/or boring	percent of total
various borings	9	31.0
horn corals	8	27.6
<i>Spirorbis</i>	7	24.1
clionid-like borings	5	17.2
auloporid corals	4	13.8
<i>Petrocrania</i>	2	6.9
tabulate coral	1	3.4
<i>Palescara</i>	1	3.4
other bryozoa	1	3.4

some on brachial umbos. *Petrocrania* probably attached to mature *S. iowaensis* that rested on their pedicle valves.

Horn corals—Seven horn corals were found, all from single pedicle valves. Apertures of the corals do not display a clear and consistent pattern of orientation toward the brachiopod's commissure. One horn coral was found affixed to the interior of a pedicle valve, demonstrating that a live brachiopod was not needed for growth of the coral.

Spirorbis—Fourteen *Spirorbis* were found on intact *Schizophoria iowaensis*; half were on pedicle valves and half were on brachial valves. No preferred location of *Spirorbis* was apparent on either valve. Two additional *Spirorbis* were found on disarticulated pedicle valves. Thus, the position of *Spirorbis* on *S. iowaensis* is similar to its position on other brachiopods in our study and supports the conclusion that *Spirorbis* larvae attached randomly to both living and dead brachiopods.

Spirorbis was found in association with *Aulopora* on three specimens and occurred with each of the following once: horn coral, *Hederella*, and *Cornulites*.

Tenticospirifer cyrtinaformis

The morphology of *Tenticospirifer cyrtinaformis* suggests that it had a functional pedicle and that its commissure was oriented upright. This species generally preserved with valves intact. Seventeen specimens of the brachiopod *Tenticospirifer cyrtinaformis* were found to host epibionts and/or borings. Because of this small sample size, only limited conclusions are drawn.

Cornulites—Seven of the 17 brachiopods studied contained one or more *Cornulites*. Eighteen *Cornulites* were present total, and 15 of these were oriented with apertures that opened toward the lateral or anterior margins of *Tenticospirifer cyrtinaformis*. One *Cornulites* was oriented with its aperture away from the brachiopod's plane of commissure, and one specimen occurred in the interarea. Thus, while most of the *Cornulites* were oriented in such a way as to suggest that they took advantage of the brachiopod's life processes and feeding currents, there are exceptions.

Hederella—Colonies of *Hederella* were observed on four *Tenticospirifer cyrtinaformis*. In general, their position and pattern suggest attachment to living *T. cyrtinaformis*.

Other epibionts—*Spirorbis* occurred on three specimens of *Tenticospirifer cyrtinaformis* and unidentified conical tubes were found on two brachiopod shells. Lacy bryozoa and an unidentified encrusting bryozoan occurred on one specimen each. Four *T. cyr-*

tinaformis contained circular borings; two of the borings were in interareas. As noted previously, circular borings like these may have been produced by polychaete worms.

Devonoproductus walcotti

Devonoproductus walcotti, a spiny productid brachiopod, probably rested on its pedicle valve, using its spines for anchorage. Our collections of *D. walcotti* bearing epibionts or borings were limited to eight intact specimens and 10 brachial valves. Occurrences of epibionts and borings were as follows (numbers refer to number of brachiopods): various borings (14), clionid-like borings (2), *Cornulites* (2), *Spirorbis* (1), *Aulopora* (1), and unidentified bryozoa (1). Position of epibionts, as in previous cases, suggests attachment to either living or dead brachiopods.

Strophonella hybrida

Twenty-nine specimens of *Strophonella hybrida*, consisting of 15 intact valves, 10 pedicle valves, and 4 brachial valves, were found to contain epibionts and/or borings (Table 7).

The curvature of *Strophonella hybrida* is such that its pedicle valve is concave and its brachial valve is convex. Thus, this species may have rested on its convex brachial valve to keep its commissure free of sediment. The positions of epifauna on *S. hybrida* suggest that their attachment took place on either living or dead specimens. The interiors of five pedicle valves contained epibionts, positive evidence that epibionts affixed to dead shells.

Cranaenella navicella

Only five specimens of the terebratulid brachiopod *Cranaenella navicella* were found to host epibionts or borings; borings were found on three specimens and bryozoa on two. Because of limited data, few conclusions are drawn. One colony of *Hederella* displayed a growth pattern toward the lateral plane of commissure and only to its edge, suggesting that the bryozoan may have benefited from the feeding currents of the living *Cranaenella*. Living *C. navicella* probably had functional pedicles and oriented with upright commissures.

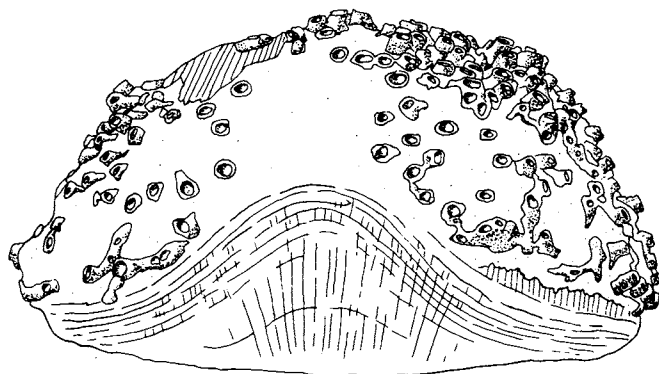


Figure 8. Colony of auloporid corals on the brachiopod *Schizophoria iowaensis*. View of brachiopod's anterior commissure showing an abundance of auloporids on the brachial valve and a complete absence of auloporids on the pedicle valve.

DISCUSSION

Epibionts and borings are common on brachiopods from the Cerro Gordo Member of the Lime Creek Formation at Rockford, Iowa. Random collections demonstrated that approximately 45 percent of *Cyrtospirifer whitneyi* contained epibionts and/or borings, whereas only 10 percent of *Atrypa rockfordensis* displayed epibionts and/or borings. For most species, 30 to 45 percent of the brachiopods were found to contain epibionts and/or borings.

Occurrences and distributions of epibionts are best explained by attachment and subsequent growth on either living or dead brachiopods. The distribution of *Spirorbis*, a calcareous worm tube, is best explained by random attachment of worm larvae on either living or dead brachiopod shells. *Cornulites*, a conical shell of uncertain affinity, commonly occurs with its aperture oriented toward the anterior commissure of brachiopods; this suggests attachment to living shells and growth in response to the brachiopod's feeding currents, or growth to consume mantle tissues at the anterior margins of brachiopods. Some tabulate corals (*Aulopora* sp.) and some bryozoa (*Hederella* sp.) display growth patterns toward or parallel to the plane of commissure of brachiopods. Such a pattern is understandable if these colonial epibionts grew on living brachiopods, taking advantage of the brachiopods' feeding currents.

Borings are present on many of the brachiopods. Circular borings with 0.5 to 0.6 mm. diameters and parallel sides are particularly common. These borings may have been produced by parasitic polychaete worms.

Dendritic grooves ("borings") of the type once attributed to clionid sponges are common on the pedicle valves of *Theodossia hungerfordi* and may have been responsible for the death of some members of this species. Similar borings occur on other brachiopods from the Cerro Gordo Member of the Lime Creek Formation.

The Cerro Gordo Member was deposited on a muddy shelf, so attachment sites for small suspension feeders were limited. Thus, brachiopod shells, living or dead, provided relatively mud-free sites for attachment locations, where the suspension-feeding epibionts could survive and grow. Horn corals served as hosts for some epibionts, too.

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